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ANATOMY OF THE COMMON INDIAN APPLE-SNAIL, *PILA GLOBOSA*.

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(Plates XVI—XVIII.)

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INTRODUCTION.

Our knowledge of the anatomy of Indian freshwater Gastropods is very meagre and except for the two recent memoirs[1] published in the "Records of the Indian Museum" practically no information is available regarding the large number of Indian forms. A memoir on the common Indian apple-snail has been long a desideratum as *Pila globosa* (Swainson) is used as a type for dissection by various universities and the only available account by Lloyd (53)[2] is far from satisfactory. Other papers on the subject only contain stray notes on various systems and are scattered in different journals in various languages. The present memoir contains a fairly complete account of the common Indian *P. globosa* and is a continuation of the various memoirs referred to already and published in the "Records of the Indian Museum."

I have to acknowledge my great indebtedness to my late chief and friend Dr. N. Annandale for the facilities he gave me for preparing this memoir and for the great interest shown by him during the progress of the work. Most of the illustrations were prepared under my supervision by the talented artists of the Zoological Survey of India, and I have to record my great appreciation of their help.

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[1] Sewell, *Rec. Ind. Mus.* XXII, pp. 217-242 (1921) and Rao, *Rec. Ind. Mus.* XXV, pp. 199-219 (1923).

[2] The Arabic numerals in brackets refer to literature cited at the end of this paper.

CLASSIFICATION.

Ampullariidae are streptoneurous gastropods and owing to their having a single auricle are placed in the order Monotocardia (=Pectinibranchia). They are assigned to the suborder Taenioglossa owing to the possession of a taenioglossid radula consisting of three teeth, one lateral and two marginals, on either side of the median tooth. Their general anatomy is also typical of the suborder. The possession of a well developed pulmonary chamber or lung in addition to the monopectinate gill is only an adaptation to peculiar conditions under which these animals live (*vide postea* p. 121), and is not of any special systematic value. Ampullariidae are usually placed next to the families Viviparidae, Littorinidae, Valvatidae, etc., but are not closely allied to any of them.

GENERAL DESCRIPTION.

Pila globosa (Swainson) with which this memoir deals is, as has been described in the systematic account of the Indian species of the family,[1] the common species in the Indo-Gangetic plain and is found in tanks, ponds, lakes, streams and rice-fields. It is particularly common in areas in which there is a large quantity of succulent aquatic vegetation. The shell and operculum have been described in the paper cited above, while figures (Pl. XVI, figs. 4, 4*a*) of the operculum are now published.

The eggs of this species are laid on moist ground on the banks of ponds or lakes or in paddy-fields. They are laid in clusters, 5-6 layers thick (Pl. XVI, fig. 3), and usually consist of two to three hundred eggs tightly adhering together. The eggs are spherical, about 4—4·5 mm. in diameter with a white calcareous covering. In Bengal eggs are usually laid in May and June at the beginning of the rainy season. The young ones come out after about a month. The young shell consists of $2\frac{1}{2}$-3 whorls (Pl. XVI, figs. 5, 5*a*) and measures 3·5 mm. × 3 mm. All the eggs appear to be fertile and there is no covering of sterile eggs as has been mentioned by Annandale in the case of the Siamese species *P. turbinis*.[2]

ANIMAL.

The body of the apple-snail (Pl. XVI, figs. 1 and 6), like that of most other Gastropoda, is divisible into three parts, head, foot and visceral mass. A large part of the animal (Pl. XVI, fig. 1) can be extended out of the shell, but the visceral mass always remains hidden. When, however, the snail is disturbed, the entire animal is withdrawn within the shell, and the mouth tightly closed by the calcareous operculum. The skin of the visceral mass is produced to form the characteristic molluscan structure, the pallium or the mantle (Mt.). This structure, besides forming a regular cloak round the anterior part of the animal, encloses the head and several other organs in a state of retraction; these structures are described further on. The edge of the mantle, which secrets the shell, is thickened, and in the extended animal is prolonged to the edge of the shell-mouth, where it is seen as a light greyish skin lining the orange coloured shell-mouth on the inside.

The head is prolonged into a partly contractile snout, which is prolonged on its two sides into two labial palps or anterior tentacles (Tl). These are merely prolongations of the antero-lateral edges on the sides of the vertical mouth (M.), and are, like the snout, con-

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[1] Prashad, *Mem. Ind. Mus.* VIII, pp. 70-73, pls. xiii, figs. 1-7 (1925).

[2] Annandale, *Journ. Nat. Hist. Soc. Siam*, IV, p. 2 (1920).

tractile. About a quarter of an inch behind them are the true tentacles (T2), which, when fully extended, measure about two inches in length, but are reduced to about a quarter of their length when contracted. When fully extended they are filamentous structures, much thicker at the base, but gradually tapering to a fine thread at the tip. The eyes (E.) are situated on small stalks arising on the outer sides of the bases of the tentacles. Projecting anteriorly over the foot and on the two sides of the head are two transverse, fleshy lobes—the nuchal lobes or the pseud-epipodia (R.P.E., L.P.E.), connecting the head with the mantle on the two sides. The left lobe is better developed and forms the large respiratory siphon, but both of them, as will be referred to further on, play an important part in the respiration of the animal. These flaps, as is proved by their nerve supply from the pleural ganglia, are prolongations of the mantle, and have not originated either from the head or the foot. They are, therefore, not homologous with the epipodia of other Gastropods which, according to Thiele (78), are innervated by branches from the central ganglia, and are, therefore, to be considered as being developed from the *anlagen* of the head. Sewell (72) is wrong in designating similar structures in *Vivipara bengalensis* as epipodia ; for in *Vivipara* also the flaps are prolongations of the mantle and have not developed from the foot.

The foot (F.), which forms the main part of the extruded animal, is roughly triangular in outline, with the apex of the triangle directed backwards, the sides somewhat arched and the angles broadly rounded. In living animals it is constantly changing its outline and is very extensile. It is much thicker anteriorly, the side on which the snout is situated, but is thinner posteriorly, where on its dorsal surface (Fig. 1, pl. XVI) it bears the operculum. The ventral surface or the sole of the foot is quite smooth, and does not show any grooves. In the fully extended animal the shell lies on the operculum, and in the creeping movements is often seen to rotate on it. The sole is of a greyish colour, being much darker along the margins. Dorsally it is light chocolate interspersed with greyish lines and orange spots ; the posterior operculiferous lobe is dark grey mottled with orange spots.

The visceral mass (M.V.) of the animal, which consists of all the main organs of the animal, is not to be seen without the removal of the shell. It occupies all the inner and the greater part of the main or the body-whorl of the shell. It is, like the shell, spirally coiled, and varies from greyish to dark brownish in colour according to the colour of the digestive gland. It is described at length in the accounts of the various organs composing it.

The columellar muscle arises from the columella in a somewhat spiral fashion, and is in *P. globosa*, as shown in fig. 7, pl. XVI, not entirely attached to the columella, but along its upper part is attached to the inner side of the penultimate whorl of the shell. In a dissected specimen the columellar muscle is seen as a broad band, rather narrowed down at its lower extremity. On the removal of the skin-covering the fibres of this muscle, as shown in text-fig. 1, are seen to run longitudinally through the upper part of the foot to the operculiferous lobe on the postero-dorsal surface. Here they form a rather ovoidal patch, which is attached to the boss of the operculum.

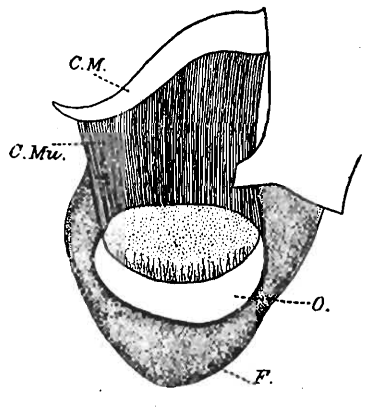

FIG. 1.—Drawing illustrating the columellar muscle and the course of the columellar muscle-fibres of *P. globosa*.
C.M. the region of attachment of columellar muscle to the shell axis ; *C.Mu.* columellar muscle fibres ; *F.* foot ; *O.* operculum.

THE MANTLE AND THE MANTLE CAVITY.

The mantle (Mt.), as has been noted already (Pl. XVI, fig. 8), forms a regular cloak round the anterior part of the animal, and encloses on the dorsal side a cavity in which the structures collectively termed as the " Organs of the pallial complex " are enclosed. Some of these organs like the gill, the pulmonary sac, the osphradium, the nuchal lobes, the hypobranchial gland and the penis or the rudimentary copulatory organ of the female together with its pouch are developed from the wall of the mantle itself, while others like the rectum, the terminal parts of the male and female ducts, a part of the anterior chamber of the renal organ and its external opening and the head with its appendages are simply enclosed in the cavity.

The mantle itself is thick and muscular, particularly along its free edge. This edge is slightly recurved outwards, and is pigmented along the edge and a little behind it. As in other Prosobranchs the mantle-fold is best developed above the foot anteriorly to the visceral mass, and largely on the left side of its main whorl. Ventro-laterally the edges of the mantle are continued to about a quarter of an inch of the attachment of the operculum, where along the greater part of its extent it is firmly united to the foot, but the edge projects as a free fringe, a couple of millimetres broad.

The mantle cavity, referred to above, is bounded above and along the greater part of the sides by the mantle, and the floor is formed by the body-wall above the foot. It is a very extensive cavity, and plays a very important part in the life of the animal. If the mantle be cut open by a longitudinal slit along the left of the gill and the two flaps turned outwards, the whole of the mantle cavity is exposed and the organs of the pallial complex and the cavity can be examined. Ventrally the cavity is seen to be divided into a small right and a large left portion by a well developed, vertically upstanding and prominent ridge (Ep.) of the body-wall. This ridge is called " bourrelet dorsal " by Bouvier (11), but in this paper I use von Jhering's (40) name " epitaenia " for it. At its origin near the beginning of the gill posteriorly the ridge is rather low, but gradually becomes higher anteriorly. It is at its anterior end in continuation of the left margin of the right nuchal lobe. The epitaenia is a very important structure and, as is explained in the account of the respiratory processes of the apple-snail (pp. 119-121), it plays a very important part in both aquatic and aerial respiration.

The pseud-epipodia or the nuchal lobes have already been mentioned, but a few further notes may here be added as to their macroscopic structure. The right lobe (R.P.E.), which is so well developed in *Vivipara* and according to Sewell's account forms the respiratory siphon (72), is in the case of *P. globosa* and other members of the genus a rudimentary structure. As noted above its left edge is in continuation of the epitaenia, and the outer or right edge forms the outer extension of the mantle cavity up to the mantle itself. The channel formed by this lobe is rather a shallow drain-like structure formed by the limiting off of the lobe. The left nuchal lobe (L.P.E.) compared to that of *Vivipara* is very highly developed, and forms the large left siphon, either as an elongate tube or as a broad funnel-shaped structure. Their functions are discussed further under respiration.

The organs of the pallial complex, which have already been mentioned, will now be described.

The *osphradium* (Os.) of the Ampullariidae (Pl. XVI, fig. 10), like that of *Vivipara*, is situated on the left side of the mantle cavity (Pl. XVI, fig. 8), but is neither ridge-like nor in close proximity of the gill. Further it is not a simple ridge, but a complex structure. In *P. globosa* it is about a quarter of an inch in length, arising from the mantle a little behind the margin and directly in line with the middle of the left pseud-epipodium. In shape it is elongated oval, rather broad in the middle, somewhat pointed along the left margin and rounded on the right inner side. It is bipectinate and consists of 22-28 rather stout, fleshy leaflets arranged along the two sides of a broad axis. The leaflets are broadest in the centre and narrow down on the two sides; each leaflet being roughly triangular. These leaflets are attached to the wall of the mantle along their bases, and to the middle axis along their inner side, while the third longest side is free. In its normal position it hangs as a frill in the course of the respiratory water current as it flows in over the left nuchal lobe; this is dealt with at length under respiration. The histology of this organ as also its homology and function are dealt with in the account of the sense organs (p. 143).

The *pulmonary sac* (P.C.) or the lung is a large pouch-like structure hanging down from the roof of the mantle cavity, and occupying the greater part of the left or the pulmonary part of the cavity. It is developed from the mantle itself, and is, except for the ventral opening into the pallial cavity, entirely closed. The dorsal wall of the pulmonary sac is formed by the mantle and is densely pigmented. The opening of the sac (P.C.O.) is situated in line with the right marginal line of the osphradium, and extends along the longitudinal axis somewhat obliquely to very near the posterior limit of the mantle cavity. The two flaps on the two sides of the opening are not of the same size, and are so situated that the anterior left one projects over the posterior right. As a result of this arrangement and the different size of the flaps the left one entirely covers over the right at the time of the closing of the opening. The walls of the pulmonary sac are moderately thickened, and are richly supplied with blood vessels. Lloyd (53) wrongly describes the inner walls as spongy. They are highly vascular, as has been noted above, but nothing like a spongy structure is ever produced.

The pulmonary sac of the Ampullariidae appears to be a new structure or only a part of the second ctenidium, which in response to aerial respiration has been developed in close association with the gill and the osphradium as a specially modified structure. This is substantiated by the embryological studies of Brooke and McGlone (15) according to whom "In a young embryo soon after the mantle is formed, a ridge or thickening of the epithelium of its inner surface indicates the region where the gill-filaments, the osphradium and the lung are to arise. The osphradium is developed from one end of this ridge, the gill-filaments from the other, and between the two the ridges become infolded into the lung, which may be regarded as a modified and invaginated gill-filament." It may also be noted here that the pulmonary sac or the lung of the Ampullariidae is not in any way related to that of the Pulmonate molluscs, and is only an example of convergence, where similar organs are evolved by different animals independently under similar physiological conditions for similar purposes.

On examining a fresh piece of the pulmonary wall (Pl. XVII, fig. 1) under the microscope we find on focussing through the outer epithelial covering that the main matrix is a homogeneous layer with large numbers of connective tissue cells (C.T.C.), calcareous particles (C.G.), pigment granules (P.G.) and muscle-fibres (M.F.) scattered through it. In addition there are large numbers of lacunar blood spaces (B.S.) passing through its substance in all directions. This structure is confirmed on examination of the fixed and stained material as also of microtome sections.

In a section running transversely (Pl. XVII, figs. 2, 3) to the long axis we find that following from above downwards there is first the external epithelial layer, which is continuous with the general epithelial covering of the body. It consists in this region of low, cubical cells (E.) with a rounded nucleus, and large numbers of very fine black pigment granules. The granules are often so numerous as to make it impossible to distinguish the cell outlines between adjacent cells. Next to the epithelium is a fine basement membrane, which in most places can only be distinguished with difficulty from the connective tissue. The connective tissue (C.T.C.), which fills up the greater part of the sections, consists of a homogeneous stratum with large numbers of Leydig's cells or what had better be called by Brock's older name "Blasenzellen," the star-shaped cells and a few calcareous granules lying in groups. A little below the epithelium is a layer of longitudinal muscle-fibres (M.F.) arranged in irregular bundles. Next to this layer, but quite separate from it, is the layer of the transverse muscles. A few vertical muscle fibres are also to be seen running slightly obliquely from above downwards. In the connective tissue there are a large number of blood spaces of all sizes running in different directions. The lower and inner surface is lined by a layer of endothelium in which the cell outlines are difficult to distinguish. It has the same basement membrane, connective tissue and its inclusions lying above it as is the case if the structures are followed from above downwards.

The only difference between the upper and the lower pulmonary walls is in the much thicker nature of the upper or the mantle wall, the absence of pigment in the lower wall of the pulmonary sac, the comparatively smaller number of blood-spaces and the much larger number of muscle fibres.

The *ctenidium* (B.) or the branchia is not visible through the thickness of the mantle. It lies in the right or the gill chamber of the pallial cavity, and hangs vertically down from its dorso-lateral edge. Corresponding to the osphradium on the left, with which, however, it is not homologous, the gill starts a little in front of the anterior limit ot that organ, and extends to the pericardium posteriorly. As was pointed out by Bouvier (11) and by Sabatier (66) before him, the right gill of *Ampullaria* appears from its blood and nerve supply to be the left gill which has been shoved to the right side by the very extensive pulmonary chamber.

It is composed of a large number of thin, triangular leaflets (Pl. XVI, fig. 9), which are attached along the base or the ctenidial axis and have the slightly rounded apex free. The free sides of the triangular leaflets are unequal in size. In its natural situation with the apex hanging downwards the right or the afferent side is shorter while the left or the efferent side is much the longer of the two. On both the anterior and the posterior sides of the flat plate-like lamellae there are a varying number of transverse ridges of the nature of pleats; these ridges gradually decrease in size from the base towards the apex. These ridges were, without any remark as to their significance, figured by Jhering (40) in the gill lamellae of *Ampullaria canaliculata*, and the efferent axis of the lamellae was given the name "Limbus."

Haller (35) later described in detail the structure of the gills of *Natica*, and called these ridges the " Querfalten " or transverse folds. As will be seen from the histological account of the gills further on I am not able to confirm his account in all details from the structure of the gills of *Pila*. No such ridges or folds have been described or figured by Dakin (24) in the case of *Buccinum*, and, as will be seen from the account of the attachment of the lamellae given above, I differ in the use of the term ctenidial axis from that in which Dakin uses it in the case of *Buccinum*. The leaflets are largest in the middle, and gradually decrease in size along the two ends of the gill. The ctenidium is of the typical monopectinate type, the leaflets being attached in a single row along the ctenidial axis.

The histological structure of the gills of Gastropods has not received the attention it deserves, and it is not possible, therefore, to give a comparative account. In *P. globosa* transverse sections of the leaflets show that each of them is formed of a double layer of epithelium supported on a thin lining of connective tissue and muscle-fibres, and enclosing a flattened cavity. The epithelial layer, which bounds the lamellae on the two sides, differs in various regions of the lamellae, and consists of three kinds of cells :—(i) non-ciliated columnar cells (E.), (ii) ciliated columnar epithelium (C.E.) and (iii) a few gland cells. The arrangement of the various kinds of cells is best seen in sections of the leaflets passing parallel to a line connecting the middle of the ctenidial axis with the apex of the leaflet. The external epithelium, which is similar over most of the surface except in the regions of the transverse furrows and in the ciliated areas (Pl. XVII, fig. 5), is of the first type noted above. It consists of non-ciliated columnar cells of slightly varying heights ; the outer surface of the sections in these regions is, therefore, irregular. The cells have rounded nuclei lying at different levels in the adjacent cells near the middle of the cells, and containing one large and a number of small chromatin granules. The protoplasm of the cells is homogeneous, more or less hyaline, and stains moderately with eosin or Orang G. In between these cells are a number of flask-shaped unicellular gland cells of the type described for various molluscs as " Becherzellen " by German authors. The ciliated epithelium is restricted chiefly along a line parallel to the longer side or the efferent axis of the lamellae on both surfaces, in addition the cells over the greater part of the transverse furrows are also ciliated. The ciliated epithelium (Pl. XVII, fig. 6) consists of regularly arranged columnar epithelial cells, which are about 1½ times higher than the non-ciliated cells. The nuclei of these cells are comparatively much larger, somewhat oval and rich in chromatin granules. The cilia are rather short, but densely line the surface of the cells. Lying next to the epithelium is a basal membrane, which is very thin and, in places, quite indistinguishable from the connective tissue next to it. Near the apex of the lamella it is thicker, but nowhere so thick as has been described by Dakin (*loc. cit.*) in the case of *Buccinum*. The connective tissue layer consists of an endothelial type of lining with a few nuclei scattered in the substance ; no cell-limits are to be distinguished in this layer. In this layer a number of obliquely running muscle fibres are also to be distinguished in places ; they are more numerous near the base. Just below the apex of the lamellae in sections one sees an elongate space (S.) intercrossed by ridges formed of connective tissue matrix and some muscle fibres. Apparently these muscle fibres by their contraction draw together the two surfaces of the lamellae thereby reducing the lacunar spaces and forcing the blood from the lacunae into the efferent vessel. I did not see any nerves in my preparations.

