

**Article VII.—THE ADAPTIVE MODIFICATIONS OF THE
ARBOREAL TADPOLES OF *HOPLOPHRYNE* AND THE
TORRENT TADPOLES OF *STAUROIS***

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PLATES XV AND XVI; TEXT FIGURES 1 TO 12

In recently summarizing the life-histories of the Amphibia, I (1927) found that the tadpole of a species frequently afforded one of the best clues as to its relationships, for the larval type was comparatively stable, and pronounced modifications when they occurred were usually common to a natural group of species. More recently, Barbour and Loveridge (1928) have described two remarkable brevicipitid toads from East Africa, one of which, at least, lays its eggs in bamboos and banana trees. It might be expected that the tadpoles which come from these eggs would differ considerably from those of the brevicipitid toads which breed in ponds. Through the kindness of Dr. Thomas Barbour I have had the opportunity of examining the unique series of eggs and larvæ of these toads collected by Mr. Arthur Loveridge and have compared them with the large embryological series of other species in The American Museum of Natural History. This study has revealed certain interesting adaptive changes in the arboreal tadpoles and has served as the occasion to examine the adaptive modifications of a number of other tadpoles, particularly those of the torrent-dwelling *Staurois* which had previously been described only in part. How many of these adaptations are hereditary characters, and how many modifications produced by the environment during each ontogeny, will have to await an experimental analysis. The present study is of interest in the confirmation it gives to the thesis previously advocated, namely, the relative stability of the tadpole type.

TWO ARBOREAL TADPOLES

Barbour and Loveridge (1928) have recently described *Hoplophryne* and *Parahoplophryne* as two new genera of brevicipitid toads from the Uluguru and Usambara Mountains of East Africa. *Hoplophryne* is represented by *uluguruensis* on the former mountain range and *rogersi* on the latter. *Parahoplophryne*, which may be described as a *Hoplophryne* with a clavicle, is known only from the latter range. Barbour and Loveridge have given an interesting account of the eggs and larvæ of *H. uluguruensis* but the tadpoles which they doubtfully refer to *P.*

usambaricus are here considered to be those of *H. rogersi*. In the first place they can not be those of *Callulina krefftii*, which was collected the same time, for the fore limbs are well developed in the two oldest larvæ, and the first finger is greatly reduced in these specimens as in both *Hoplophryne* and *Parahoplophryne*, but not in *Callulina*. Secondly, I have found these mature tadpoles to be provided with thin cartilaginous procoracoids but no clavicles such as would be expected in *Parahoplophryne* at this stage, the beginning of metamorphosis. They differ further from *Parahoplophryne* in having T-shaped terminal phalanges. The adult female of *H. rogersi* is unknown and the male, which exhibits an enormously developed pectoral musculature, lacks all trace of the cartilaginous procoracoids found in the larvæ. Hence, until the female and young of *H. rogersi* are discovered, some doubt will remain as to the specific status of the larvæ to be discussed below. From the data at hand it seems probable that the loss of the procoracoid is a peculiarity of the adult male. The tadpoles are certainly referable to *Hoplophryne* and their specific status does not affect the conclusions to be reached below.

Hoplophryne uluguruensis lays its eggs between the leaves of the wild banana or within the stems of bamboos which have been split sufficiently to permit the entrance of a small and greatly depressed frog. Some rain-water is retained between the leaves of the wild bananas and Loveridge was unable to determine whether or not the eggs were actually submerged. The eggs in the bamboos were certainly exposed to the air (Fig. 1), for the internodal chambers, while moist, contained little or no free water. The tadpoles which develop from eggs in the bamboos would rarely if ever have enough water to cover them. Hence, we may conclude that some, possibly all, of the eggs of *H. uluguruensis* are laid exposed to the air and the tadpoles which develop live either in a very small basin of water between the leaves of the wild banana, or exposed to the atmosphere within the split stems of bamboos. It is also possible that some of the tadpoles between the banana leaves may not reach the pockets of water but live exposed to air as do the tadpoles in the bamboos. This suggestion will appear more probable when the structure of the tadpole has been described below.

On several occasions I have pointed out (1926, 1927) that all Brevicipitidæ which pass through a tadpole stage, except certain African forms of independent origin, are characterized by a single distinctive type of larva. This is the more remarkable in that the species are found in both the Old and New World and that the larvæ develop in waters of considerably different temperatures and surroundings. No brevicipitid

larvæ had previously been reported to pass their larval life in such restricted quarters as *Hoplophryne* and I welcomed the opportunity of examining the material described by Barbour and Loveridge with a view to determining the degree of divergence in this series from the conditions found in the pond-breeding brevicipitids. For comparison, I have used chiefly a series of eggs and larvæ of *Gastrophryne carolinensis* collected by Byron C. Marshall at Imboden, Arkansas, but I have also drawn upon the other developmental material of Brevicipitidæ in the American Museum.

In my summary of the life-histories of the Amphibia (1927), I omitted reference to the account of *Hemismus mormoratum* as given by Bles (1907). There seemed some doubt as to the identity of the material Bles described, the tadpoles not having been carried through to metamorphosis. Very recently, Mr. Vincent Wager has sent me a complete developmental series of this species, which fully confirms the account of Bles and demands further consideration of this form. *Hemismus* agrees with *Cacosternum* and some of its allies of South Africa in having a tadpole with the usual horny teeth. The external nares appear early, the spiracle is sinistral. None of the "brevicipitid characters" as defined by me in 1925 appear. In the case of *Cacosternum* it was possible to trace the origin of this genus directly to the smaller ranids of Africa (Noble, 1926), but *Hemismus* is so modified that the problem is more difficult. *Hemismus* has both procoracoid and clavicle present. It has considerable resemblance to *Breviceps* but lacks the large glandular area on the roof of the mouth. It is specialized in having the pectoral girdle articulating with the skull and in having a sharply pointed snout, a pouched tongue, etc. Whether *Hemismus* is related to the other South African brevicipitids having a ranid-like tadpole will have to await a detailed comparison of their anatomy. For the present it may be grouped with these forms and assumed to have had an independent origin from some ranid by that frequently repeated process, a loss of the maxillary teeth and a slight expansion of the sacral diapophyses. In this connection I may add one more case of dental loss to the series previously recorded. I find, on an examination of the type of *Allophryne ruthveni* Gaige, that this "bufonid" is really a toothless hyloid. It lacks an omosternum and possesses T-shaped terminal phalanges and intercalary cartilages. It is thus closely allied to *Centrolenella* but differs in having a distinct canthus rostralis with eyes laterally directed. It is unique among Salientia in the scalelike patches of roughened epidermis strewn over head and back. The ovarian eggs are small and pigmented.

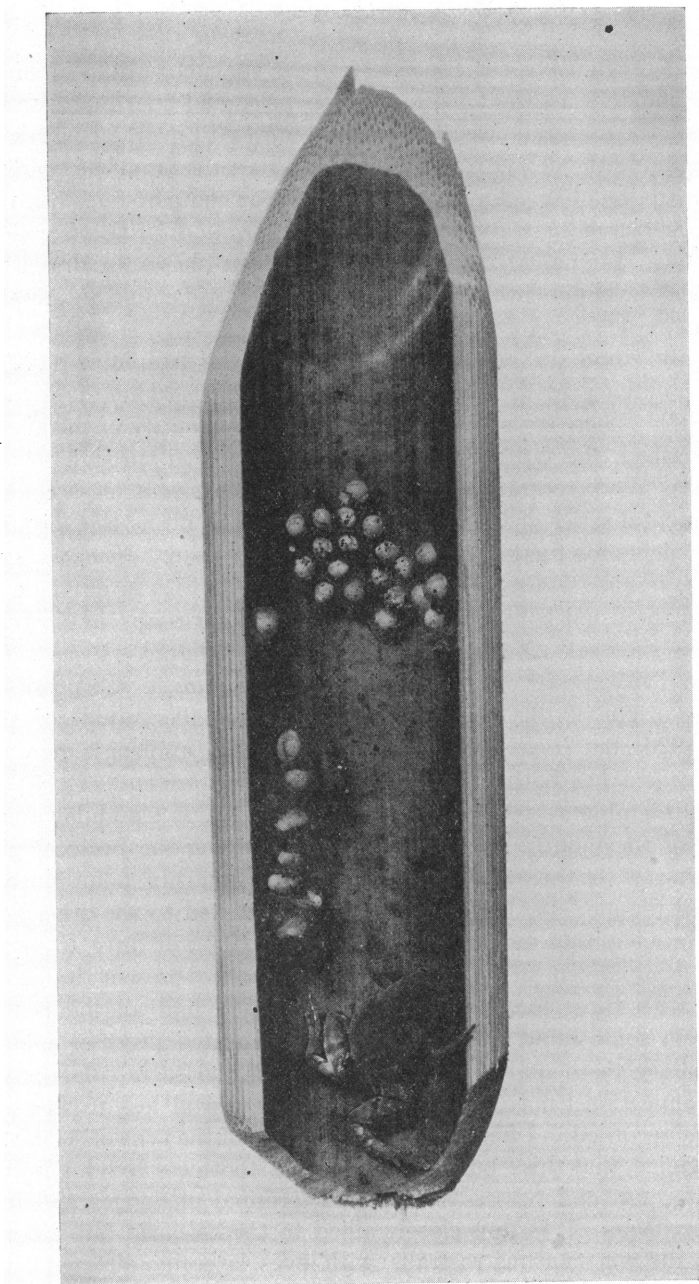


Fig. 1. Female *Hoplophryne uluguruensis* and its eggs within a piece of bamboo. About natural size. Photographed from preserved material.

A. ruthveni cannot be directly derived from any known species of *Centrolenella* but it may be described as having descended from this genus by a loss of teeth.

The eggs of *Hoplophryne uluguruensis*, as noted by Barbour and Loveridge (1928), are laid in a single layer on the inner wall of living bamboo stems (Fig. 1) or on wild banana plants, between leaves and stem. There are two egg-capsules and a very thin adherent vitelline membrane present (Fig. 2b). The outer capsule is soft and apparently adhesive, for its contour is molded by the substratum and by the adjacent eggs (Fig. 1). The inner capsule is more resistant and spherical in form. The cap-

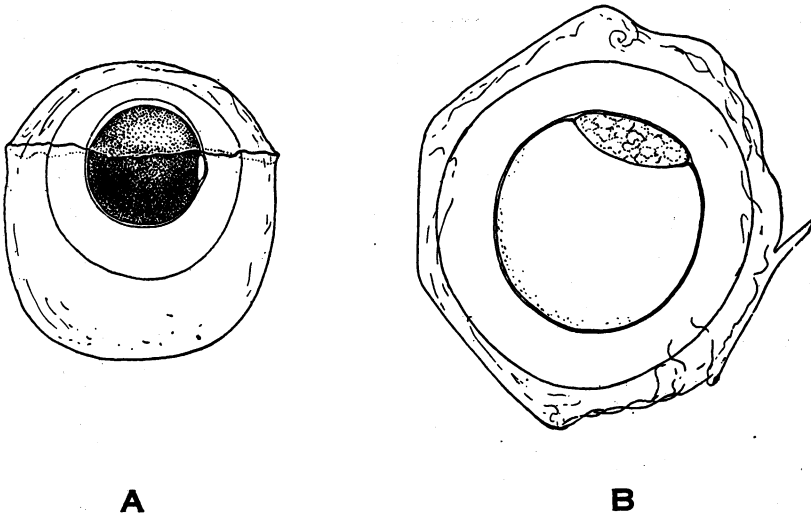


Fig. 2. The egg of *Hoplophryne uluguruensis* (b) compared with that of *Gastrophryne carolinensis* (a). $\times 15$.

sules vary considerably in thickness but the inner is in nearly all cases thicker than the outer. There is no cap or flattened pole to the outer capsule as previously reported to be typical of brevicipitid eggs laid floating in water. In addition to *Gastrophryne* (Fig. 2a) and *Kaloula* (Noble, 1927), I strongly suspect that the eggs of *Kalophrynus stellatus* as reported by Taylor (1920) are equipped with this flattened pole to the outer capsule. Taylor describes the condition as a rim, and in many of my formalin-preserved eggs of *Gastrophryne carolinensis* the modification appears to be more an encircling ridge than a flattening of the upper pole.

Some eggs of *H. uluguruensis* collected October 5, 1926, at Nyange, Uluguru Mountains, Tanganyika Territory, are in the blastopore stage.

