

## PART I.—ANATOMICAL.

By R. B. SEYMOUR SEWELL.

The body of *Vivipara bengalensis*, as in practically all Gastropod molluscs, is composed of three distinct parts or regions. In the fully-expanded animal the central portion forms a somewhat conical-shaped foot, by means of which the animal is able to crawl over the supporting surface. When fully extended the central aspect of the foot or sole is, roughly speaking, a broad oval, rather broader in front than behind, with a crescentic anterior margin. In young examples the shape of the sole is more elongate and tapers behind to a rounded point. In colour the sole is slate-grey, dotted over irregularly with spots of golden yellow pigment, and just within the anterior margin is a narrow but distinct line of demarkation, indicated by a grey streak, which corresponds to a groove between the more heavily pigmented anterior fleshy border and the less pigmented muscular sole. Above the expanded sole the foot rapidly tapers and on the upper aspect of the posterior region is situated the horny operculum.

The operculum is roughly oval in shape tapering somewhat towards its right side,<sup>1</sup> so as to adapt it accurately to the shape of the mouth of the shell. It is horny in structure and is composed of a number of concentric layers so that it is considerably thicker in the centre, where the opercular muscle is attached, than at the margin, which is often somewhat frayed and irregular in outline. The nucleus is situated excentrically about one-third of the distance from the anterior margin. The colour varies in different regions: around the nucleus it is a deep red-brown and immediately external to this is a narrow band of a pale yellow colour: outside this again the colour often deepens to a golden brown, while the extreme margin is of a blackish tint. The operculum is not absolutely flat, but is somewhat depressed in the central region owing to the pull of the columellar muscle. On the body aspect or lower surface the central portion of the operculum is occupied by the muscular scar to which the opercular muscle is attached. Surrounding this is a smooth ring, which during life is in close apposition to a thin fold of glandular tissue (*vide* Simroth, 1896-1907, pl xviii, fig. 16). In the living animal this fold almost exactly covers the whole of the body surface of the operculum lying outside the scar: owing to the muscle scar being slightly asymmetrical, the fold is somewhat broader on the right side than on the left. It is by the gland cells of this fold that the operculum is secreted.

---

<sup>1</sup> In the following description the terms right and left, anterior and posterior, etc., refer to the position in the fully extended condition of the animal.

The main mass of the foot is divided into two layers. The lower layer, which forms the sole and consists of soft greyish-

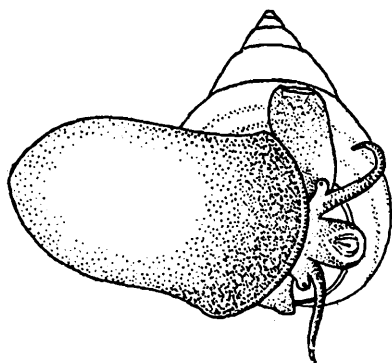


FIG. 1.—Living male of *V. bengalensis* as seen from below.

coloured spongy tissue, is traversed by a network of muscle-fibres, which is in turn covered by a layer of columnar epithelium. [It is this tissue that forms the whole surface on which the animal crawls]. The upper and posterior portion of the foot is composed of white muscle-fibres. This mass of muscle, which arises from the operculum, becomes continuous with the columellar muscle, which runs upwards in

the floor of the mantle chamber and is inserted into the columella about half-a-turn of the spiral above the mouth of the shell. Between the sole and the opercular muscle is a layer of tissue, consisting of a somewhat open reticulum, the meshes of which enclose numerous irregular spaces, and lying free in these are oval or rounded deeply-staining bodies, which closely resemble starch grains. Similar bodies are also found scattered through the reticulate tissue of the edge of the mantle. Between the two tissues of the foot the pedal nerves and the terminal portion of the cephalic artery pass backwards, and the central region is also occupied by a large venous sinus, running antero-posteriorly in the middle line.

The anterior part of the body forms a well-marked 'head,' which is produced forwards in the middle line in a short trunk-like snout, on the anterior and central aspect of which lies the oral aperture. Projecting upwards and forwards on either side of the base of the snout is a slender tapering tentacle. Each tentacle arises from a short thick base which is produced on the outer side in a short wide pedicle bearing at its tip a well-marked globular, pigmented eye. Each eye is hemispherical in outline and is situated on the anterior and inner aspect of the pedicle. It consists of a clear cornea superficially, which is usually outlined with golden yellow pigment, and the optic cup is lined by a black, heavily-pigmented retina and encloses an almost spherical lens.

In the female both tentacles are symmetrical, but in the male the right tentacle is somewhat thickened and is curved in a sickle-shaped manner. In this latter sex this tentacle is traversed throughout its whole length by the ejaculatory duct, which opens through a small orifice at the extreme tip. The whole tentacle forms an intromittent organ or penis. Immediately behind and below the base of the tentacles the body surface is produced on either side in a fold—the epipodium. On the left side, the epipodium is triangular or quadrate in shape and is prolonged backwards along the side of the head almost to the point of origin of the mantle. On the right side the epipodium is more complex. Immediately below

and to the outside of the tentacle is a small narrow fold with a rounded anterior margin and a free external border; this forms a gutter in which the base of the right tentacle and the right eye rest. As we trace the fold forwards and backwards it is seen to commence on the under-surface of the snout close to the junction of the snout and foot, it then runs backwards along the right side of the snout and near the base of the tentacle it curves out-

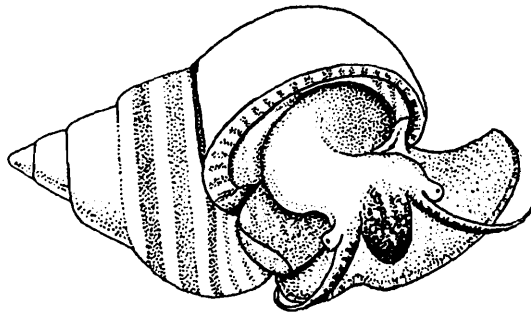


FIG. 2.—Living *V. bengalensis* extended from the shell as fully as possible.

wards and forwards and becomes continuous with the syphon. The syphon is formed by a thin leaf-like process the two edges of which are curved upwards so as to form a tube, which is exhalent in function. The mouth of the syphon looks outwards and downwards and when fully extended, backwards. The inner fold of the syphon is continued backwards and becomes continuous with the branchial fold, which passes backwards and towards the left on the floor of the branchial chamber. The whole of the upper surface of the foot and the head as well as the epipodia and syphon are covered with ciliated epithelium the only region devoid of cilia is the clear cornea of the eyes. The head is heavily pigmented with black, variegated with dots and splashes of golden-yellow in varying degrees of intensity. In examples taken from the tank in the Indian Museum compound the snout is frequently an almost uniform black, unrelieved by any lighter pigment and in some cases the tentacles are alternately banded in yellow and black. The syphon is as a rule of a golden colour.

The part of the body enclosed within the shell is the visceral hump and in a fully-grown example possesses  $5\frac{1}{2}$ —6 spiral whorls. The skin covering the visceral hump also shows a certain degree of pigmentation, which varies however in different areas as well as in different individuals. In the upper whorls it is often of a deep black colour, while in the lowest or body-whorl the pigment usually follows the lines of the blood sinuses, but as a rule the males are more heavily pigmented than the females. The upper  $2\frac{1}{2}$ —3 body-whorls are occupied by the liver and the stomach: this latter organ appears on the surface between the lobes of the liver on the right and posterior aspects of the 3rd body-whorl. The penultimate body-whorl, when viewed from above, is seen to be occupied on the left side by a loop of intestine, in front of which is an area of thin skin separating it from the kidney and the upper end of the testis in the ♂ or the albumen gland and shell gland in the ♀. The whole of the lowest or body-whorl is occupied by the branchial chamber, and a series of organs extend throughout its whole length attached to its thin roof. On the extreme left of the

branchial roof, running obliquely forward from left to right, is the line of attachment of the gill, and close to it in front and to the

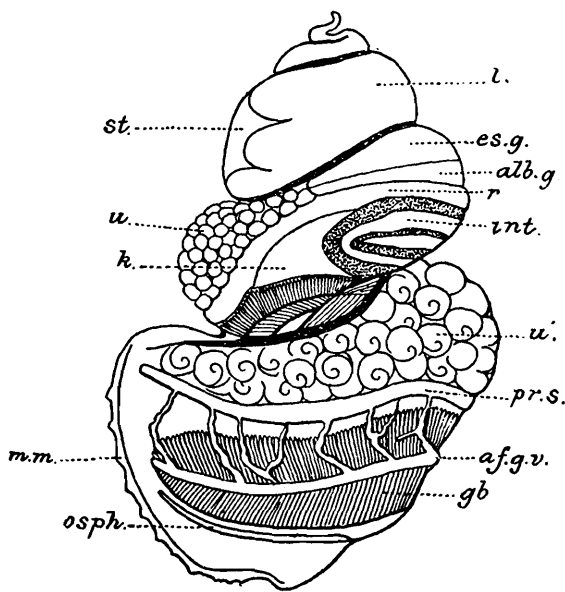


FIG. 3.—*Vivipara bengalensis*: view of the visceral hump from above. *af. g.v.*, afferent gill vein; *alb.g.*, albumen gland; *es.g.*, egg-shell gland; *gb.*, gill base; *int.*, intestine; *k.*, kidney; *l.*, liver; *mm.*, mantle margin showing traces of processes; *osph.*, osphradium; *pr.s.*, perirectal blood sinus; *r.*, rectum; *st.*, superficial area of stomach; *u.*, *u.*, upper and lower parts of uterus.