In dissected specimens (Pl. XVI, fig. 8), the rectum is seen to lie to the left of the ctenidium and between it and the genital duct. As seen in the opened up mantle cavity it is seen to run in a somewhat arched course from the point of its entrance into the cavity at its extreme posterior end to a little less than a quarter of an inch from the anterior edge in line with the middle of the right nuchal lobe. The opening of the anus, which is situated at its end, is surrounded by a large number of papillae, and not only by eight as is described by Lloyd (53).

The male and the female ducts, according to the sex of the individual, lie next to the rectum. These and the copulatory organs are described in detail in the account of the generative organs.

A small reddish, elliptical part of the anterior chamber of the renal organ projects into the right ctenidial part of the pallial cavity in its posterior end near the origin of the epitaenia, though the greater part of it lies in the visceral mass. It is in this part that the external opening of the renal organ is situated. The opening is an oblique transverse slit situated in a narrow depression in the posterior half of the renal chamber along its left side a little further than the origin of the epitaenia.

ALIMENTARY CANAL.

Blainville (7) in the earliest account of the anatomy of any species of the family Ampullariidae included a short description of the alimentary canal, and noted that the secretions of the liver were poured into the stomach through a single hepatic duct. Quoy and Gaimard (62) later described the alimentary canal of *Ampullaria celebensis* (=*P. ampullacea, forma typica*)[1]; but their account is very brief and inaccurate in many respects. Troschel (80), who followed, described the buccal mass and the radula of *A. urceus*, and included a short account of the general course of the alimentary canal. He did not say very much about the liver or the digestive gland, but noted that there were a large number of hepatic ducts, which opened both into the stomach and the intestine. Bouvier (11) gave the first detailed account of the system as a whole, and noted the presence of a caecum. He described two hepatic ducts opening into the stomach, and included a figure of the dissected stomach, showing the position of the folds and the openings of the ducts and the caecum. H. Fischer (28) did not himself investigate the liver of the Ampullariidae, but gave a good summary of the work of previous authors. In view of Semper's (70) observation regarding the development of the liver of *Ampullaria* from two distinct rudiments, he was of the opinion that Bouvier's observation as to the presence of two hepatic ducts from the two lobes of the liver appeared to be correct. Amaudrut (1) gave a fairly detailed description of the buccal mass, the salivary glands, the oesophageal pouches and the anterior part of the oesophagus, but, as will be demonstrated later, his description is rather difficult to follow, and is not accurate in all respects. Lloyd's account (53) of the alimentary canal of the Indian *P. globosa* is very superficial, and he repeats Troschel's mistake in describing several hepatic ducts opening into the stomach.

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[1] Prashad, *Rec. Ind. Mus.* XXII, p. 479 (1921).

The mouth (M.), as has been stated already, is situated at the end of the partly retractile snout ; it is an elongated, vertical, slit-like opening in the middle of the snout. The margins of the opening are surrounded by a sort of low frill, which is formed by the edges of the opening being plicate ; these form the secondary lips, there being no true lips. The two labial palps or anterior tentacles on the sides of the snout have already been described.

Buccal-mass and *Oesophagus* :—On opening the floor of the pallial cavity by a median slit starting between the anterior tentacles and prolonged backwards to the extreme posterior limit of the pallial cavity, and turning back the flaps, we find that there is a large, somewhat pyriform structure lying at the extreme anterior end and forming the first part of the alimentary canal. This is the buccal mass. Into it the mouth opens anteriorly and it is the apparatus for the mastication of food. It is described at length further on (p. 101). The oesophagus (Text-fig. 2, O.), which follows, starts from the dorsal posterior edge of the buccal mass, and, after a short course in the middle line, turns to the left and then enters the visceral mass, to open into the stomach. A short distance behind its point of origin the oesophagus is somewhat swollen and becomes barrel-shaped, but I cannot distinguish any area corresponding to Amaudrut's. " Jabot," nor can I agree with his interpretations and description of what he terms the two pairs of " bourrelets "—pads or cushions in the buccal mass. The oesophagus after entering the visceral mass passes on the right into the pericardium and after running along the anterior extremity of the digestive gland enters the stomach. The salivary glands and oesophageal pouches are described below (p. 109).

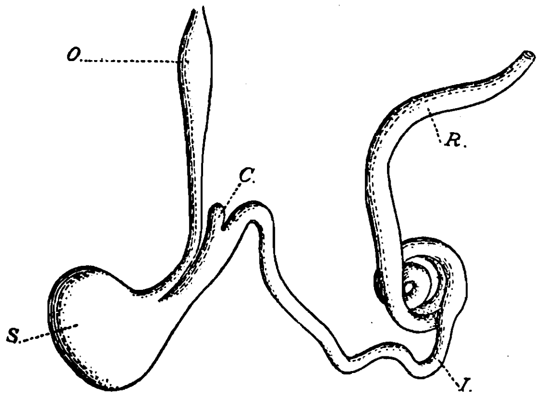

FIG. 2.—Outline diagram of the Alimentary Canal of *P. globosa* excluding the buccal mass.
C. Caecum ; *I.* Intestine ; *O.* Oesophagus ; *R.* Rectum ; *S.* Stomach.

Stomach :—The stomach (S.) begins on the left side just below the pericardium and runs backwards as a blind pouch on the postero-lateral sides of the main whorl of the visceral mass. Externally it is seen as a quadrate patch of a dark reddish colour. Its lower margin is nearly straight, while the posterior margin curves up to be continued over the edge to the inner or columellar axis and is embedded in the digestive gland. At this point it forms a rectangular wedge. Its anterior margin thus starts from the columellar axis on the inner side along the anterior side of the rectangular wedge and curves on the outer side to the pericardium, where the intestine starts to the outer side of and dorsally to the opening of the oesophagus.

The upper and outer wall of the stomach in a freshly dissected specimen is, as has been described above, of a deep red colour, but along the greater part of the outer surface this colour is disguised by a thick coat of muscular fibres on the outer surface of the stomach between the stomach-wall and the outer epithelial covering. On being opened from the outer side the stomach (Pl. XVII, fig. 7) is seen to have a broad **U**-shaped cavity, which in its greater part is of a rosy-red colour. The opening of the oesophagus on the lower side leads into the posterior chamber or the cardiac region of Bouvier, while the intestine begins anteriorly from the upper pyloric region. There is a somewhat arched transverse ridge (R.) arising from the lower wall and running between the two limbs of the U from the right to the left. The ridge is thicker in its outer or left half, and gradually narrows to the right. In front of the ridge and on the right upper side lies a semilunar pit (D.G.O.) with alternate ridges and grooves radiating from the opening of the duct of the digestive gland. There is in it the single opening for the two ducts of the digestive gland, which unite just before entering the stomach-wall. The opening is semilunar, and, owing to its ventro-lateral position and the arrangement of the radiating ridges and grooves, the secretion is very efficiently distributed. The posterior chamber (P.C.) forms the main part of the stomach and has its entire wall lined by longitudinal folds running close together from one side to the other and which make it look like a corrugated surface. In the preserved specimens these folds can also be seen on the outer wall after the skin and the muscular coat are removed. The anterior chamber of the stomach (A.C.) consists of the second or right limb of the U and is somewhat tubular. It differs from the posterior chamber in being somewhat yellowish. Its wall is thrown into transverse folds, while a vertical fold arising from its dorso-lateral wall projects down to the opening of the duct of the digestive gland as a lappet. The opening of the caecum (C.O.) is on the outer lower side a little behind the origin of the intestine.

The question ot the caecum is of some importance. It was described trom dissections only by Bouvier (11), but no mention was made of the crystalline style. Robson,[1] from the situation of the caecum as described by Bouvier, was of opinion that it probably had the function of forming the crystalline style in the Ampullariidae. In *P. globosa* the caecum (Text-fig. 2, C) is a pyloric structure arising from the outer, lower wall of the pyloric chamber of the stomach as a small, bluntly rounded pouch. Its opening into the stomach is much lower down as the greater part of it is enclosed in the stomach wall, but there is no internal communication of the type described by Robson[2] for *Paludestrina.* In large numbers of dissections I have failed to find any crystalline style in the caecum and I consider it to be simply a blind diverticulum of the stomach.

Intestine and *Rectum* :—After leaving the stomach the intestine (I.) runs up along its anterior edge and further along the digestive gland below the posterior chamber of the kidney, and then turns backwards and upwards in the visceral mass. It then forms $2\frac{1}{2}$-3 coils between the uterus ot the female or the vesicula seminalis of the male in front and the digestive gland behind. Then, turning upwards, it runs forwards along the anterior edge of the posterior renal chamber to enter into the pallial cavity, whence the rectum starts. The rectum (R.) has already been described in the account of the pallial cavity (p. 98).

Digestive Gland :—This structure has generally been called the liver by the English school. Indeed, Dakin (24) is really the only author of that school who has called it by the more appropriate name of " digestive gland." The French zoologists have similarly called it the " foie " or liver, while the German authors indiscriminately refer to it as " Leber "

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[1] Robson, *Proc. Malacol. Soc. London,* XV, p. 42 (1922).

[2] Robson, *Quart. Journ. Microsc. Sci.* LXVI, p. 164, fig. 3 (1922).

or " Mitteldarmdruse." The name liver is quite unsuitable, for the gland combines the functions of the various digestive glands of the Vertebrates and is in addition the chief organ for the absorption of the digested food. I have, therefore, adopted for it Dakin's term " digestive gland."

The digestive gland (Text-fig. 3) may be described as a somewhat triangular plate, or rather a cone with a very convex outer and a more or less flat inner surface. The cone is spirally coiled from the tip of the visceral mass downwards. Along the upper and partly on the inner edge of the first $2\frac{1}{2}$-3 whorls the genital gland is attached in the two sexes, while the stomach is embedded in the situation described already. In the embryo the digestive gland arises from two distinct rudiments (*vide* Semper 70), but in the adult the two areas are fully fused, and their line of demarcation is only to be distinguished by the position of the stomach, which is wedged in between them, and by the separate ducts of the two areas from in front of and behind the stomach. I cannot agree with Lloyd (53), who describes the liver of *P. globosa* as consisting of two distinct lobes with a large number of ducts opening into the stomach. The gland is of a brownish green to dirty green colour, and is, when fresh, quite soft after the removal of the skin covering. It is made up of fine tubules bound together by connective tissue. The tubules unite with one another, forming secondary tubules, which come to the surface on the columellar side and unite into two ducts, an anterior (D.D.1) and a posterior duct (D.D.2), arising respectively from the anterior and the posterior areas of the digestive gland. The two tubes later unite with one another just before opening into the stomach in the anterior lower angle of the rectangular wedge on the columellar face.

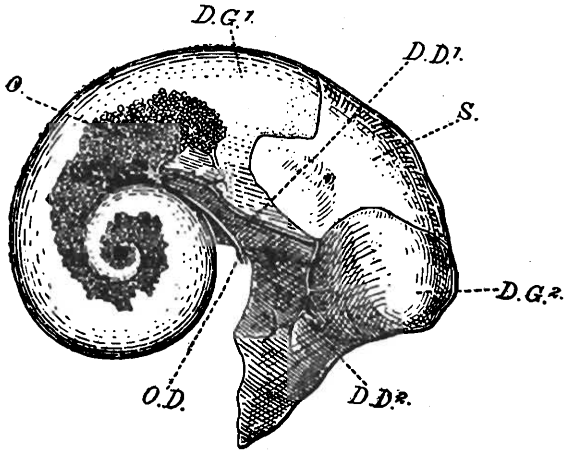

Fig. 3.—Inner view of the digestive gland and associated structures.
D.D.1. and *D.D.2.* Ducts of the anterior and posterior areas of the digestive gland ; *D.G.1.* and *D.G.2.* Anterior and posterior areas of the digestive gland ; *O.* Ovary ; *O.D.* Oviduct ; *S.* Stomach.

Buccal Mass :—This very complicated part of the alimentary canal of the Ampullariidae has been neglected by most authors. Bouvier (11) gives only a very imperfect and inaccurate account, and the only other author to deal with it is Amaudrut (1). This latter account, which is included in the author's famous monograph on the anterior part of the alimentary canal of the Gastropods, is unfortunately very confused and incomplete in the case of *Ampullaria.* My own results differ from both accounts as to the number and relationships of the cartilages of the buccal mass, the arrangement and number of the muscles and the structure of the buccal cavity and its glandular areas.

Starting first with the so-called " cartilages," we find three pairs of them mentioned in Amaudrut's account. These are (i) the " cartilage lateral supérieur " (labelled *ls* in his fig. 36), (ii) " cartilage lateral inférieur " and " cartilage antérieur " united into a single cartilage on each side (*li* and *a* in his fig. 38), and (iii) the structure he labels *p* in figure 37 and considers to be " un nouveau cartilage," but which is apparently no more than a part of the united inferior lateral and anterior cartilages. In *P. globosa* I have found only two pairs of cartilages. These, from their homologies and position, I term the superior and lateral cartilages.

The superior cartilages are somewhat triangular in outline, with their upper surfaces greatly arched and projecting directly into the buccal cavity except for a thin layer of epithelium over their surface. In a transverse section of the buccal cavity they appear as arched wings on the two sides of the radula, connected with each other along their ventral internal edges by the " elastic membrane " of Amaudrut, which runs ventrad of and closely attached to the radula and is a continuation of the ventral membrane of the radular sac. These cartilages are very thin.

The lateral cartilages of *P. globosa* appear from their homologies with a form like *Patella* to be the result of the fusion of all the other three pairs, probably brought about by the great condensation of the muscles of the odontophoral mass and the very short, but broad radula. In the Indian species the cartilage is not like an inverted **V**, as is figured by Amaudrut in his figure 38 of the transverse section of the buccal mass of *A. insularum*, but appears somewhat **S** shaped. The plates are really somewhat obliquely situated, vertical cartilages in the odontophoral mass, one on each side, and have a greatly thickened lower edge. Their dorsal anterior part is quite thin and makes an angle with the lower posterior half, owing to the upper part being curved inwards and partly lying over that of the opposite side. Along its lower half the cartilage is greatly hollowed on both the inner and outer sides for the attachment of the muscles. Externally they are seen as whitish ridges on the ventrolateral sides between the muscles, the bulk of the plates being embedded in the odontophoral mass. Owing to all the muscles of the odontophore being attached to these plates either directly or indirectly, they form the centre of all the movements of the radular apparatus.

In connection with the very complex movements of the buccal mass and its constituents the muscular system is very highly organized, but the action of the various muscles is hard to interpret. I propose dealing with them under the following heads :—

I. The protractor series of muscles of the buccal mass.
II. The sphincter muscles of the buccal mass, and the superficial coats of longitudinal and transverse muscles.
III. Muscles of cartilages.
IV. Muscles connecting the cartilages and the elastic membrane.
V. Depressor and retractor muscles of the elastic membrane and the radula.

I. The protractor muscles are best developed as they are required for the protrusion of the buccal mass, while the retractors are very poorly represented. Indeed, the only two muscles, which can be assigned to this series in *P. globosa*, have probably a depressor function as well. This is easily understood when one remembers that the retraction of the mass is probably brought about partly by the protractor muscles themselves, after the contraction of the muscles is over and the muscles resume their normal state while the attached blood vessels, the nerves and the oesophagus pull it backwards. Of the protractor series, the muscles on the dorsal surface(Text-fig. 4) consist of (i) a median dorsal (M.D.) which arises in front of the middle of the buccal mass, and running forwards as a broad band is attached to the skin anteriorly, (ii) three pairs of dorso-laterals (L.D. 1-3), which arise further forwards than the median dorsal and are similarly attached to the skin. Of these the outermost muscle, as shown in text-fig. 4, is situated very much on the lateral side, and (iii) two pairs of posterior dorso-laterals (D.L.1 and D.L.2), which arise a little in front of the buccal ganglion of each side from broad fan-like bases, and after running up to the anterior edge become attached to the skin, the outer pair being attached more medially. This pair may probably have a rotatory function in addition to that of protraction. The muscles of the ventral face consist of :—(i) three anterior muscles (Text-fig. 5 ; M.V.), a median and two laterals. All the three muscles are rather short and originate shortly behind the anterior edge of the snout ; and (ii) a pair of long and strong muscles (M″.P″.), one on each side. Each originates from the ventral inner edge of the lateral cartilage as a broad band, and curves downwards and forwards on the sides of the radular sac and is continued to the anterior end to be attached to the ventral body-wall. Before attachment, however, it divides into two, and the points of attachment of the two branches are internal to the insertions of the posterior dorso-laterals. The action of these muscles is very hard to interpret ; it is partly of the nature of depressors, but they are probably of use in the protrusion forwards of the lateral cartilages, or they may help in the protrusion of the mass as a whole. These are the muscles labelled *m″p″* in Amaudrut's figure and in text-fig. 5.

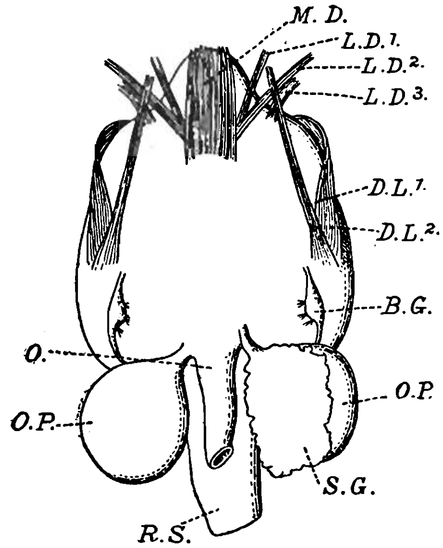

FIG. 4.—Outline drawing of the buccal mass as seen from above ; the salivary gland on the left side has been removed to show the oesophageal pouch, while the radular sac is shown drawn backwards under the Oesophagus.
B.G. Buccal ganglion ; *D.L.1.*, and *D.L.2.* Posterior dorso-lateral Muscles 1 and 2 ; *L.D.1. L.D.2.* and *L.D.3.* Anterior dorsolateral muscles 1-3 ; *M.D.* Median dorsal muscles ; *O.* Oesophagus ; *O.P.* Oesophageal pouch ; *R.S.* Radular sheath ; *S.G.* Salivary gland.

