THE DEVELOPMENT OF ANURAN KIDNEY.

Part I. The Development of the Mesonephros of Rhacophorus maculatus* Boulenger.

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Introduction.

"Investigations are greatly needed on the embryology of Anura outside the genus Rana...........it will be only after greatly extended studies on different species that we shall have a really comprehensive idea of typical Anuran development."

* The genus Rhacophorus includes forty-two known species. Twenty of them are found in India and its dependencies and six occur in other parts of the oriental region. Four are known from China and Japan while the rest are confined to Madagascar. The genus is so closely allied to Rana that their characters run into each other and Gadow considers the distinguishing characters between the two genera as unimportant. Rhacophorus maculatus Boulenger is confined to India and Ceylon. It is popularly known as the "Chunam Frog". It is arboreal in habit and like Rh. schlegeli of Japan lays its eggs in a foamy mass on the margin of tanks.

† The terminology of Peter Gray (1930) has been employed in this work.
It is nearly 20 years since this almost complaining remark of Graham Kerr (1919) was made and yet no attempt has been made to remedy this defect. In the present paper the author proposes to deal with the development of the mesonephros in *Rhacophorus maculatus*.

Spengel (1876), Nussbaum (1880), Hoffmann (1886), Marshall and Bles (1890) and Farrington (1892) have worked on the development of the amphibian kidney. But the works of Hall (1904) and Filatow (quoted by Gray, 1930) alone were exclusively devoted to the development of the mesonephros in *Rana sylvatica* and *R. esculenta* respectively. Peter Gray (1930) worked on the development of the mesonephros of *R. temporaria*. The last author gave an excellent summary of previous work on the subject. The present author is not aware of any previous work on the development of the kidney of *Rhacophorus maculatus*.

**Material and Method.**

Egg masses of *Rhacophorus* were collected within the University area and were allowed to hatch and develop in the Laboratory. Later on the tadpoles were transferred to open-air tanks in the University gardens. The advanced and metamorphosing stages were procured from the open-air tanks while the earlier stages were selected from those developing in the Laboratory. The tadpoles used in the course of this work were graded according to the length from the tip of the snout to the end tip of the tail. The characteristics of the tadpoles of the selected stage-lengths are noted below:

<table>
<thead>
<tr>
<th>Stage</th>
<th>Length</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>5-7 mm</td>
<td>with yolk sac.</td>
</tr>
<tr>
<td>II</td>
<td>12-14</td>
<td>with external gills disappearing.</td>
</tr>
<tr>
<td>III</td>
<td>18-21</td>
<td>with external gills completely disappeared. Hind legs evident.</td>
</tr>
<tr>
<td>IV</td>
<td>23-25</td>
<td>hind legs developed. Front legs evident.</td>
</tr>
<tr>
<td>V</td>
<td>36</td>
<td>with front and hind legs.</td>
</tr>
<tr>
<td>VI</td>
<td></td>
<td>with mouth widening and tail disappearing.</td>
</tr>
</tbody>
</table>

Further the various stages in the formation of the mesonephros seem to correspond to the different stage-lengths of tadpoles selected out as above.

Bouin's fluid was invariably used for fixing the material. The material was left in the fixative for 10-12 hours. It was then washed in 70 per cent. alcohol till the yellow colour was removed. After dehydration it was cleared in cedar wood oil. The usual method of embedding in paraffin was followed. In the case of advanced tadpoles where the skull formation has begun, the material was left in 2.5 per cent. nitric acid in 70 per cent. alcohol for about 15 days. Then it was washed in 70 per cent. alcohol till there was no trace of acid. The intestines of the tadpoles at this stage always contain grit.
entire gut was therefore completely removed before embedding. In the case of these advanced tadpoles cold impregnation with xylol and paraffin was also used. Further these were left in the bath from 1½ to 2 hours whereas in the case of the earlier stages ½ hour to ¾ hour was quite sufficient.

In all cases 12 μ sections were cut along transverse, sagittal and frontal planes. Delafield’s haematoxylin with eosin as counter stain gave excellent results. In a few cases iron-alum-haematoxylin was also employed.