left and extending back for only a comparatively short distance from the mantle margin is an opaque whitish-yellow narrow streak, which denotes the position of the osphradium, while extending for the whole distance along its right and posterior border is a brown band, the branchial gland. On the extreme right of the branchial cavity in the ♂ is the crescentic spirally-twisted testis, which is usually of a bright yellow or orange colour, though this character is often obscured by the dense black pigmentation of the skin; in the ♀ this position is occupied by the thin-walled distended uterus, which seems invariably to contain eggs and young in the sexually mature examples, no matter at what season of the year they are taken. To the left of the uterus is a narrow clear line which denotes the course of the ureter, and beyond this again is a broad brownish band, indicating the course of the rectum. The central portion of the roof of the branchial chamber is thin-walled and is traversed by numerous blood-sinuses which commence in the perirectal sinus on the right and pass transversely across to the left to open into the afferent gill vein which runs along the course of the branchial gland. The free edge of the mantle underlies the peristome of the shell, and is thickened and covered with ciliated epithelium. In young specimens it is produced into a series of blunt finger-like processes, which are usually of a golden-yellow colour (*vide infra*). These tend to disappear as age advances, but traces of them can still be made out in the adult. There is often a quite noticeable one situated on the mantle margin opposite the commencement of the gill, and the yellow pigment-splashes on the mantle margin possibly denote the former positions of others that have since disappeared.

Immediately behind the free edge of the mantle, running parallel to it, is the shell-gland. This is most highly developed, as one would naturally expect, during early life, when the rate of growth is most rapid. A similar band exists in *Vivipara vivipara* and has been noticed by Villepoix (1895, p. 513). Laterally the

left and extending back for only a comparatively short distance from the mantle margin is an opaque whitish-yellow narrow streak, which denotes the position of the osphradium, while extending for the whole distance along its right and posterior border is a brown band, the branchial gland. On the extreme right of the branchial cavity in the ♂ is the crescentic spirally-twisted testis, which is usually of a bright yellow or orange colour, though this character is often obscured by the dense black pigmentation of the skin; in the ♀ this position is occupied by the thin-walled distended

mantle, where it joins the sides of the body, is thickened owing to wing-like expansions of the body muscle which pass outwards and upwards within its substance. Posteriorly the edge of the mantle is continued round the lower aspect of the body, between it and the upper surface of the foot, as a narrow pigmented ridge. Running upwards in the floor of the branchial chamber is the branchial fold. This structure presents a somewhat different appearance in the two sexes. In the female it forms a thin crenated fold, which passes upwards to the extreme apex of the branchial cavity, and finally becomes closely connected with the upper end of the gill immediately in front of the pericardium. Below, it is continuous with the left fold of the syphon and the ridge passing forwards beneath the right tentacle on the right side of the snout. Throughout its whole length it bears on its right side a small subsidiary ridge or fold, which is usually of a brown colour and which lodges a blood sinus. In the male the ridge consists of a stout basal portion, which is surmounted by a thin lamella. The reason for this difference in the two sexes lies in the fact that in the ♂ this ridge accommodates throughout almost its entire length the vesicula seminalis. According to Moore (1901, p. 470, note to fig. 1, pl. xxv) in the closely-related mollusc, *Neothauma tanganyikense*, Smith, this ridge serves as a protection for the gill against damage from pressure against the distended uterus and contained young, and is better developed than in *Vivipara vivipara*. It is always a matter of some difficulty to compare living examples of one species with the published descriptions and figures of others, but it seems to me that in *Vivipara bengalensis* this branchial fold is every whit as well developed as in *Neothauma tanganyikense*, and a study of the living animal has convinced me that Moore is wrong in his view of its function. If a fully-expanded example of *V bengalensis* be examined in the live state, it will be seen that the branchial fold extends vertically, inclining slightly to the right from the floor of the branchial chamber till its upper free border almost if not actually reaches the roof of the chamber, thus dividing the branchial chamber into two almost completely separate parts. On the left of this ridge is a wide cavity the upper and left wall of which is formed by the gill, and a little behind the mouth of the shell, the tips of the gill-filaments are in close apposition to the free border of the fold. A transverse section about half way up the body-whorl shows that the tips of the gill-filaments may actually pass across above the upper edge of the fold and project into the cavity on its right side. The cavity to the right of the branchial fold is never completely occluded by the uterus; there is always a free interval between the two which becomes continuous below with the syphon tube. The ridge is covered with a tall columnar ciliated epithelium, very similar to that covering the gill lamellae and the margin of the mantle. The presence of an equally well-developed branchial fold in the male indicates that Moore's explanation is not the true one and I entirely agree with Cuvier (1817, p. 6) that its function is respiratory, though it is

well known that the syphon is exhalent and not inhalent as he supposed (*l.c.*, p. 4).

The middle portion of the mantle is, as has already been mentioned, thin, and by carefully cutting through along this line and everting the two sides we are able to see the various structures contained within the cavity. The left side of the mantle is the same in both sexes. Commencing in the middle line in front and running backwards and to the left is the line of attachment of the gill. This is of the pectinate type and comprises roughly some three hundred filaments. Each filament or plate is of an elongate triangular shape, with a narrow base of attachment and tapering towards its extremity. The basal attached portion is to the left and the free margin of the gill lies towards the right side. Each gill-filament is covered with ciliated epithelium. Immediately on the right and, owing to the oblique course of the gill, a little posterior to it, is a raised, brownish-coloured ridge, the hypo-branchial gland, which extends upwards along the whole length of the gill-base. It is covered with a tall columnar epithelium and lying immediately above it is a large blood sinus, the afferent gill-vein, which collects blood from the viscera and conducts it to the gills, where it is aerated. To the left and in front of the gill and extending backwards from just behind the edge of the mantle to a point about one-third the length of the gill is a raised narrow ridge of a whitish yellow colour; this is the osphradium, and from its upper end a narrow white line is continued upwards, parallel to the gill-base as far as the extreme apex of the mantle cavity. As already mentioned, the mantle cavity is divided into right and left halves by the branchial fold. Water entering the mantle cavity passes into the left of this fold, and having traversed the branchial chamber passes out again down the right side and through the syphon. From the position of the osphradium, which commences a little to the left of the middle line and runs outwards and backwards on the left and in front of the gill, it is evident that all the water entering the cavity must first pass over the osphradium before it can reach the gill-filaments. The osphradium forms a very sensitive sensory organ. It is covered with ciliated epithelium and on its gill-surface it bears a number of small microscopic pits, which are also lined by columnar epithelium. These pits are difficult to see in the natural state, but in some cases indications of them can be made out owing to the mouths being faintly outlined with yellow pigment. The organ is supplied by a special nerve or series of nerves, the osphradial nerves, which arise from the anastomosis between the mantle nerve, coming from the left pleural ganglion and the first gill-nerve arising from the suprainestinal ganglion of the right visceral nerve (for a detailed account of this organ in *Vivipara vivipara* see Bernard, 1890, pp. 244-250).

On the right of the mantle chamber are the rectum and ureter and, in the female, the uterus also. These pass down close together on the right wall of the mantle chamber and open close

to the mantle margin in the angle formed by the roof and floor of the cavity opposite the syphon, so that all excreta are at once carried out of the chamber away from the body.