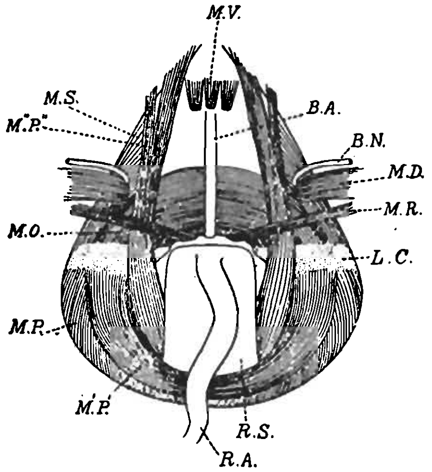

FIG. 5.—Ventral view of the buccal mass to show the musculature.
B.A. Aortic branch supplying the mass ; its lateral branches are not shown ; *B.N.* Buccal nerve branch of the cerebral ganglion ; *L.C.* Lateral cartilage ; *M.D.* Depressor muscle of the elastic membrane ; *M.O.*, *M.P.*, *M′P′*. *M″ P″*. The Superficial muscles of the ventral surface of the buccal mass ; *M.R.* Retractor muscle of the radula ; *M.S.* Sphincter muscle ; *M.V.* Ventral protractor muscles ; *R.A.* Artery of the radular sheath ; *R.S.* Radular sheath.

II. The sphincter muscle (M.S.) is a fairly broad coat of circular muscles, running round the anterior third of the buccal mass. Ventrally it is covered by a thin layer of longitudinal muscles, but dorsally it is quite free. The two jaws lie embedded in the substance of the muscle on the dorso-lateral sides internally in the buccal cavity, being separated from the muscle by a layer of epithelium only. The other muscles of this series are the thin longitudinal muscle fibres covering the buccal mass ventrally in front of and behind the cartilage, as shown in text-fig. 5, and a transverse band of superficial muscles running on the posterior surface of the mass transversely over and behind the radular sac. These muscles correspond to the muscles marked *m o*, *m p*, *m′ p′*

and *m″p″* in Amadraudt's fig. 54 on pl. VII of the buccal mass of *Ampullaria insularum*.

III. The muscles of the cartilages can be best described beginning from the ventral surface of the buccal mass. The first muscle band, corresponding to *mlii* of Amaudrut,[1] is broad and thick; it begins posteriorly on the anterior ventral edge of the lateral cartilage, and runs forwards and inwards to be attached to the lateral cartilage of the opposite side. It may thus be described as a somewhat obliquely running transverse muscle lying under the superficial longitudinal muscle fibres, and connecting the lateral cartilages of the two sides. On removal of this muscle, we find a second similar but less broad and more forwardly placed, deep seated transverse muscle, which also runs from the lateral cartilage of one side to that of the other; it corresponds to *mlis* of Amaudrut.

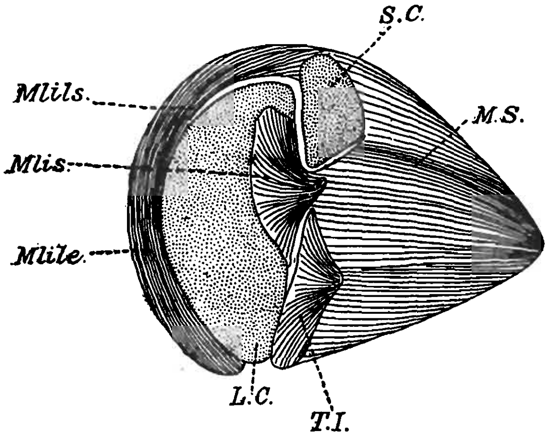

Fig. 6.

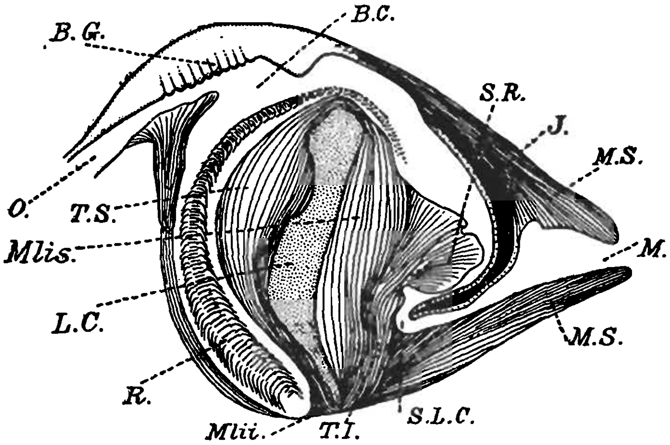

Fig. 7.

Fig. 6.—Vertical longitudinal section of the buccal mass to the left of the middle line.

Fig. 7.—Vertical longitudinal section of the buccal mass about the middle.

B.C. Buccal cavity; *B.G.* Buccal gland on the roof of the buccal cavity; *J.* Jaws; *L.C.* Lateral cartilage; *M.* Mouth opening; *Mlii, Mlis.* Transverse muscles connecting the lateral cartilages anteriorly; *Mlile., Mlils.* Dorso-posterior transverse muscle bands connecting respectively the superior and lateral cartilages and the elastic membranes of the two sides; *M.S.* Sphincter muscle; *O.* Oesophagus; *R.* Radula; *S.C.* Superior Cartilage; *S.L.C.* Sublingual cavity; *S.R.* Subradular organ; *T.I.* Tensor inferior muscle; *T.S.* Tensor superior muscle.

Posteriorly on each side thick bands of muscle fibres arise on the dorsal posterior surface of the bulb and run transversely under the superficial muscles. There are two muscles in this series one connecting the superior and lateral cartilages of the two sides and the other the elastic membrane (Text-figs. 8 and 9). These bands of muscle fibres correspond to *mlils* and *mlile* of Amaudrut. Another rather weak muscle of this series is a vertical muscle on each side, arising from the inner edge of the superior cartilage, and running up to the lateral cartilage of the same side to be attached to its upper, inner edge; it corresponds to *malss* of Amaudrut.

IV. The two pairs of tensors of the elastic membrane are the only muscles of this series. The more strongly developed of these, corresponding to *tsm*—the tensor superior of Amaudrut—arises from the internal surface of the lateral cartilage of each side, and runs upwards

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[1] For the sake of uniformity these muscles are labelled identically in text-figs. 4-8.

and forwards to be attached to the elastic membrane on each side. The second muscle, corresponding to *ti*—the tensor inferior of Amaudrut—arises further back on the posterior edge of the lateral cartilage, and runs between the muscles *mlii* and *mlis* to be attached to the elastic membrane just behind the subradular organ.

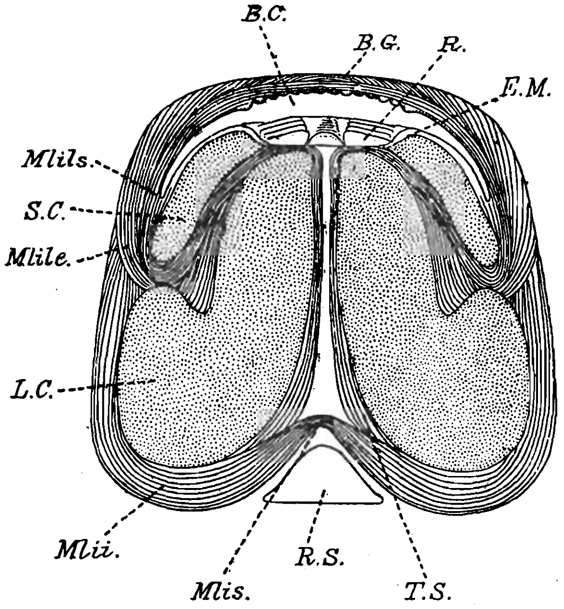

Fig. 8.

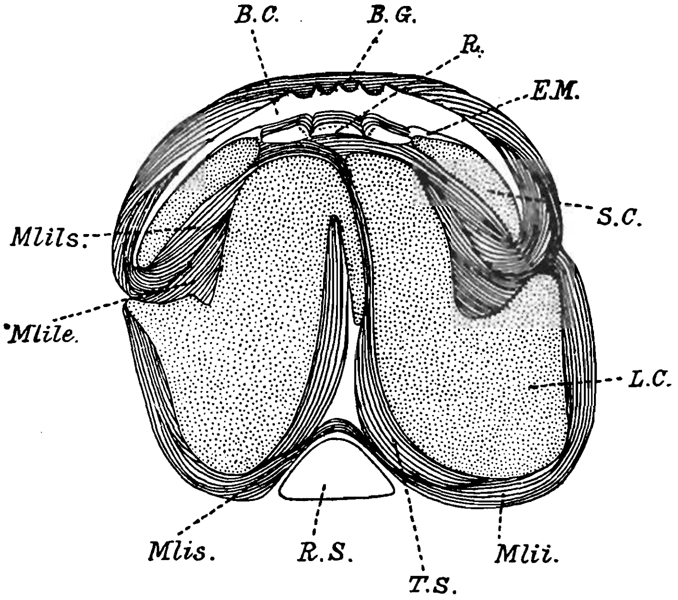

Fig. 9.

Fig. 8.—Transverse section of buccal mass to show the position of the cartilages and the attachments of various muscles.

Fig. 9.—Transverse section of buccal mass in front of one reproduced as text-fig. 7.

B.C. Buccal cavity; *B.G.* Buccal gland; *E.M.* Elastic membrane; *L.C.* Lateral cartilage; *Mlii, Mlis.* Transverse muscles connecting the lateral cartilages; *Mlile.* and *Mlils.* Dorso-posterior transverse muscles connecting respectively the superior and lateral cartilages and the elastic membrane on the two sides; *R.* Radular teeth; *R.S.* Radular sac; *S.C.* Superior cartilage; *T.S.* Tensor superior muscle.

V. There are two pairs of muscles of this series (i) the depressors, and (ii) the retractors of the elastic membrane and the radular sheath. The depressors (M.D.) are darkish, vertical muscle bands piercing out of the *mlii* muscles with the V nerve branch (B.N.) supplying the buccal mass from the cerebral ganglion. These muscles are attached ventrally to the floor of the body-wall, and above to the elastic membrane on its ventral surface. The retractors (M.R.) are thick strand-shaped muscles which come out of the bulb one on either side of the middle line in front of the radular sac. Ventrally they are attached to the body-wall and above to the elastic membrane near the posterior edge of the superior cartilage of each side. They retract the radula by their contraction.

Buccal Cavity :—The cavity of the buccal mass may be divided into two parts, the areas in front of and behind the jaws; the first of these is labelled 'vestibule' by Amaudrut.

The vestibule is very short, and has the mouth opening into it anteriorly. There are no definite lips, but the skin all round is thickened and plicate with the folds running longitudinally throughout the anterior part of the vestibule. Its posterior extent is marked off by the two jaws which lie dorso-laterally.

The remainder of the cavity is a rather complicated structure. Its greater part is taken up by the massive odontophore or tongue-mass. Anteriorly the cavity is somewhat tubular, but extends as two narrow chinks under the ventral margins of the jaws. It is then continued over the subradular organ, which is described further on, and then rises up over the odontophoral mass. Anteriorly, under the subradular organ (Text-fig. 7, S.R.), there is also a small pouch-like backwardly directed prolongation of the cavity; this may be termed the sublingual cavity (S.L.C.). The cavity of the mass then leads over the radula as a somewhat arched, but pressed tube in transverse section, till it widens out behind in the region where the oesophageal pouches open into the cavity at the junction of the buccal mass with the oesophagus. The roof of the cavity is not simple, but bears a longitudinally furrowed glandular area (Text-fig. 7, B.G.), a little over a quarter of an inch in length, on each side, from the openings of the oesophageal pouches onwards. This area was described by Amaudrut (1) as consisting on each side of the " bourrelets "—the " supérieur " and " inférieur " —with a depression in between (see his pl. viii, fig. 67). Simroth (75) copied this figure on plate xxxv, fig. 7, designating them as " Leitwulste " or directing pads. Amaudrut rightly considered them by comparison with *Cyclophorus* and *Lanistes* to be a part of the greatly reduced " Jabot " of other forms. Simroth based his description on the above, and gave a short summary. In *P. globosa* the condition of these buccal glands, as they may be termed, is as follows :—From the openings of the oesophageal pouches on each side to about a quarter to a third of an inch forwards is an elliptical pad, which is divided into two by an oblique, longitudinal furrow. The two constituent pads are further cut up by transverse furrows into grooved pads. The openings of the salivary ducts are one on either side, and situated in the pad of each side about the middle. A few further remarks about these dorsal pads may also be included here. Their structure, which corresponds to that of the " Jabot " of the French and " Drusenmagen " of the German authors, leads one to think that the disappearance of the " Jabot " in this family has led to the anterior part of it being absorbed in the buccal mass. It is not possible to be certain about their exact function, but their structure points to their being of the nature of accessory digestive glands.

The position of the subradular organ in the buccal cavity has already been noted. Amaudrut marks it *bo* in his figure, apparently considering it homologous with " bourrelets." Simroth in his copy of Amaudrut's figure labels it " Muskelpolster "—muscle pad— ; this is certainly a misnomer, as the pad is by no means a muscular structure. It is the same structure which has been described as the subradular organ in *Patella* by Wilcox (85). In *P. globosa* the structure when examined macroscopically (Pl. XVII, fig. 11) is a somewhat rounded area, divided into two by a median vertical furrow, and itself appearing mulberry-shaped owing to the entire surface being cut up by transverse furrows. It lies just in front of and below the anterior limit of the radula. Its microscopic structure is described further on.

There are two jaws, one on each side, situated dorso-laterally in the sphincter muscle region of the buccal cavity. The jaws of the two sides are connected together by a cuticular membrane, which is thin and structureless. Each of the jaws is somewhat quadrate in outline, with a regularly arched posterior margin, and somewhat incurved upper and lower margins. The anterior cutting edge is truncate, and shows in addition to the minute irregular serrations, two or three large, triangular, toothlike processes. At a distance of about a third from its anterior margin, it has a fairly thick ridge (Pl. XVI, fig. 15 M.A.), which helps in the attachment of the jaws to the sphincter muscle. The jaw is not equally thickened throughout, but according to the different degrees of chitinisation of the different parts it may be divided into two parts :—(*a*) the greater part of the anterior two thirds which is thick and dark brownish in colour and bears the cutting edge (C.E.), and (*b*) the posterior third (M.P.) which is much thinner and lighter in colour, and is apparently the region in which growth is taking place. Examined under the low power of a microscope the jaws show very fine, vertical lines. From their structure and connections the jaws appear to be simply local thickenings of the cuticular lining in these areas, being secreted by the low, cubicular epithelium, which lines the inner surface of the sphincter muscle. As has been noted already there are no definite muscles of the jaws, and the movements of the jaws are brought about by the sphincter muscle to the inner surface of which they are attached.

Radula :—The radula of *P. globosa*,[1] in general with that of the Taenioglossa, consists of seven teeth in each transverse row, two marginals and a lateral on each side of a central or rachidian. The formula is 2, 1, 1, 1, 2. In ten specimens, in which the number of transverse rows was counted, it varied from 38-42. The radula of *P. globosa* was described by Troschel in 1857 (81), and I will, therefore, only include a short account of it here. As a general point it may be noted that the teeth are all simple, and do not bear any secondary ridges or folds as in the Melaniidae, or basal teeth as in most of the Hydrobiidae. The central or the rachidian tooth is somewhat rectangular, with the posterior edge broader, and drawn out into points along the sides ; the anterior side is nearly straight and the lateral sides are slightly concave. The anterior free edge is formed by the reduplication of the anterior edge, and is roughly triangular, bearing a broad triangular median cusp, and two or three lateral cusps on each side. The lateral teeth are rhomboidal, with rounded margins and greatly broadened out along their toothed edge, being very much more so on the outer side. As a result the broadest central cusp comes to lie near the inner margin, and has only a single cusp internal to and two cusps external to it. Of the marginal teeth the outer is narrower than the inner, but otherwise the two teeth are similar. Each bears two cusps, a large broadly pointed main cusp and a much smaller second cusp on its inner side.

The radular sac, which has already been mentioned, is rather short, and appears like a broad band about 2 mm. in breadth. It projects ventrally out of the buccal mass in the mid-ventral line, and in the natural situation lies turned forwards with the artery from the cephalic aorta entering at its tip. The radula lies in this sac as a broad membraneous structure formed by the teeth lying embedded in the basal membrane. The dorsal wall of the radular sac terminates in the floor of the buccal cavity behind the superior cartilages. The ventral wall is continuous with the so-called elastic membrane under the radula, and connects the superior cartilages of the two sides.

Radular Action :—Cuvier (21) believed that in the action of the radula " the tongue-plate is essentially passive and that its movements depend upon the protraction, retraction, divergence and approximation of the cartilages ";[2] later (22) he developed this idea still further. Troschel (80) stated in the case of *Ampullaria urceus* " Sie ruht wie überall wo sie vorhanden ist, auf zwei neben einander gelegen durch Haut verbundenen und durch viele muskeln beweglichen Knorpelstücken von weise Farbe, welche gemeinschaftlich eine umgekehrte Rinne bilden," thereby implying that the radular movement is direct, and is brought about by the action of the muscles attached to the cartilages ; he did not add any-

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[1] For figure of radula of *P. globosa* also see Annandale and Prashad, *Rec. Ind. Mus.* XXII, p. 8, fig. 1A (1921).

[2] Quoted from Huxley, *Phil. Trans. Roy. Soc. London* CLXIII, p. 54 (1853).

thing about the action of the elastic membrane or of the jaws. Huxley (37) from a study of a large number of living and preserved forms was of opinion that " the action of the intrinsic muscular bands (having the insertions described) must be to cause the ' elastic plate ' and with it the ' dentigerous plate ' to traverse over the ends of the cartilages ; just like a band over its pully, the cartilages themselves being entirely passive in the matter. The extrinsic bands must serve to protract the whole mass and thurst it more or less firmly against the object to be acted upon." His observations on living Heteropods further led him to assert this " chain-saw movement " as being the only real movement. Troschel in his monumental work on the radulae (81) went into the question in greater detail, and came to the conclusion that the radula has no movement of its own, but that all its movements are dependent on the elastic membrane on which it rests. At the same time the cartilages with their strong muscles help in and control the movements of the radula. Geddes (31) reverted to Cuvier's view, which was similar to Troschel's later ideas, in that the radula itself was regarded as passive, its action being due to the up and down movements of the whole apparatus and particularly the cartilages. Oswald (57) was of opinion that both the movements played a part, and Dakin (24) agreed with him, adding, however, that the chain-saw movement described by Huxley was the more important. Amaudrut (1, pp. 131-177), who gave a very elaborate summary of previous work, was the first to include the action of the jaws with that of the radula, and divided the Gastropods for the radular mechanism into three groups, (*a*) molluscs with a single median jaw and with numerous little differentiated teeth, as in Pulmonates ; (*b*) forms with two stout lateral jaws, with numerous teeth, but the laterals very slender, as in Taenioglossa, Diotocardia and Monotocardia ; and (*c*) snails without or with very rudimentary lateral jaws, teeth very strong, but not numerous, as in carnivorous forms like *Buccinum*, etc. The second of these groups, to which *P. globosa* belongs, he considered to be constituted by primitive forms with powerful jaws and many long and slender lateral teeth. According to him it was difficult to conceive that the feebly developed radula of these forms played the principal part and that the well developed jaws were merely passive. On the other hand he considered the action of the jaws as being similar to that of a pair of scissors for cutting up the food into thin strips, which were then taken hold of by the radular teeth and carried back to the oesophageal opening. The movements of the radula are chiefly in the transverse plane, being brought about by the action of the muscles of the cartilages alternately deepening and flattening the radular gutter thereby drawing in and flattening the radula, this results in a change in the direction of the radular teeth, which now hook on and sweep back the food particles by the backward and forward movements of the radula ; the teeth conjointly acting as two brushes, one on each side.