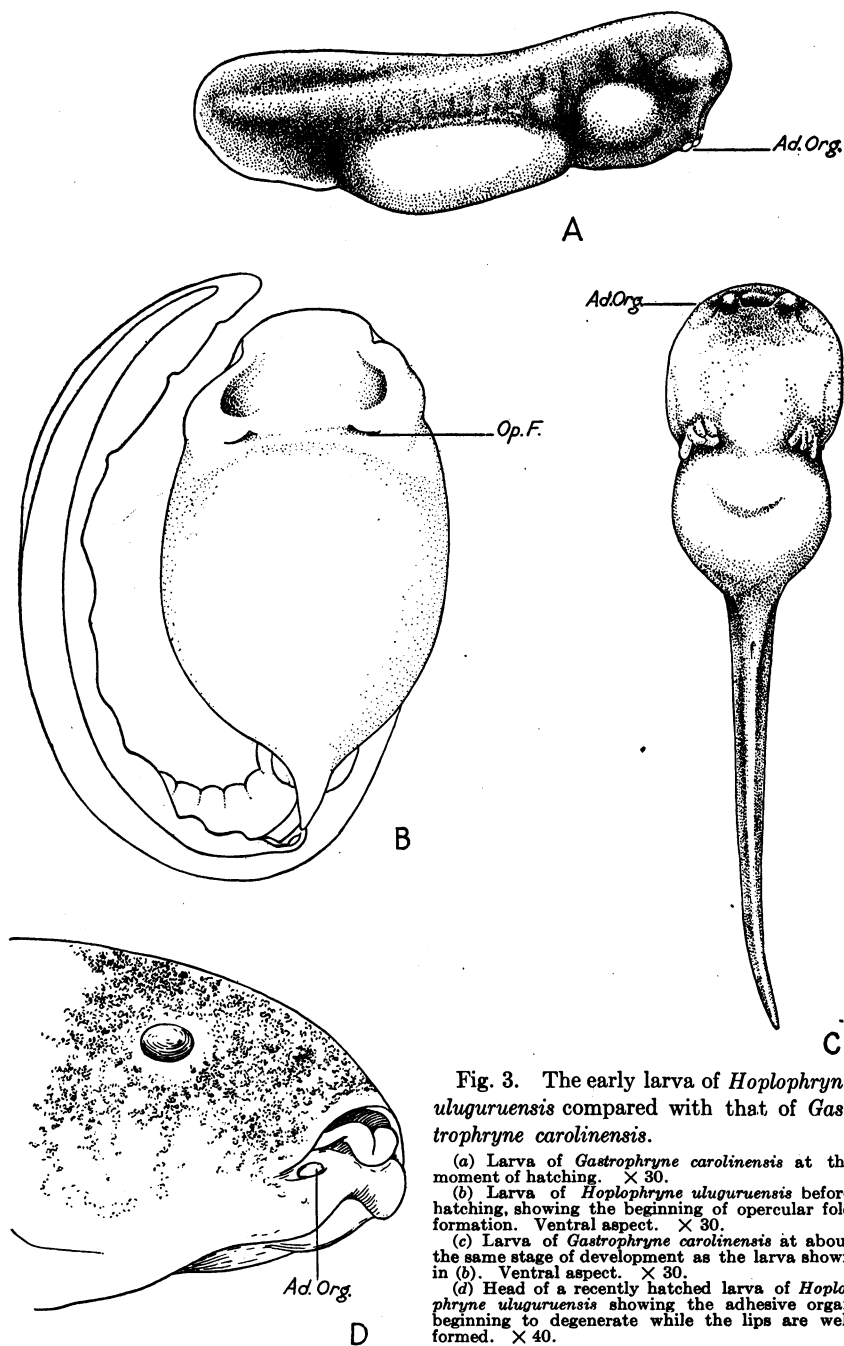


Fig. 3. The early larva of *Hoplophryne uluguruensis* compared with that of *Gastrophryne carolinensis*.

(a) Larva of *Gastrophryne carolinensis* at the moment of hatching. $\times 30$.
 (b) Larva of *Hoplophryne uluguruensis* before hatching, showing the beginning of opercular fold formation. Ventral aspect. $\times 30$.
 (c) Larva of *Gastrophryne carolinensis* at about the same stage of development as the larva shown in (b). Ventral aspect. $\times 30$.
 (d) Head of a recently hatched larva of *Hoplophryne uluguruensis* showing the adhesive organ beginning to degenerate while the lips are well formed. $\times 40$.

They are pigmentless and measure 2.5–3 mm. in diameter. The inner egg-capsules measure 3.8–4.5 mm. in diameter, the outer 4.5–5 mm. in this series fixed in formalin and preserved in alcohol. By contrast the eggs of *G. carolinensis* are densely pigmented (except for the yolk-plug which is creamy white and the dorsal lip of the blastopore which exhibits a conspicuous “gray crescent”), are much smaller than those of *Hoplophryne*, and lie excentric in the upper half of the egg-capsules (Fig. 2a). The diameter of the egg is 1.5 mm., the outer capsule 3 mm. in the eggs pre-

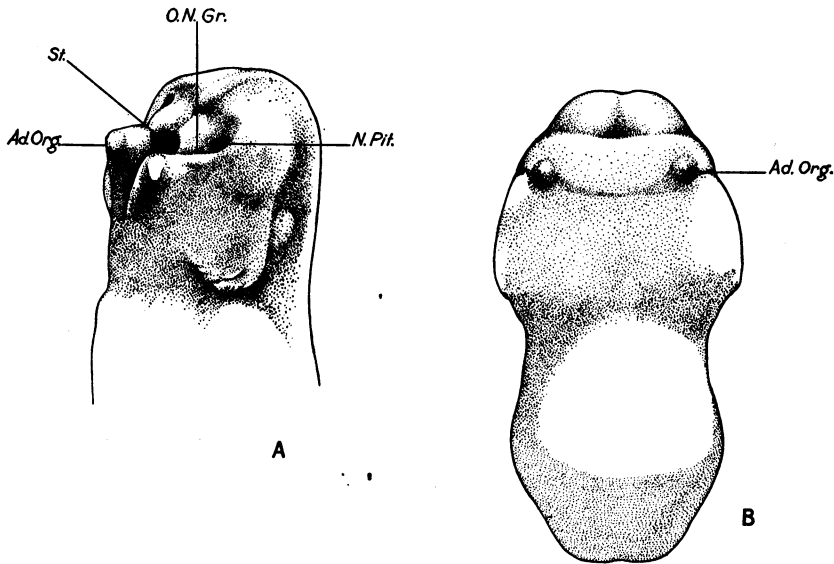


Fig. 4. The development of the head of *Gastrophryne carolinensis*. $\times 60$.

(a) Head at oblique angle showing the nasal pits and oro-nasal groove.

(b) Whole embryo. Ventral aspect showing the development of the adhesive organs at the points of a pigmented crescent.

served in formalin. In brief, the eggs of *Hoplophryne* differ from those of *Gastrophryne* in their respiratory medium, crowded position, simpler egg-capsules, greater yolk and lack of pigmentation.

On October 5 there was also collected another lot of eggs (Mus. Comp. Zoöl. No. 13792) which are much more advanced. The larvæ, although well-formed, show no sign of hatching. It is interesting to note that they have attained such a high state of development before hatching. The mouth is formed and the lips are beginning to develop. The tail is longer than head and body and is wrapped across the ventral surface of the body. Hind-leg rudiments are clearly visible. The vent is

median in position and already open (Fig. 3b). It is noteworthy that in spite of the advanced stage of development there is no indication of external gills. This is not due to the fact that they have been covered over by an operculum. The latter is just beginning to form and appears as a small pouch on each side of the throat immediately posterior to the hyoid ridge. The two pouches are directed backward and partly toward

one another. Adhesive organs have already formed and are represented by two widely separated disks one below each corner of the mouth. Pigmentation has begun to appear uniformly over the surface of head and body as a delicate reticulation which is less distinct on the tail and dorsal fin.

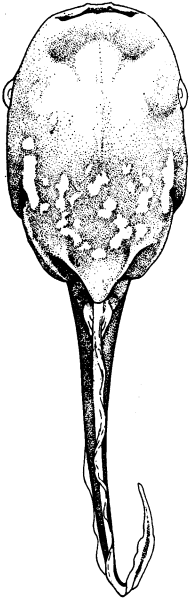


Fig. 5. Mature tadpole of *Gastrophryne carolinensis*. Ventral aspect. $\times 10$.

All these conditions are very different in the small-yolked *G. carolinensis*. As shown in figure 3a the larva at hatching has a very short tail and a prominence where the gills will later appear. Adhesive organs are very conspicuous, while the frontal organ is indicated by a pigmented streak which fades into the general dark color of the larva. The optic and pronephric regions are marked by swellings. Olfactory pits and stomodæum are well differentiated. Of special interest is a pronounced oro-nasal groove extending from the pit to stomodæum on each side. Kurepina (1926) has described a similar groove in *Pelobates* and *Rana*, and has pointed out its significance in the development of the internal nares which he, in contrast to earlier writers, finds homologous throughout vertebrates. The stomodæum appears very early in development (Fig. 4a) and the adhesive organs differentiate (Fig. 4b) at either end of a pigmented arc as in the case of

Hyla andersoni (Noble and Noble, 1923). The larva of *G. carolinensis* develops external gills (Fig. 3c) a short time after hatching but the opercular folds soon grow backward, fuse, and form an enormous median sac which completely covers the ventral surface. Before the hind legs have begun to develop the spiracle has attained its final position directly ventral to the vent and invisible unless the fold of skin at the posterior corner of the abdomen is turned forward (Fig. 5). *Hoplophryne* apparently never develops the abdominal sac. Mature larvæ of *H. uluguruensis* are unknown but the spiracle has an anterior position in *H. rogersi* (Fig. 6).

The larvæ of *H. uluguruensis*, preserved on October 6, show a distinct advance in growth over those preserved on the 5th. The lips are better developed (Fig. 3d), the olfactory organs are visible through the skin but, as on the previous day, there is no indication of external nares. The opercular folds have grown together leaving a broad, semicircular opening, the spiracle, in the midline of the body at a level immediately behind the fore limbs which are visible through the semitranslucent skin as whitish buds. The hind limbs are more developed than on the previous day but are still represented by a mere bud on each side. The most important feature is that behind each angle of the jaw, in other words, behind each hyoid and slightly towards the midline, there has appeared a whitish prominence which in later stages is destined to grow into a cutaneous appendage.●

By the 19th, approximately thirteen days after hatching, the tadpoles have increased to 16 mm. total length, 6 mm. head and body-length. They are more pigmented above and below. The adhesive organs have been entirely lost. The cutaneous appendages appear as a pair of whitish lunate flaps, very conspicuous on the more or less pigmented ventral surface. The hind limbs are better developed and the three segments marked out. The spiracle has moved slightly posteriorly and the opening has grown relatively narrower. At this stage it is clear that the tadpole of *H. uluguruensis* agrees essentially with the "brevicipitid type." It has a toothless and beakless mouth with a folded lower lip divided in the midline. No external nares are present. The spiracle and vent are both median. Except for the peculiar cutaneous appendages no important specializations are externally visible in these tadpoles other than the large yolk, the hastened development, the early differentiation of parts, and the elongate tail.

A series of larvæ of the same species was collected at Vituri, Uluguru Mountains, on the 29th of October. These show a great range of variation in degree of development. Some are hatched and are nearly as well developed as the Nyange larvæ preserved on the 19th. Others in the same lot are in the early stages of development and show neither limb rudiments nor opercular folds. The lips are just beginning to form and there is only the barest indication of pigmentation. This series is of interest for it clearly demonstrates that external gills are never present at any stage of development. I have dissected one of the larvæ which had apparently just hatched from the egg-capsule. In this specimen, only 5 mm. in head and body-length (15 mm. in total length), the lungs are well developed, inflated, and extend two-thirds the length of the body-

cavity. The larynx is open and I had no trouble in passing a fine bristle through the orifice into the lungs. Only a single branchial arch is present and, though the epithelium covering this arch is greatly folded and a series of short villousities flank the cleft, there are no typical branchiæ. This is radically different from the conditions in other brevicipitid larvæ, such as in those of *Gastrophryne* and *Microhyla*, where well-developed branchiæ occur. The lungs of *H. uluguruensis* can not be said to be greatly hypertrophied in compensation for the lost branchiæ. In a larva of *G. carolinensis*, only 3 mm. head and body-length, the glottis is open, the lungs are partly inflated and extend half the length of the body-cavity. In an older larva, 8.5 mm. head and body-length, the inflated lungs extend three-fourths of the body-cavity. *G. carolinensis* differs from *H. uluguruensis* in that it hatches before the lungs are formed but the reduction of the branchial region in the latter is correlated with the absence of water rather than with a disproportionate growth of the lungs. In brief, we may say that the larva of *H. uluguruensis* is highly specialized in that lungs are functional at the time of hatching, no external gills ever appear, and the internal gills are reduced to a few minute villousities on a single branchial arch. Respiration from the time of hatching would appear to be largely pulmonary but the greatly elongate tail would suggest that cutaneous respiration might play an important part. The tadpole, although a typical larva externally, employs throughout development the respiratory mechanisms of an adult rather than those characteristic of aquatic larvæ. This would suggest that the larvæ do not swim in the water caught between the banana leaves but remain on the edges of it or merely wriggle in damp crannies between the leaves. This conclusion is supported by other evidence to be discussed below.