In the female the uterus and ureter open close together. These two ducts run down side by side on the extreme right of the branchial cavity, the ureter being to the left of the uterus, and the rectum lying above and to the inner side of the ureter. The terminal portion of the uterus is known as the vagina: it forms a prominent rounded papilla, the walls of which are thick and spongy, and the orifice is situated at its apex. This orifice is extremely distensible and in the contracted condition is oval or slit-like. The aperture of the ureter lies above and to the outer side of the vagina. It is much smaller and is provided with a sphincter muscle. The rectum passes down above and to the inner side of the ureter, it is continued further forward, towards

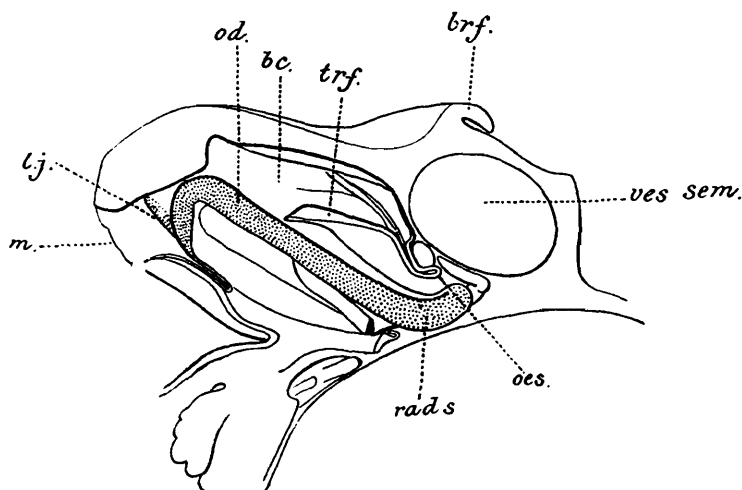


FIG. 4.—*Vivipara bengalensis*, view of the right half of the buccal cavity, cut in the sagittal plane. *bc.* buccal cavity; *br.f.* branchial fold; *lj.*, lateral chitinous jaw; *m.*, mouth aperture; *od.*, odontophore; *oes.*, oesophagus; *rad.s.*, radular sac; *trf.*, transverse fold above and behind odontophore; *ves.sem.*, vesicula seminalis cut in oblique section.

the mantle margin than either the uterus or ureter and having passed the terminations of these ducts it bends downwards and to the right and opens at the tip of the anal papilla. The terminal papilla and orifice of the anus is usually of a bright golden-yellow colour.

In the male, the rectum and ureter occupy the relative positions as given above, but the position of the uterus is now occupied by the orange yellow testis.

#### *The Alimentary System.*

The mouth is situated ventrally at the anterior end of the snout and forms an oval aperture, bounded by fleshy lips, between which the radula is thrust out during the process of feeding with a rotary motion from above downwards. The mouth leads backwards and upwards into the cavity of the buccal mass and each lateral wall is furnished with a low ridge, running from above

downwards and backwards. These ridges are yellowish in colour and are armed with a simple chitinous plate. The buccal mass is heart-shaped. In front it becomes continuous with the lips of the mouth, while behind it is produced in two ventral and posterior rounded prominences, between which lie the radular sac below and the oesophagus above. The buccal mass is plentifully supplied with muscles. On cutting through the skin in the middle line of the dorsum of the head and reflecting it outwards, numerous delicate strands of muscle, the protractors, can be seen passing backwards from the sides and dorsum of the skin of the snout to the buccal mass. Below the buccal mass a pair of rather stouter bands passes downwards and forwards to the skin. These are the depressors. The anterior region of the buccal mass is plentifully supplied with intrinsic muscles, as follows:—

- (1) Superficially and somewhat towards the ventral aspect on each side is a fan-shaped muscle, which arises by a narrow tendon from the lateral region of the ventral aspect and spreads out fan-wise as it passes forwards to be inserted into the oral tube.
- (2) Immediately deep to this is a sphincter muscle, the fibres of which run concentrically around the tube.
- (3) A band of muscle, rather narrower behind than in front, arises from the sides of the buccal mass, immediately posterior to the buccal nerve, across which it passes forwards, spreading out to be inserted round the oral tube.

Two pairs of strong muscles, the fibres of which are of a shining white colour in contradistinction to the fibres of the preceding muscles which have a reddish tinge, arise from the main muscle mass of the body and pass forwards to be inserted into the buccal mass. These are the anterior and posterior retractors:—

- (4) The anterior retractors are inserted into the anterior ventral aspect of the buccal mass by narrow tendons; passing backwards side by side they cross the pedal commissure dorsally and can be seen to arise from the main muscle mass near the base of the antennae.
- (5) The posterior retractors arise from the main muscle mass and pass forwards and slightly upwards external to the pleuro-pedal commissure of the central nervous system. Here each gives off a slip to the lateral wall of the oesophagus. It then continues forwards internal to the cerebro-pedal commissure and finally joins the side of the buccal mass as a fine tendon which can be traced forwards below the buccal ganglion and ends in a delicate expansion internal and deeply to the muscle (3) noted above. These two muscles are not quite symmetrical for that of the left side arises from the main muscle mass of the body at a higher level than that on the right.



A series of small muscle strands, usually three in number, arise close to the origin of the above muscle and pass forwards and upwards to be inserted into the surface of the radular sac.

The upper wall of the buccal mass is thin and on cutting through it in the antero-posterior line we get a view of the buccal cavity. In the middle line in front arising from the floor is a stout pyriform mass the narrow end of which projects upwards and forwards; this is the odontophore and it can be seen to carry the radula which disappears posteriorly into the radular sac. The radula is a yellowish narrow ribbon, which carries a series of small spinose teeth. These teeth are divided according to their position and dentation into three series. In the middle line is the median row, consisting of a single central tooth, as it is called. The anterior border of this tooth is recurved and is cut into a series of denticles. There is a wide rounded median denticle and five smaller triangular denticles on either side. On each side of the central tooth are a pair of laterals. In both cases we get the rounded median denticle and a series of smaller triangular or claw-like denticles on each side of it.

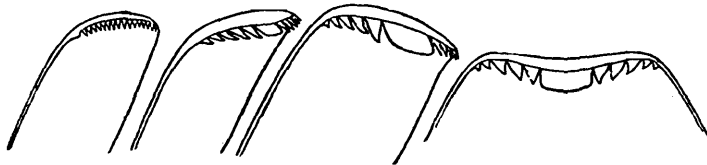


FIG. 5.—Radular teeth of *V. bengalensis*.

As a rule there are five of these claw-like denticles on either side of the median denticle in each of these teeth, but occasionally we find that there are six denticles on the outer side of the second lateral tooth. This variation may occur in a portion of a radula the rest of which shows the normal condition. The marginal tooth is usually curved inwards towards the middle line, and bears on its margin a uniform series of small denticles. In some cases as in the radula figured, there may be a broad sharp extra denticle at the extreme margin. The radula of *Vivipara bengalensis* was figured by Fischer (1887, fig. 499, p. 732), but a comparison of his figure with that given above will render unnecessary any apology for refiguring it here.

Lying behind and above the odontophore is a transverse fold with a crescentic anterior margin, the median portion of which is somewhat thickened and is slightly notched. Each lateral wall of the buccal cavity is thick and swollen and contains a cartilaginous mass—the odontophoral cartilage. Each cartilage is roughly oval in shape, the anterior end being somewhat more sharply rounded than the posterior, and is concavo-convex, the concavity being towards the middle line. The lower border is thin and is curved inwards. From the outer aspect a little below and behind the centre of the cartilage numerous muscle-fibres

arise and spread out in the lateral walls of the buccal mass. At the posterior end of the buccal mass beneath the oesophagus lies the radular sac, in which the radular ribbon is secreted. It is a short stout tube having a somewhat dorsally directed nipple-like posterior end. Above the odontophore the cavity of the buccal mass is hour-glass shaped the upper portion having a very thin-walled roof. Opening into the cavity are the ducts of the salivary glands.

The salivary glands are irregular asymmetrical racemose glands, consisting of a number of branching and anastomosing lobules. It is impossible accurately to separate the gland into right and left portions, and hence in this respect *Vivipara bengalensis* offers a marked contrast to *Neothauma tanganyikense* in which the salivary glands are separate and form compact lobulated masses (vide Moore, 1901, fig 2, pl. xxv). The main mass of the salivary gland lies on the dorsal side of the oesophagus behind the central nervous ring and is intimately bound up with the supra-oesophageal nerve as it crosses the oesophagus from right to left. A pair of delicate narrow salivary ducts arise anteriorly and pass forwards beneath the cerebral commissure.

The oesophagus is thin-walled and usually presents a greenish appearance due to its contents. It passes backwards and to the left and then turns towards the right again to pass up the columellar aspect of the visceral hump. During its course backwards in the floor of the branchial cavity it lies beneath the branchial fold and above the main muscle mass: on its left side lies the supra-intestinal nerve, and during this part of its course it lies in a well-marked venous sinus and is in close relationship to the cephalic aorta. At the posterior end of the mantle cavity the oesophagus passes upwards in the floor of the pericardial chamber and so reaches the liver. Finally in the upper part of the visceral hump the oesophagus curves round and opens into the stomach. This is a wide cavity occupying the third and fourth whorl. On cutting away the superficial wall of the stomach the cavity is seen to be incompletely divided into three regions, of which the upper two represent the cardiac portion of the stomach, while the lower part is the pyloric cavity. The junction of oesophagus and stomach is marked by a crescentic fold, just beyond which lies the orifice of the duct from the upper lobe of the liver. On the inner aspect, and dividing the cardiac region into two, is a broad longitudinal fold which passes downwards, and which carries a well-marked blood vessel. Below, this ridge divides into right and left folds which diverge and form the line of separation between the cardiac and pyloric regions. In the right half of the cardiac chamber the wall of the stomach is thrown into a series of longitudinal parallel folds, each fold being marked with a brown streak. The lower portion of this cavity is lined by a thin layer of chitin, which becomes thicker and more marked over the ridge separating the cardiac and pyloric cavities.