Reverting now to my observations on the movements in *P. globosa*, it may be noted that my views are in entire agreement with those of Amaudrut. There is only a very limited amount of secondary " chain-saw movement " of the radula, and the chief movements are the result of the concerted action of the jaws and the radula through the elastic membrane and the cartilages brought about by the action of their muscles. The sphincter muscle and the protractor muscles of the bulb or the first and second series of muscles of the present account, by their alternate contraction and relaxation bring the jaws to the mouth opening, and here there is a regular cutting action, but not of the scissor-type described by Amaudrut. The leaves of the aquatic plants—the chief food of the apple-snail—are cut up by the movements of the jaws from above downwards and backwards. Meanwhile the contraction of the transverse and vertical muscles of the third series (*mlii, mlis, mlile, mlils* and *malss*) has drawn the lateral and superior cartilages outwards thereby flattening the elastic membrane and with it the radula. The two tensor muscles of the second series (*tsm* and *ti*) have also meanwhile pulled the radula forwards through the elastic membrane by their oblique action. The radula is thus flattened out, and the backwardly and inwardly directed cusps of its teeth come to point forwards and outwards. These taking hold of the cut up strips of food scoop back the same to the posterior part of the buccal cavity. This is brought about by the depressors and retractors of the fifth series and the retractors of the radular sac contracting, depressing and pulling back the radula. The united and alternate action of all the muscles through the elastic membrane and the cartilages brings about the slight alternate forward and backward movements of the radula, which are necessary for the food to be pushed back, while the jaws perform the main function of the cutting up of the food. The radula barely comes up to the mouth opening anteriorly and, as has been noted already, does not perform any rasping function.

Salivary Glands :—There are two salivary glands which lie one on each side of the posterior limit of the buccal mass, and often partially cover the oesophagus which issues dorsally from the buccal mass. The glands are triangular in outline, with the surface and the margins greatly cut up, resulting in a somewhat branched type of glands. The duct of each gland starts near its internal, anterior corner and immediately entering the muscles of the dorsal surface of the buccal mass follows a nearly straight course for about a third of an inch, when it opens internally into the cavity of the buccal mass in the region of the buccal glands described already (p. 106).

Oesophageal Pouches :—The oesophageal pouches, as shown in text-fig. 4, are two in number, one on each side, and lie below the salivary gland of each side. In *P. globosa* they are somewhat rounded bags, a little over a quarter of an inch in diameter, and of a creamy colour. Though intimately bound up with the salivary glands by connective tissue and blood vessels, they are not in any way connected with them, and by careful dissection can be separated from them. Each opens by a short duct at the point of junction of the buccal cavity and the oesophagus dorso-laterally near the posterior ends of the buccal glands described already.

None of the authors except Amaudrut (1) and Simroth (75), who gives a summary of the former author's work, mention these pouches. They are simple backwardly directed prolongations of the oesophagus, or that part of it which represents the "Jabot" of other forms. The internal cavity is quite simple except for a few longitudinal folds in its ventral wall.

Histological Structure of the Alimentary Canal and Associated Structures :—In the following account only the main points regarding the structure of the alimentary canal are dealt with. The cell-lining of the various parts is described and short notes regarding the muscular and connective tissue coverings are also included.

The *vestibule* is lined by an elongate cubical epithelium similar to the epithelial covering of the general body-surface with which it is continuous. The cells are only more elongate, more cubical and have a thick cuticular lining on their inner free surfaces. The nuclei, which are large, spindle-shaped and richly filled with chromatin granules, lie near the basal membrane. The cells lining the area next to the mouth opening contain large numbers of pigment corpuscles. External to this epithelium is a very fine basement membrane, while external to it are the muscular coats embedded in connective tissue. The muscular coats except for differences in degree of development of the muscle layers in different parts of the alimentary canal have the same arrangement. They consist of an inner layer of longitudinal muscle fibres and one or many layers of circular muscle fibres lying external to the longitudinal layer.

In the *buccal region* the inner epithelial covering changes in character. It consists of elongated cells which on their inner free surface bear rodlets [1] or "stabchen." In between the rodlet cells are a number of flask-shaped gland cells. As these gland cells occur all through the intestinal tract, a general description of these cells may be included here. The cells are flask-shaped structures, broader at the base and with a narrow neck opening into the cavity of the alimentary canal. The plasma is finely granular with a number of vacuoles. The nucleus is large, usually oval in shape, and lies in the basal part. It contains a nucleolus and a large number of chromatin granules. A number of 'eosinophil' cells can also be distinguished in some places in the buccal region.

The *oésophagus* (Pl. XVII, fig. 8) is comparatively thin walled owing to the layer of longitudinal muscles being feebly developed. The epithelial lining consists of cells (E.) similar to those of the buccal region; only the cells here are taller and the rodlets are better developed. The number of gland (G.C.) and 'eosinophil' (E.C.) cells in this region is also larger.

The *stomach* has a very thick muscular covering on the outside consisting of (i) a small number of longitudinal fibres running through a connective tissue layer, and (ii) a thick many layered covering of circular muscle fibres which take their origin in the middle along the ridge of the stomach (*antea* pp. 100, 101). The muscular coat is thicker on the lower surface of the stomach. The inner epithelial lining consists of cells which are similar to those of the oesophagus, but are not so high, and their rodlets are less developed. In between the epithelial cells are a large number of gland cells and a fair number of cells similar to those decribed as 'eosinophil cells' by Dakin (24) in the alimentary canal of *Buccinum*. These cells are somewhat spindle-shaped with an ovoidal nucleus lying about the middle of the cell and containing large quantities of fat-globules in the plasma, which is somewhat granular. These cells appear to help in the absorption of the food.

The *intestine* (Pl. XVII, fig. 9), which shows a large number of villi-like process internally, has the same structure as the oesophagus except that there are a larger number of 'eosinophil cells' in this area.

The *rectum* (Pl. XVII, fig. 10) is peculiar in that it has internally a longitudinal ridge (R.) on the ventral wall running throughout its length. The epithelial covering of this ridge is similar to that of the rest of the rectal wall, while the core of the ridge is filled up with connective tissue and a few muscle fibres running through it. The epithelium bears long rodlets and appears as if it was ciliated. Gland cells and 'eosinophil cells' are present in large numbers.

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[1] See Stephenson and Prashad, *Trans. Roy. Soc. Edinburgh*, LII, pp. 459, 460 (1919).

The *subradular organ* (Pl. XVII, fig. 12) is peculiar in that its high cylindrical epithelium (E.) is at least 1½ times as high as that of the area round about. The cells, which do not bear rodlets, have a large oval nucleus full of chromatin granules lying about the middle of the cell and the plasma is granular. In between the epithelial cells there are a large number of gland cells (G.C.). The subepithelial mass consists of connective tissue cells and muscle fibres. There are no nerve cells reaching the surface and I have failed to find any nerve ganglion or plexus in the subepithelial area.

The structure of the *buccal glands* is similar to that of the buccal region except that the epithelial cells on the surface are higher and the gland cells are more numerous. No rodlets or cilia are present on the cells.

The *radular sac* (Pl. XVII, fig. 13) is, as has been described already, closed posteriorly and in transverse sections appears as a flattened tube with vertical plugs hanging into the lumen from both the dorsal and ventral surfaces ; the ventral plug is prominent near the extreme posterior end only and gradually becomes reduced anteriorly to a low ridge. Externally the sac is surrounded by a thin layer of connective tissue and internal to it the lumen of the sac is lined by odontoblasts which vary in height. The dorsal plug is formed of odontoblasts (*O.C.*), while the ventral plug consists only of connective tissue (C.T.) with blood vessels running through it. This ventral plug in the extreme posterior end of the sac divides the sac into two parts. Each part is lined internally by the odontoblasts (O.C.) or the cells which secrete the radular teeth and forms the membrane in which the bases of the teeth are embedded. The length of the cells varies according to the situation of the teeth ; they are longest at the extreme posterior end and along the outer and dorsal sides of the sac and gradually decrease in height in the situations of the teeth. Further on the epithelium becomes continuous with the epithelium of the buccal cavity. Each cell is elongate and has a rounded or ovoid nucleus with a number of deeply staining granules, usually lying near the end of the cell. The protoplasm of the cell is homogenous. The odontoblasts in the active region of secretion are connected by ciliate processes with the bases of the developing teeth (R.T.).

On examining serial sections of the *salivary gland* it is found that the gland is formed as a result of the continued branching of the salivary duct, which thus results in a greatly branched mass. The epithelial linings of the ducts are only separated by a few strands of connective tissue, which also envelopes the terminations of the ducts ; a few blood vessels are also found in the interstices. The main duct is lined by a non-ciliated cubical epithelium, with fair sized oval nuclei lying near the basal part of the cells ; the cells are filled with a homogeniously staining protoplasm. Here and there a few rather ovoid cells are to be seen in between the cubical epithelial cells ; these do not show any nuclei, and are filled up with rounded, minute granules. The lining of the smaller tubules (Pl. XVII, fig. 14) is also similar, except that the cells are much bigger, and have larger nuclei ; even these cells have no cilia. The interstices, which mark the endings of the tubules, are formed of quadrate or polygonal cells, with large nuclei, and very little of protoplasmic contents ; the rest of the cell is either filled up with minute granules or shows a few vacuoles and some colourless, non-staining inclusions. The structure of the salivary glands is thus quite similar to that of the salivary glands of other Gastropods, but the entire absence of ciliated cells in the ducts is exceptional. I have tried fixing the glands in different ways and have also tried various stains, but have failed to distinguish any ciliated tracts.

The histological structure of the *oesophageal pouches* (Pl. XVII, fig. 15) is, like their macroscopic structure, quite simple. Externally they are surrounded by a thick sheath of connective tissue of the ordinary type, and internally they are lined by a single layer of very tall epithelium. The cells are not ciliated in any part of the sacs. They have a large ovoidal nucleus lying near the base of the cell, and the protoplasm of the cells is somewhat granular. The cells appear to be of the type of simple unicellular glands, and probably secrete some kind of an enzyme for the digestion of food.

The *digestive gland* resembles that of other Gastropods. As already described it is formed by repeated division of a tubular structure and the numerous tubules resulting from its division end as blind caecae. The space between the tubules is occupied by connective tissue with large numbers of blood vessels running through it. The tubules (Pl. XVII, fig. 16) are circular in transverse sections and the inner lining consists of two kinds of cells :—(i) Gland cells (G.C.), which are roughly cylindrical, rather broader near the base and narrowing gradually towards the lumen of the acini. Their nuclei are nearly circular and lie about the middle of the cell. The protoplasm is vacuolar and large numbers of small granules and fat globules are found in it. (ii) Ferment cells (F.C.), which are broadly triangular, with a broad base and gradually narrowing to the free end. The nucleus is large ovoidal and lies near the base. The protoplasm is very granular and a number of fat globules are also seen in these cells. I have not been able to distinguish any lime cells or "kalkzellen" as Barfurth (2) calls them, in my sections of the digestive gland of *P. globosa*. The epithelial cells lining the main ducts except for having longer rodlets or cilia are similar to those of the stomach layer.

The structure of the so called *cartilages* of the buccal mass of Ampullariidæ was described for *A. wernei* by Schaffer.[1] My results are entirely in agreement with him and so only a few notes will be added here. In sections the cartilagenous areas are found to be formed of large polygonal cells (Pl. XVII, fig. 17) with the greater part of the cell consisting of a non-staining ground substance. The outlines of the cells are thick, and in this area ovoidal nuclei are present. This area of the cells stains deeply with Delafield's haematoxylin. Here and there one finds between the cells fairly broad areas with a fibrillar structure and a number of nuclei. Apparently in these areas the transition into cartilagenous structure has not yet taken place.

BLOOD VASCULAR SYSTEM.

Of the earlier authors Quoy and Gaimard (62) included a few notes about the heart and the arteries arising from it. Troschel (80) gave a good account of the heart, and shortly described the arterial system and the branchial and pulmonary veins, but the relations of the latter are not correctly given. Jourdain (42) in his account of the respiratory system included a few, in some respects inaccurate, notes on the general anatomy of the animal and the circulatory system. According to him the blood from the renal organ passes directly

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[1] Schaffer, *Verhandl. Zool. Bot. Ges. Wien*, LVI, pp. 215-219 (1906).

into the heart. Sabatier (66), who gave a more detailed account, did not agree with Jourdain, and stated that the blood from the renal organs did not directly pass into the heart, but had to go through the respiratory organs. He further gave a very ingenious explanation of the way in which the lung and the branchial organs serve for the purification of the blood during aerial and aquatic respirations, but this, in view of his faulty description of the connections of the branchial and pulmonary vessels, does not hold good. Bouvier (11) in his account of the venous system relied almost entirely on Jourdain and Sabatier, and as a result of his own investigations agreed with Jourdain as to the course of the blood from the posterior chamber of the kidney. He is also the only author who has given a detailed account of the arterial system and the heart. Lloyd (53) made a few remarks on the structure of the heart, but did not say very much about the circulatory system as a whole.

Pericardium :—The pericardial cavity of *P. globosa* is situated on the left side of the body-whorl, and is visible after the removal of the shell lying between the posterior limit of the pulmonary sac and the chambers of the renal organ anterior to it, while the stomach with a part of the digestive gland lies posteriorly. Ventrally it extends to the level of the oesophagus, where the latter enters the visceral mass. It is roughly triangular in outline, and extends dorsally between the two chambers of the renal organ. Its cavity is quite spaceous, and communicates with that of the posterior chamber of the kidney through a reno-pericardial pore in the septum separating the two chambers ; this will be referred to in the account of the renal organ. In spite of careful examination I have failed to find any pericardial glands of the type described by Grobben[1] for various Gastropods.

Heart :—(Pl. XVIII, fig. 1). In common with other Monotocardia, except *Cypraea*, *P. globosa* has a single auricle (A.), and one ventricle (V.). The chief peculiarity of the structures in connection with the heart of this species, as indeed of all Ampullariidae, consists in the presence of an aortic ampulla (A.A.) in the course of the cephalic aorta (C.A.) shortly after its origin from the main aortic trunk. The auricle, the ventricle, the main aortic trunk and the first parts of its branches and the aortic ampulla are all enclosed in the pericardium. The auricle lies near the dorsal edge, and has the ventricle lying below it and in the same vertical axis. The aortic trunk arises from the ventricle at its ventral apex and immediately divides into two branches. These two branches run longitudinally at right angles to the axis of the other divisions of the heart, the cephalic branch (C.A.) forwards and the visceral (V.A.) backwards. The anterior or the cephalic branch has the aortic ampulla developed on it.

The auricle is a thin walled sac, and is capable of great extension. It is somewhat triangular in outline, with the apex of the triangle situated dorsally. The efferent ctenidial sinus (E.C.V.) and the efferent renal (E.R.V.) from the posterior chamber of the kidney open into its apex, and the pulmonary vein (P.V.) opens at a slightly lower level on the anterior side. The lower broad end is connected with the ventricle through the auriculo-ventricular opening. The opening is guarded by two semilunar valves situated transversely and attached by muscular fibres to the walls of the ventricle. The attachments of the valves is such as to allow the blood to flow from the auricle into the ventricle, but not in the opposite direction.

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[1] Grobben, *Arb. Zool. Inst. Wien*, IX, pp. 35-56, pl. i (1890).

The ventricle is ovoidal, and has very thick spongy internal walls owing to large numbers of muscle fibres running in various directions from one end to the other, and forming a very coarse mesh-work; these fibres greatly reduce the cavity of the ventricle. As mentioned already the aortic trunk originates from the ventricle at its lower end. This opening, like the auriculo-ventricular opening, is provided with two valves, a large right and a much smaller left semilunar valve. The action of these valves is similar to that of the auriculo-ventricular valves, in that they do not allow the blood to flow back into the ventricle from the aortic trunk.

The aortic trunk immediately after its origin from the ventricle divides into (i) an anterior branch or the so called cephalic aorta (C.A.), and (ii) a posterior branch or the visceral aorta (V.A.). The aortic ampulla, as has been noted already, is situated on the cephalic aorta a short distance from its origin. It has fairly thick walls, and I have observed it alternately contracting and dilating in the living individuals. The ampulla probably thus helps in the circulation of the blood in the anterior part of the body. The opening of the ampulla into the aorta is quite simple, and is not provided with any valves.

Histology :—Externally the auricle, the ventricle, the main aortic arch and the aortic ampulla are all lined by a thin endothelium. It consists of a thin layer of protoplasm, with large numbers of rounded to ovoid nuclei arranged in a single row. No cell limits are to be distinguished. There is no internal epithelial or endothelial lining, and the connective tissue with the muscles, or the latter alone project directly into the cavity.

The wall of the auricle consists of a thin connective tissue layer under the endothelial layer already mentioned. The connective tissue layer is filled up with a fair number of very fine muscle fibres running in various directions in the form of rather thin bundles. Most of the bundles, however, have a longitudinal course.

The auriculo-ventricular valves similarly consist of connective tissue and muscle fibres but the mass of connective tissue is greatly reduced, and the muscle fibres predominate. The muscles of the valves originate from the muscles of the ventricular wall, and thus cannot be pushed back into the auricle at the time of the contraction of the ventricle.

The wall of the ventricle on the other hand consists almost entirely of muscle fibres. These fibres are arranged as (i) a rather thin, outer circular coat, (ii) a very thick coat of longitudinal fibres running longitudinally, and (iii) many bundles of cross fibres running obliquely from in between the two coats, and forming the meshwork seen in the cavity of the ventricle. On the internal surface the muscle-cells with their nuclei are arranged in a row and look like an endothelial lining.

The valves between the ventricle and the aortic trunk consist entirely of longitudinal muscle fibres, which take their origin from the wall of the aorta.

The wall of the aortic trunk, as has been noted already, has the outer endothelial lining, and is followed on the inside by a fairly thick layer of connective tissue cells with many longitudinal muscle fibres running in between them. A few circular muscle fibres are also to be distinguished. The connective tissue cells are large, polygonal, with the protoplasmic layer very thin and restricted along the walls as a thin lining. The elongate nucleus is situated along one of the sides or in one of the angles in the protoplasmic lining. The rest of the cell appears to be empty and does stain with Orange G., or eosin.

The wall of the aortic ampulla is similarly built of the outer endothelial lining, muscle fibres and connective tissue cells. The layer of muscle fibres is thick, and has become more or less separated from the connective tissue ; there being only a few scattered connective tissue cells in it in some places. The muscle fibres consist of two coats :—(i) a rather thin outer circular coat, and (ii) a thick coat also of circular fibres, but running at right angles to the fibres of the first coat, and from one end of the wall of the ampulla to the other. Internal to the muscular coats is a thick layer, six to seven cells deep, of large connective tissue cells of the same type as on the inner surface of the aortic wall. There is no true lymphoid tissue in the wall of the ampulla, as was believed by Lloyd (53).

Arterial System :—The main aortic trunk, as it originates from the ventricle, and its branching into the anterior or the cephalic aorta (C.A.) and the posterior or the visceral aorta (V.A.) have already been described. The aortic ampulla (A.A.), which is developed on the anterior aorta, has also been referred to.