As Barbour and Loveridge (1928) state, a series of tadpoles of the related *Hoplophryne rogersi* were collected at Amani in the Usambara Mountains on December 3, 1926. They are all more mature than the larvæ discussed above and some are metamorphosing. They are relatively much larger than the tadpoles of *H. uluguruensis*. One tadpole which has its hind limbs only slightly more differentiated than the largest larva of *H. uluguruensis* in the series measures 28 mm. total length. 9.5 mm. head and body-length. They differ markedly from the tadpoles of this species in having the integument of the snout and upper lips covered with a series of prominent papillæ which are visible even from the ventral surface (Fig. 6). The lower lip has the same folds and ridges of *H. uluguruensis* but these have different proportions which may be best seen by removing the upper lip (Fig. 7a). The two more anterior flaps

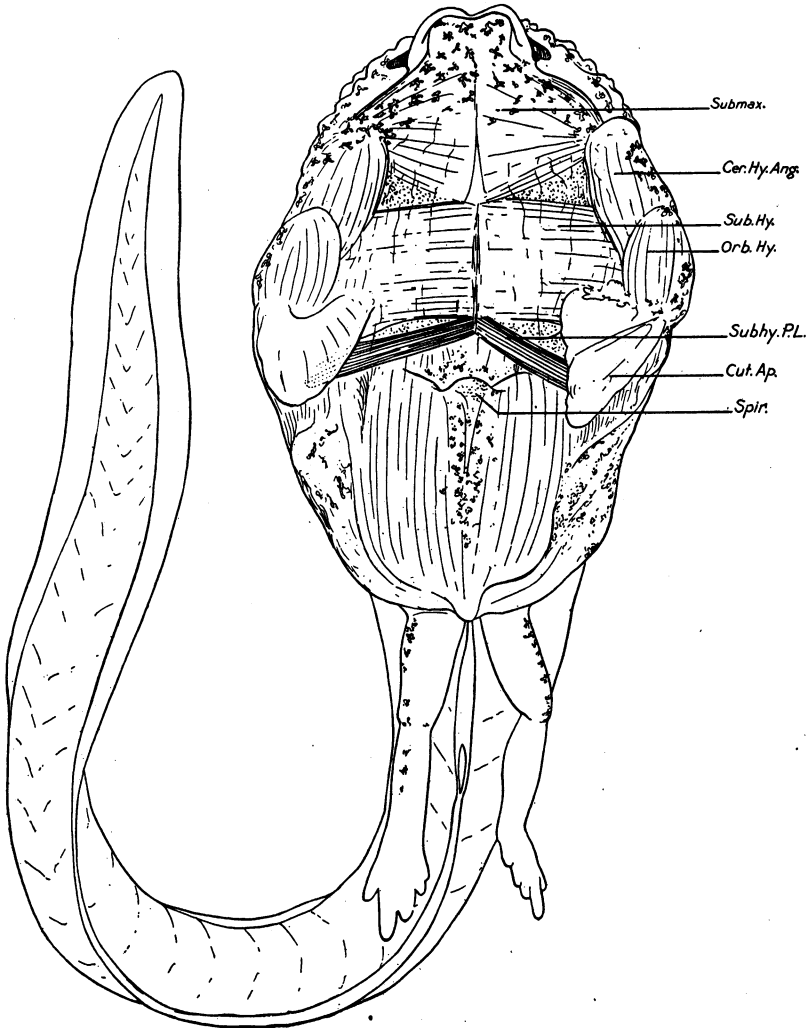


Fig. 6. Mature tadpole of *Hoplophryne rogersi*. Ventral aspect showing the locomotory appendages and their musculature. $\times 20$.

are short and curled downward and hence not visible from above. Further, the anterior or infrarostral segment of the lower jaw is more marked off from the posterior or mandibular segment. The same folds and ridges of the *Hoplophryne* jaw occur in *Gastrophryne carolinensis* (Fig. 7c) but the marginal flap curls upward and not downward. Further, the anterior segment, together with its folds, is proportionately much

smaller in *Gastrophryne*. The larvæ of *H. rogersi* agree with those of *H. uluguruensis* in the toothless and beakless jaws, the median spiracle and vent, and in the absence of external nares. Being older than the larvæ of *H. uluguruensis* before me they show additional "brevicipitid characters." The external nares form just before metamorphosis. Further, the toes are broadly webbed until metamorphosis (when the web is entirely lost). The larvæ exhibit the elongated tail of *H. uluguruensis* and have the cutaneous appendages of the throat well developed (Fig. 6).

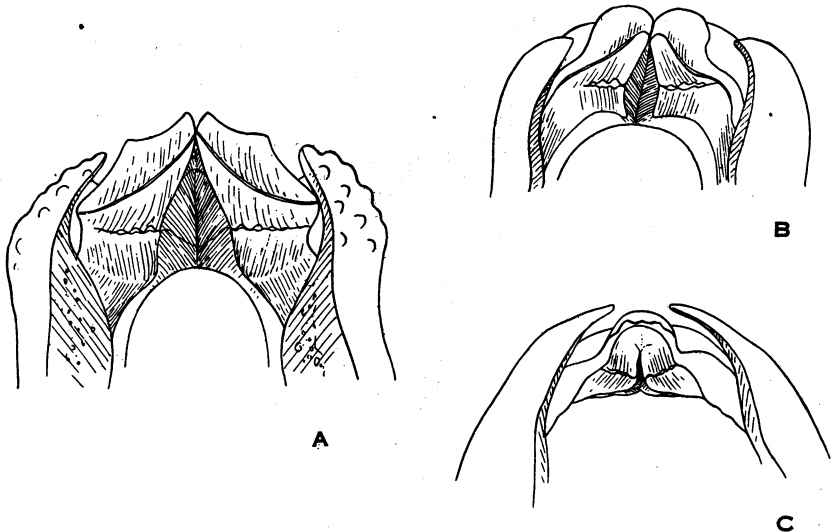


Fig. 7. Comparisons of the lower lips of *Hoplophryne* and *Gastrophryne* tadpoles after removal of the upper lips. The lower jaw is viewed from the dorsal aspect after part of the upper jaw has been cut away. $\times 30$.

- (a) *Hoplophryne rogersi*.
- (b) *Hoplophryne uluguruensis*.
- (c) *Gastrophryne carolinensis*.

I have dissected two larvæ of *H. rogersi* and have fully confirmed my observations made on *H. uluguruensis*. Lungs are well developed, the larynx open. Only one branchial arch is present (Fig. 8). A single opening occurs on each side between pharynx and opercular sac. This cleft is bounded by loose folds of epithelium and a few villisities but no typical branchiæ occur. It is apparent that *H. rogersi* agrees with *H. uluguruensis* in using its lungs and skin rather than its branchial apparatus for respiration during its larval life.

The most remarkable feature of the *H. rogersi* tadpoles is the cutaneous flaps which extend posteriorly, one on either side of the throat. They

are somewhat variable in shape but tend to have a triangular form. Preserved in alcohol they are grayish white, and much more opaque than the integument covering the ventral surface of the body. Under the highest binocular powers the individual cells may be readily noted, especially as each cell is more or less free, at least on its distal end, from the neighboring cells. As the cells are arranged in irregular rows the appendage has the appearance of being covered with minute, slightly

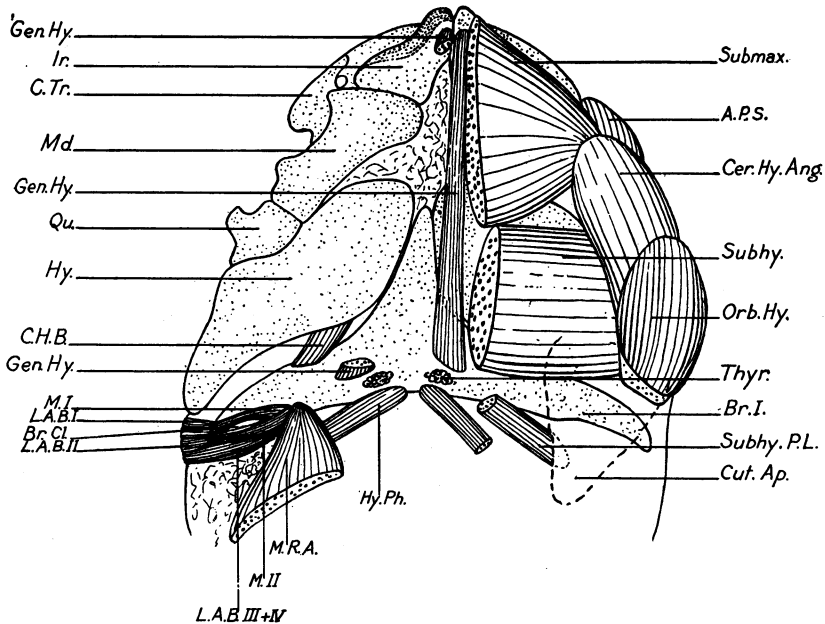


Fig. 8. Hyobranchial skeleton and musculature of *Hoplophryne rogersi* tadpole. Ventral aspect. $\times 20$.

overlapping scales. This illusion is strongest on the periphery of the appendage where the slightly projecting distal borders of the cells form a serrated edge to the whole border of the appendage.

Sections of one of these appendages (Plate XV, fig. b) reveal that each consists of a pad of connective tissue covered with a greatly thickened epidermis. The cells of the superficial layer are found to be practically free from one another but tend to overlap posteriorly. The appendage could obviously be pulled forward easily but the plate-like edges would tend to catch when drawn backward. The cells of the epidermis immediately underlying the superficial layer are also partly free, at least distally. The

epidermis of the appendage is three to four times as thick as that of the adjacent integument. Its cells, and especially their nuclei are much larger than those of adjacent epidermis. They are arranged in four to five instead of in two to three layers as in the skin of the abdomen where the cells are also more flattened. The cells of the basal layer of appendage epidermis are vertically elongated, those of the middle layers are nearly square, while the two superficial layers are flattened. The cells of the basal layer are, for the most part, bluntly pointed at their proximal end, and in contact with a series of fine collagenous fibers which tend to form a thin basal membrane. No capillaries are found in the epidermis. A thick bundle of muscles forms a firm attachment to the inner (dorsal) surface of the underlying pad of connective tissue. It is clear that the appendages in spite of their position in the branchial region can have no respiratory function.

In the larvæ of *H. rogersi* preserved in alcohol, the integument of the ventral surface is semitranslucent (Fig. 6). It is clearly visible that each appendage has firmly attached to its more distal portion a slip of the subhyoideus muscle. The relation of muscle to appendage is shown in the figures (Fig. 6; Plate XV, fig. *b*). The terminology employed is that of Schulze (1892) and Luther (1914), except for a few cases where the name given to the homologous muscle in the adult frog seemed preferable. In the case of the *M. hypopharyngeus*, topographical relations suggested the use of this term usually given to a urodele muscle (Göppert, 1898).

A dissection of the muscles of the branchial region has revealed that the appendage fits as a loosely adjusted cap or pad applied to the tip of the hyoid and branchial arch of each side. A dilation of the hyoid would stretch the skin of the throat and carry the appendage of each side forward and laterally. On the other hand a contraction of the powerful subhyoideus muscle would bring the appendages backward and toward the midline. This migration and rotation of the pad would be further extended by a contraction of the muscular slip attached to the distal part of each pad. In the larva figured, the appendage on the left side chanced to be more flexed than that on the right and the tip of the first will be seen to occupy a more posterior position than that of the second.

The relation of the appendages to hyoid cartilages and musculature strongly suggests that they are locomotory organs of use to the tadpoles in wriggling from one damp cranny to another. The histological structure of the pad supports the same view. They are not respiratory organs for they are only slightly vasculated and on the other hand are covered

with a thick friction surface similar to that of the pads of tree frogs (Noble and Jaeckle, 1927). A snake usually employs its long tail and body in wriggling over the ground but on emergency is able to move its ribs as props to push itself forward. By comparison it would seem probable that the *Hoplophryne* larva usually employs its greatly elongated tail in locomotion but is also equipped with a push mechanism. The latter would function to a certain extent every time the larva extended and contracted its buccal cavity in gulping air into the lungs, but an additional "kick" would be given to this movement by the contraction of the muscular slip attached to the posterior part of each appendage.

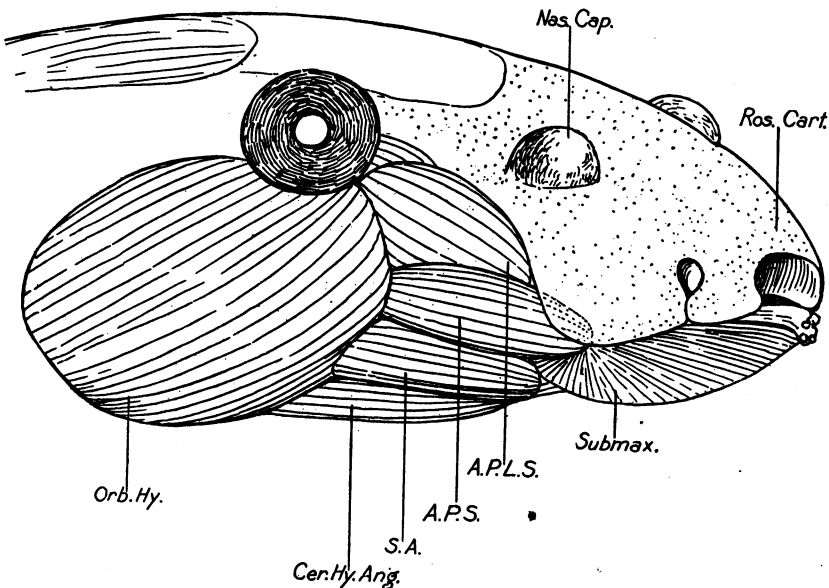


Fig. 9. Head of *Hoplophryne rogersi* tadpole, showing the diagnostic brevicipitid characters of musculature and rostral cartilage. $\times 30$.