The pyloric portion of the stomach is a wide cavity that

gradually tapers towards its lower end. Running across the posterior wall is a double fold, of which the upper lip is often much more prominent than the lower. Between these two folds is a narrow gutter into which the ducts of the right and left lobes of the liver open. The junction of stomach and intestine is very clearly defined owing to the different character of the lining mucous membrane. The stomach is lined by tall columnar ciliated cells, which give the wall a soft velvety appearance, whereas the intestinal wall has a yellowish colour and is lined with a layer of chitin which gives it a smooth bluish metallic look.

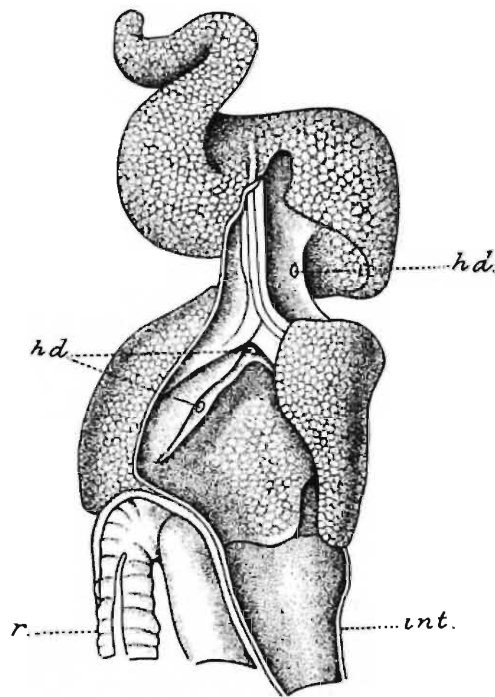


FIG. 6.—*Vivipara bengalensis*, view of inner wall of gastric cavity after removal of superficial wall. *hd.*, openings of hepatic ducts; *int.*, intestine; *r.*, rectum.

The liver, owing to the bulging of the stomach on its outer surface and the passage through it internally of the oesophagus, is incompletely divided into three lobes, an apical, occupying the upper turns of the spire, and a right and a left lobe inferiorly. The organ has a golden brown colour, which is, however, frequently obscured owing to heavy pigmentation of the overlying skin. It is a racemose gland, with elongate acini the tips of which reach the surface. Each acinus is hollow and is lined with a columnar or cubical epithelium. Each lobe is furnished with a separate duct, that of the upper lobe opening into the left part of the cardiac portion of the stomach, while the ducts of the right and left lobes open on the posterior wall of the pyloric cavity between the folds noted above. According to Leydig these folds probably serve to regulate the flow of bile.

The intestine passes forwards and to the right in the penultimate body-whorl and then turns sharply back again, forming a loop which overlies the pericardial cavity. In the first part of its course the lumen gradually narrows: it is lined by a yellow-coloured epithelium covered with a thin chitinous layer and running along its posterior aspect is a gutter with fleshy lips which are pigmented brown. At the apex of the loop, the character of this gutter becomes somewhat modified and the right-hand fold becomes proportionately larger and now appears to form a longitudinal ridge or typhlosole projecting from the posterior wall. The intestine having again reached the liver turns sharply forwards

once more and is now continued on as the rectum. It passes forwards on the right of the whorl, lying on the surface; in the ♀ it is in close apposition to the albumen- and shell-glands, and passes downwards and forwards immediately to the outer side of the kidney and the first part of the ureter. In the body-whorl it passes forwards, as we have already seen, in the roof of the branchial chamber and opens at the anus. In this latter part of its course its walls are thrown into numerous transverse folds. The contained faeces are moulded into small oval compact masses.

#### *The Vascular System.*

The heart lies in the pericardial chamber at the apex of the branchial cavity and on the inner side of the penultimate body-whorl. It is a closed cavity the walls of which are in places extremely thin and delicate and hence are very liable to become torn or ruptured. On its inner aspect the pericardium is separated from the shell only by thin membrane, above and in front it is bounded by the kidney, and above and behind is the loop of the intestine and the liver; on its right or outer side lie the genitalia and the rectum; while below it lie the oesophagus, the termination of the supra-intestinal and sub-intestinal nerves and the splanchnic ganglion and, in the female, the loop of the oviduct. On its outer and upper aspect the cavity of the pericardium communicates with the kidney through the reno-pericardial opening, the position of which will be studied when dealing with the kidney itself.

The heart consists of two chambers. Anteriorly is the soft-walled whitish-looking auricle, the walls of which are usually thrown into a series of irregular folds. In almost every adult example examined, the auricular wall was seen to contain a number of small round white bodies. These are cysts of an Echinostome Agamodistome and are present in such large numbers that they may almost fill the whole organ. The wall of the auricle is thick and glandular, and is said to form the haematic gland that is present in other molluscs (*vide* Perrier, 1889, p. 178). The ventricle lies posteriorly and is a rounded body of a pale brownish colour and its walls are thick and muscular. The auriculo-ventricular aperture is tube-like and projects into the cavity of the ventricle. From the inferior aspect of the ventricle arises a short wide aorta. In *Vivipara vivipara* (*vide* Perrier, 1889, pl. viii, fig. 38 x.) there is said to be a valve-like flap at the point of origin of the aorta from the ventricle, which prevents the regurgitation of blood during the ventricular diastole. Leydig (1850, p. 170) on the other hand states that there is a crescentic valve situated between the auricle and ventricle. In *Vivipara bengalensis* I have failed to find any indication of either. The common aorta almost at once bifurcates into two wide trunks, which run in opposite directions. One branch, the *cephalic aorta*, passes forwards and downwards to the inner side of and close to the oesophagus. In this position it passes forwards

below the floor of the mantle cavity and high up in the chamber it gives off a large branch that diverges towards the left side and, where the mantle margin merges into the foot, breaks up into branches. The main trunk of the cephalic aorta is continued on, crossing beneath the oesophagus to reach its right side. In this situation it has the sub-intestinal nerve, lying in a blood sinus, on its right and in the ♂ the vesicula seminalis lying directly above it. At the anterior end of the branchial chamber it comes into relationship with the radular sac, and passes forwards on its right side. It then dives ventrally, and below and behind the pedal commissure it gives off a branch to the snout and then divides into anterior and posterior branches which run to the respective regions of the foot. Throughout its course beneath the branchial chamber it gives off a number of fine branches to the muscles of the body.

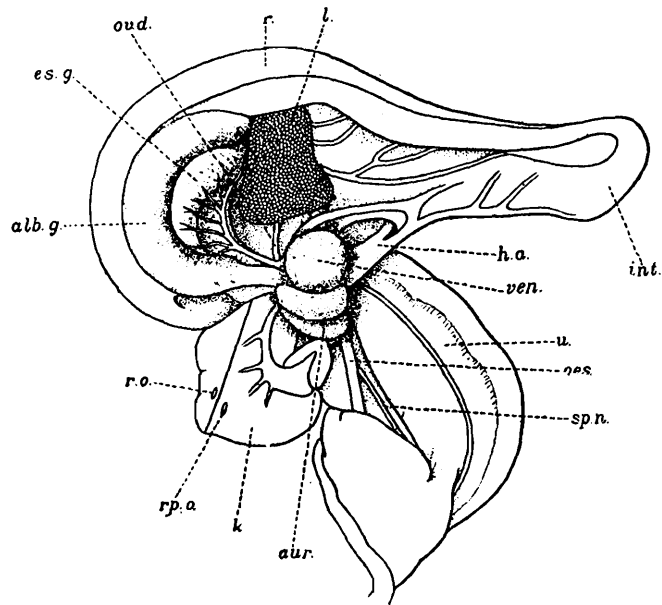


FIG. 7.—*Vivipara bengalensis*, view of the pericardial chamber. The loop of intestine has been turned over to the left side and the kidney downwards and to the right. *alb.g.*, albumen gland; *aur.*, auricle; *es.g.*, egg-shell gland (receptaculum seminis); *h.a.*, hepatic aorta; *int.*, intestine; *k.*, kidney; *l.*, liver; *oes.*, oesophagus; *ov.d.*, oviduct; *r.*, rectum; *r.o.*, renal orifice into ureter; *rp.o.*, reno-pericardial opening; *sp.n.*, supra-intestinal nerve; *u.*, uterus; *ven.*, ventricle.

The *hepatic aorta* passes upwards and backwards in the floor of the pericardial cavity, immediately to the left of the oesophagus. It almost at once gives off a large branch which passes at first slightly inwards and upwards to reach the lower wall of the intestine, where it subdivides into two main branches. One of these curves forwards and runs along the under aspect of the first part of the intestine, supplying branches to it, and the main vessel passes at first forwards as far as the bend of the intestine and then continues on along the second part of the intestine, lying immediately beneath the typhlosole-like ridge on its under aspect. The other branch curves forwards and to the right, crossing behind the oesophagus, and sends branches to the testis in the ♂. In the ♀, after supplying branches to the albumen and shell glands, curves backwards and to the left and reaches the wall of the uterus where it finally divides into ascending and descending branches, the latter of which is much the longer and larger of the two and runs down the ventral wall as far as the point where the wing-like

expansion of the body muscle meets the mantle margin. The main hepatic artery is continued upwards between the liver and stomach, where we have already noticed it lying in the longitudinal fold on the posterior wall of the cardiac portion of the stomach, and ends in branches supplying the liver in the apical whorls.