**Development of Mesonephros.**

**Stages 1 and 2.**—In stage 1, the mesonephros is represented by an irregular retro-peritoneal tract of cells the ‘‘Blastema’’ which occupies the dorso-median wall of the archinephric duct. As Furbringer (1887) and Gray (1930) have pointed out this tract of cells is derived from specialised mesenchyme cells. From this tract of cells the mesonephric units arise.

Series of transverse sections of stage 2 reveal the condensation of the cells of the blastema into spherical vesicles, the nephroblast vesicles. Each nephroblast vesicle is composed of 10 to 12 loosely packed blastema cells. There are 6 to 8 vesicles on either side. This number varies in different tadpoles I have examined. In no case however, I found more than 8 vesicles. These vesicles do not have any segmental arrangement. To begin with each vesicle is spherical. Later on due to the reorientation of the inner mass of cells they assume a oval shape.

The nephroblast vesicles seem to arise at the same time. There is no indication whatever to show that the posterior units are developed earlier than the anterior ones. In fact, there is no regular line of development of these units after their appearance. In some, posterior ones are in a much advanced stage of development. There are also cases where anterior and central units show more advanced development than the posterior units.

As in the case of *Rana* (Gray, 1930) the units of the left side are invariably better developed than those of the right side. This asymmetry becomes even more prominent (or pronounced) in the development of the later units.

Each nephroblast vesicle then develops a lumen and elongates at either end. The end near the archinephric duct forces its way into it and the other end grows downwards towards the peritoneal wall. At the same time the latter end develops a dilatation as a result of the proliferation of the cells at its free end. These cells (R.M.G. Fig. 1) are the rudiment of the malpighian glomerulus. This cellular mass grows inwards into the lumen of the growing tubule and ultimately severs its connection with the tip (E.M.C. Fig. 2). Thus a completed glomerulus results. But it will be noticed that the glomerulus results a vascular connection throughout its functional condition.
Fig. 1 shows the formation of the malpighian glomerulus. Outside the wall of the malpighian capsule is another thickening (R.F.N.) These are proliferated from the squamous epithelium of the malpighian capsule. This is the rudiment of the early peritoneal funnel.

Now as the cells of the walls of the tubule divide the tubule increases in length and is thrown into a characteristic 'S'-shaped loop. This is the 'Henle's loop' of other forms. The later coiling of the tubule becomes too complicated to follow. In Figs. 1, 2 and 3 transverse sections of these coiled tubules (T) are seen.

![Diagram of development of the funnel rudiment](image1)

**Fig. 1.**—The development of the funnel rudiment in connection with the squamous epithelium of the malpighian capsule.

![Diagram of funnel rudiment separated from the squamous epithelium](image2)

**Fig. 2.**—The funnel rudiment lying separated from the squamous epithelium.

![Diagram of early peritoneal funnel with inner opening](image3)

**Fig. 3.**—The early peritoneal funnel with its inner opening into the blood-vessel.
Stage 3.—Towards this stage as a result of growth and coiling of the nephroblast vesicle tubule the malpighian capsule with its glomerulus is pushed towards the peritoneal wall. During this process the group of cells (R.F.N. Fig. 1) which were proliferated from the squamous epithelium of the malpighian capsule get detached from the wall of the capsule and lie very close to it (F.N. Fig. 2). In this condition they appear as if they were a condensation from the blastema cells. Then there takes place a reorientation of the cells resulting in the formation of a lumen within them. The plane of the small tubule thus formed is transverse to the malpighian capsule. Cilia are now developed in the lumen of the tubule (F N. Fig. 3). As the malpighian capsule approaches the peritoneal wall this ciliated tubule or peritoneal funnel of the early malpighian units is wedged in between them. It ruptures the peritoneal wall and establishes a communication with cælom (O.N. Fig. 6). Its inner end (I N. Figs. 3, 5 and 6) opens into a blood vessel. Here the peritoneal funnels like those of *Rana* establish a direct communication between the cælom and blood-vessels.
Figs. 5–8.—Show the degeneracy of the early malpighian glomerulus.