The anatomy of the tadpole of *H. rogersi* is strikingly different from that of *Rana*. I have examined the musculature of two brevicipitid larvæ from different parts of the world to determine how many of these peculiarities of *Hoplophryne* were peculiar to the genus and how many were family characters. *Microhyla pulchra* and *Gastrophryne carolinensis* agree with *Hoplophryne* in the complete absence of a separate supra-rostrale. Further, the M. adductor mandibulæ posterior subexternus of Luther, 1914, is very muscular in these species and inserts as in *Hoplo-*

phryne on the rostral (trabecular) cartilage (Fig. 9, A.P.S.). These two features may be considered family characters which distinguish the brevicipitids, considered here at least, from the tadpoles of other families. The loss of the suprarostrale gives the brevicipitid tadpole its distinctive convex upper lip.

The tadpoles of *G. carolinensis* and *M. pulchra* agree among themselves and differ remarkably from those of *Hoplophryne* in having a mandibulolabialis muscle on each side, a small submentalis and an enormous subbranchial muscle which extends posteriorly over the abdomen as the ventral wall of the large branchial sac. This latter muscle is remarkable in having both horizontal and longitudinal fibres. The loss of this enormous muscle in *Hoplophryne* larvæ is correlated with the great reduction and loss of the posterior branchial arches described above. The loss of the submentalis and mandibulolabialis muscles is correlated with the great development of the infrarostrale and mandibulare cartilages which are much more powerful than in *Gastrophryne* or *Microhyla*. How these powerful jaws are used in *Hoplophryne* is difficult to say. The greater development of the rectus muscles in *Hoplophryne* larvæ is correlated with the development of the peculiar locomotory apparatus described above. The rectus abdominis is a powerful muscle attaching to the first branchial arch. It does not adhere to the ventral integument as in stream-dwelling tadpoles to be described below. Hence, it is not likely that the venter in *Hoplophryne* functions as an adhesive organ.

There are three aortic arches and the rectus is attached to the first branchial cartilage between the first and second of these arches.

I have examined the contents of the stomachs and intestines of twelve tadpoles of *Hoplophryne rogersi*. In seven of the specimens this food material consisted of the débris of animal and plant tissue. Among the former, three ants were identifiable. The greater part of the material consisted of partly digested plant tissue. Two tadpoles contained in their stomachs a small amount of yolk obviously from eggs they had eaten. Two others had their stomachs greatly dilated with pieces of frog eggs and with comminuted yolk. Some of the larger egg fragments were slightly pigmented but the greater part was pigmentless. This observation is of interest for it is clear, from the account of the habitat of *H. rogersi* given by Barbour and Loveridge, that no other species of frog lays eggs in the situations where the tadpoles were found. It would thus seem that the larvæ wriggle about in the crevices at the base of banana leaves and pick up with their toothless but powerful jaws what bits of

animal or plant débris may occur there. Eggs of their own species which they are able to reach are devoured, for the available food within the crevices where they live is doubtless limited and competition must be at a maximum. None of the tadpoles of *H. uluguruensis* examined had begun to feed but it may be assumed that they also have the voracious habits of *H. rogersi*.

The digestive tract of the tadpoles of both species is comparatively short. In *H. rogersi* there are only two and one-half or three loops of the small intestine and these have the general arrangement found in the adult frog. There is no spiral coil so characteristic of the intestines of most tadpoles, including *Gastrophryne*. This remarkable shortening of the digestive tract in *Hoplophryne* would seem to be correlated with the highly nutritious yolk diet of the tadpoles.

From the above account it is obvious that the eggs and larvæ of *Hoplophryne* differ from those of *Gastrophryne* in a number of important ways. It is not unlikely that some of these differences may be due to the direct effect of the environment acting during each ontogeny. Unfortunately, I have been able to compare the developmental series of *Hoplophryne* with only one other brevicipitid which lays its eggs out of water. This species is *Breviceps rugosus*, collected in the Uluguru Mountains by Mr. A. Loveridge, and kindly loaned me for study by Dr. Thomas Barbour. Its eggs are enormous, being 4 mm. in diameter without the egg-capsules. Two egg-capsules and a vitelline membrane are present as in *Hoplophryne*. These are molded by adjacent egg-capsules and no flattened "cap" is present. All of the eggs are in a single stage of development. The embryo is well marked out and it lies flat on the large yolk half encircling it. The eyes and olfactory organs are visible, and four limb-buds of subequal size are present. The tail is round but there are no indications of external gills. Thus, *Breviceps rugosus*, which skips over the tadpole stage, very probably will show in its encapsuled larva no distinctive features characteristic of the brevicipitid type of tadpole. A great many genera of Salientia have succeeded in increasing the size of their eggs and we have previously concluded (Noble, 1927) that egg size alone was of little phylogenetic significance.

COMPARISONS WITH OTHER AMPHIBIA

From the above description it is clear that the tadpole of *Hoplophryne* agrees in external features with the typical brevicipitid larva but differs remarkably in the possession of a pair of integumentary flaps attached to the hyoid region and moved by branchial muscles. These I interpret as locomotory structures. The tadpole is also distinctive in the almost complete suppression of its larval branchial apparatus. It would seem that pulmonary respiration early asserted itself, and that neither external nor internal gills are ever formed. Modifications having a more obscure functional significance are the elongation and narrowing of the tail and the great development of the lower jaw. In attempting to correlate these modifications with functional differences some comparison may be profitably made with the larvæ of other groups of frogs having a similar mode of rearing their young.

First may be mentioned the larvæ of the pelobatid *Sooglossus sechellensis* as described by Brauer (1898). The eggs are laid exposed to the air and the larvæ undergo their complete development while adhering to their parent's back. The developmental history of *Sooglossus* agrees with that of *Hoplophryne* in that the eggs are large-yolked, the larvæ hatch with hind leg rudiments visible, neither external nor internal gills appear at any stage of development, and the tail of the larvæ is long and narrow. *Sooglossus* larvæ differ from those of *Hoplophryne* in that lungs appear very late in development, tadpole mouth-parts are never formed and, although branchial "limbs" would doubtless be of service to the *Sooglossus* larvæ in wriggling over their parent's back, there is no indication of such structures.

Although *Sooglossus* and *Hoplophryne* lack external gills during development there are many other Salientia laying large-yolked eggs on land or away from water and yet possessing such gills. This is particularly true of *Cryptobatrachus* which transports its eggs exposed on the back of the female. Some species of *Eleutherodactylus* which practice direct development have external gills at an early stage (Noble, 1927). *Phyllomedusa* and *Centrolenella* lay their eggs exposed to the air on leaves. The larvæ, while within the egg-capsules, have very large gills. The same is true of *Chiromantis xerampelina* which beats considerable quantities of air into the egg-mass. It must be admitted that it is not clear why *Hoplophryne*, *Sooglossus*, and a few other species such as *Hemisus* have been able to dispense with their external gills while other species have not.

Continuing the detailed comparison of *Hoplophryne* tadpoles with those of other Salientia, some reference may be made to the Hylidæ of Jamaica. All four species of *Hyla* from this island lay their eggs in bromeliads (Dunn, 1926). The crevices at the bases of the leaves usually retain a small amount of rain-water in which the tadpole lives in very much the same way as Barbour and Loveridge reported for *Hoplophryne*. As the tadpoles develop, the water, according to Panton quoted by Dunn, becomes about as viscid as glycerine. The viscosity is apparently due to the disintegrating egg-capsules and although no exact measurements have been made it is possible that the liquid in which the larvæ of *Hoplophryne* swim would have much the consistency of that in the "nests" of the Jamaican hylas. It may be, therefore, of some interest to compare the tadpoles of the Jamaican hylas with those of the less modified Hispaniolan species, with a view to determining what adaptation, if any, develops in tadpoles which swim in slime. Again I am indebted to Dr. T. Barbour for the loan of valuable material.

Hyla brunnea of Jamaica is very closely allied to *H. dominicensis* of Hispaniola (Dunn, 1926; Noble, 1927). Both lay their eggs in stagnant water, the first in small quantities between bromeliads, the second in larger pools in forest and open country. In Barahona, Santo Domingo, I found *H. dominicensis* breeding in a small tank, placed at some distance from the ground to catch rain-water. The chief difference between this breeding site and that of *H. brunnea* was its greater size, more exposed position and the less viscid medium throughout development. Nevertheless, the tadpole of *brunnea* differs markedly from that of *H. dominicensis*. Its tail is twice as long in larvæ of the same head and body-length. The tail fin is much narrower. The body of *H. brunnea* is slimmer and flatter than that of *H. dominicensis* and the head is slightly marked off from the body. The latter feature is due in part to the great reduction of the branchial arches. All four are present but they are much smaller than those of *dominicensis*. Only a short fringe of branchial villousities projects ventrally from these arches and not the extensive brush found in *dominicensis*. A dissection reveals that the rectus abdominis muscles are much better developed in *brunnea*; further, they extend forward to attach to the base of the first branchial arch. In other words, the anterior part of the rectus is not marked off as a distinct element, the *M. diaphragmatobranchialis medialis* of Schulze (1892). In apparent correlation with this the other median branchial muscles (*M. basihyobranchialis* and *M. ceratohyobranchialis*) are much thicker in this

species. It would seem that *H. brunnea* made much greater use of its ventral musculature and less use of its branchial apparatus than *H. dominicensis* did.

This reduction of the branchial apparatus is not correlated with a greater development of the lungs in *brunnea*. In a tadpole of *brunnea*, having its hind limb-buds beginning to differentiate segments, the lung extends the whole length of the body cavity. The same condition is found in a larva of *H. dominicensis* of the same stage of development and also in a tadpole of *H. heilprini*. The latter live in rushing cascades and might be expected to get along with branchial respiration alone, especially as lungs have been assumed to be detrimental buoyant organs in animals living in mountain brooks.

The lungs did not hypertrophy with the reduction of the gills. Might not the elongation of the caudal appendage, which obviously functions in cutaneous respiration, be considered a compensatory change? This may be true, but there are certain other facts to consider. The tail elongation and narrowing are found in mountain-brook tadpoles, also in species such as *Borborocætes miliaris* which live only partly immersed in water flowing over rocks. It similarly occurs in *Cycloramphus* recently described by Lutz (1928), which during its larval life lives only partly immersed in water. The elongation of the tail is not merely an expression of a need for greater respiratory surfaces.

Could the reduction of the branchial arches and the elongation of the tail be directly produced during each generation by an environment of great viscosity? Such a question could be easily answered by experiment. In the meantime the following correlations are of interest. Tadpoles living in foam-nests have usually an elongate and narrow tail. In *Eupemphix* and to a less extent in *Leptodactylus* the tail is proportionately longer and slimmer while the larva is still within the disintegrating mass of egg-capsules than later when free in the water (Noble, 1927, Fig. 18). Some years ago Babák (1907) showed the direct effect of increased oxygen supply on reduction of branchiæ in *Salamandra*. It is hard to believe that the slimy liquid in the "nests" of the Jamaican hylas would be saturated with oxygen. Hence the failure of the branchiæ to develop fully may be due to an inhibitory effect of a dense medium on gill growth.

I have dissected the larvæ of all four species of *Hyla* from Jamaica and find that they agree in the reduction of branchial arches and gills. It has been pointed out elsewhere (Noble, 1927) that mountain-stream life tends to reduce gill growth, but the gills of *H. heilprini* are far

better developed than in any of the Jamaican species of the same size. Further, in all four species the rectus abdominis is well developed. The species differ in the extent to which the rectus attaches to the integument of the abdomen or is continued forward to the branchial arches. The tadpoles are all comparatively slim and flattened. The tail is long and is equipped with only a narrow fin, but it differs considerably in length from species to species. It is proportionally most developed in *brunnea* and least in *wilderi*. The tail of the latter species agrees well in length and height with tadpoles of *heilprini* of the same body length. It is, however, less muscular than that of *heilprini*. A mountain torrent, such as *heilprini* frequents, would not foster the development of a broad tail fin, nor would living in shallow water be conducive to its growth in height. The narrow tail fin of the Jamaican hylas would seem to be directly correlated with their life in shallow and viscid water. We may conclude that the narrow, elongate tail of *Hoplophryne* is equally adapted primarily not for respiratory needs but for locomotion in the viscid mass formed by disintegrating egg-capsules in a minimum amount of water.

A further parallelism between the tadpoles of *Hoplophryne* and those of the Jamaican hylas is the similarity of diet. *Hyla brunnea* which lives in a habitat differing from that of its relative *H. dominicensis*, chiefly in size, has discovered, so to speak, a nutritious article of diet in the freshly laid eggs of tree frogs and presumably those of its own species. Of fourteen tadpoles of *H. brunnea* which I dissected, six had their stomachs greatly dilated with eggs which had been swallowed whole, five had only insect and vegetable débris in their digestive tracts. Roaches, flies and ants were recognizable among the former food material. Three tadpoles contained both eggs and vegetable food. There was no correlation between size and diet. All the eggs seemed undeveloped and no remains of other tadpoles were in the stomachs. The digestive tract was shorter than in *Hyla versicolor* tadpoles. When the stomach was full of eggs it covered most of the ventral surface of the tadpole and its contents was visible through the integument. Of seven digestive tracts of the Jamaican *H. wilderi* examined, three contained only eggs, two only insects and vegetable débris, and two a mixed diet. Of seven of *H. marianæ*, five contained eggs, one, other material, and one, eggs and vegetable material. The one tadpole of *H. lichenata* examined had eggs, insect and plant food. The eggs in the last species were distinctly larger and more pigmented than those devoured by the other species. This suggests but does not prove that the tadpoles devour eggs of their own species.