The venous system consists very largely of wide spaces or sinuses, whose walls are very thin and in consequence are very difficult to define. Occupying the central portion of the foot, between the dense white muscle and the grey spongy tissue of the sole, is a wide irregular sinus, the blood from which, according to Leydig, passes upwards and backwards to reach the venous sinus on the ventral posterior aspect of the kidney. This sinus appears to be joined at the left posterior angle of the kidney by a venous sinus, which runs up the right side of the branchial fold in the floor of the mantle cavity, and it is also joined by a sinus crossing from right to left along the posterior and upper margin of the kidney and having its origin in the perirectal sinus. The conjoined vessel passes down superficially on the left side of the kidney between it and the branchial gland. This vessel is known as the afferent gili-vein. Lying to the right of the kidney in the body-wall is a large sinus which receives blood from the organs lying in the upper coils of the visceral hump; this passes downwards and at the apex of the kidney joins the afferent gill-vein that we have already seen passing down the left margin along the branchial gland. The afferent gill-vein can be traced down the whole length of the branchial gland on the right of the gill-base almost as far as the mantle margin; below the level of the kidney it is joined by a further series of small branches which arise from the perirectal sinus and pass across the thin median portion of the mantle roof. The perirectal sinus also received tributaries in the female from the wall of the uterus. The afferent gill-vein supplies branches to the gill-filaments and the blood after being aerated returns to the efferent gill-vein which lies on the left side of the base of the gill, this vein passes from below upwards and at the apex of the mantle cavity opens into the cavity of the auricle. A large vein runs down beneath the floor of the branchial chamber on the right side of the oesophagus. Superiorly it receives tributaries from the liver, and in the ♀ from the albumen gland and egg-shell gland while a large branch passes up on the inner aspect of the uterus and then crosses over behind the sub-intestinal nerve to join it near the apex of the branchial cavity.

### *The Renal System.*

The kidney is a triangular pyramidal organ of a pale greenish colour, lying in the roof of the mantle cavity at its extreme apex. Along the external or right margin runs the rectum and the perirectal blood sinus, below which lies the commencement of the ureter, while along the left or inner margin is the commencement of the afferent gill-vein and the base of the gill. The posterior

border is connected with the loop of the intestine by an intervening fold of thin membrane. Of the four surfaces of the kidney, the upper lies just under the skin against the shell. The apex of the kidney lies to the front, and the left surface forms the upper part of the right-hand wall of the mantle cavity and is in close relationship with the terminal portion of the branchial fold. The base of the kidney, which is triangular in shape with the apex of the triangle directed ventrally, faces backwards towards the upper part of the visceral hump and forms part of the anterior boundary wall of the pericardial chamber. The right surface of the kidney is in relationship with the upper part of the ureter, which separates it from the testis in the male or the uterus and shell-gland in the female. A thin fold of membrane passes outwards and backwards from the right-hand border of the base of the kidney to the testis in the male and the shell-gland in the female and forms the upper boundary limit of the ureter.

The kidney is provided with two orifices that open respectively into the ureter and the pericardium. Both these apertures are situated close together near the right posterior border. The reno-pericardial opening is situated on the posterior or pericardial surface of the kidney near the supero-external angle: it is oval in shape and has thin walls. The external or ureteral orifice is situated on the external surface, close to the reno-pericardial aperture, but separated from it by the conjoined pericardium and wall of the ureter. It possesses thick protuberant lips, which are covered with ciliated, columnar epithelium and are often marked by a ring of black or brown pigment. The ureter is a thin-walled tube having in cross section a triangular lumen. Its right wall is bounded by the testis in the male or the uterus and part of the albumen- and shell-glands in the female: the left wall is thin and separates it from the branchial chamber, while its upper or superficial wall is formed partly by the rectum and perirectal blood sinus and a thin-walled portion in contact with the superficial skin. The orifice of the ureter lies, as we have already seen, near the right-hand margin of the mantle edge, in the angle between the rectum and the vagina in the female, or in the corresponding position to the left and above and behind the anus in the male.

### *The Genital System.*

*Vivipara bengalensis* like all members of the genus is dioecious, or in other words the two sexes are separate. We have already seen that sexual differences are apparent in the structure of the right tentacle, which in the male is thickened and recurved and acts as a penis or intromittent organ. This change does not seem to have proceeded quite as far in *Vivipara bengalensis* as in the European species *Vivipara vivipara*, for in the former the modified tentacle is sickle-shaped, whereas in the latter it is figured as being completely contracted up into a rounded projection (*vide* Fischer, 1887, fig. 501, p. 733), which may actually be

enclosed in a small pocket (*vide* Baudelot, 1863, p. 218, pl. v, figs. 14-15).

♂ The testis in *Vivipara bengalensis* forms a compact semi-lunar organ lying on the right of the branchial chamber, and occupying the same position as the uterus in the female. It is of a bright orange-red colour and extends to the upper end of the branchial cavity, where its apex is in close relationship with the pericardial cavity and is connected by a thin fold of membrane with the lower surface of the liver. The gland is flattened from side to side, the right surface being in contact with the shell while the left surface forms in part the right wall of the ureter and below this the right wall of the mantle cavity. In possessing a testis formed of a single mass in this position in the body *Vivipara bengalensis* differs markedly from *Vivipara vivipara*, in which the testis consists of two distinct portions, the upper occupying the extreme apex of the visceral hump and the lower lying at the lower margin of the liver between the stomach and the coil of the intestine (*vide* V. Siebold, 1836, p. 241, and Simroth, 1896-1907, pl. xliii, fig. 9; also Erlanger, 1891, pp. 665-666).

Although the testis in *Vivipara dissimilis* (Müller) occupies the same position as in *V. bengalensis*, it differs in having a more or less quadrilateral extension from its upper pole, which passes upwards on the outer side of the pericardial cavity and abuts against and is firmly united to the lower aspect of the liver, from which, however, it can be readily recognised by its golden orange colour. This upward expansion is clearly demarcated off from the rest of the organ, which closely resembles the whole testis of *V. bengalensis*, and partakes more of the nature of a second lobe. *V. dissimilis* in this respect is intermediate between *V. vivipara* and *V. bengalensis*.

A series of narrow delicate ducts, the vasa efferentia, arise from the lower border of the testis and passing respectively upwards and downwards along its lower border converge to form a narrow tube, the vas deferens, which passes to the left beneath the floor of the branchial chamber, crossing above the sub-intestinal nerve, to reach the vesicula seminalis. The first part of the vas deferens is sometimes dilated to form a spindle-shaped swelling, but the portion of the duct near the vesicula seminalis is narrow. The vesicula seminalis forms a wide tube which passes downwards and forwards from just in front of and below the pericardium to the base of the right tentacle beneath the floor of the branchial chamber approximately in the middle line and exactly beneath the branchial fold. The upper portion of the organ curves round to the right to meet the vas deferens. The whole organ is pigmented and possesses an iridescent appearance like mother-of-pearl. Cuvier (1817, p. 7) described this structure in *V. vivipara* as the copulatory organ, but Treviranus subsequently referred to it as a seminal vesicle, and there seems to be some doubt as regards its true function. Later authors refer to it either as the vesicula seminalis or the prostate gland. Erlanger



(1891, p. 665), appears to consider it to be an ejaculatory duct, in which view Simroth (1896-1907, note to fig 9, pl. xliii) concurs. Baudelot (1863, p. 217), on the other, hand seems to consider that it is of the nature of a prostate gland, and describes the internal surface as consisting of a series of transverse lamellae, running parallel to each other. In *V bengalensis*, this region of the duct is surrounded by a layer of circular connective tissue fibres and the lining mucous membrane is thrown into folds as described by Baudelot, though these are narrower and more numerous than he figures them. A transverse section shows that these folds are supported by a connective tissue lamella, on each side of which is a layer of cubical epithelium. The whole organ is glandular in character and is in my opinion a 'prostate' gland. The terminal portion of the male duct is comparatively narrow. It passes up the right tentacle and opens by a small orifice at its extreme tip. In this part of its course the duct-wall is thick and muscular, and constitutes an ejaculatory duct.