Figs. 9–11.—Illustrate the mode of constriction of the later peritoneal funnel from the funnel-forming tubule.

N.B.—Read 'B.V.' in the place of 'B.Y.' in Text-Figs. 7, 9, 10, 13, 15 and 20.
As these early mesonephric units are developed the archinephric duct is pushed away from the blastema. But there are 4 to 5 outgrowths from the archinephric duct which maintain a connection between the two. Each one of these outgrowths to start with arises from condensations of blastema along the dorso-median side of the archinephric duct resembling those of the rudiments of the early nephroblast vesicles (F.St. Fig. 16).

Stage 4.—The condensations (F.St Fig 16) on the archinephric duct develop into well-defined straight tubules (St. Figs. 12, 18 and 19) Their lumina become continuous with the lumen of the archinephric duct (A.D. Figs. 19 and 12). At the growing end of the straight tubule is a group of cells (A.M.C. Figs. 12 and 19) which resemble the condensation of blastema cells from which early malpighian capsules are developed But this rudiment never gets perfected. This is the abortive malpighian capsule described by Gray (1930) in the case of Rana.

Fig. 12.—The straight tubule with two outgrowths.

Along the length of each straight tubule outgrowths or secondary tubules (O.St1, O.St2. Fig. 12) are developed at regular intervals. In most cases only three outgrowths are developed. The lumen of each secondary tubule is continuous with that of the straight tubule. At the free end of the straight tubule is the abortive malpighian capsule (A.M.C.).

Figs. 13 and 14.—Show the formation of latter peritoneal funnels from the funnel-forming tubule.
In this stage the blastema, which has been separated from the archinephric duct, is arranged in the form of dorsoventrally hanging tracts from the straight tubules. In each tract generally three and rarely four condensations of the blastema cells—the capsuloblast vesicles—appear. The first vesicle which is formed is pushed downwards by the other two which are formed above it a little later. The condensations give rise to the later malpighian capsules.

In Fig. 15 is a string of three malpighian capsules (M.C.₁, M.C.₂ and M.C.₃). The lowest capsule is the best developed. This is the first formed capsule which has been pushed down by the formation of the other two capsules above it. Just in front of the lowest malpighian capsule (M.C.₁) is a peritoneal funnel (F.N.). In connection with the middle malpighian capsule (M.C.₂) is another funnel which is cut in a transverse plane. In connection with the uppermost malpighian capsule (M.C.₁) is a condensation of cells (R.F.N.). This is the rudiment of the peritoneal funnel to be developed later on.

Fig. 15.—Shows a string of later malpighian capsules with their corresponding peritoneal funnels developed between them and the peritoneal wall.

The structures outlined above are formed in the way:—The lowest capsuloblast vesicle develops into malpighian capsule. As the other two capsuloblast vesicles above it are developed it is pushed downwards towards
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the peritoneal wall. As each malpighian capsule approaches the peritoneal wall a condensation of the blastema cells is distinguished between the malpighian capsule and the peritoneal wall. This condensation gives rise to the peritoneal funnel which is found in connection with every later malpighian capsule.

This condensation or the rudiment of the later peritoneal funnel is formed near the peritoneal wall itself. It is not formed in front of the malpighian capsule and carried to the peritoneal wall as the capsule is pushed downwards as in the case of Rana (Gray, 1930). When the malpighian capsule is away from the peritoneal wall no condensation can be made out in front of the capsule. Neither is there one near the peritoneal wall. But as the malpighian capsule approaches the peritoneal wall the condensation makes its appearance near the peritoneal wall. The approach of the capsule appears to stimulate or initiate the condensation of the blastema cells near the peritoneal wall. Further development of the rudiment of the peritoneal funnel is similar to the process outlined by Gray (1930) for Rana.

Each malpighian capsule develops a small tubule at the end opposite to that which faces the peritoneal wall. This tubule grows upwards and fuses with an outgrowth from the straight tubule. Thus each malpighian capsule indirectly communicates with the lumen of the archinephric duct through the straight tubules and then outgrowths just as described for Rana by Gray (1930). As has been pointed out by Gray (1930), the straight tubule with its outgrowths is the collecting trunk of earlier authors.