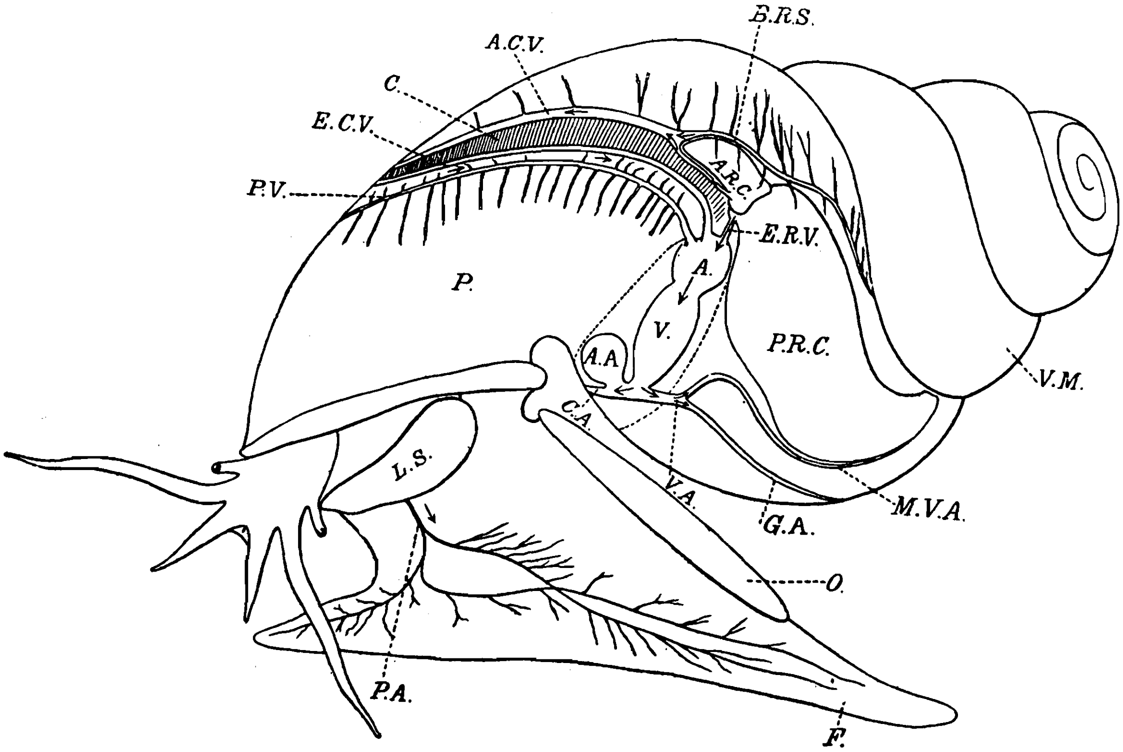

FIG. 10.—Diagrammatic view of the animal as seen from the left side to show the position of the heart and the principal vessels. The ctenidial area is shown more to the left for making the drawing complete and the outline of the pericardial region is shown by dotted lines. The arrows indicate the course of circulation of the blood.

A. Auricle ; *A.A.* Aortic ampulla ; *A.C.V.* Afferent ctendial sinus or vein ; *A.R.C.* Anterior renal chamber ; *B.R.S.* Branchio-renal sinus ; *C.* Ctenidium seen through the mantle ; *C.A.* Cephalic aorta ; *E.C.V.* Efferent ctenidial vein ; *E.R.V.* Efferent renal vein of the posterior renal chamber ; *F.* Foot ; *G.A.* Gastric artery ; *L.S.* Left siphon ; *M.V.A.* Main visceral artery ; *O.* Operculum ; *P.* Pulmonary chamber area ; *P.A.* Pedal arteries ; *P.R.C.* Posterior renal chamber ; *P.V.* Pulmonary vein ; *V.* Ventricle ; *V.A.* Visceral aorta ; *V.M.* Visceral mass.

The anterior or the cephalic aorta immediately after the ampulla gives off on the outer surface (i) a fine branch to the skin, (ii) a fairly thick branch on its lower side, which subdivides very often and supplies the part of the oesophagus lying immediately beneath the pericardial cavity before it enters the visceral mass, and (iii) another thick branch on the outer and upper side to the left side of the mantle, the ospharadium, the left siphon and the skin. On the inner side, *i.e.*, the side of the visceral mass, it gives only a small branch, which sends a couple of small branches to the pericardial wall, and then penetrating through it enters the cavity of the posterior renal chamber and sends branches to the walls of the two renal chambers and the part of the genital organ projecting into the cavity. The aorta (C.A.) has now passed into the perivisceral sinus or the space surrounding the buccal mass, oesophagus, etc. ; and after running along the left of the oesophagus for a time crosses over and comes to lie on the right of it. During this part of its course it gives many small branches to the oesophagus. The main vessel after crossing over to the right side appears as a thick branch, and besides several branches to the floor of the cavity, sends a thick branch which divides and supplies the right side of the mantle (R.P.A.), the right siphon (R.S.A.) and the copulatory organs in both the sexes. The main trunk now turns underneath the oesophagus, and there, after giving a few branches to the floor and the oesophagus, sends a broad ribbon-shaped branch (R. A.) to the radular sac. From the artery of the radular sac a fairly thick branch rises up ; shortly after its origin this branch divides into two, each in turn dividing and, as shown in text-fig. 11, supplying the oesophageal pouches, the salivary glands and a part of the buccal mass. The main branch of the radular sac pierces through the radular sac and runs forwards (B.M.A.) in the middle line of the ventral wall of the buccal mass to the extreme anterior end, where the branch divides into two and spreads into the sphincter muscle of the buccal mass. In its course it also gives many minute branches to the muscles of the buccal mass. The main aortic branch has meanwhile continued forwards over the nerve connectives, and after giving two branches to the eyes (O.A.) and the tentacles (T.A.) of the two sides, divides into two pedal arteries (P.A.). The two pedal arteries, which are of considerable size, enter the mass of the foot and run in a dorso-ventral direction to about the middle, when each divides into a small anterior and a much larger posterior branch. Each of these branches divides repeatedly to form the irregular network in the mass of the foot. The great expansion of the foot is brought about by blood being forced into this extensive network.

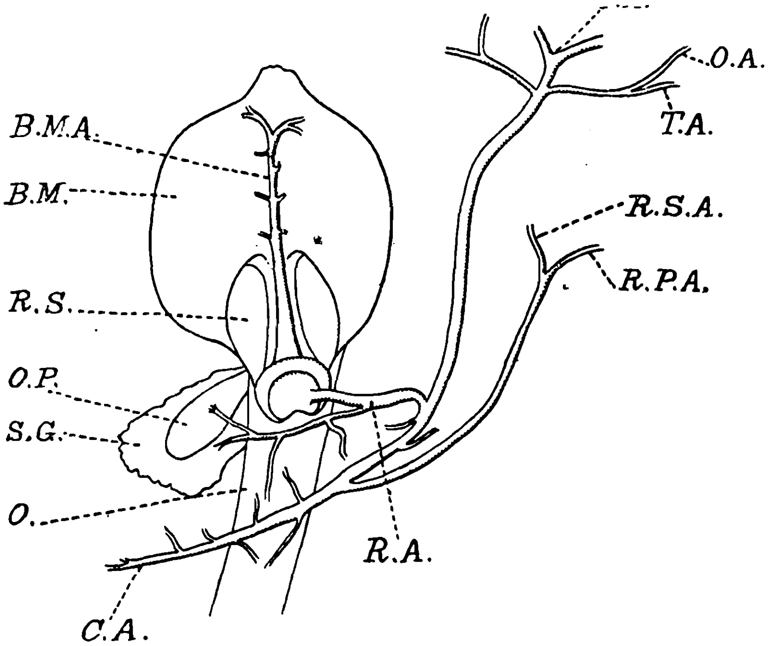

FIG. 11.—Diagrammatic view of the buccal mass and the anterior part of the oesophagus turned upside down with the cephalic aorta shown as in the natural position crossing over the oesophagus from the right to the left. The salivary gland and the oesophageal pouch of the left side are not shown in the drawing. *B.M.* Buccal mass ; *B.M.A.* Artery of the buccal mass ; *C.A.* Cephalic aorta ; *O.* oesophagus ; *O.A.* Arterial branch to the eye-stalk and eye ; *O.P.* Oesophageal pouch ; *P.A.* Pedal arteries ; *R.A.* Artery of the radular sheath ; *R.P.A.* Right pallial artery ; *R. S.* Radular sac ; *R. S. A.* Right Siphonal artery ; *S. G.* Salivary gland ; *T. A.* Artery of the tentacles.

The posterior or visceral aorta shortly after its origin gives off a small branch on its outer side ; this branch divides into many branches and supplies the wall of the pericardium, the anterior part of the digestive gland and its skin covering. A little further it sends somewhat ventrally a large gastric branch (Text-fig. 10, G.A.), which enters the thick muscular coat on the outer surface of the stomach, and sends a number of branches to the various regions of the stomach. The main trunk continues over the surface of the intestine running parallel to the gastric branch along the left margin of the posterior renal chamber. It sends many small branches to this part of the intestine and a couple of branches to the skin covering the posterior renal chamber. On reaching the posterior limit of the stomach it sends a large branch to the digestive gland, which in turn branches repeatedly and supplies various parts of the digestive gland and the gonad. The main branch of the aorta still continues along the upper edge of this coil of the intestine, and curves forwards with it. After sending many branches to the intestine throughout its course and a few to the roof of the anterior renal chamber and the terminal part of the genital duct, it terminates in the rectal wall.

Venous System :—The blood, which is distributed by the arterial trunks to various parts of the body, is in turn passed into small lacunae. These lacunae unite together and open into large central sinuses. In some places the lacunar spaces are quite well marked and simulate real capillaries connecting the arterial with the venous system. They are, however, mere excavations in the tissues, and are not like the arteries true vessels with definite walls. The chief sinuses may be considered under the following four heads :—(i) the anterior perivisceral sinus, (ii) the posterior peri-intestinal sinus, (iii) the branchio-renal sinus, and (iv) the pulmonary sinus.

The anterior perivisceral sinus lies above the foot and below the floor of the pallial cavity surrounding the anterior part of the alimentary canal. The blood from this large sinus runs along three channels. The two more important are the sinuses which carry the blood to the anterior renal chamber and the pulmonary sac through many small branches. The third course is more direct, and here the blood from the rectal wall and the terminal part of the genital duct is collected in the main perivisceral sinus and from there taken to the renal organ or to the pulmonary sac. A number of branches from this region also pass directly into the afferent ctenidial sinus.

The peri-intestinal sinus, 'sinus rectal' of Sabatier or 'la grand lacune perirectal' of Bouvier lies on the collumellar axis next to the intestine and the terminal part of the genital duct. It runs along the coils of the intestine to the junction of the posterior with the anterior renal chamber. It collects blood from the viscera, the digestive gland and the greater part of the genital system. Anteriorly it becomes regularly tubular, and near the seminal vesicle in the male or the uterus in the female divides into two branches. The right branch passes into the floor of the anterior renal chamber and forms the ventral or afferent renal sinus of that organ ; its further distribution is discussed fully in the account of the renal system. The second or the left larger branch bends upwards to the roof of the posterior renal chamber and forms its afferent renal vein.

The branchio-renal sinus (B.R.S.) begins on the right side dorsally over the intestine, and after receiving a number of fine branches follows the outline of the anterior renal chamber along the right side. In its course it receives branches from the roof of the posterior renal chamber (P.R.C.). It also directly receives branches from the surface of the root of the anterior renal chamber (A.R.C.) along its left side. The afferent ctenidial sinus

(A.C.V.), as it may now be termed, then runs forwards over the rectum and receives branches from the terminal part of the genital duct and the rectal wall. All along its course it sends large number of minute branches downwards and inwards, one into each of the ctenidial leaflets, thus pouring into the gill all the blood which it had collected. The efferent sinus (E.R.S.) of the anterior renal chamber, which is situated along the roof of the anterior renal chamber (see p. 123), also opens into the afferent ctenidial sinus at its extreme posterior limit, *i.e.*, the point of junction of the anterior renal chamber and the pallial cavity. The blood from the ctenidial leaflets passes into the efferent ctenidial sinus (E.C.V.), which anteriorly receives branches from the mantle and the copulatory organ, and runs a little to the left of and parallel to the afferent ctenidial to the pericardial cavity, where it opens into the auricle.

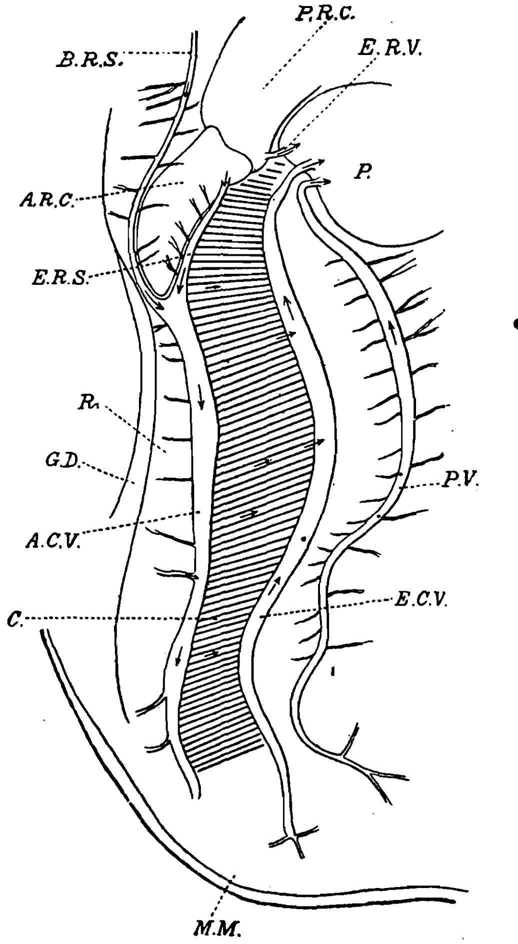

FIG. 12.—Diagram showing the circulation in the branchial and pulmonary region with connections. The arrows indicate the course of blood circulation.
A.C.V. Afferent ctenidial vein; *A.R.C.* Anterior renal chamber; *B.R.S.* Branchio-renal sinus; *C.* Ctenidial area seen through the mantle; *E.C.V.* Efferent ctenidial vein; *E.R.S.* Efferent renal sinus of the anterior renal chamber; *E.R.V.* Efferent renal vessel of the posterior renal chamber; *G.D.* Region of the genital duct; *M.M.* Marginal region of the mantle; *P.* Pericardium; *P.R.C.* Posterior renal chamber; *P.V.* Pulmonary vein; *R.* Rectal region.

The afferent vessel of the posterior renal chamber called ' la grosse gland ' by Sabatier is situated on the roof of this organ and originates, as already described, from the peri-intestinal sinus. As is described below in the account of the posterior renal chamber (p. 124) it divides continuously, and forms a very thick plexus with the branches of the efferent vessel of this chamber. The blood from this plexus is collected in branches which unite to form the efferent vessel. This efferent vessel (E.R.V.) on entering the pericardium opens into the auricle to the right of the opening of the efferent ctenidial sinus. The blood in this vein is not aerated, and thus the blood, which is redistributed from the heart, is mixed. Sabatier correctly described the afferent and the efferent vessels of the posterior renal chamber, and called the arrangement a true portal system, but wrongly described the connection of the efferent vessel, which according to him opens into the renal organ or the anterior renal chamber of the present account.

The upper and lower walls of the pulmonary sac receive a large amount of blood from the anterior perivisceral sinus. As is described by Sabatier the large vessels, which bring the blood to the pulmonary chamber, break up into minute capillaries in its walls and then unite to form the main trunks which in turn by their union form the pulmonary vein. The blood after aeration is collected from both the roof and the floor of the sac by a large number of sinuses, which unite to form the pulmonary vein (P.V.). This vessel lies in the roof of the sac about a quarter of an inch to the left of the efferent ctenidial, and as described already, opens into the auricle on the anterior side slightly to the left of the efferent ctenidial. I have not been able to find any connection between the pulmonary vein and the efferent ctenidial sinus as is described by Sabatier.

Blood Circulation :—The course of circulation of the blood in *P. globosa* may be summarized as follows :—

The blood from the ventricle is supplied to the head and associated structures, a part of the mantle, the buccal mass, oesophagus, copulatory organ and the columellar muscle through the anterior or cephalic aorta, while the whole of the visceral mass and its parts are supplied by the posterior or visceral aorta.

From the various parts of the body the blood is collected in two main sinuses, the perivisceral and peri-intestinal. From these sinuses the blood is either passed into the pulmonary sac, and after aeration returned to the heart, or is carried into the renal sinuses. Some of the blood from the peri-intestinal sinus, which is conveyed into the posterior renal chamber through the afferent vein of that organ, passes into the heart without aeration. The rest of the blood, after the excretory products have been taken from it in the anterior renal chamber, passes into the ctenidium and thence after aeration into the auricle.

During aerial respiration the greater part of the blood from the perivisceral sinus passes into the pulmonary sac, and only a small quantity is carried into the gill through the anterior renal chamber. The reverse, however, is the case during aquatic respiration.

RESPIRATION.

The respiratory peculiarities of the Ampullariidae were studied by a number of observers during the latter half of the last century, and fairly complete accounts of the processes exist in literature. Of the various accounts those of Jourdain (42), Fischer and Bouvier[1], Bouvier (12), Bavay (4), Semper (71) and the quite recent one by Robson (65) are of special interest in connection with the Neotropical forms, while the fairly detailed account of the same phenomena by Ramanan (63) deals with the Indian species commonly found in Madras. Ramanan in his paper describes the respiratory and locomotory habits of what he calls *Ampullaria globosa,* but this is apparently the name he gives to the common Madras species, *P. virens* (Lam.). I do not, in view of the already noted publications, propose dealing with the mechanism of respiration in great detail, but will content myself with giving a short general account and add a few further notes to complete Ramanan's description. It may be noted here that the mechanism of respiration is, so far as my observations go, identical in various Indian species.

The respiratory processes, as is well known for the members of this family, have to be dealt with under two distinct heads :—(i) aquatic respiration by means of the ctenidium, and (ii) direct aerial respiration by the pulmonary sac. At certain times it is impossible to decide as to which of the two processes is functioning.

Aquatic Respiration :—True aquatic respiration takes place when the animal lies quietly at the bottom of a tank or an aquarium, or is swimming or suspended in midwater, attached

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[1] Fischer and Bouvier, *Compt. Rend. Acad. Sci. Paris* CXI, p. 200 (1890).

to weeds, etc. At times the animal may be seen fully expanded with the shell lying backwards on the operculum, with the foot, the snout, the two nuchal lobes and tentacles fully expanded. The expansion of both the nuchal lobes is at this time about equal, and they appear as somewhat shallow channels. After a time, however, the left one increases a little in size and forms a distinct gutter, in which a definite current of water is seen running inwards. The course of the water from this point onwards is somewhat oblique from under the osphradium to the right posterior angle of the left or the pulmonary part of the pallial cavity. Then, crossing over the ridge of the epitaenia the water current passes into the right or the gill chamber. Here, after washing the entire length of the gill, the water flows forwards and out through the right nuchal lobe. On several occasions I have seen a current flowing in at the edge of the left nuchal lobe and out of the right one. Full observation of the phenomenon can only be made in fully expanded animals which are slowly crawling along the bottom of a shallow aquarium or are lying quietly on the bottom. It is greatly facilitated by the addition of powdered carmine particles. The only important factors for this type of respiration appear to be the alternate raising and lowering of the floor of the mantle cavity by the protrusion and retraction of the snout and the currents set up by the ciliary patches on the ctenidial leaflets. Another point also observed in the course of these experiments was the selective influence of the osphradium on the quality of the water that was flowing in. When, for example, the quantity of carmine particles was increased the animal immediately withdrew itself inside the shell, and put an end to aquatic respiration. Even later, when it again expanded, the mode of respiration adopted was not aquatic but aerial. Aquatic respiration was only renewed when the water in the aquarium was changed.