According to Smith (1881, p. 221) the right tentacle of the male *Vivipara vivipara* is merely the sheath of a true penis, "which, at the time of copulation, protrudes through it." As regards this statement he appears to be at variance with other authors. Simroth (1896-1907, p. 617) states that the short 'penis' can be coiled up in a pouch of skin at the outer side of the tentacle, and Baudelot (1863, p. 218, pl. v, fig. 14) shows this condition very clearly. It is this coiled up portion of the tentacle which is the 'penis,' and no portion of the genital duct is protruded through it during the act of copulation, for, as Baudelot points out, the terminal portion of the duct, which I have considered to be an ejaculatory duct, is intimately connected with the skin of the tentacle and could not possibly be everted. In this respect *Vivipara vivipara* and *V bengalensis* appear to be identical. In this latter species the terminal portion of the ♂ genital duct is closely bound to the skin of the tentacle by connective tissue. I have not been able to observe the act of copulation, but the structure of the right tentacle in this species shows that here also it is the tentacle itself which is the intromittent organ.

The seminal fluid contains two quite distinct forms of spermatozoa. The first form, which appears to be that of the mature functional spermatozoon, consists of an elongate spiral head, with 6-7 turns in the spiral and of a refractile appearance: behind this is a single long flagellum. The second form is usually described as 'worm-shaped'; it may be straight or spirally twisted, is much stouter than the spiral kind and terminates in a tuft of numerous short flagellae. From the time of their discovery these two forms of spermatozoa have interested zoologists and accounts of them and their mode of development have been given by V Siebold (1836), Leydig (1850), Baudelot (1863), Simroth (1891-1907) and others, but we are still ignorant of the function of the worm-shaped type.

♀ The genital organs of the female *Vivipara bengalensis* appear to agree exactly with those of *V vivipara*. One of the best

accounts of these organs is that given by Baudelot (1863, pp. 218-220, pl. v, figs. 16-20). Erlanger (1891, p. 664) in his description claims to have followed Baudelot and to have reproduced his illustration of this system. But a comparison of the two figures serves to show how misleading the results of such a procedure may be, for Erlanger (*l.c.*, fig. 3) shows no trace of the duct of the albumen gland, though this is clearly seen in Baudelot's figure (*l.c.*, fig. 16).

In *Vivipara bengalensis*, the ovary consists of a few small scattered follicles along the commencement of the oviduct. It is of a red-brown colour and so in spite of its small size can be distinguished from the liver tissue: it lies in the third body-whorl, in close contact with the posterior wall of the cardiac region of the stomach and along the course of the hepatic artery. The various follicles contain numerous small ova, which have a diameter of 0.021-0.025 mm. The oviduct passes downwards as a fine tube, also of a red-brown colour, to the lower margin of the liver and is then continued on along the floor of the pericardial cavity on the right of the oesophagus. At this point it is joined by the short wide duct of the albumen gland. This gland is situated just below the skin on the right of the pericardium. It is connected by a thin fold of membrane with the loop of the intestine on the upper surface of the pericardium and the rectum passes forwards and downwards along its superficial aspect, which is grooved to receive it. Below, the gland is intimately bound down to the U-shaped egg-shell gland, or receptaculum seminis as it is usually termed. The albumen gland is tongue-shaped and slightly curved. It is of a bright orange-red colour and its apex is in contact with the lower surface of the liver. From its inner and posterior border a wide duct arises which passes backwards internal to the first part of the egg-shell gland and joins the oviduct. The combined duct is then continued downwards and inwards for a short distance and then turns back again towards the apex of the visceral hump. This portion of the duct is of a brown colour and it can be traced to the lower and inner limb of the egg-shell gland, into which it opens at its extreme end on a smooth rounded papilla.

The egg-shell gland is, as already mentioned, a wide U-shaped tube the walls of which have a yellow-brown colour very similar to that of the liver. The ascending limb of the U is at first narrow, but as it passes upwards towards the liver it gradually dilates and then turns sharply round on itself and passes downwards again on the right of the ascending limb and in close contact with the shell. On opening the tube, the inner wall is seen to be thick and glandular and is thrown into a series of folds. At first these folds run parallel to the length of the tube, but as we trace them up they become more and more oblique curving towards the right and in the descending limb of the gland they run spirally. On the posterior aspect of the descending limb a smooth whitish ridge with a gutter on its right side can be seen to

arise at the upper and posterior end, passing downwards to the orifice through which the shell-gland opens into the uterus. At this point the smooth ridge becomes continuous with a longitudinal fold, which, as we shall see later, passes down the whole length of the lower wall of the uterine cavity. I have throughout referred to this U-shaped portion of the genital duct as the egg-shell gland. In the earlier descriptions of *V. vivipara*, such as that given by von Siebold (1836 p. 244), it is referred to as a receptaculum seminis, because free spermatozoa were found in the contents. That it serves as a repository for semen is beyond doubt, but it seems to me that its true active function is to produce the thin membranous covering which surrounds the eggs. The egg-shell gland opens below by a wide crescentic mouth into the thin-walled uterus. This is a wide cavity, which we have already seen lying on the right of the mantle cavity throughout the whole length of the body-whorl. It invariably contains eggs and developing young when once sexual maturity has been reached. Running along the whole length of the floor of the uterine cavity is a double fold of opaque-white colour which is in marked contrast with the thin translucent side walls. This double fold has a narrow base of attachment and the left-hand or inner fold is thin and convoluted while the outer fold is thicker and has a straight margin. This outer fold is covered with a ciliated epithelium and beneath this fold, between it and the floor, the seminal fluid, which has been introduced by the male is conducted up to the shell gland. The terminal portion of the genital duct is comparatively narrow and thick-walled. It opens on the right of the branchial chamber by an oval orifice, the vagina, which is situated terminally on a small papilla. During copulation the right antenna of the male is introduced through this orifice and the seminal fluid is deposited within the uterus.

The members of the genus *Vivipara*, as their name implies, produce live young, but they are actually ovo-viviparous. If we examine the contents of the uterus during the breeding season we find that the lower region of the duct contains numerous young, with  $2\frac{1}{2}$  turns in the shell, ready to be born, but as we pass further and further upwards the state of maturity of the young becomes less and less, until at the extreme upper end we find large ova containing an extremely minute embryo, with only half a turn in the spiral of the visceral hump. These eggs are large and are pyriform or globular in shape. They are surrounded by a thin delicate membrane, which at one point is twisted up and produced into a kind of free pedicle. Filling the whole egg, and surrounding the young embryo is a mass of faintly blue albuminous material, which under the higher powers of the microscope, can be seen to contain large numbers of spermatozoa, so that it would appear that the seminal fluid of the male serves the double function of fertilizing the ovum and providing in part for the nourishment of the embryo. In addition to the spermatozoa we find numerous fine spicules which dissolve readily on the addition of glacial

acetic acid and are presumably calcareous in nature. It is probably from these spicules that the young embryo derives the calcareous substance necessary for the production of the shell.

#### *The Nervous System.*

A very full and complete account of the nervous system of *Vivipara vivipara* has been given by Bouvier (1887, pp. 63-72, pl. iv, figs. 15, 16) and that of *Vivipara bengalensis* agrees in almost every particular, so far as I have been able to ascertain. The type of nervous system is that known as 'dialyneurous,' in that the connection between the sub-intestinal nerve and the right pleural or parietal ganglion is an indirect one, brought about by the union of a branch arising from the right pallial nerve and a branch from the sub-intestinal nerve. A similar anastomosis exists on the left side of the body, between the left pallial nerve and a branch from the supra-intestinal ganglion. Moore (1903, p. 276) has distinguished three different types of nervous system, based on the relative positions of the three main ganglia of the central nervous system—those forms of nervous system in which, as in *Vivipara*, "the pleural ganglia are more or less half-way between the cerebrals above and the pedals below the oesophagus" he terms 'dystenoid.'

The cerebral ganglia are situated in the base of the snout on either side of the commencement of the oesophagus, immediately behind the buccal mass. Each ganglion is roughly triangular in shape, with the base posteriorly and the apex pointing forwards and outwards. On the external aspect a shallow groove divides the ganglion into two parts, an anterior 'labial' portion and a posterior 'cerebral' portion. Each ganglion is of a red-brown colour and is connected with its fellow across the dorsal aspect of the oesophagus by a wide, short cerebral commissure. The ducts of the salivary glands pass forwards close to the middle beneath this commissure and above the oesophagus. The 'labial' portion of the cerebral ganglion is flattened dorso-ventrally and from its outer and antero-internal borders a number of nerves arise. From the antero-internal border two fine nerves arise close together and pass forwards over the dorsum of the buccal mass to the skin of the snout. Near the apex of the ganglion, but still from the inner border, a stout nerve arises and passes forwards on the side of the buccal mass to the snout and lips. At the extreme apex of the ganglion three nerves arise close together: (i) this runs forwards on the side of the buccal mass to the lips and snout; (ii) this is the stoutest of all three and is the buccal nerve. It first passes downwards and forwards on the lateral aspect of the buccal mass towards the ventral aspect: here it turns upwards and passes deep to the lateral retractor muscle of the lips, and just above and behind the origin of this muscle from the side of the odontophoral cartilage it ends in a rounded or triangular yellowish-brown body, the buccal ganglion, which lies just in front of and below the point of entrance of the salivary duct into the buccal cavity.