The Jamaican hylas have undergone a great reduction of the larval tooth-rows. Is this correlated with the soft substratum on which they rest, or with an egg diet? The larval lips are reduced to either a nearly complete ring of tubercles or to a shallow cup-like fold surrounding the mouth and are studded with low tubercles. The larval tooth-rows are greatly reduced. They are entirely absent from the lower lip of all species except *wilderi* which has a circle of widely spaced teeth surrounding the mouth (Dunn, 1926, Fig. 4). No larval teeth occur in *marianæ* at all, while *brunnea* and *lichenata* retain a single row in the upper lip more or less complete. In addition, *lichenata* has a few scattered teeth on a few of the tubercles of the lower lip. The mandibles are well developed in all species and in most have a smooth, not denticulated edge. The mandibles of *brunnea* extend more laterally and are less curved than those of *dominicensis*. There is a considerable gape in all the Jamaican species. In the diminutive *H. wilderi* the mandibles when opened are found to extend beyond the limits of the cup-shaped fold around the mouth. They are proportionately wider than those of either *dominicensis* or *heilprini*. In correlation with this great development of the mandibles the jaw muscles in the four Jamaican species are proportionately much more developed than those of the Hispaniolan species. The muscles are broader and less tendinous. Most remarkable is the fact that the masseter (M. adductor mandibulæ posterior subexternus of Luther, 1914) attaches not to the tendon of the subtemporalis (M. adductor posterior longus profundus of Luther, 1914) but to the suprarostrale in the Jamaican species but in none of the Hispaniolan forms. This would make the closing of the mandibles in the Jamaican species much stronger. It would be interesting to know how many of these modifications could be produced in a single generation by forced change of food habits in the Hispaniolan forms. Some years ago Powers (1907) recorded remarkable changes in *Ambystoma tigrinum* larvæ which had become cannibalistic. The mouth of *Hoplophryne* is toothless, but so is that of all brevipitid larvæ except the African forms of independent origin. Obviously the pond-dwelling tadpoles of *Microhyla* must take very different foods than those *Hoplophryne* utilize, but whether the pronounced difference in the size of the lower jaw of these forms has any functional significance is unknown. In this connection it should be noted that the diet of the four Jamaican species of *Hyla* is very similar and yet the details of mouth structure differ considerably from species to species. It seems, nevertheless, more than a coincidence that *Hoplo-*

phryne and the Jamaican hylas, which differ from their nearest relatives in adding eggs to their diet, should both have developed powerful jaws.

Another point of similarity is the short digestive tract and expansive stomach found in both groups. The character of the food is known to have a great effect on the length and width of the alimentary tract of tadpoles and it would seem from the experiments of Yung (1905) and Babák (1905) that the mechanical effect was greater than the chemical effect. Thus, whether or not nutritious yolk would tend to shorten the digestive tract, it would seem probable that the enormous size of the stomach was directly correlated with the great quantities of whole eggs engulfed. It would be interesting to know the effect of a pure vegetable diet on the digestive tract of these tadpoles, for in view of the extensive experiments of Babák, 1903, 1905, 1905*a*, 1911, Yung, 1904, 1905, and Elven, 1928, it seems certain that the direct effect of bulky food during each ontogeny would be considerable.

THE TORRENT TADPOLE OF *STAUROIS*

The ranid genus *Staurois*, including the *Rana formosa* section of *Rana*, is characterized by a distinctive type of tadpole. It possesses a large suction disk just posterior to the buccal apparatus. The tadpole lives in mountain-brooks and adheres to stones by means of its disk. Hora (1922) has shown that the tadpole when lifted free of the water could support with its disk a stone sixty times the weight of the whole tadpole. There is therefore no doubt as to the efficiency of the disk as a holding mechanism.

Staurois is so closely related to *Rana* that the distinction between the two groups is still an unsettled matter. I have pointed out (1927) that all species having tadpoles with suction disks form a natural group to which I apply the name *Staurois*. In view of this close relationship it would seem that the beginnings of disk formation would be found in some species of *Rana*. A detailed study of the disk has been made by Annandale and Hora (1922) in *S. afghana* (= *S. latopalmata*). They claim that the disk apparatus "seems . . . to have arisen strictly *de novo*," and make no attempt to homologize the muscles which they describe in this apparatus with those found in the ventral body-wall of *Rana* tadpoles. I have examined a large series of well-preserved larvæ of *Staurois ricketti* collected in Fukien, China, by Mr. Clifford H. Pope, and find myself in disagreement with many points in the account of Annandale and Hora. Before pointing out these

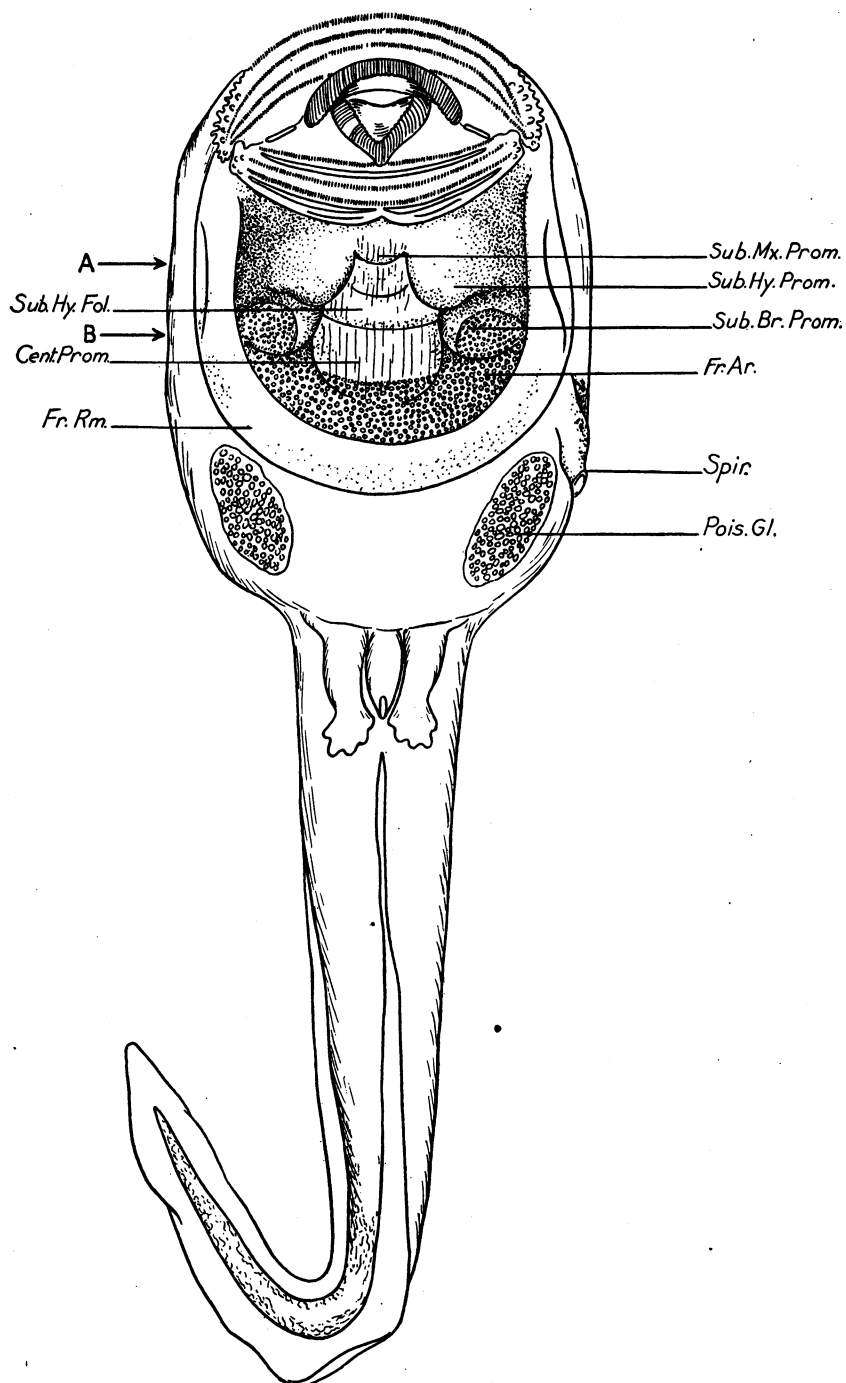


Fig. 10. Tadpole of *Staurois ricketti*. Ventral aspect. $\times 8$.

discrepancies I wish to describe briefly the essential features of the suctorial disk of the tadpoles before me.

The form of the suctorial disk of *S. ricketti* as viewed from below is seen in figure 10. The free edge forms a semicircle which meets anteriorly the ventral lip. Within the free edge is a depression marked by several prominences and a fold. There are two prominences on each side and two less distinct ones in the midline, separated by a narrow, flat space and a fold (Fig. 10). I have given names to these areas for they have different functions in the suction process. Under the higher binocular powers a roughened area (Fig. 10, *Fr. Ar.*) of the disk is readily distinguished from the remainder of the ventral integument. It forms a crescent-shaped area immediately anterior to the posterior part of the rim. It extends forward to partly cover each of the subbranchial prominences (Fig. 10, *Sub. Br. Prom.*) but avoids all but the posterior edge of the central prominence. The roughening is produced by an irregular series of very fine protuberances.

The ventral surface of the tadpole of *S. ricketti* is also distinguished by two large clusters of poison (granular) glands. The mouth is large and directed ventrally. The teeth are in 3, 1-1: 1-1, 2 rows, but the occurrence of several folds between the tooth rows in the lower jaw tends to obscure the arrangement.

With a sharp razor the ventral integument, together with its attached muscles, was removed from the remainder of a tadpole's body (Fig. 11). Serial sections were made of two other tadpoles. With this material it was possible to follow out all structures attaching to the disk.

An examination of the dorsal surface of the removed suctorial disk (Fig. 11) reveals that the muscles attaching to the disk have much the same arrangement as those in the ventral body-wall of *Rana clamitans* and may be readily homologized with them. The chief difference lies in the fact that the posterior half and the two anterior corners of the disk are covered by more or less continuous pads of connective tissue to which the muscles are attached.

At the anterior end of the disk there are five ligaments extending between connective tissue pad and overlying skeletal elements. The subquadrate and the subhyoid ligaments fan out as they approach the pad, while the median submaxillary ligament maintains a narrow base. By transmitted light the relation of the ligaments to the prominences on the other side of the pad may be readily recognized. The submaxillary ligament overlies the submaxillary prominence. The

subhyoid and subquadrate ligaments of each side are above the subhyoid prominence of that side

The subbranchial muscle is much narrower than in *Rana clamitans*. It arises from two heads, one of which originates from the subcutaneous

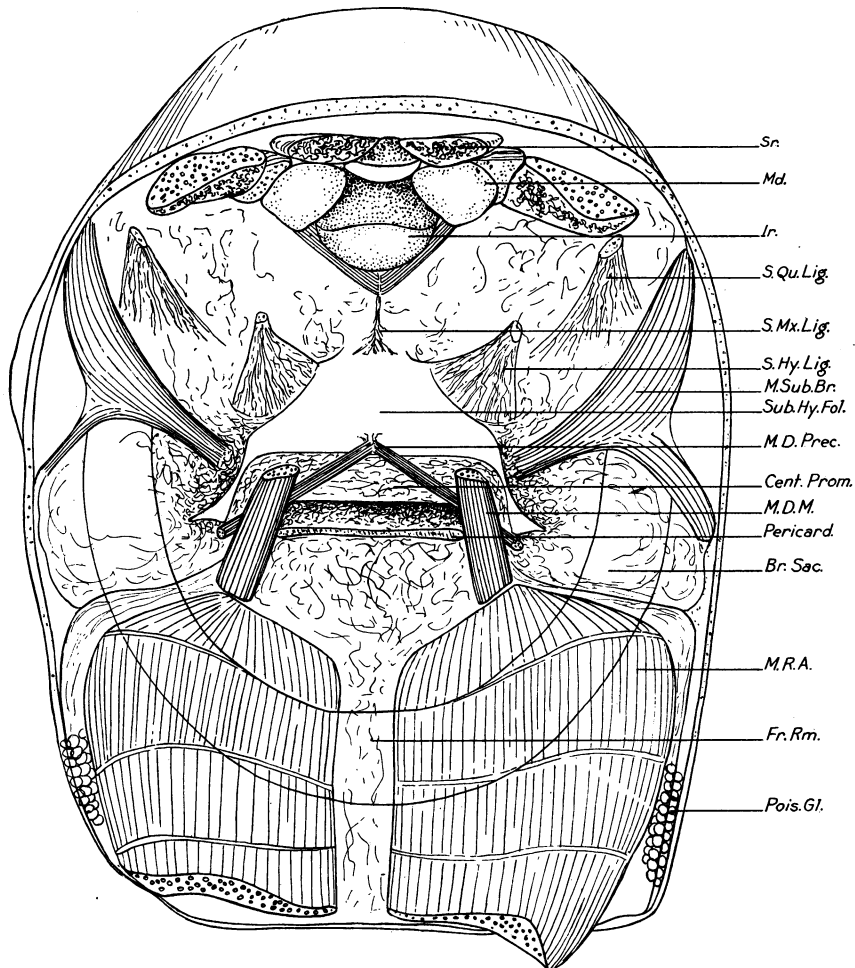


Fig. 11. Suctorial disk of tadpole of *Stauroids ricketti*. A visceral aspect after removing the disk and associated structures from the remainder of the tadpole. $\times 20$.

connective-tissue sheath just lateral to the posterior end of the mandible, the other from the connective-tissue sheath covering the branchial arches. As shown in figure 10 the two heads soon form a narrow muscle-band which inserts on the disk-pad immediately over the sub-

branchial prominence on the ventral surface of the disk. This relation of the subbranchial muscle to the pad is also shown in the cross-section of this region (Plate XVI, fig. b).