Examination of a series of transverse and longitudinal sections of this stage reveals that the early malpighian capsules which maintained a direct communication have by now disappeared. In somewhat earlier sections can be made out degenerating tubules attached to the dorsomedian wall of the archinephric duct. Towards the peritoneal wall are also seen malpighian capsules which have lost their blood connection, in a state of degeneracy. Figs. 5, 6, 7 and 8 illustrate this process of degeneration and disappearance of the early malpighian capsules (D.G.). Their function is now taken up by the strings of later malpighian units. But the peritoneal funnels of the early units do not degenerate. They alone persist of the entire early mesonephric units (F.N. Figs. 5, 6, 7 and 8).

Stages 5 and 6.—Serial sections of these stages show that the peritoneal funnels of the later mesonephric units outnumber the malpighian capsules. The occurrence of this large number of peritoneal funnels is brought about in the following manner:—
Figs. 16–18.—Show the origin of the rudiment of the straight tubule and its subsequent development into the straight tubule.

Lying in the course of the blood-vessel are the coils of a tubule. This tubule to begin with arises from a group of cells (R.F.N.T. Fig. 12). This is the rudiment of the funnel-forming tubule. This tubule does not form any connection at all with the straight tubule. The tubule grows ventrally, closely following the peripheral blood-vessels. The lumen of its lower extremity is ciliated and lies parallel to the peritoneal wall. On reaching the peritoneal wall the ciliated tip is constricted off (F.N. Figs. 9, 10 and 11). The outer end of the severed tip establishes a connection with the coelom (O.N. Figs. 9, 10 and 11). The inner end opens into the blood-vessel (I.N.). Thus the tubule lying in the blood-vessel is the funnel forming the tubule described by Gray (1930) in *Rana*.

In Fig. 13 is the first funnel (F.N. Fig. 13 and F.N. Fig. 14) which has been developed from the funnel-forming tubule (F.N.T.) Fig. 14 shows two peritoneal funnels (F.N. and F.N.) which have been developed from the funnel-forming tubule (F.N.T.). Figs. 9, 10 and 11 show the actual process by which a peritoneal funnel is constricted off from the funnel-forming tubule.
The straight tubule which has acquired its connection with the archinephric duct.

After giving rise to the peritoneal funnel (F.N. Fig. 11) the tip of the tubule (F.N.T. Fig. 11) turns upwards. At some distance from the first peritoneal funnel (F.N.¹ Fig. 14) it gives rise to another funnel (F.N.² Fig. 14).

An abnormal peritoneal funnel showing a very long tail,
The formation of the peritoneal funnels in this manner is not indefinite. Each tubule as far as I have examined never gave rise to more than three peritoneal funnels at this stage.

Thus in a metamorphosed *Rhacophorus* there are three kinds of peritoneal funnels:—

1. The peritoneal funnels of the early mesonephric units, which persist. These are derived from the proliferation of the cells of the squamous epithelium of the early malpighian capsules.

2. The peritoneal funnels which are developed in connection with the later malpighian capsules. These are derived from groups of blastema cells which are condensed near the peritoneal wall under the influence of the approach of the malpighian capsule towards the peritoneal wall.

3. The peritoneal funnels which are developed from the funnel-forming tubule.

**Discussion.**

The development of the mesonephros in *Rhacophorus* is almost similar to that of *Rana* (Gray, 1930). To begin with, we have the formation of the early malpighian units from nephroblast vesicles which have a direct communication with the archinephric duct. These units later disappear and we then have the development of the later malpighian units. Here the communication of the units with the archinephric duct is indirect. The malpighian capsules are connected with the archinephric duct by means of the straight tubules and their outgrowths.

**Formation of the Peritoneal Funnels.**—A consideration of the formation of peritoneal funnels shows certain deviations from those of *Rana*. The rudiments of the peritoneal funnels of the early units are developed from the thickenings of the squamous epithelium of the external walls of the malpighian capsules. The cells which are proliferated become columnar and get detached from the capsular wall. The rudiment then elongates and develops a lumen. It is pushed by the downwardly growing malpighian capsule towards the peritoneal wall, where it lies parallel to the latter. The lumen gets ciliated and opens into the coelom externally and into the blood-vessel internally.