Aerial Respiration :—Aerial respiration of *P. globosa* is a much more interesting process than the aquatic. Earlier authors, basing their accounts on what they had observed in the case of the Neotropical forms, described this type of respiration as taking place through a long siphonal tube formed by the rolling up of the edges of the left nuchal lobe, one over the other. Ramanan (*loc. cit.*) for the Madras species, on the other hand, considered this tube to be only of use in assisting the animal to gain the surface of the water, after which, to quote his own words :—" the siphonal tube, after it has reached the top, increases enormously in calibre at the expense of length. The orifice maintains the diameter, as a rule, till the completion of the aerial respiration, and slowly contracts afterwards till the lumen comes to be only 5 millim. in diameter." The broadened opening is, according to Ramanan, formed by the nuchal lobe only along its lower half, the upper half being formed by the " basal part of the peristome." This is apparently a mistake, for it is the mantle lobe in this region which forms the outer rather than the upper half of the broad siphonal opening. I have carefully observed the process in *P. globosa,* and have also examined some of the other Indian species. In all of these the conditions for aerial respiration are very highly evolved, there being actually a combination of the conditions described for the Neotropical forms by Bouvier and Semper, and that described by Ramanan for the Madras species. Ramanan seems to have missed the first condition of aerial respiration in his observations.

Starting with an animal lying fully expanded at the bottom of an aquarium or attached to plants, we find that it either begins to swim to the surface by the active lashing movements of its snout and tentacles, or else slowly crawls up the sides of the aquarium. Before, however, the animal has actually reached the surface the left nuchal lobe has begun to expand both in length and breadth, and forms by the rolling up of the right edge over the left an elongated tube (S.), measuring as much as 20 mm. in length (Pl. XVI, fig. 1). It is this tube which first reaches the surface, and, breaking the surface film of water, projects above it, thus bringing the left or pulmonary chamber of the pallial cavity into direct communication with the atmosphere. The tube is also at this time the only support by which the animal is kept suspended. When the surface is covered by aquatic vegetation or other molluscs, the animal remains suspended by the long tube and goes on respiring through it like the Neotropical species, without ever having recourse to the broadening of the tube as is described by Ramanan. On the other hand, if the surface is more or less free, the tube soon after the arrival of the animal near the surface begins to broaden out with a corresponding shortening in length, and gradually draws up the animal. The tube now becomes transformed into a broad funnel-shaped aperture (Pl. XVI, fig. 2). The aperture projects about a centimetre above the surface of the water, and with it a part of the shell also lies above the surface. At this time it is quite easy to observe the pulmonary chamber through the funnel-shaped opening. On looking into it one finds that the pulmonary sac is fully extended and fills up about $\frac{2}{3}$ of the pulmonary chamber. At the same time the right branchial part of the cavity is quite shut off from the left by the epitaenia closely pressing against the lower wall of the sac. The opening of the pulmonary cavity is now seen as a nearly circular hole lying near the posterior limit of the funnel-shaped structure of the siphon. The inspiration of air is a pure suction process resulting from the expansion of the sac, which is highly contracted before the air is drawn into it. From time to time alternate contraction and expansion of the pulmonary cavity takes place, and these movements result in the expiration and inspiration of the air. The process, when the animal is respiring air through the long tube instead of the broad funnel, is quite similar to that described above, and there is no continuity between the pulmonary opening and the tube brought about by the extension back of the posterior edge of the tube, as is implied by Bavay (4) and Bouvier (12). This indeed would be quite impossible in the case of a species like *P. globosa*, where the opening of the lung is situated far back in the pallial cavity. Robson's observations on living *A. vermicularis* had also led him to deny any such connection. As has been stated above, the epitaenia or the " repli palleal " of French authors certainly helps in definitely separating off the pulmonary part of the pallial cavity from the ctenidial, though the ridge is of no use in keeping the water out of the pulmonary part as the course of the respiratory water current is from the pulmonary into the ctenidial chamber. I agree entirely with Robson that the main function of the epitaenia, in the Ampullariidae at least, is the direction of the respiratory water current. It probably also assists in keeping the urinary secretions from entering into the pulmonary part of the pallial cavity.

There are thus two distinct methods of aerial respiration in the case of the Indian species, and the choice of the method to be adopted depends almost entirely on the surroundings in which the animals are living. My views on the adaptational value of the siphon are, as was stated by Robson, quite in agreement with what has been so fully expounded by him.

In addition these animals often make long excursions on land both for going from one source of water to another and for the purpose of laying eggs. At this time they must respire air directly through the pulmonary sac. My own observations on this point are limited to what I have seen in the case of animals which had crawled out of the water in the aquarium, and remained still expanded. At this time no long siphon is formed, but the left nuchal lobe is broadened out, and the opening lying along the right nuchal lobe is fully closed by the mantle pressing tightly against it. At the same time the pulmonary sac is fully expanded and full of air, and the left chamber is quite cut off from the right by the lower wall of the sac pressing against the epitaenia, precisely as is the case when Ampullarids in water resort to aerial respiration.

While living in water the animal adopts aerial and aquatic respiration alternately with a more or less definite regularity, but sometimes one is resorted to in preference to the other. If the water in the aquarium, for example, is not changed for some time and thereby becomes poor in the quality of air held in solution, the aerial mode of respiration becomes the more usual, and *vice versâ* if the water is changed too frequently.

The only other phase of respiration of these amphibious animals is that which takes place when they either lie buried in more or less dry mud, or rest with the body fully retracted and the operculum tightly closed at the bottom of a tank or aquarium. Under these circumstances the activities of the animal are very greatly reduced, and the molluscs are in a state of hibernation or aestivation, and probably the only respiration that goes on is through the oxygen stored in the pulmonary sac. That air is stored by animals in this condition in the lung chamber was easily proved by placing animals in this condition in water. They floated at the surface for some time, and on the opening of the opercula a few bubbles of air were extruded out. It is this air stored in the pulmonary sac which enables the animals to remain in a state of hibernation for long periods. Further, probably the same stored air makes it possible for Ampullariidae to be sent long distances. We in Calcutta have received specimens from Burma, the Malay Peninsula and Siam packed dry, and these on being placed in water immediately revived and were after a time quite as active as animals from the Calcutta tanks. The more or less classical cases of Ampullariidae sent by D'Orbigny to Europe from South America, and of Troschel also receiving specimens alive in Germany from the same area are too well known to need further reference. I have also kept animals dry for many months in a cupboard without them being any the worse for it; on being placed in an aquarium they revived and after a time became quite active.

RENAL SYSTEM.

The renal system of Ampullariidae has received attention from early times. In spite of Sachwatkin's (67) very lucid recent review of the previous works on the subject I have, to make this paper complete, thought it necessary to include a short summary here.

Troschel (80) recognized only the anterior chamber of the renal organ, and gave a short description of it. He was certainly wrong in describing the external opening as being situated near the anus. Sabatier (66) and Jourdain (42) in their papers on respiration shortly refer to the renal organ. The former does not mention the external renal opening, and the latter describes it like Troschel as being near the anus; in other respects also their accounts are inaccurate and far from complete. Bouvier (11) recognized that the renal organ consisted of two parts and described the macroscopic structure of these in detail. He failed to find the reno-pericardial opening, and his account of the renal blood-supply is inaccurate. Erlanger (27) on purely theoretical grounds was of opinion that a reno-pericardial pore between the lamellar kidney (anterior chamber of the present account) and the pericardium would certainly be found to be present if the structures were properly investigated. This proved to be the case as a result of Burne's work (18) on *Ampullaria urceus,* but the pore was found between the posterior vascular chamber and the pericardium. Lloyd's account (53) of the structures in *P. globosa* is both incomplete and inaccurate. He recognized only the anterior chamber, and designated the second as a visceral cavity, which, according to him, is not coelomic, and does not communicate with the exterior or any other organ. The whole structure has recently been fully re-investigated by Sachwatkin (67) for *A. gigas,* and the results of Burne confirmed in all important details. He has further fully discussed the morphological significance of the two parts of the renal organ of the Monotocardia generally. He disagrees with Perrier (60), and has come to the same conclusions as Lang and Heschler (48), Drummond (26) and other authors, according to whom the kidney of the Monotocardia, whether it consists of one or two chambers, corresponds to the left kidney of the Diotocardia, while the right kidney in this order has been modified to form the genital duct. This view is supported by the morphology and development of the genital and renal systems of the Monotocardia.

The renal organ of *P. globosa,* as of all Ampullariidae, consists of two chambers, (i) a right anterior, and (ii) a left posterior which lies somewhat to the left of and posterior to the anterior chamber. These two parts though they are homologous with the two chambers in other Taenioglossa are not similar in structure to that of any form in which the renal organ has been properly investigated. In the following account I refer to them by the non-committal names of the anterior and the posterior renal chambers.

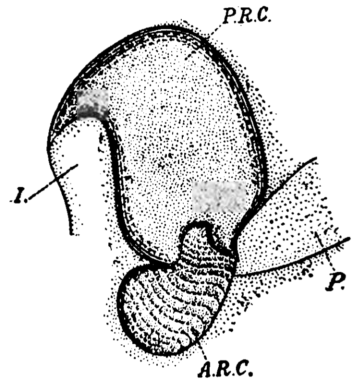

Fig. 13.—Diagram of the Renal area as seen from above. *A.R.C.* Anterior renal chamber; *I.* Intestine; *P.* Pericardium; *P.R.C.* Posterior renal chamber.

Anterior Renal Chamber :—The anterior chamber of the renal organ of *P. globosa* is visible on the upper side of the animal directly after the removal of the shell as a reddish organ, somewhat ovoidal in outline, and lying to the right of the whitish pericardium and the dusky green posterior chamber of the kidney. As noted already (p. 98) the anterior chamber projects into the mantle cavity, and opens into it in a deep crypt by an elongate opening to the right of the epitaenia. The organ, as seen in text-fig. 13, has on its upper surface rather shallow transverse furrows corresponding to the internal lamellae. On opening the chamber by the removal of the roof it is found that the roof has a thick, whitish median axis—the efferent renal sinus—with triangular lamellae regularly arising from its two sides. The floor similarly has a median axis—the afferent sinus (A.R.S.)—situated more to the posterior side and also beset with lamellae along its two sides. The ventral axis, however, is not simple like the dorsal, but is forked a little distance from the wall between the anterior and posterior chambers (Text-fig. 14). This is the afferent vessel of the anterior renal chamber and is the right branch of the peri-intestinal sinus. All along its axis the vessel has lamellae, similar to those of the dorsal sinus arranged on the two sides. Corresponding to the external opening of the chamber into the mantle cavity, noted already, there is an internal opening (O.) along the floor situated in front of the anterior branch of the forked afferent vessel (Text-fig. 14). The second opening (C.) through which the anterior chamber communicates with the posterior lies a little above the point of entrance of the afferent sinus into the anterior renal chamber. There is very little of a cavity in this chamber of the renal organ as practically the whole of the space is taken by the lamellae which project into it from both the roof and the floor and are interleaved with one another.

The arrangement of the vessels in the anterior chamber described above is similar to that described by Bouvier, but differs in minor particulars from both Burne's and Sachwatkin's accounts.

In longitudinal sections (Pl. XVIII, fig. 2) of the anterior chamber of the renal organ one finds that the roof of the chamber is formed by the usual body epithelium (E.), and the connective tissue layer interspersed by a thin layer of longitudinal muscle fibres. Underneath the connective tissue layer are the minute ramifications of the efferent blood sinus, which communicate with the sinuses in the lamellae. Here and there one also sees the blood vessels which communicate directly with the efferent renal vessels. The floor is similarly formed by a single layered cubical epithelium with a layer of connective tissue lying above it and the ramifications of the afferent sinus above the connective tissue. The dorsal and ventral lamellae are similar in structure, being covered by a cubical epithelium (Pl. XVIII, fig. 2). The cells are filled with a finely granular protoplasm, and have a large rounded to ovoid nucleus, rich in chromatin granules, lying about the middle. There are no vacuoles in the cells, and I have failed to find any " Blaschens " or the vacuolar layer on the outer free margins of the epithelial cells, as is mentioned and figured by Sachwatkin. Underneath the epithelial layer on each side of the axis of the lamellae is a thin layer of connective tissue, which here and there sends in fine processes forming bridges in the cavity. The cavities or the sinuses of the lamellae are in continuation with the capillary network of the afferent and efferent sinuses. The canal of the external opening of the chamber is lined by rather high epithelium of the same type as the one on the outer surface of the floor of the chamber. The lining of the pore between the anterior and posterior chambers is similar, but the cells are not so high. I did not find any ciliated cells lining any part of the chamber or the canals.

Posterior Renal Chamber :—Posterior to the anterior chamber and lying to the left of the rectum before its entrance into the pallial cavity, and to the right of the pericardium and the digestive gland is a broad, somewhat hook-shaped area (Text-fig. 13) of brownish to dusky grey colour; this is the roof of the posterior chamber of the renal organ. On cutting this area laterally and along the posterior edge and reflecting the cut surface forwards, we find that there is a spaceous cavity lying underneath it. In the cavity are a few coils of the intestine (Text-fig. 14, I.) and a part of the genital duct. The roof of the cavity, which Lloyd (*loc. cit.*) wrongly describes as " shreddy glandular," appears spongy on its inner surface after the removal of the skin. This is due to two large blood vessels on its inner surface, which divide again and again and form a thick and complicated plexus. The two main blood vessels are the afferent (A.R.V.) and the efferent (E.R.V.) vessels of the posterior renal chamber. The pericardium (P.), which lies to the left of the chamber, is separated from it by a thin vertical partition. In this reno-pericardial septum there is a fine, elongated reno-pericardial pore (R.P.P.), surrounded by thickened whitish lips, and connecting the cavities of the pericardium and the posterior chamber of the kidney. In *P. globosa* there is no pericardial process of the type described by Burne for *Ampullaria urceus.* Anteriorly the chamber is separated from the anterior chamber by the posterior wall of the latter, and the only communication between the two is through the pore described already. The floor consists of a thin lining of tissue separating the cavity from the organs which project into it.

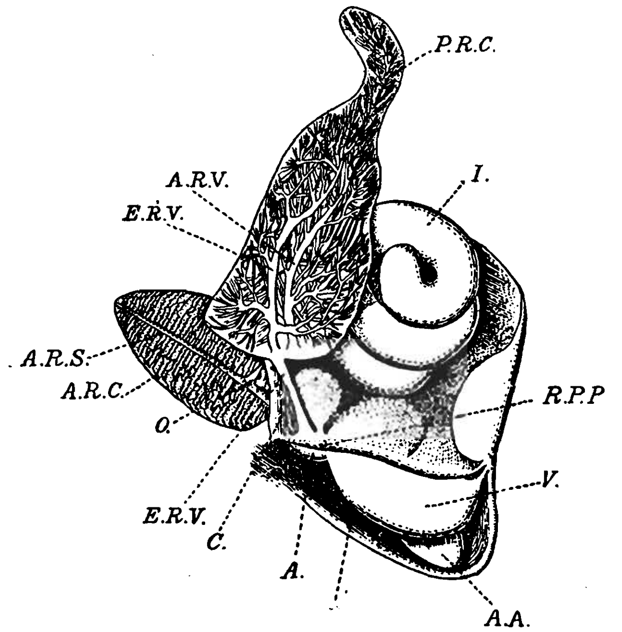

FIG. 14.—Diagram showing the pericardium and the two chambers of the renal organ. The roof of the anterior renal chamber has been removed, while that of the posterior renal chamber is drawn from the ventral surface; it is shown somewhat stretched. *A.* Auricle; *A.A.* Aortic Ampulla; *A.R.C.* Anterior renal chamber; *A.R.S.* Afferent renal vessel of the anterior renal chamber; *A.R.V.* Afferent renal vessel of the posterior renal chamber; *C.* Opening in the wall separating the anterior from the posterior renal chamber; *E.R.V.* Efferent renal vessel of the posterior renal chamber; *I.* Intestinal coils in the cavity of the posterior renal chamber; *O.* External opening of the anterior renal chamber into the pallial cavity seen from the inner side; *P.* Pericardium; *P.R.C.* Posterior renal chamber; *R.P.P.* Reno-pericardial pore; *V.* Ventricle.

In sections of the posterior chamber the roof is seen to have the usual skin covering above, and the plexus of blood vessels and connective tissue below it. In transverse sections (Pl. XVIII, fig. 3) the lower region is found to consist of numerous channels (C.) separated from one another by closely packed connective tissue cells (T.C.). The channel of the vessels is surrounded on the outside by a thin layer of connective tissue, with numerous amoebocytes embedded in it, and is lined on the inside by a single layer of renal epithelium. In the upper areas a few strands of connective tissue are also found running through the channels. The renal epithelium of the posterior chamber, as described by Sachwatkin, consists of two kinds of cells :—(i) the general lining of the chamber and of the lower main sinuses, and (ii) the cells surrounding the secondary branches above.

The first type of cells (A.) are from cubical to cylindrical in outline, being mostly broader along their distal free edge. The protoplasm is usually confined to the basal half and contains a rounded nucleus. The rest of the distal half of the cell is taken up by a large vacuole, which contains either a single, large irregularly shaped granule, or many small granules of the excreta. Such granules are also to be seen in the amoebocytes. It appears, therefore, that the excretory products are collected from the blood by the amoebocytes, and passed on into the vacuole through the basal protoplasm of the cell. In many places one also finds cells without the distal vacuoles, and the protoplasm in a greatly degenerated condition. It appears that in these cells the condition is similar to that described by Perrier (60) in *Littorina littorea,* in that the vacuoles with the excretory granules have separated from the rest of the cell, and dropped into the cavity of the renal chamber. The cells themselves also after the separation of the vacuole probably degenerate and are replaced by new cells.

The second type of cells (B.) are rather broader than the first type, and are distinguished by having a much smaller quantity of protoplasm and a much larger vacuole. The contents of the vacuole are also different, being of the nature of minute granules which stain deeply with Orange G. or eosin. The vacuoles in the cells often show openings at their distal free ends through which the excretory products are discharged. In the protoplasmic portion one often finds amoebocytes with vacuoles enclosed in the cells. These apparently collect the excretory products from the blood and bring them to the renal epithelium.

The epithelial lining of the reno-pericardial pore consists of non-ciliated, narrow cylindrical cells, with ovoidal nuclei. The passage from the flat epithelium of the pericardium to the cylindrical cells of the reno-pericardial pore is quite gradual.

Excretion :—The mode of excretion in *P. globosa* and other Ampullariidae appears to be similar to that in other Prosobranchs, except that probably both the chambers in this family have an excretory function, and the posterior is not of the nature of a nephridial gland. Owing to the single external opening excretory products from the posterior chamber are also collected together and poured into the anterior chamber, whence they are discharged into the mantle cavity.

REPRODUCTIVE SYSTEM.

In *P. globosa*, as in all Ampullariidae, the sexes are separate and the males are generally much smaller with the body-whorl of the shell less swollen. Rudimentary copulatory organ is present in the females also, but the organ and its sac in the female as shown in figs. 13, 14, pl. XVI are much less developed than in the male, figs. 11, 12, pl. XVI. The organs of the two sexes will be described separately.