To the posterior margins of the disk-pads the two rectus abdominis muscles are firmly attached. I have included a photograph of a section

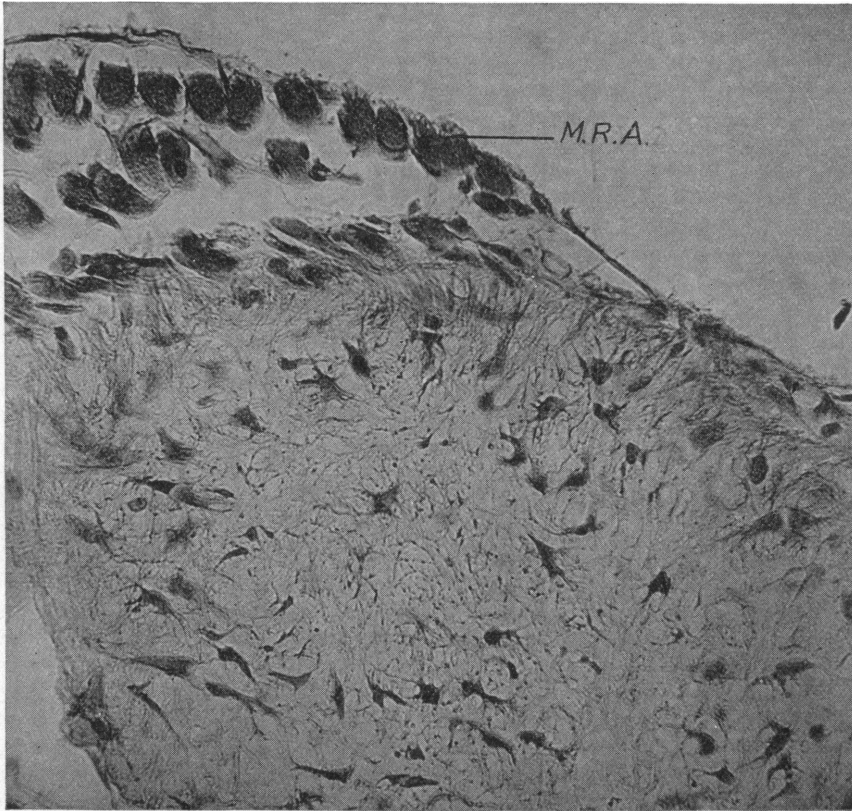


Fig. 12. Area of attachment of the rectus abdominis muscle to the connective tissue pad of the suctorial disk. $\times 280$.

made at one of the points of junction. The thickness of the pad as well as the interweaving of connective tissue and muscle fibres will be noted (Fig. 12). Immediately anterior to each of the rectus muscles is the *M. diaphragmatobranchialis medialis* of that side inserting on the pad. It arises from the base of the branchial skeleton as in *Rana clamitans* tadpoles.

The posterior wall of the pericardium differs from that in *Rana* tadpoles in being far more tendinous and in firmly attaching to a thickened portion of the pad (Plate XVI, fig. *a*). It is provided with some smooth muscle fibers and these together with a thick sheet of collagenous fibers extend dorsally from the pad. It divides into two ligaments which at the junction of skull and first vertebra divide again, one half of each extending posteriorly and attaching to the ligamentous sheath covering the ventral surface of the dorsal musculature and the other half extending forward to attach to the otic capsule of that side.

The M. diaphragmatopræcordialis is a slim muscle arising from the anterior wall of the abdominal cavity immediately posterior and mesial to the developing fore limb. It inserts on a papilla of connective tissue immediately anterior to the connective-tissue pad which forms the central prominence (Fig. 11). It differs from the homologous muscle of *Rana clamitans* chiefly in its insertion on to the integument of the ventral surface.

The muscles attaching to the suctorial disk of *Staurois* occupy nearly the same position as homologous muscles in *Rana* tadpoles. The process of suction in *Staurois* is essentially a contraction of the ventral musculature which in turn would lift the connective-tissue pads and form a vacuum within the rim provided the mouth was held closely to the substratum. The work would be done chiefly by the rectus abdominis, diaphragmatobranchialis medialis and the subbranchialis, but obviously as the body was arched and the snout pressed into the substratum the tendons extending from the pad to the quadrate and hyoid of each side would tend to lift the two anterior corner pads. The movement of the pads in a vertical direction is complicated by the thin central area of the disk which in preserved specimens forms a slight fold. This region obviously stretches as the pads are lifted and, as the subbranchial muscles are inserted at a very acute angle to the medial edge of the lateral pads, they would tend to raise only the inner portion of these pads. This fact will be more readily recognized if figure 11 and Plate XVI, fig. *b* are compared.

The tendinous posterior wall of the pericardium as well as the two small diaphragmatopræcordialis muscles would have only a secondary function in the lifting movement. It would seem that the diaphragm sheet assisted the two diaphragmatobranchialis medialis muscles in opposing the contraction of the powerful rectus muscles and by this action affecting a raising of the posterior pad. The function of the

slim diaphragmatopræcordialis muscles is apparently the holding of the thin subhyoid fold of skin tense while the other ventral muscles are contracting.

That the major part of the work is done by the posterior pad is further suggested by the distribution of the fine epidermal tubercles. These are formed wholly within the epidermis out of little groups of cells which may be so crowded together that the tubercles may seem to be only one cell wide at the base (Plate XV, fig. *a*). It is more usual for several cells to be found in a cross-section of the base of one of the tubercles. The superficial cells are extensively cornified but not always flattened. As shown in Plate XVI, figure *a*, the tuberculated epidermis is markedly thicker than adjacent epidermis. A layer of collagenous fibers separates it from the underlying pad of connective tissue.

The function of the tubercles would seem to be to increase the friction of the suctorial disk. In this they agree with the overlapping cells on the branchial appendages of *Hoplophryne* or with the friction epidermis (Noble and Jaekle, 1927) on the pads of tree frogs. The tuberculated area of *Staurois* differs from these other friction surfaces markedly in structure, for each friction unit is not a single cell but a cluster of cells, a veritable papilla of the epidermis.

The above account of the suctorial apparatus of the tadpole of *Staurois ricketti* differs in almost every detail from that of *S. afghana* as given by Annandale and Hora (1922). Only one tadpole of this species has been available for dissection but this one was well preserved and I have had no difficulty in working out the main features. In *S. afghana* or *S. latopalmata* as the species is now called, the suction disk has nearly the same form as in *S. ricketti*. There are two pairs of prominences formed by pads of connective tissue and a medial fold of thin integument. This fold is not transverse to the body axis as in *ricketti*, but longitudinal. There is a crescentic patch of cornified and finely roughened epidermis occupying, as in *ricketti*, the posterior part of the cup within the rim. The rectus abdominis is very powerful and inserts, as in *ricketti*, to the posterior part of the cup just within the rim. It is opposed by two diaphragmatobranchialis medialis muscles having the same relationship as in *ricketti*. An important difference appears in the subbranchialis muscles which attach in the usual way to the dorsal side of the subbranchial prominences but are much more powerful than in *ricketti*. Further, they extend almost straight dorsally to attach by a powerful ligament partly to the base

of the skull and partly to the connective-tissue sheath covering the anterior part of the dorsal body muscles. The more anterior part of the disk exhibits the same form and attachments as in *ricketti*. A few minor differences occur, such as in the subhyoideus muscle which sends a few strands to attach to the subhyoid fold. Annandale and Hora have numbered but not named the muscles which they found in their specimen attaching to the disk. I assume their No. 1 is the subbranchial muscle, their No. 2 the diaphragmatobranchialis medialis and their tendon the pericardium. The points of origin of these two muscles are very different from those Annandale and Hora described. Further, they overlooked the very important part the rectus muscle must play in the suction process.

From the above description it is clear that the tadpole of *Staurois latopalmata* differs in regard to its suctorial apparatus from that of *S. ricketti* chiefly in having a more powerful and dorsally directed subbranchial muscle. The tadpole is more specialized than that of *ricketti* in having a greater number of tooth-rows in its dorsal lip, but it is less specialized in lacking poison glands. In regard to its suctorial apparatus *S. latopalmata* is obviously the more specialized but it differs only in detail from the tadpole of *S. ricketti*. Annandale and Hora state that the suctorial apparatus of *S. livida* agrees with that of *S. latopalmata* and I have found very little difference in the external form of the disk of *S. hainanensis*. We may conclude that the suctorial apparatus of *Staurois* is essentially the same in all species and its parts may be readily homologized with structures already existing in the ancestral *Rana*.

The tadpole of *S. latopalmata* available is not sufficiently well preserved to permit a histological study of its suctorial disk. The account of the histology of this structure as given by Annandale and Hora is so much at variance with the conditions in the same tissues in *S. ricketti* described above that I suspect that Annandale and Hora's material was not adequately prepared. Thus, the epidermis in *S. ricketti* is not a syncytium, the cornified outer layers are not a "chitinized cuticle," the connective-tissue pad has its deeper fibres running not at right angles to the epidermis but in various directions. Annandale and Hora do not mention that the roughening of the epidermis is confined to a crescentic region in the posterior part of the pad. Their main point that the ventral disk in *Staurois* functions both by friction and by suction is fully confirmed. The additional details given above are of importance in defining more precisely the degree of divergence from conditions found in the ancestral, pond-dwelling tadpole.

COMPARISONS WITH OTHER AMPHIBIA

No genus of Salientia other than *Staurois* has tadpoles equipped with a suctorial disk behind the mouth. Until recently some species of *Staurois* have been referred to *Rana* but, as I have pointed out elsewhere (1927), these species are more properly allied with *Staurois*. If the suctorial disk characterizes all species of *Staurois* and no other tadpoles have it, how may we trace the steps by which the disk came into existence?

Many other tadpoles live in mountain brooks. Most of them have the mouth enlarged into a suctorial-friction apparatus similar in general structure to the enlarged mouth of *Staurois*. Whether any of these are able to use the abdomen as a suction apparatus is unknown. All mountain-brook tadpoles of *Rana* and *Hyla* which I have examined have the rectus abdominis much more developed than in pond-dwelling tadpoles of the same groups. A few show a progressive fusion of the rectus abdominis to the integument of the ventral surface, obviously an important step in the direction of the *Staurois* tadpole. This is well shown in the hylas of Hispaniola where the condition reaches its extreme in *Hyla heilprini*. No abdominal disk is formed in any of these species, but the tadpoles of *H. heilprini* hold themselves so tightly to rocks in cascades that it would seem probable that the specialized ventral musculature assisted the mouth in maintaining the tadpole's grip.

In the mountain-brook tadpole of *Heleophryne rosei*, a South African bufonid, there is found a modification of the ventral musculature to stream life in a different direction from that followed by *Staurois*. The subbranchial muscle of each side is enormously developed and originates from the lateral process of the quadrate cartilage to insert by a broad head on the outer part of the rectus abdominis. The muscle must be of great service in swimming, for the lateral muscle-bundles of the rectus are continuous with it, making a single muscle-mass extending from the lower side of the tail base to the quadrate of each side. In *Staurois* the subbranchialis is attached to the suctorial disk and is not continuous with the rectus, but *Heleophryne* is instructive in showing the extent to which this muscle may be modified. The other branchial muscles of *Heleophryne* agree closely with those of *Rana* tadpoles but are better developed than in most species. This is particularly true of the diaphragmatobranhialis medialis which is continuous with the rectus as in *Hoplophryne*.

In brief, many mountain-brook tadpoles are equipped with large mouths but none are known at the present time to be intermediate in regard to their ventral musculature between *Staurois* and *Rana* tadpoles. Nevertheless, mountain-brook tadpoles of other families exhibit certain resemblances in their ventral musculature to that of the tadpoles of *Staurois*.