The origin of the funnel-forming rudiment is different from that of *Rana*. It arises as a condensation of blastema cells in front of the malpighian capsule and is later carried to the peritoneal wall. There is no difference in the further development of the funnel.

The formation of the rudiments of the early peritoneal funnels is comparable to that of the urodelan peritoneal funnels (*Triton*, Gray, 1933). But in
Triton the rudiment remains in connection with the malpighian capsule and establishes a connection between the cœlom and the cavity of the malpighian capsule.

The main part of the development of the peritoneal funnels in connection with the later malpighian capsules is similar to that of Rana. But here in Rhacophorus the blastema cells are not condensed in front of the malpighian capsule and carried to the peritoneal wall. The condensation of the blastema cells takes place near the peritoneal wall itself as the malpighian capsule approaches the peritoneal wall.

The production of the peritoneal funnels by the funnel-forming tubule is exactly similar to that described for Rana. In all the three types the peritoneal funnels never communicate with the cavity of the capsule but invariably establish a connection with the cœlom on the one hand and the blood-vessel on the other.

*Function of the Peritoneal Funnel.*—Gray (1932) has explained the establishment of a direct communication between the cœlom and the blood circulation by the peritoneal funnels, by attributing a very important function of collecting a secretion from the cœlom and passing it on to the blood circulation. In fact, Gray (1932) considers this function as a primary one and the process of excretion by the peritoneal funnels as only of secondary importance. The present author is in complete agreement with this view.

This direct communication between the blood circulation and the cœlom cannot be without some physiological significance. It is impossible to see how such a connection is helpful, in a process of excretion. This certainly points to an important function other than that of excretion by the peritoneal funnels. Then we are also faced with their prodigious multiplication. If they were merely excretory the funnels developed in connection with the malpighian capsules would have been quite sufficient. The multiplication of the funnels indicates the primary nature of this collection and conduction of the secretion from the cœlom.

In Rhacophorus we have the retention of the peritoneal funnels of the early units, when the entire early mesonephric units have disappeared. Gray (1930) however has not stated whether the early peritoneal funnels are retained or not in Rana. When there is need for more peritoneal funnels and when there is the development of a special tubule towards their multiplication, why should already functioning early peritoneal funnels disappear?

In Rhacophorus it is noted that its larval life after the fore legs have become evident, is very short. In fact, their appearance heralds the end of
its larval life. Immediately afterwards the mouth widens, tail disappears and the metamorphosis is completed. It will be remembered that it is at this stage that the funnel-forming tubule is developed and the peritoneal funnels are multiplied. This results in bringing about a rapid collection and conduction of the important secretion from the cœlom.

Can it be possible then, that this secretion is in some degree responsible in shortening the larval life of the animal? If it were possible we have to expect the disappearance of at least some of the funnels after the metamorphosis is completed and the adult stage is reached. But there is no indication of such a disappearance in the metamorphosed animal. In the adult condition it has been demonstrated in other forms that these funnels are found in a very active state and Gray (1936) has pointed out recently the development of even accessory peritoneal funnels in the post-metamorphic kidney of *Rana* in addition to the already existing peritoneal funnels. Hirt (1930) has also shown the existence of an extensive nerve-net correlated with the presence of these funnels in the adult animal.

The development of the mesonephros of *Rhacophorus* and other Anura proceeds along such lines as to bring about a rapid collection and conduction of this important secretion from the cœlom into the blood circulation. In what manner this secretion is important we are at present neither in a position to state nor is it our concern in this communication. But this much can be said. This secretion is essential to the animal both in its larval and adult life. Even in Urodela this secretion is collected from the cœlom by the peritoneal funnels and conducted in an indirect manner into the blood circulation. The long larval life of Urodela does not necessitate the multiplication of the peritoneal funnels such as seen in Anura for the collection of this secretion.