From each buccal ganglion three nerves arise, two of these pass obliquely upwards towards the dorsal aspect of the buccal mass, but the third and largest passes backwards and downwards around the posterior aspect of the buccal mass, below the oesophagus and above the radular sac, to the ganglion of the opposite side. This is the buccal commissure. (iii) This nerve arises just external to the buccal nerve and passes forwards and downwards to the lower part of the lip of the mouth, it gives off a branch which passes

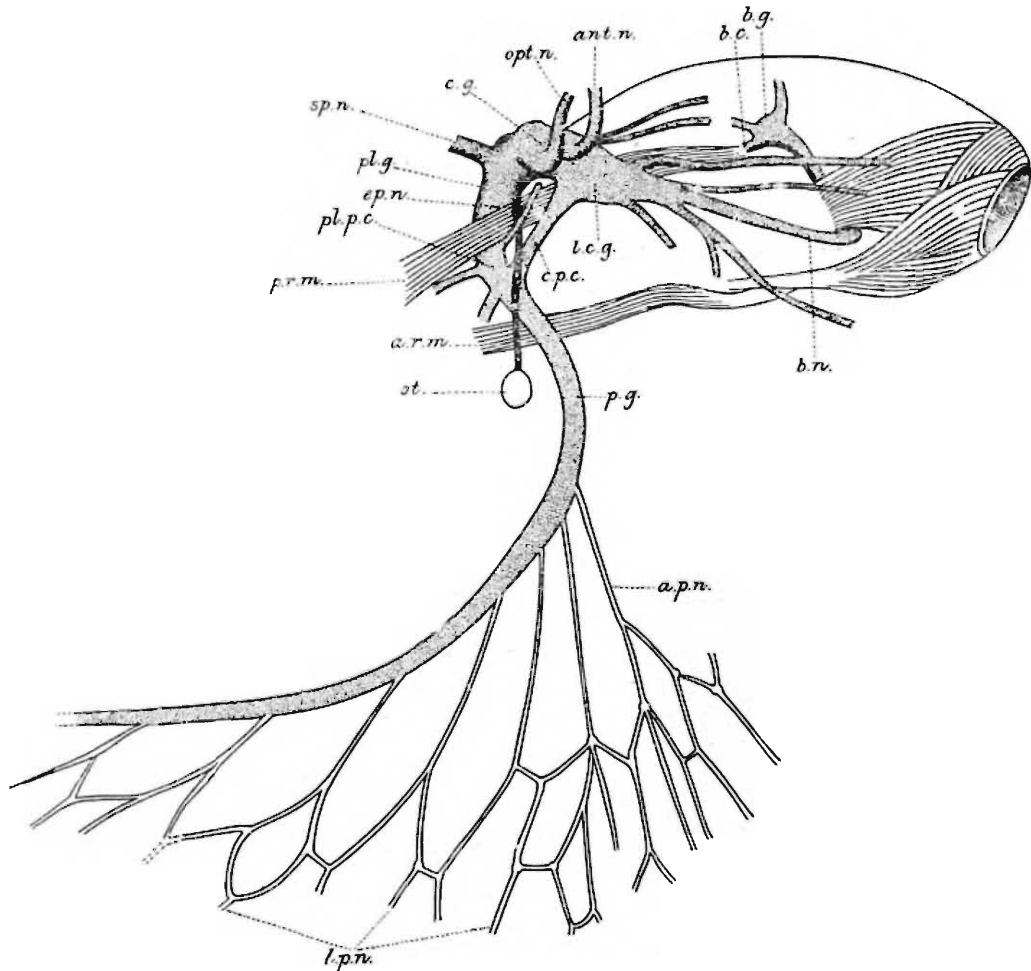


FIG. 8.—*Vivipara bengalensis*, nervous system of the right side. *ant n.*, antennal nerve; *a.p.n.*, anterior pedal nerve; *a.r.m.*, anterior retractor muscle of buccal mass; *b.c.*, buccal commissure; *b.g.*, buccal ganglion; *b.n.*, buccal nerve; *c.g.*, cerebral ganglion; *c.p.c.*, cerebro-pedal commissure; *e.p.n.*, epipodial nerve; *l.c.g.*, labial portion of the cerebral ganglion; *l.p.n.*, lateral pedal nerves; *opt.n.*, optic nerve; *ot.*, otocyst; *p.g.*, pedal ganglion; *p.r.m.*, posterior retractor muscle of buccal mass; *pl.g.*, right pleural ganglion; *pl.p.c.*, pleuro-pedal commissure; *sp.n.*, supra-intestinal or right parietal nerve.

across below the oral tube, joining with its fellow of the opposite side to form the labial commissure. Three nerves arise from the rounded upper and outer aspect of the cerebral portion of the cerebral ganglion. From the upper aspect a stout nerve, the antennal nerve, arises and passes forwards and outwards to the antenna; although in the male the right antenna serves the double function of a tactile organ and the intromittent organ, the nerve that supplies it shows no obvious increase in size. From

the posterior and outer surface of the ganglion the optic nerve arises and passes forwards and outwards external to the antennal nerve and ends in the sensory epithelium of the eye. As we trace this nerve backwards to the brain it can be seen to end in a quite distinct rounded swelling which forms a localised prominence on the external and posterior margin of the cerebral ganglion. From the side of the cerebral ganglion immediately below the origin of the optic nerve a small nerve arises, which can be seen to pass directly downwards. This small branch, which is the nerve to the otocyst, passes down external to the lateral retractor muscle of the buccal mass and the pedal ganglion and finally ends in the otocyst, which lies a little behind and to the outer side of the pedal nerve

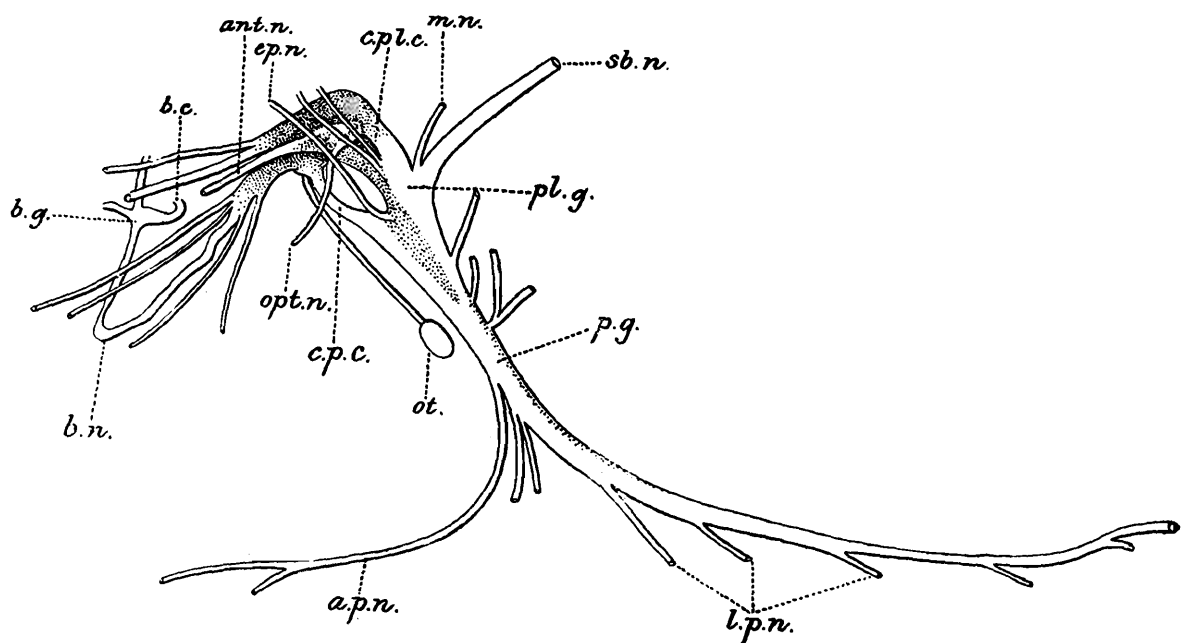


FIG. 9—*Vivipara bengalensis*, nervous system of the left side. *ant.n.* antennal nerve; *ap.n.*, anterior pedal nerve; *b.c.*, buccal commissure; *b.g.*, buccal ganglion; *b.n.*, buccal nerve; *c.p.c.*, cerebropedal commissure; *c.pl.c.*, cerebropleural commissure; *ep.n.*, epipodial nerve; *l.p.n.*, lateral pedal nerves; *opt.n.*, optic nerve; *ot.*, otocyst; *p.g.*, pedal ganglion; *pl.g.*, pleural ganglion; *sb.n.*, sub-intestinal or left parietal nerve.