Male Genital Organ :—Of the earlier authors Troschel (80) was the first to note the occurrence of the penis in *A. urceus*, and briefly described the mantle process from which the penis is developed as a flagellar structure. Jhering (40) gave an elaborate, but very confused description. He called the entire flap-like process of the mantle the penis, and noticed on it a gland, which he described as " Anhangsdrüse," and which corresponds to the hypobranchial gland of the present description ; the true penis he designated as the flagellum. In his second paper (41) he elaborated his first account and described a pouch—"Gaîne de l'appendice filiforme " for the flagellum, and gave rather poor figures. For the flat process, which he still designated as the penis, he described the pouch and the groove as follows :—" Cette gaîne on sac n'a qu'un orific situé à la base vers le corps du pénis, dont la rainure (*rai*, fig. 1) se prolonge dans la base de la gaîne, comme le montrent les figs. 1 et 2." Bouvier's account (11) is more accurate, and with few exceptions as to details is applicable to the structures in *P. globosa.* He, however, does not mention the hypobranchial gland. Lloyd (53) is very confused, and apparently as in the case of the female organs failed to find the true genital gland. Sachwatkin (67) in his very detailed account deals fully with the male organs, but, as is discussed further on, his account of the penis and its appendages, as found in *A. gigas*, is not applicable to the structures of *P. globosa.*

Male organs (Text-fig. 15):—These consist of (i) the testis with its fine vasa efferentia, (ii) vas deferens with the vesicula seminalis, and the terminal glandular part of the vas deferens, (iii) the hypobranchial gland, and (iv) the penis and its sheath.

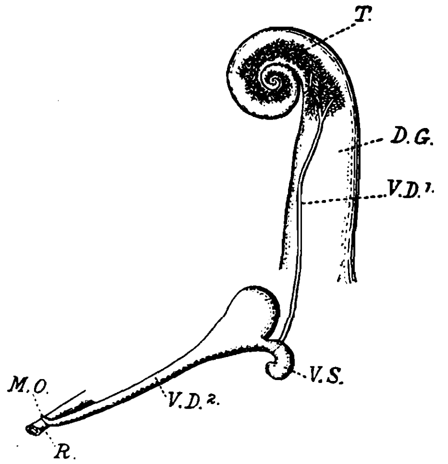

FIG. 15.—Male genital organs of *P. globosa.* The penis and its accessory structures are not shown. *D.G.* Digestive gland ; *M.O.* External opening of the vas deferens ; *R.* Rectum ; *T.* Testis ; *V.D.1.* Thin tubular portion of the vas deferens ; *V.D.2.* Terminal glandular part of the vas deferens ; *V.S.* Vesicula seminalis.

The testis (T.) is a flat plate-like structure, somewhat triangular in outline, which lies in a spiral along the upper area of the first 2½-3 whorls of the shell, attached to the digestive gland (D.G.) on its upper and a little along the inner or columellar edge. It is separated from the shell by rather thin skin, and is closely attached to the liver, though it is easier to separate from the liver tissues than the ovary. Its boundaries can be easily distinguished from those of the liver owing to its creamy colour. From its different parts minute ducts—the vasa efferentia—lead downwards where they either unite with one another or directly open into the vas deferens.

The vas deferens may be treated under three heads, (i) the thin tubular part (V.D.1) as it starts from the testis, (ii) the vesicula seminalis (V.S.), and (iii) the thick glandular part (V.D.2), which ends near the anus. The thin vas deferens starts from near the posterior end of the testis, and runs just below the skin along the inner or columellar edge up to the posterior renal chamber. It then turns to the left, and after reaching the pericardium once again turns upwards and to the right to open into the vesicula seminalis on its ventral side, a little further than the extreme posterior limit. The vesicula seminalis lies to the right of the pericardium and immediately below the line of junction of the anterior and the posterior renal chambers. It is a somewhat curved, swollen flask-shaped structure with its posterior blind end broadly rounded. The terminal glandular part of the vas deferens into the blind end of which the vesicula seminalis opens on the left side, and which has been given the unfortunate name of " Prostata " by Sachwatkin, starts from the vesicula seminalis and after a very short course passes into the mantle cavity near the origin of the gill and the epitaenia. In the mantle cavity it lies closely attached to the left side of the rectum and runs along it to terminate in a small papilla, about a quarter of an inch behind the anus. The papilla is free and lies over the rectum. The terminal part of the vas deferens is white in colour and has thick glandular walls which easily distinguish it from the rectum.

About a quarter of an inch to the left of the extreme right limit of the mantle cavity the mantle edge on its inner surface bears a thick glandular process of a yellowish colour. The process is attached on the right side, but is free on the left, and is greatly rolled in along the edge to form a sheath or pouch for the penis. In A. *gigas* Sachwatkin has described a very elaborate apparatus consisting of a penis sheath, a penis sac, the penis and the well developed canal on the penis sheath ; he further noticed that the apparatus in the males is of a brick-red colour, and this he considered to be a secondary sexual character of great importance for determining the sex of the individuals from the examination of the external characters alone. In *P. globosa* the conditions are very different and the structure is much simpler (Pl. XVI, fig. 11). The penis sac is only an outgrowth from the inner surface of the mantle in the situation described above. In the region of the hypobranchial gland, which is situated on the right outer half of the pouch, it is much thickened, and has a true glandular structure. The gland in the male is found in the same position as in the female. Its free edge is curved upwards and inwards, and thus forms a definite pouch for the penis. There is no trace of a groove on the inner side, as has been described by Sachwatkin, nor is there any distinction between the penis sac and the penial pouch to be made out. The penis (Pl. XVI, fig. 12) itself is a flagellar structure, about half an inch long, arising from the attached right side of the flap of the mantle. It is seen lying as a somewhat curved structure inside the flap, and is swollen at the point of attachment; from here it gradually tapers to the free tip. The penis is rod-like and has a deep groove (Pl. XVIII, fig. 4, G) running along the middle on its inner surface from the base to the tip. Sachwatkin's description of this part is rather involved and difficult to follow. He does not describe the macroscopic appearance of the penis, beyond referring to its great length and discussing its relations with the penis sheath. In the histological account he describes the canal of the penis, which he calls the vas deferens. He does not deal with the course of this duct in his description and does not say anything regarding its external opening, but from his description and figures it is clear that he considers the penis to be bored through by a fine microscopic duct. Such a fine tube not in direct continuation with the terminal part of the vas deferens would, owing to the very fine calibre of the tube, be quite useless for the transference of the spermatic fluid. In view of the great differences between Sachwatkin's and my observations, I am of opinion that the structure of the penis of *A. gigas* needs re-investigation.

Histology :—The structure of the male organs of *A. gigas* has recently been described in detail by Sachwatkin (*loc. cit.*) and I can confirm his results in practically all details. For the sake of completeness I include here a short summary, but have not thought it necessary to give figures of the various structures.

The testis consists of a compact glandular mass formed of a large number of seminal tubules, bound together by connective tissue. In a transverse section one finds that the outermost layer of the testis wall consists of a single layer of cubical epithelium. The cells are nearly squarish, with a large nucleus and very many minute pigment granules. Next to the epithelial layer is a thin, clear basal membrane, which is followed by two layers of connective tissue with a few muscle fibres. Up to this layer the structure is quite similar to that of the general body-covering, and is apparently only a continuation of it. Underneath follows a thick layer of connective tissue formed of Leydig's cells, with large numbers of blood spaces. At this level the seminal tubules separated from one another by bands of connective tissue appear in the connective tissue layer. Each tubule is covered by a definite, but thin and structureless coat of connective tissue. Internal to it is a thick layer of protoplasm with large numbers of nuclei of sperm-mother cells and numerous rounded fat droplets of a yellowish colour. It is not possible to demarcate the boundaries of the sperm-mother cells, as no cell walls are to be distinguished. Besides the nuclei of the sperm-mother cells there are some much larger nuclei surrounded by definite layers of protoplasm, but also without definite walls. These seem to correspond to the "basal cells" of Platner (61), and probably have a nutritive function. The sperm-mother cells develop into spermatogonia while still in the protoplasmic layer, and are distinguished by their much larger nuclei, with large chromatin spiral, and projecting with their protoplasmic covering into the cavity of the tubules. I do not propose dealing with the complicated process of spermatogenesis, and would only note that the spermatogonia now separate from the wall, and develop into the spermatozoa in the cavity of the tubule, after passing through the spermatid stage in the channel of the tubule.

The spermatozoa of *P. globosa*, as of all Monotocardia and of most of the Prosobranchs, are of two kinds :—(i) the hair-shaped, which Meeves (54) called the " eupyrene " sperms (Pl. XVIII, fig. 5), and (ii) the worm-shaped (Pl. XVIII, fig. 6), which Siebold (74) designated as the " oligopyrene " sperms. For a detailed discussion of the forms and the possible functions of the two kinds of spermatozoa reference may be made to Brunn (16), Simroth (75), Retzius (64) and Buchner (17). It may, however, be noted that only eupyrene or the hair-shaped spermatozoa are capable of fertilising the ova. The worm-shaped or the oligopyrene sperms, which are not capable of any movements, have probably some secondary function. Brunn (*loc. cit.*) does not figure but has described the spermatozoa of *Ampullaria* sp. from Katapang Island near Java. Sachwatkin (*loc. cit.*) has recently described the two types of sperms of *P. globosa* and published good figures The eupyrene sperms of *P. globosa* are 25·2μ in length, the head being 7·2μ, the middle piece being 6μ and the single ciliated tail 12μ. The proportions of the various parts are thus similar to those given by Brunn, but the sperms are about $\frac{2}{5}$ the size ; they are, however, about $1\frac{2}{3}$ times as long as those of *A. gigas*, and differ in proportions of the various parts. The sperms in the corkscrew spiral portion are 1·2μ in width. The oligopyrene sperms are about $1\frac{1}{2}$ times the size of those of *A. gigas*, and about $\frac{7}{10}$ the size of those described by Brunn. The head and middle-piece area are not to be distinguished, and both together measure 14·4μ ; while the tail is 18μ and consists of four or five cilia. The width of the anterior region in its broadest part is about 3μ.

The first or the thin tubular part of the vas deferens consists of a very narrow canal surrounded by a cubical epithelium. External to the epithelial layer is a fairly thick coat of circular muscle fibres, surrounded by a thin connective tissue layer. The cells of the epithelium are ciliated, cubical, about three times as high as broad, and have a large ovoid nucleus near the base. The protoplasm of the cells is somewhat granular. The cilia are only slightly shorter than the cells, and are connected by cytoplasmic fibres with the double row of desmochondria a little below the free margin of the cells.

The channel of the vesicula seminalis is not simple like that of the first part of the vas deferens, but is traversed by a large number of vertical longitudinal folds. In transverse sections these folds appear as finger-like processes, and are covered by ciliated epithelium, while their cavity is filled up with connective tissue. This tissue is a continuation of the general connective tissue which surrounds the vesicula seminalis all round. In this connective tissue a layer of muscle fibres is also to be distinguished. The ciliated epithelium of this part resembles that of the first part of the vas deferens, except that the cells are a little narrower, have larger nuclei and their protoplasm is more vacuolated.

The last part of the male duct has a very thick glandular wall and a rather narrow semilunar lumen running through it. The canal here also is lined by ciliated epithelium of the same type as that of the vesicula seminalis. The thick wall consists of glandular tissue with the canals of the glands uniting together and opening into the main canal, and large numbers of blood spaces running through its entire length. The glandular tissue consists of large numbers of unicellular, inverted flask-shaped glands with the tips of the necks reaching up to the channels of the smaller canals in between the ciliated epithelial cells lining them. The gland cells are smaller in structure to those described by Sachwatkin for *A. gigas*, and have a large nucleus lying near the base. The rest of cell in sections contains a finely granular secretion, which stains faintly with eosin.

The minute structure of the penis is similar to that of the rudimentary copulatory organ of the female. Only the muscular coats and the epithelial lining of the groove are more highly differentiated, and the structure is much larger in size.

The hypobranchial gland (Pl. XVI, fig. 11, H.G.) is not a deep seated gland, but the cells in this area are much taller, with a small basal nucleus and the rest of the cell either filled with a granular secretion, which stains feebly with eosin, or quite empty. The surface of the glandular area is somewhat pleated, but there is no duct, and the secretions of the gland cells are apparently directly poured on the surface.

Female Genital Organs :—Blainville (7) in his paper correctly described the position of the ovary of the Ampullariidae, but Jhering (40), who followed him, remarked on the absence of the ovary in the situation corresponding to the testis of the male in the Brazilian *Ampullaria canaliculata*. He was not certain, however, as to whether he had been able to distinguish the ovary, but was of opinion that the ovary was probably represented by the follicular gland which lies closely attached to the albumen gland—the receptaculum seminis of the present account. His description of the structure of the albumen gland also is inaccurate, in that he described it as being cut up into compartments by means of septa. Bouvier (11), who gave the first detailed account and figures of the anatomy of *Ampullaria*, was similarly wrong in his interpretation of the structures, and in his paper definitely described the receptaculum seminis as the ovary. He refers to the discovery of both male and female organs in the same individual, which he considered to be an evidence of the ancestors of these forms being hermaphrodites. This conclusion was based on the presence of both the male and female glands and of the penis in a rudimentary condition in a single individual. The former fact is of no value as Bouvier certainly mistook the receptaculum seminis for the ovary and what he considered to be the testis was the real ovary, while the presence of what he considered to be the penis is quite normal, in that a rudimentary structure of this nature is present in all females. This fact had been noted by Quoy and Gaimard (62), whose description of the other anatomical features is very scanty. Bouvier further does not mention the hypobranchial gland. Lloyd (53) makes the same mistakes in his account of the female organs as Bouvier and Jhering, but has described the rudimentary copulatory organ of the female. Sachwatkin (67) was the first author to give a correct account of the various structures, but his description of the receptaculum seminis is wrong, and he does not describe the rudimentary penis of the female. Jhering in his second paper (41) merely repeats the account given in his first paper but mentions the presence of a rudimentary copulatory organ in the females corresponding to that of the males; this he compares to the clitoris, and concludes that it affords a proof of the ancestral forms of the Ampullariidae being hermaphrodites.

Female organs (Text-fig. 16) :— Like the male organs the generative organs of the female consist of (i) the ovary with its numerous minute ducts, (ii) the main oviduct, (iii) the receptaculum seminis, (iv) the uterus, (v) the vagina, and (vi) the hypobranchial gland with the rudimentary copulatory apparatus.

The ovary (O.) lies in the same position as the testis, but is not so extensive. It is closely attached to the liver and is covered by a thin, but stout skin coat; it occupies the upper and inner surface of the first 2-2½ whorls. Whereas the testis lies in its greater part along the upper edge of the whorls and is only slightly extended on the inner or the columellar edge, the ovary on the other hand lies mainly along the inner surface, and only a part of it is extended on the upper edge, so that in the dorsal view the greater part of it is only visible after the whorls have been separated apart. Sachwatkin describes the ovary as being situated on the " Aussenseite " *i.e.*, the outer side, but in *P. globosa* the ovary is certainly more on the inner surface. Owing to the opaque nature of the skin-covering and the close attachment of the ovary to the liver, it is rather difficult to distinguish it, but on the removal of the skin it is seen as a much branching structure of a light orange colour; in fully ripe individuals the colour is much darker. The branches of the ovary consist of one layered acini, which are somewhat flask-shaped, with the closed rounded ends directed outwards, and the necks coming down to meet those of the adjacent acini to form minute ducts, which in their turn open into the main oviduct.

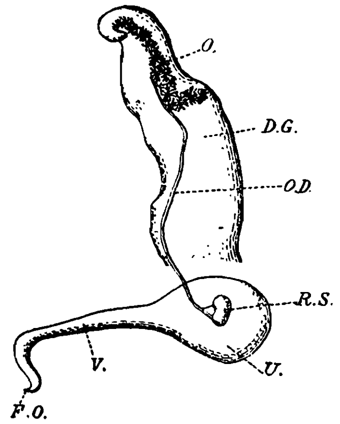

FIG. 16.—Female genital organs of *P. globosa.* The rudimentary penis and its accessory structures are not shown.
D.G. Digestive gland; *F.O.* External opening of the vagina; *O.* Ovary; *O.D.* Oviduct; *R.S.* Receptaculum seminis; *U.* Uterus; *V.* Vagina.

The oviduct (O.D.) is situated along the lower boundary of the ovary and can be followed to about the middle of the ovary. In fresh specimens it is seen as a fine transparent tube lying immediately under the skin and shining through it. About the level of the renal organ it turns downwards along the margin of the liver, and then upwards to enter through the pouch of the receptaculum seminis into the receptaculum itself.

The receptaculum seminis (R.S.) is a bean-shaped structure, lying in the cavity of the posterior renal chamber on the outer left side (topographical) of the uterus, and closely attached to it. It lies near the left outer margin of the uterus, and transversely to the long axis of the animal; the regularly arched long axis of the bean is the upper one, and the point of attachment is along the anterior notched side. Along this notched side the receptaculum seminis passes into a thin-walled pouch, which arises directly from the wall of the uterus. The oviduct enters the receptaculum seminis through the thin-walled pouch from its lower apical or the anterior angle, and runs through it along the outer side to pass into the receptaculum. On clearing the receptaculum in clove oil or acetic acid, one finds that the oviduct (Pl. XVIII, fig. 7) forms a closely wound spiral along the long axis of the receptaclum, running from the right to the left, where the tube slightly broadens out, and turns inwards to enter into the uterus. This structure of the Ampullariidae, as has already been pointed out, was wrongly interpreted as the ovary by all the older authors, and Sachwatkin is the first author who understood its exact nature. It corresponds to the " reservoir spermatique " of *Vivipara*, as described by Baudelot (3). Sewell (72) calls the same structure in *V bengalensis* by the name of " egg-shell gland," but the structure is a non-glandular one formed by the spiral coiling of the oviduct in this region. In the Monotocardia the receptaculum may be either a simple pouch-like widening as in Rachioglossa or may take the form of an accessory structure attached to the uterus, and with a spirally coiled area of the oviduct lying embedded in its upper part ; such is the case in *P. globosa*, other Ampullariidae, and in *Oliva peruviana* (Küttler, 44). The structure is non-glandular, and is only produced for the great coiling up of the oviduct in this area for the fertilisation of the eggs before the yolk has been secreted round them in the uterus. The finding of spermatozoa in the canal by both Küttler and myself adds weight to this supposition.

The uterus (U.) is a large, pyriform, deep yellow coloured structure, which is to be seen on removal of the shell lying inside the main or the body-whorl. The terminal part of the intestine, before its entry into the mantle cavity to form the rectum, lies along its upper margin, and outside it to the left side are the two chambers of the renal organ. The structure, as I have described above, is pear-shaped, with the apex lying forwards ; this is continued as the vagina ; while the posterior end is broadly arched and somewhat rounded, and the opening of the receptaculum seminis is on the outer side.

The vagina (V.) is clearly marked off by its white or somewhat creamy colour, and is seen from the outside as a band-like structure lying immediately under the skin and extending from the uterus to the upper end of the columellar muscle. On opening the mantle cavity, the vagina is seen to enter the cavity at its extreme right, posterior corner, and continues in a somewhat arched manner to a little behind its anterior limit, lying closely attached to the rectum. The outer opening (F.O.) is narrow slit-like, and is situated about a quarter of an inch behind the anus on a small papilla ; the papilla itself is free and, as shown in fig. 8, pl. XVI, lies over the rectum.