LUNG REDUCTION AND ITS CAUSES

In the tadpoles of both *Staurois ricketti* and *S. latopalmata* the lungs are small and apparently non-functional for almost the entire larval period. In a mature tadpole of the former species, 37 mm. in total length and 15 mm. in head and body-length, the lungs are only 2 mm. in length. In a tadpole of the latter species of the same total length and 14 mm. head and body-length, the lungs are only 1 mm. long although the hind limbs are as well developed as in the former specimen. In a tadpole of *Heleophryne rosei*, 44 mm. in total length, 20 mm. head and body-length, the hind limbs are well developed but the lungs are only 2 mm. in length. By contrast it is found that with many pond-dwelling tadpoles, such as those of *Pseudis paradoxa* and *Microhyla pulchra* in the same stage of development, the lungs are inflated and extend the full length of the body-cavity. In others, such as in *Hyla versicolor* and *Gastrophryne carolinensis*, the lungs extend four-fifths of the body-cavity at the same stage of ontogeny. In the tadpoles of *Rana clamitans*, which have been used for comparison above, the lungs are also extensive. Thus, in a specimen having a total length of 56 mm. and a head and body-length of 24 mm. the lungs are 9 mm. long and inflated. This tadpole is in approximately the same stage of development as the tadpole of *S. ricketti* described above. From these data it would seem that mountain-brook tadpoles tend to have far less developed lungs than pond-dwelling species of the same ontogenetic stage.

A closer examination of the problem will reveal, as I have pointed out previously (Noble, 1925), that the rule does not always hold. Other mountain-brook tadpoles, in particular those of *Hyla heilprini* and *H. vasta*, have the lungs as well developed as *Rana clamitans* and many other pond-dwelling forms. How may we account for this difference in lung length between tadpoles living in swift water? The only difference known at present between the average habitat of *Hyla heilprini* and that of *S. ricketti* tadpoles is one of temperature. I found that in midsummer the mountain torrents of Santo Domingo inhabited by

H. heilprini ranged from 74° to 78° F. C. H. Pope, in Fukien Province, China, found at the same time of the year the streams frequented by *S. ricketti* tadpoles varied from 63° F. to 73° F. The latter species was found in both large and small streams, the larger being the warmer.

It is highly probable that the streams frequented by *S. ricketti* have on the average a higher oxygen content than those inhabited by *H. heilprini*. Both streams flow over bare rocks and are well churned by the projecting ledges. Cold water absorbs more oxygen than warmer water and, as the conditions other than temperature seem equal in the two cases, it appears that the Fukien stream would have the higher oxygen content.

What effect would increased oxygen supply have on the growth of lungs? In 1925, when describing the changes in heart and skin correlated with a reduction of the lungs, I reviewed briefly the explanations which had been given for the reduction of lungs in Amphibia and found reason for believing that the greater oxygen supply in cold and running water was a factor permitting Amphibia living in this medium to succeed with cutaneous respiration alone (supplemented in some cases by buccopharyngeal respiration). More recently, Dunn (1928) has criticized this point of view on what seems to me insufficient grounds and hence it may be well to review briefly the evidence as to the causes of lung reduction in Amphibia in general as this has an important bearing on the conditions in *Staurois*.

In 1893, Bridge and Haddon (p. 305), while discussing fish living in mountain torrents, pointed out "the utter uselessness and probable harmfulness of an air bladder as a hydrostatic organ under such conditions is no doubt the cause of its degenerate and rudimentary condition." However, the air bladder of fish has been reduced or lost in other habitats besides the mountain brook, and Bridge and Haddon recognize that "in so many Physoclist Teleostei the assumption of a purely ground habitat of life is probably the most important" factor leading to this degeneration. The correlation of air bladder degeneration with life in mountain torrents has been discussed by later authors and particularly by Hora in the hill-fish of India. Lonnberg (1899), recognizing the importance of lungs in salamanders as hydrostatic organs, as had been previously described by Camerano, pointed out that some salamanders with reduced or lacking lungs have adopted a ground habit of life in the water. In 1920, Wilder and Dunn stressed for the first time in salamanders the other correlation which had been previously made in fish. They considered lungs a decided disadvan-

tage to salamanders living in a current, for the lungs would act as hydrostatic organs and prevent their owner from quickly reaching a protection among the rocks on the bottom. They went so far as to say that all cases of lung reduction, or loss, in salamanders arose in a mountain stream and Dunn (1928) has recently attempted to defend this point of view against certain obvious difficulties.

There is no doubt that natural selection acting in a mountain stream would tend to favor species which, due to a reduction of lungs, had adopted a ground habit of living. Species with large buoyant lungs could not make progress against the current and would be eliminated. This assumption receives confirmation in the measurements of Camerano (1896) and Lonnberg (1899) of lung-length in a series of salamanders. No species living in mountain brooks had lungs which reached the maximum proportions attained by certain buoyant pond species. On the other hand the mountain-brook species as given by Camerano do not invariably have smaller lungs than forms not living in this habitat. For example, the terrestrial *Salamandra salamandra* is described with the same relative lung-length as the stream frequenting *Euproctus asper*, and with shorter lungs (as compared with head and body) than *Euproctus platycephalus* (= *rusconi*) which is even more of a brook dweller than *E. asper*. Further, *Tylotriton verrucosus*, which according to Wood-Mason (1877) is terrestrial in at least part of its range, has relatively shorter lungs than any of these brook species or than *Chioglossa lusitanica* which is well known to inhabit the borders of brooks. *Salamandra* and *Tylotriton* are not known to have had mountain-brook ancestors and hence their lung reduction would be inexplicable according to the theses of Dunn (1928). In the collections of the American Museum there is an extensive series of Caudata. I have examined the lungs of representatives of different species to see at first hand how far the lung reduction was correlated with a mountain-brook habitat. It was at once obvious that several species living today in streams, and so far as known always inhabitants of this type of habitat, manage well with fairly large lungs. Thus, C. H. Pope found *Pachytriton brevipes* only in streams. It occurred regularly with *Staurois ricketti* tadpoles and Pope observed the salamander moving over the bottom, feeding on the tadpoles of this species as they adhered to rocks with their disks (Pope, 1927). The lungs of five adult *Pachytriton brevipes* collected by Pope average 36.6 per cent of the head and body-length and 19.1 per cent of the total length. They agree well in relative size with the lungs of another archaic type and one which

we may feel sure has lived for long periods in currents, for its nearest relatives date back to the Miocene (Noble, 1928). This form is *Cryptobranchus alleganiensis* which has lungs which average in two specimens 35.9 per cent of head and body, and 22.1 per cent of total length. This proportion is also practically the same in another species, *Salamandra caucasica*, which seems to be primarily a stream form (Cyren, 1911). In the one specimen available its lungs are 34.3 per cent of head and body-length, 18.2 per cent of total length. By way of comparison I find the lungs of two specimens of *Ambystoma maculatum* average 49 per cent of head and body-length, 26.1 per cent of total length. In three *Ambystoma macrodactylum* these proportions are 49.1 per cent, and 25.8 per cent as an average for the same measurements, and in three *A. tigrinum* are 44.1 per cent and 24.7 per cent respectively.

The variation of relative lung-length found in the different species within a genus is frequently not correlated with the current factor. Thus, Citterio (1928) found that within the genus *Euproctus* the shortest lungs were found in *asper*, the longest in *montanus* and yet Bedriaga (1897) makes it clear that *montanus* is more a torrent dweller than *asper* and hence would more frequently find its hydrostatic organs a disadvantage to it. To judge from the account of Despax (1923), *asper* lives in colder water than the other species of the genus. It is well known that frogs can live successfully under water at low temperatures while they quickly drown if the temperature is raised. It would be interesting to know the degree to which the metabolic processes are slowed down in Amphibia which live only at high altitudes. In the meantime it may be emphasized again that species living at high altitudes or in cold water frequently show a reduction of lungs. Thus *Salamandra atra* has a lung as reduced as many brook forms. When fully extended it is 36.1 per cent of the head and body-length and 20.8 per cent of total length. But these figures give no idea of the degree of reduction. Recently killed specimens I find to have only 52 alveoli in each lung while, by contrast, *Ambystoma maculatum* exhibits approximately four times this number. Dunn (1928, p. 243) states, "Among salamanders *Hynobius keyserlingii*, dwelling north of the Arctic Circle at Verkoyansk, the North Pole of cold of the entire world, with perfectly good lungs, is evidence of the comparative inefficacy of this factor of temperature. . . . " But I find that the lungs of two specimens of *H. keyserlingii* average 36.4 per cent of head and body-length, 22 per cent of total length. These proportions agree well with those of the brook-dwelling *Pachytriton brevipes* and are but little more

than those of *E. platycephalus* as averaged from two preserved specimens. The proportions rise to 38.7 per cent and 22.4 per cent average in two Korean specimens of *Hynobius leechii*. There is a considerable chance for error when measuring preserved specimens and hence I have attempted so far as possible to check my measurements with those obtained from fresh material. I can confirm Citterio that the lungs of *E. platycephalus* are longer than those of *E. asper*. I find the lungs of the former when inflated in fresh material are 29 per cent of head and body-length while they are only 20 per cent in the latter. As I do not find a great discrepancy in my figures for fresh, inflated as compared with preserved, extended lungs, I assume that the measurements given are essentially correct.

In my previous paper I stressed the correlation of cold water with lung reduction. This correlation was most noticeable in *Ascaphus* which, while both a larva and adult, has the greatest reduced lungs of any frog. It also frequents the coldest streams. There are many other frogs which live when adult in streams and seek refuge by diving into the water. *Staurois ricketti*, according to Pope, is a good example. In this frog the lungs of the adult average 51.7 per cent of head and body-length in the male (two specimens) and 35.2 per cent in the female (two specimens). In the streams of the same region is *Rana spinosa* with measurements of 34.9 per cent and 33.9 per cent and *R. graminea* with 35.5 per cent and 25.6 per cent as averages for the same ratios in two specimens of each sex, respectively. In *Hyla heilprini*, which I have seen swim successfully in swift streams, the lungs are even larger. As none of the waters frequented by these species are as cold as those inhabited by *Ascaphus*, it would seem that cold was a factor checking lung growth. But cold running water does not always necessitate a great lung reduction. Lonnberg (1899) finds that, although the lungs are more reduced in the stream-dwelling *Ranodon sibiricus* than in *Ambystoma*, they are still of good size. I find that *Dicamptodon ensatus* when adult has a lung only 32.5 per cent of head and body-length, and a larva slightly less than this. The species as a larva is found in the same stream as *Ascaphus* but is not subjected to so long a period of stream life as *Rhyacotriton* which is another inhabitant of these streams and has much smaller lungs.

There is no evidence that cold running water affects the growth of lungs directly. In my previous paper I suggested that mountain streams might foster cutaneous respiration because of the great oxygen content of the water. It is generally recognized that ponds inhabited

by such typical lunged salamanders as *Ambystoma* and *Triturus* are poorer in oxygen than mountain brooks (compare Shelford, 1913, p. 151 with p. 99). This is due largely to the great quantities of decaying vegetation in the former. Of course the surface of a pond whipped by a squall, or the water immediately adjacent to quantities of green water-plants after long exposure to sunlight, might be saturated with oxygen, but these are special cases and do not concern the average conditions in most salamander ponds. The oxygen content in the large lakes described by Birge (1908) and quoted by Dunn (1928) has no bearing on the amount to be expected in the small pools reeking with decaying vegetation where I have found newts and *Ambystoma* abundant. Nor is the paucity of oxygen in certain streams inhabited by Michigan trout any indication that the mountain brooks where plethodontids thrive will be equally poor in oxygen. Local conditions may affect enormously the oxygen content of a stream or pond. In general, mountain streams are colder than ponds, they are more free of decaying vegetation and they are more aerated. We would, therefore, expect them to have a greater oxygen content.

Very recently Powers (1929) has made a study of the mountain streams of a section of the Great Smokies, a region which is very rich in plethodontid salamanders. The figures given by Powers fully confirm this expectation of high oxygen content. I quote from this paper:

"The temperature, as is always the case in mountain streams, is lowest at high altitudes and highest at low altitudes in any one stream system. . . . It is common knowledge that typical mountain stream waters are supersaturated with oxygen. . . . By inspection of figures 1 and 2 it is seen that the actual oxygen content falls with the lowering of the altitude, but the oxygen tension does not necessarily fall, and might actually rise, due to the rise in temperature of the water. . . . All samples showed a decrease in oxygen content with ageing."

In his conclusions Powers states: "The oxygen contents increase and the carbon dioxide tensions, as a general rule, decrease with increasing altitude."

There is another aspect of the subject which should not be neglected, I have found by experiment (Noble, 1925, p. 371) that a lungless salamander lives longer submerged in running than in still water. Cameron (1921) had previously shown that a frog could live completely immersed in running water for long periods. This would seem to be due to the fact that more oxygen is brought to an animal by moving than by still

water. There is every reason to believe that more oxygen is available to salamanders in mountain brooks than in the usual salamander pond. Hence it seems that the greater oxygen content and its availability for cutaneous respiration has been one of the factors in mountain brooks tending to permit the reduction of the lungs of Amphibia living in these waters.

Bridge and Haddon (1893) found that degeneration of the swim-bladder occurred in fish not only in mountain torrents but also outside of this habitat. The lungs of some salamanders have been similarly reduced outside of this habitat. Mention has been made above of the reduced and poorly vasculated lungs of *Salamandra atra*. This condition which was studied in freshly killed specimens does not appear in the account of Camerano (1896). It is important to note further that *S. atra* never occupied a mountain-brook habitat (Noble, 1927, p. 49).