close to its origin. Each otocyst is a small oval sac, the long axis of which is vertical; it has a shining refractile appearance and its cavity is filled with a number of small calcareous concretions of varying shape, the otoliths. [For more detailed descriptions of this organ, the reader is referred to the accounts given by Leydig (1850), and Lacaze Duthiers (1872).] The position of the pleural ganglia and consequently the arrangement of the nerve commissures that arise from the cerebral ganglia differ on the two sides of the body. On the left side, the pleural ganglion lies mid-way between the cerebral and pedal ganglia and the arrangement of the ganglia and commissures conforms to Moore's definition of the 'dystenoid' type of nervous system. On this side of the body two commissures, that differ markedly from each other, arise from the ventral aspect

of the hinder portion of the cerebral ganglion. The anterior cerebro-pedal commissure is long and narrow and of a white colour; it passes downwards external to the lateral retractor muscle of the buccal mass to join the pedal ganglion. The posterior cerebro-pleural commissure is broad and ribbon like, and can be seen to consist of two parts, an anterior brownish-coloured portion and a posterior white portion. Inferiorly it fades into a very ill-defined left pleural ganglion. Below this ill-defined ganglion a short broad commissure passes downwards, being joined by the cerebro-pedal commissure to the pedal ganglion. On the right side of the body there is no distinct cerebro-pleural commissure. The right pleural ganglion lies close against the posterior end of the cerebral ganglion and is only separated off from it by an ill-defined neck. The pleuro-pedal commissure is in consequence proportionately long. On this side of the body the arrangement of these ganglia conforms to what Moore (1903, p. 276.) terms the 'epiathroid' type of nervous system.

From the pleuro-pedal commissures several fine nerves arise; of these one, usually the largest, can be seen to arise from the commissure low down near its point of union with the cerebro-pedal commissure. This is the epipodial nerve and that on the left, which is usually slightly the larger, supplies the epipodium on that side, while the right supplies the fold beneath the right tentacle and the inner or left half of the syphon. The other nerves pass upwards and outwards to the tissues at the base of tentacle. The pedal ganglia are long ribbon-like structures of a brown colour, which are connected above with the cerebro-pedal and pleuro-pedal commissures. Each of these ribbons is composed largely of ganglionic nerve-cells, and in consequence the whole length of the structure must be regarded as being homologous with the more compact pedal ganglia of other molluscs. Immediately beneath the radular sac the two pedal ganglia are connected together by a wide short pedal commissure which passes from side to side below and in front of the posterior retractor muscles of the buccal mass, and behind and above them the terminal portion of the cephalic aorta passes downwards and backwards in the middle line. From this point the two ganglia pass downwards and backwards lying between the white muscle mass of the foot and the soft grey tissue of the sole. At first the two cords diverge somewhat, but posteriorly they again converge towards the middle line. A series of three or four transverse commissures pass across from side to side uniting them together at different points in their length. A series of nerves arise from the pedal ganglia and spread forwards and outwards. The first pedal nerve arises from just below the pedal commissure and passes forwards towards the anterior margin of the foot; it sends off a branch which passes inwards towards the middle line and forms an anastomosis with its fellow of the opposite side. The remaining nerves pass outwards in a radiating manner and form a very elaborate anastomosis around the margin of the foot. The nerves divide and

anastomose in a series of loops and at certain points of the network so formed slight swellings can be detected, which probably correspond to local collections of ganglion cells. From the posterior surface of the pedal ganglia and the pleuro-pedal commissure several nerves pass backwards and enter the muscles of the foot. Each parietal ganglion gives rise to two nerves. The most anterior and smaller of the two is the mantle nerve, and the larger and more posterior is the parietal nerve. The two parietal nerves pass backwards and form a figure-of-eight loop in the visceral hump. Each nerve crosses over to the opposite side of the body from which it originated, and having done so sends off a lateral branch which anastomoses with the mantle nerve of that side, thus forming the 'dialyneural' connection.

The right parietal nerve, or supra intestinal nerve as it is called, passes obliquely across the upper aspect of the oesophagus just behind the buccal mass. In this portion of its course it is closely connected to, and surrounded by the branching follicles of the salivary glands. Having reached the left side it gives off a large branch, the anterior branchial nerve, which passes to the left and, having given off a small branch to join the mantle nerve, breaks up into a number of fine branches which supply the anterior region of the gill and the osphradium. At the point where the anterior branchial nerve arises from the supra-intestinal nerve a slight swelling is to be seen, this is known as the supra-intestinal ganglion. From this point the nerve passes up beneath the floor of the branchial chamber on the left side of the oesophagus. During this part of its course it gives off a series of fine branches to the gills and finally, at the extreme apex of the branchial cavity, a considerably larger branch, which soon subdivides into smaller twigs, is given off to the upper part of the gill.

The left parietal or sub-intestinal nerve crosses over from left to right below the oesophagus. It then diverges somewhat to the right and gives off a branch which again subdivides; one twig passes forwards and outwards to join the mantle nerve of the same side and the conjoined nerve so formed supplies branches to the outer wall of the syphon and the terminal portions of the excretory and genital ducts and the anus. The main nerve continues backwards above the columellar muscle at some distance from the oesophagus and gives off a series of branches to the mantle roof and its dependent structures. At the apex of the branchial chamber both nerves are continued up for a short distance in the floor and outer wall of the pericardium and then unite to form a loop, in front and to the inner side of the U-shaped bend of the oviduct in the ♀. At the apex of the nerve loop the nerve is slightly swollen and is known as the visceral ganglion. From it a series of branches arise which supply the neighbouring viscera.



## REFERENCE LIST

- Baudelot., 1863 Recherches sur l'appareil générateur des mollusques gastéropodes.  
*Ann. Sci. nat. Zool.* XIX, pp. 134-222, and 268-294, 5 pls. Paris.
- Bernard, F., 1890 "Recherches sur les organes palléaux des gastéropodes Prosobranches."  
*Ann. Sci. nat. Zool.* (7) IX, pp. 89-404, 15 pls. Paris.
- Bouvier, E. L., 1887 "Système nerveux morphologie générale et classification des gastéropodes Prosobranches."  
*Ann. Sci. nat. Zool.* (7) III, pp. 1-510, 18 pls. Paris.
- Cuénot, L., 1890 "Sur la glande de l'oreillette (*Paludina Vivipara*) et la glande néphridienne (*Murex brandaris*)."  
*Compt. rend.* CX, pp. 1275-7. Paris.
- Cuvier, 1817 Mémoires pour servir l'histoire et l'anatomie des Mollusques. No. XVI, Sur la Vivipare d'eau douce, les Turbo, les Trochus, etc., pp. 120, 1 pl. Paris.
- Erlanger, R. von., 1891. "Zur Entwicklung von *Paludina vivipara*."  
*Morphol. Jahrbuch.* XVII, pp. 337-379 and 636-630, 6 pls. Leipzig.
- Fischer, P., 1887 "Manuel de Conchyliologie. Paris.
- Lacaze Duthiers, H., 1872. 'Otocystes ou capsules auditives des Mollusques.'  
*Arch. Zool. expér.* I, pp. 97-168, 6 pls.
- Leydig, F., 1850 "Ueber *Paludina vivipara*." *Zeitsch für wissenschaft. Zool.* II, pp. 125-197, 3 pls. Leipzig.
- Moore, J. E. S., 1901 "Further researches concerning the Molluscs of the great African Lakes."  
*Proc. Zool. Soc.* II, pp. 461-470, 2 pls. London.
- Moore, J. E. S., 1903 "The Tanganyika Problem." London.
- Perrier, R., 1889 "Recherches sur l'anatomie et l'histologie du rein des Gastéropodes Prosobranches."  
*Ann. Sci. nat. Zool.* (7) VIII, pp. 61-311, 13 pls. Paris.
- Siebold, C. T. Von., 1836. Fernere Beobachtungen über die Spermatozoen der wirbellosen Thiere."  
*Müller's Archiv. für Anat. Physiol.*, pp. 232-255, 1 pl. Berlin.
- Simroth, H., 1881 'Das Fussnervensystem der *Paludina vivipara*.'  
*Zeitschrift für wissenschaft. Zool.* XXXV, pp. 141-149. Leipzig.

- Simroth, H., 1896— “Mollusca: Gastropoda Prosobranchia.”  
1907. Bronns Thier-Reich. Part 2, Vol. III,  
Leipzig.
- Smith, E. A., 1881 . ‘Remarks upon Mr. Wood-Mason’s paper  
“On the Discrimination of the sexes in the  
genus *Paludina*.”  
*Ann. Mag. Nat. Hist.* (5) VIII, pp. 220-221.  
London.
- Speyer, O., 1855 .. “Zootomie der *Paludina vivipara*.” Cassel.  
(I have been unable to refer to this  
work.)
- Villepoix, M. de, 1895 “De la formation de la coquille dans les  
mollusques.”  
*Compt. Rend.* CXX, pp. 512-513. Paris.
- Wolff, G., 1887 . “Einiges über die Niere einheimischer  
Prosobranchiaten.”  
*Zool. Anzeiger* X, p. 317. Leipzig.