In the face of a short larval life Anura have evolved a process of multiplication of these funnels to effect a rapid collection of this secretion from the cœlom. Further the efficiency of the conduction of this secretion into the blood circulation is enhanced by the establishment of a direct communication between the blood circulation and the cœlom.

There is no doubt whatever that the Anuran mesonephros is evolved from a Urodelan type. The modification of the mesonephros in Anura is conditioned by different life-history of the animals. The formation of the rudiments of the peritoneal funnels of the early mesonephric units of *Rhacophorus* are certainly to be regarded as pointing towards Urodelan ancestry.

*Summary.*

(1) The general development of the mesonephros in *Rhacophorus* is similar to that of *Rana* (Gray, 1930).
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(2) The early malpighian units arise from nephroblast vesicles.

(3) Each nephroblast vesicle is a condensation of 10–12 loosely packed blastema cells.

(4) Six to eight nephroblast vesicles are developed.

(5) Each early peritoneal funnel arises as a thickening of the squamous epithelium of the early malpighian capsule.

(6) This thickening later severs its connection with the malpighian capsule, develops a lumen and opens externally into the cœlom and internally into a blood-vessel.

(7) The early peritoneal funnels persist.

(8) The early malpighian capsules and their tubules degenerate and disappear.

(9) The later malpighian capsules arise from capsuloblast vesicles.

(10) A string of three capsuloblast vesicles appears in a dorso-ventrally extending tract of blastema near each straight tubule.

(11) The straight tubules and their outgrowths arise from 4 to 5 condensations of blastema on the dorso-median wall of the archinephric duct.

(12) At the free end of the straight tubule is an abortive malpighian capsule which never reaches perfection.

(13) The peritoneal funnels in connection with later malpighian capsules are developed from condensations of blastema cells.

(14) The condensation of the blastema cells does not take place in front of the malpighian capsule as has been described in Rana; but takes place near the peritoneal wall as the malpighian capsule approaches the peritoneal wall.

(15) The later peritoneal funnels also establish a direct communication between the cœlom and the blood circulation.

(16) A funnel-forming tubule arises from a condensation of cells near the straight tubule.

(17) Thus tubule never gets connected with the archinephric duct.

(18) Its lower tip which lies parallel to the peritoneal wall gets ciliated and follows the course of the blood-vessels closely.

(19) By a repeated process of constriction it gives rise to three peritoneal funnels which also open into the blood-vessels internally and into the cœlom externally.

(20) The present author agrees with the view put forward by Gray (1932) that the peritoneal funnels have a primary function of collecting an important secretion from the cœlom and conducting it into the blood circulation.
(21) It is suggested that in Rana as in Rhacophorus the early peritoneal funnels might persist.

(22) The formation of the rudiments of the early peritoneal funnels of Rhacophorus are regarded as pointing towards Urodelan ancestry of the mesonephros.

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REFERENCE LETTERS.

A.D. Archinephric duct.
A.M.C. Abortive malpighian capsule.
B. Blastema.
B.V. Blood vessel.
C.F.N. Point at which the peritoneal funnel is constricted off.
D.G. Degenerating malpighian glomerulus.
E.C. Capsule of the early malpighian unit in which the glomerulus has completely disappeared.
E.M.C. Early malpighian capsule.
F.N. Peritoneal funnel.
F.N.1 & F.N.2 Peritoneal funnels produced from funnel-forming tubule.
F.N.T. Funnel-forming tubule.
G. Glomerulus.
I.N. Opening of the peritoneal funnel into the blood-vessel.
M.C.1, M.C.2 & M.C.3 Later malpighian capsules developed from capsuloblast vesicles.
O.N. Opening of the peritoneal funnel into the coelom.
O.St.1 & O.St.2 Outgrowths of the straight tubule.
P.W. Peritoneal wall.
R.F.N. Rudiment of the peritoneal funnel.
R.F.N.T. Rudiment of the funnel-forming tubule.
R.M.G. Rudiment of the early malpighian glomerulus.
R.St. Rudiment of the straight tubule.
St. Straight tubule.
T. Tubules.