A second species of terrestrial habits and without known mountain-brook ancestors, but with the lungs reduced to mere vestiges, is *Salamandrina ter-digitata*. Much has been written on the habits of this species but the most comprehensive account is that of Bedriaga (1897). As Dunn has recently emphasized this species in his discussion of mountain-brook forms it may be well to quote in some detail from Bedriaga, 1897, pp. 263-266 (translation).

"It occurs by preference in the proximity of mountain waters, and also in moderately dry places, leaving however in this case its hiding place only at times of rain. Ramorino found it also in damp places in the castaneous woods, as also in treeless meadows and states that it seeks water only to lay its eggs and at shedding time and that stagnant water is entirely avoided. . . . In hot and dry places far from water, such as are found so frequently on the Ligurian coast, *Salamandrina* seeks refuge in the gardens where it sets up its abode along the north side of the walls and often dozens are found together under leaves and piles of half decayed objects, it even enters the Gardens of Genoa. Shade, coolness and a certain degree of moisture are unquestionably necessary for it. . . . Also it is said not to climb high into the mountains but increases in numbers the more one approaches the valley bottoms where it has the greater opportunities of coming upon springs and small accumulations of water in its nocturnal wanderings. . . . The spawn is laid by preference where the mountain brook forms small protected water basins. The Spectacled Salamander takes refuge only unwillingly in the water and never spends a long time in it; in the water this animal remains motionless, appears as if covered with a

silvery snow and makes in a short time undoubted efforts to reach the upper surface, but sinks always to the bottom again. Specimens which through accident were left a single night in the water were drowned. . . . "

This account of *Bedriaga* is substantiated for the most part by other writers. Werner (1912, p. 127), in the most recent review, states that *Salamandrina* cherishes "a strong antipathy" to water. *Salamandrina* lives in mountain valleys but is not a brook form. In the discussions of brook species no one has considered *Salamandra salamandra* a brook species and yet this form also lives in mountains and deposits its eggs in flowing water (Werner, 1912, p. 134). The larvæ have a more prolonged life in this medium than have *Salamandrina* larvæ in their sheltered pools. *Salamandrina* might be subjected to a swift current on the occasion of a storm. But its larval life lasts only 55 days and hence would not be influenced by this factor as much as *Salamandra salamandra* would. Nevertheless, the latter species, in contrast to *Salamandrina*, has well-developed lungs. They average 44.8 per cent of head and body-length, 27.5 per cent of total length in two specimens.

There is one feature of the habitat of *Salamandrina* which is common to that of many lungless forms. This is its wetness and its proximity to cool running water. I found that in all Amphibia which undergo lung reduction the superficial capillaries by one method or another have come to lie nearer the surface than in related forms possessing lungs. This means that lung reduction was correlated with an increase in the efficiency of cutaneous respiration. One of the ideal spots for cutaneous respiration is the vicinity of cold mountain-brooks. The salamanders when out of water would move continuously over or under wet rocks or other surfaces and their highly vasculated skin would not be subject to drying influences which many newts and other salamanders migrating away from ponds frequently must suffer. I found that *Salamandrina* shows in its eggs and larvæ no adaptation to stream life and assumed that *Salamandrina* owed its reduction of lungs to the great possibilities for cutaneous respiration existing in its adult habitat. This view is supported by the fact that lung reduction has occurred in *Salamandra atra* which lives also in cool, damp situations. In brief, lung reduction just like air-bladder reduction has occurred under several different environmental conditions. The most complete cases of reduction among salamanders did not occur in thoroughly aquatic stream forms, but in those which spend much of

their adult life in wet, cool crannies. If increased possibilities for cutaneous respiration was an important factor in the reduction of the lungs, the increased oxygen content of mountain streams may have influenced lung reduction in *Staurois*. It is equally possible that the cold factor alone, by slowing down metabolism, would shift the balance of cutaneous and pulmonary respiration in favor of the former method.

CONCLUSIONS

(1) The tadpoles of the African brevicipitid *Hoplophryne* live either in bamboo stems or between leaf and stalk of banana plants and are either exposed to air or possibly crowded into small basins of water. Nevertheless, the tadpoles retain the usual diagnostic characters of brevicipitid larvæ.

(2) Lungs are functional at the time of hatching, no external gills ever appear and the internal gills are reduced to a few minute villousities on a single branchial arch.

(3) A pair of cutaneous flaps moved by special branchial muscles develops in the hyoid region. The epidermis of these structures is thickened, its superficial layers modified into a toothed surface which has a resemblance to the surface of the adhesive disks of tree frogs. The flaps apparently serve as locomotory appendages.

(4) The tadpoles of *Hoplophryne* agree with those of the hylas of Jamaica in feeding on frogs' eggs as well as on insects and vegetable matter. They further agree in having comparatively large and powerful jaws, and a short digestive tract. In the Jamaican tadpoles the gills are reduced but not to the extent found in *Hoplophryne*.

(5) The typical brevicipitid larvæ, so far as known, are characterized by the absence of a suprarostal cartilage and by having the M. adductor mandibulæ posterior subexternus insert on the rostral or trabecular cartilage.

(6) The suctorial disk of the stream-dwelling tadpoles of *Staurois* bears along the posterior edge of the cup a crescentric area of tuberculated epidermis which functions as a friction surface.

(7) The muscles attaching to the suctorial disk may be readily homologized with muscles found in *Rana* tadpoles.

(8) The chief difference between the suctorial apparatus of *Staurois* and the ventral body-wall of *Rana* tadpoles lies in the free fold of integument which forms the lip to the cup and in the attachment of the ventral musculature to the integument within this rim.

(9) Mature tadpoles of *Staurois* and *Heleophryne* have reduced lungs unlike certain other mountain-brook tadpoles.

(10) Lung reduction in tadpoles and in urodeles is correlated in some but not in all cases with a life in mountain brooks. The increased oxygen content of mountain-stream water is one of the factors permitting lung reduction in Amphibia living in these waters. Another factor for urodeles is the availability of wet, cool crannies out of water, where cutaneous respiration can function to best advantage during adult life.

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EXPLANATION OF FIGURES AND PLATES

Ad. Org. = Adhesive organ

A.P.L.S. = *M. adductor mandibulæ posterior longus superficialis* (= *M. temporalis*)

A.P.S. = *M. adductor mandibulæ posterior subexternus*

B. Mbr. = Basal membrane

Br. I = Branchiales I

Br. Cl. = Branchial cleft

Br. Sac. = Branchial sac

Cent. Prom. = Central prominence

Cer. Hy. Ang. = *M. ceratohyo-angularis*

C. H. B. = *M. ceratohyo-branchialis*

C. Tr. = Cornu trabeculi

Cut. Ap. = Cutaneous appendages

Fr. Ar. = Friction area

Fr. Rm. = Free rim

Gen. Hy. = *M. geniohyoideus*

Hy. = Cartilago hyoidea

Hy. Ph. = *M. hyopharyngeus*

Ir. = Infrarostrale

L. A. B. = *Mm. levatores arcuum branchialium I-IV*

L. Ct. Pd. = Lateral pad of connective tissue

M. = *Mm. marginales I-II*

Md. = Mandibulare

M. D. M. = *M. diaphragmatobranchialis medialis*

M. D. Prec. = *M. diaphragmatopræcordialis*

M. R. A. = *M. rectus abdominis*

M. Sub. Br. = *M. subbranchialis*

- Nas. Cap.* = Nasal capsule
N. Pit. = Nasal pit
O. N. Gr. = Oro-nasal groove
Op. F. = Opercular fold
Orb. Hy. = M. orbito-hyoideus
Per. = Ligamentous posterior wall of pericardium
Pericard. = Ligamentous posterior wall of pericardium, cut edge
Pois. Gl. = Poison Gland
Qu. = Quadratum
Ros. Cart. = Rostral cartilage
S. A. = M. suspensorio-angularis
S. Hy. Lig. = Subhyoid ligament
S. La. = Superficial layer of epidermis
S. Mx. Lig. = Submaxillary ligament
Spir. = Spiracle
S. Qu. Lig. = Subquadrate ligament
Sr. = Suprarostrale
St. = Stomodæum
Sub. Br. Prom. = Subbranchial prominence
Subhy. = M. subhyoideus
Subhy. Fol. = Fold over M. subhyoideus
Subhy. P. L. = Subhyoideus pars locomotorius
Subhy. Prom. = Subhyoid prominence
Submax. = M. submaxillaris
Sub. Mx. Prom. = Submaxillary prominence
Thyr. = Glans thyroideum

PLATES XV AND XVI

PLATE XV

Friction epidermis of the tadpoles of *Hoplophryne* and *Staurois* compared.

(a) A vertical section of the tuberculated epidermis from the posterior part of the suctorial disk of *Staurois ricketti*. $\times 1200$.

(b) Section of a locomotory appendage of *Hoplophryne rogersi*. $\times 315$.

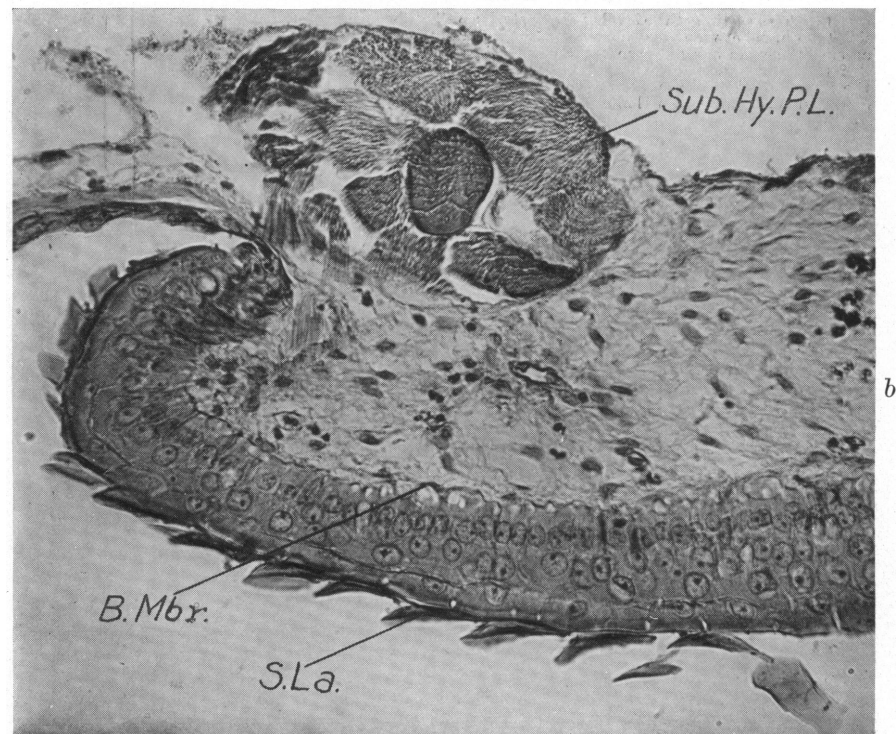
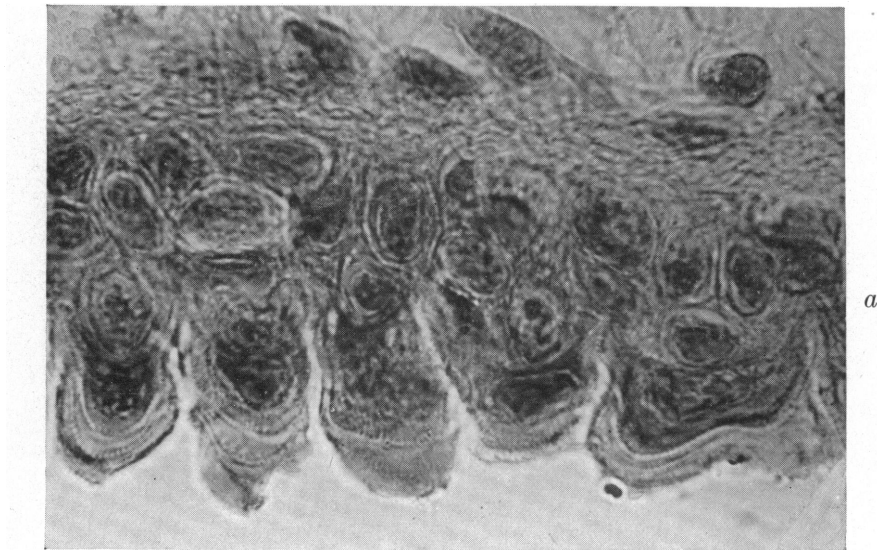


PLATE XVI

The suctorial disk of *Staurois ricketti*.

(a) Cross-section at the level of the posterior wall of the pericardium (level B in Fig. 10) showing the point of union between the connective-tissue pad and the pericardium. Showing also the different character of the epidermis of the central and lateral parts of the cup. $\times 35$.

(b) Cross-section at the level of the insertion of the subbranchial muscle (level A in Fig. 10) showing the subhyoid fold and the subbranchial pad of connective tissue, together with the point of origin and insertion of the subbranchial muscle. $\times 35$.