The rudimentary penis (Pl. XVI, fig. 13,P.') of the female specimens is seen on reflecting the glandular fold backwards by cutting along the edges. It is a thin flagellar structure with a rudimentary groove along its inner surface as is found in the penis of the male. The flagellum is about a quarter of an inch in length, of nearly the same thickness throughout except at the tip, where it is a little pointed. In the female there is no trace of the foldings of the flap like those in the male but there is a rudimentary glandular thickening in the hypobranchial gland area.

In the introductory part of the description of the female genital organs I have included references to the descriptions of the rudimentary copulatory organ of the female Ampullariidae by other authors, and a few further notes regarding the other Molluscs may be added here. Amongst the Taenioglossa Gegenbaur (32) noticed in a form of *Pterotrachea coronata* a female specimen with the external sexual characters of the male. This was further confirmed and elaborated by Paneth (58), who in colourless individuals of *Pterotrachea coronata* found that out of the thirteen females examined by him, six had a " Saugnapf " or an acetabulum—a secondary structure of the males in *Pterotrachea*—but no penis, while two had a penis but no acetabulum ; in the coloured individuals of the same species he found three individuals with an acetabulum but no penis. These structures he considered as being of the nature of secondary sexual characters of the males, which sometimes make an appearance in the females. Grobben (33), while agreeing with Paneth as to the explanation regarding the appearance of the penis in the females, was of opinion that the occurrence of the acetabulum in some of the individuals of *P. coronata* is of the nature of the recurrence of an organ, the development of which had been arrested in the genus ; a view which is upheld by comparison with the nearly allied genera *Carinaria* and *Atlanta,* in which the acetabulum is present in both the sexes. Simroth (75), after referring to the observations of the two authors, brings forward the suggestion that the penis of the females may be taken as a proof of the ancestors of these forms being hermaphrodites, a suggestion already made by Jhering (41). The penis or other accessory male organs may be present either as rudimentary organs in all female specimens as in *Carinaria, Atlanta, Pila* and probably other Ampullariidae, or may occasionally occur as a reversion as in *Pterotrachea coronata.* Reference may also be made here to the very interesting observations of Pelseneer (59), according to whom hermaphrodite condition is secondary and is evolved from a primitive dioecious state. In this paper Pelseneer further states that in the evolution of the hermaphrodite stage it is the female individuals which take on the sexual characters of the males and show a tendency to hermaphroditism. In support of this view a number of examples from various groups of animals including molluscs are cited, and *Ampullaria* is also included as an example of a mollusc in which certain individuals of one sex produce both the male and female elements. No reference is included as to the source from which this information is taken, but I believe this to be based on the observation of Bouvier (*loc. cit.*), which, as Sachwatkin has remarked and I have said already, appears to have been a mistake.

Histology :—Sachwatkin has recently described at length the minute structure of the genital organs, and it is not necessary, therefore, to go into it in great detail. In the following notes I deal with the outstanding features or the parts which have been misinterpreted or entirely missed out. The ovary is covered by a one-layered epithelium, which is the continuation of the epithelial covering of the skin over the rest of the body. Underneath the epithelium is a thin layer of connective tissue, in which a large number of longitudinal muscle-fibres running parallel to one another are also present ; underneath the connective tissue layer is a fairly thick layer of the so-called Leydig's cells, which have comparatively small nuclei and contain small quantities of protoplasm in their bodies. In the connective tissue there are besides a fair number of blood vessels, and a nerve here and there. The true flask-shaped tubules of the ovary are embedded in the connective tissue, which, except for its more or less circular arrangement, is quite similar to the rest of the connective tissue in the ovarian wall ; underneath it is a thin basal membrane, and then follows the germinal epithelium, which surrounds the channel of the tubule. This germinal epithelium consists of somewhat cubical cells with nearly rounded nuclei lying about the middle of the cells. The eggs in various stages of growth are to be seen lying attached to the epithelial cells and suspended in the canal of the tubule. I do not propose going into the development of the eggs in greater detail, as my observations on the subject are as yet not complete.

The fine oviducal branches and the main oviduct are similar in structure, except that the finer tubules are much narrower and have a thinner connective tissue coat. The channel of the main oviduct is lined by a somewhat cylindrical epithelium ; the cells are ciliate and have large nuclei. Outside the epithelium is a thin layer of connective tissue of the same type as the one described already in the account of the ovary ; in the connective tissue a few muscle fibres are also present.

The receptaculum seminis is, as has been mentioned already, not a glandular structure. In its upper area the greater part of its long axis is occupied by the coiled oviducal tube. The canal is here also, as in the case of the true oviduct, lined by a ciliated epithelium, but the cells are more cubical and the cilia are not so long. The canal is surrounded by a thick sheath of connective tissue in which a fair number of muscle fibres are to be seen ; the connective tissue on its outside has a thick coat of circular muscle fibres.

The uterus, which follows next, is a true glandular structure with very thick walls and a rather narrow canal ; the canal has a very wavy course, and is, therefore, in transverse sections cut more than once. The thick wall itself consists of gland cells surrounding fine tubules, which collect the secretion from the gland cells and then open into the main duct of the uterus, either directly or after union with one another. The gland cells themselves are large, somewhat rounded, and have a rather small nucleus of irregular outline; their entire body is filled with a granular secretion. The canals of these glandular areas are lined by a flat, low, ciliated epithelium in which the outlines of the cells are very hard to distinguish. The main canal of the uterus is lined by a high, cylindrical, ciliated epithelium, which is covered by a very thick layer of connective tissue. In the connective tissue there are a large number of blood sinuses.

The wall of the vagina is also quite thick, consisting of a non-ciliated, high epithelium on the inside of the canal and surrounded by a thick coat of connective tissue with a large number of muscle fibres. In addition there are a few blood sinuses traversing the walls in the longitudinal direction.

The rudimentary copulatory organ of the female is similar in structure to the penis of the male. It is covered by a cubical epithelium with a thin circular coat on its outside. The epithelium, except for being a little less deep, is identical with that of the mantle round it. In the groove (see macroscopic account, p. 132) the epithelium is a little higher, but less broad than the rest of the structure. Below the epithelium is a fine basal membrane, and then a layer of circular muscle fibres. The rest of the core is filled up with bundles of longitudinal muscle fibres separated by masses of connective tissue ; here and there a few transverse muscle fibres are also present. Running through the entire length of the structure in a longitudinal direction are two large blood sinuses of the same type as are found in the penis of the male. A few smaller lacunar spaces are also present, and in transverse sections the nerve branch is also to be seen. The structure of this organ supports the view that it is of the nature of a degenerate or rudimentary organ.

NERVOUS SYSTEM.

Troschel (80) was the first author who published a short account of the nervous system of an Ampullarid—*A. urceus*. Jhering (39) included a few notes on the nervous system of *A. ovata* in which, owing to his being unable to find the connective between the right pleural ganglion and the supra-intestinal, he was led to erroneous conclusions. Bouvier (9) in his memorable work on the nervous system of the Prosobranchs gave a detailed account and figures of a number of species of the family ; I am in the main able to confirm his results. Jhering (40) in the same year as Bouvier's above cited work published detailed notes on the nervous system of the South American *A. canaliculata,* but in this paper also he failed to correct the mistakes in his previous work. Bouvier in his monograph on the anatomy of *A. polita* (11) rightly criticised Jhering and fully confirmed his previous work. In 1891 Jhering (41) made a further contribution to the subject and agreed in general with Bouvier. Burne (19) also published some very valuable notes on the nervous system of an unidentified species of *Ampullaria* and gave a good account of the pedal ganglion and the nervous supply of the foot. Lloyd (53) only published an incomplete account. Ghosh (34) gave a fairly detailed account of the nervous system of *P. globosa*, but his account is inaccurate in many respects and his terminology is often faulty.

In the following account I do not propose going into details regarding the terminology of the various ganglia and nerves as expounded by Jhering (39), Spengel (76), Simroth (75) and Bouvier (9), but have followed the generally accepted names of Spengel. The main ganglia (Pl. XVIII, fig. 8) are termed *cerebral, buccal, pedal, pleural, supra-* and *sub-intestinal* and *visceral.* The nervous connections between similar ganglia of opposite sides are termed *commissures,* while those between dissimilar ganglia of the same or opposite sides are called *connectives.*

The nervous system of *P globosa* will now be described, and a short general discussion regarding the form and affinities of the nervous system of this family is included at the end.

Buccal Ganglia :—There are two buccal ganglia, one on each side (Pl. XVIII, fig. 8, L.B.G.) and lying on the dorso-lateral side of the buccal mass at its junction with the oesophagus and a little in front of the situation of the salivary glands. Each ganglion is triangular with the apex of the triangle directed towards the ventral surface, and is partly enclosed by the muscles of the buccal mass. The two ganglia of the two sides are connected with one another by the buccal commissure which is a fairly stout nerve. It begins from the posterior angle of the buccal ganglion of each side and curves downwards to the ventral side of oesophagus on the posterior side of the buccal mass. It sends a branch on each side which divides further into a number of branches and supplies the posterior part of the buccal mass and the radular sac ; it is the *s*1 branch of Bouvier (9). Each ganglion is also connected to the cerebral ganglion of the corresponding side through the fine cerebro-buccal connective which is given off from the main nerve from the anterior angle of the buccal ganglion. This connective runs backwards and downwards and becomes connected with the cerebral ganglion of the side on its upper surface. The nerves from the buccal ganglion of each side are as follows :—

(i) A thick nerve from the anterior angle of the ganglion and from which the already noted cerebro-buccal connective is given off. It runs forwards and supplies the muscles of the buccal mass anteriorly after dividing into two main branches, which again divide in their turn.

(ii) Three fairly stout and a fine nerve from the dorso-lateral margin of the ganglion supply the median part of the dorsal surface of the buccal mass.

(iii) Three rather fine nerves from the ventro-lateral margin of the ganglion, best seen by turning the ganglion upwards, supply the ventro-lateral posterior half of the buccal mass.

(iv) From the posterior angle of the inverted triangular ganglion a stout nerve runs backwards. It gives a fine branch to the buccal mass in its posterior dorsal part, and then curves backwards to the oesophagus. It sends branches to the salivary glands, the oesophageal pouches and continues over the greater part of the oesophagus giving a number of branches. It is the *s*2 branch of Bouvier.

Cerebral Ganglia :—There are two cerebral ganglia (C.G.), connected with each other by a cerebral commissure (C.Cm.). Each is somewhat triangular in shape, and is situated

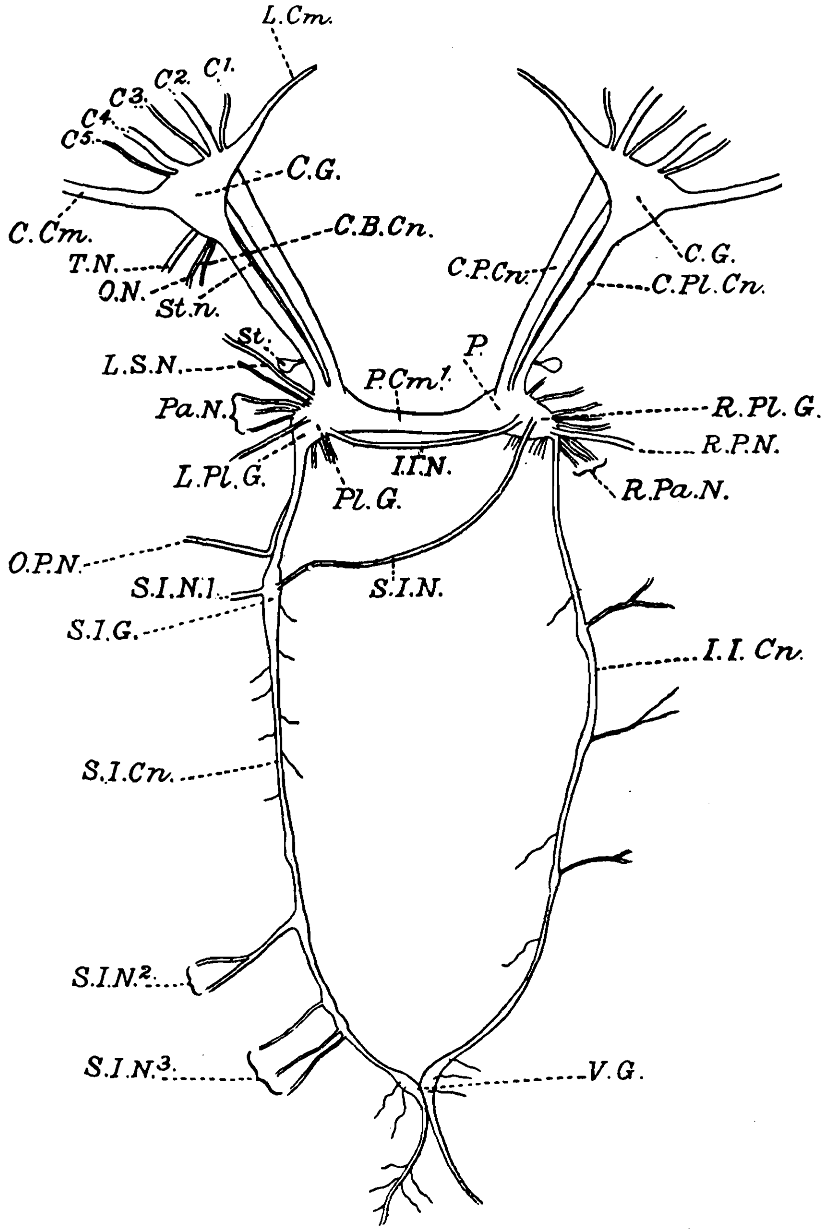

Fig. 17.—Diagrammatic outline of the nervous system of *P. globosa*. The buccal ganglia are not shown. *C.1-C.5* Nerve branches 1-5 of the cerebral ganglion ; *C.B.Cn.* Cerebro-buccal connective ; *C.Cm.* Cerebral commissure ; *C.G.* Cerebral ganglion ; *C.P.Cn.* Cerebro-pedal connective; *C.Pl.Cn.* Cerebro-pleural connective ; *I.I.Cn.* Infra-intestinal visceral connective ; *I.I.N.* Infra-intestinal nerve ; *L.Cm.* Labial commissure ; *L.Pl.G.* Left pleural ganglion ; *L.S.N.* Left siphonal nerve ; *O.N.* Optic nerve ; *O.P.N.* Osphradio-pallial nerve ; *P.* Right pedal ganglion ; *Pa. N.* Parietal nerves of the left side ; *P.Cm.1.* 1st pedal commissure ; *Pl.G.* Left Pleural ganglion ; *R.P.N.* Right pallial nerve ; *R.Pa.N.* Right parietal nerve ; *R.Pl.G.* Right pleural ganglion ; *S.I.Cn.* Supra-intestinal visceral connective ; *S.I.G.* Supra-intestinal gangilon ; *S.I.N.* Supra-intestinal nerve ; *S.I.N.1—S.I.N.3* Nerves of the supra-intestinal visceral connective ; *St.* Statocyst ; *St.N.* Nerve of the statocyst ; *T.N.* Nerve of the tentacles ; *V.G.* Visceral ganglion.

anteriorly on the dorso-lateral side of the buccal mass. The cerebral commissure is fairly thick, flattened, band-shaped, and runs dorsally over the buccal mass. In addition the two cerebral ganglia are connected with one another by a fine nervous strand which arises near the apex of the inverted triangular ganglion and runs ventral to the buccal mass (L.Cm.); it is what Bouvier calls the " commissure labiale." It also gives a few branches to the parietal wall. The ganglion of each side is connected with the buccal ganglion of that side through a fine cerebro-buccal connective (C.B.Cn.), which, as already noted, starts from the ganglion in its posterior third on the dorsal surface, and becomes connected with the buccal ganglion on its outer, lower side. With the corresponding pleural and pedal ganglia the cerebral ganglion of each side is connected by thick band-shaped cerebro-pleural (C. Pl. Cn.) and cerebro-pedal (C.P.Cn.) connectives. These connectives lie ventro-laterally on the sides of the odontophoral mass. The cerebro-pedal starts from the inner angle of the cerebral ganglion and the cerebro-pleural more external to it.

The branches of the cerebral ganglia of the two sides, owing to the identical areas being supplied by them, are the same. These will be treated under two heads according as they arise from the inner anterior surface or the outer surface of the ganglion.

(*a*) Inner anterior nerves :—

(i) A very thin nerve (C.1) from outside the cerebral commissure and supplying the snout-skin outside the labial palp.

(ii) A thick strand arising from the outer side (C.2), it divides almost immediately and the two branches continue forwards to near the anterior margin where the nerves ramify into the skin of the snout.

(iii) Another branch rather thicker than the preceding (C.3) originates internally to it and goes to the base of the labial tentacles in the substance of which it divides into two. Both the branches supply the skin of the tentacle. In some dissections a fine branch for the skin was found to originate between the two branches.

(iv) A fairly thick branch (C.4) arising internally to the preceding goes to very near the margin of the snout, and supplies the skin on the ventro-lateral margins of the buccal mass.

(v) Arising quite close to and nearly as thick as the above branch is a nerve (C.5) which after a short forward course divides into two, one of the branches supplies the anterior part of the buccal mass on the ventral side and the other supplies the parietal wall.

(*b*) Outer nerves :—

(i) A thick nerve (T.N.) from about the middle of the ganglion to the tentacle. Near its origin it gives two fine nerves to the skin round the base of the tentacle.

(ii) Rather medially situated and somewhat thinner than the preceding branch is the optic branch for the eye (O.N.). This also shortly after its origin gives off two branches, one to the skin round the base of the eye-stalk, and the other to the stalk itself.

The nerve of the statocyst (St.N.) is a fine branch running along the cerebro-pleural connective on its ventral surface and is given off next to the optic branch from the cerebral ganglion.

Pleuro-pedal Ganglionic mass :—The pleuro-pedal ganglionic mass of each side is somewhat rectangular in shape and lies with the long axis of the rectangle at an acute angle to the long axis of the animal. There is only a slight delamination in the form of a notch between the pleural and pedal ganglion of each side, but there is no furrow of the type mentioned by Bouvier, who in his first paper (9) says " En examinant attentivement les deux masses, on aperçoit que chacune d'elles est divisée en deux portions presque égales par un léger étranglement." Jhering (39) calls this ganglion the secondary palliopedal, and says " An jedem Palliopedalganglion kann man eine grosse vordere Partie, das Pedalganglion, unterscheiden, von einer Furche gegen jene abgesetzten, den Commissuralganglion." In his second paper (40) the figure of the nervous system of *A. canaliculata* is certainly diagrammatic, and the pedo-pleural ganglionic mass is shown with a more or less distinct furrow. Lloyd (53) says that the ganglia are closely united but can easily be distinguished from one another. In his figure he shows a deep emargination on the left ganglionic mass and a quadrate united mass on the right side. Ghosh (34) describes " the ganglia being closely opposed to, although distinct from, each other," and represents the two ganglia on each side as quite distinct star-shaped masses lying side by side ; his representations of the pedal commissure and the secondary commissure between the two pleural ganglia is also faulty. As stated above it is not possible in *P. globosa* to distinguish betwen the two ganglia of each side except by the notch, the points of union of the cerebro-pleural and cerebro-pedal connectives and the nerves arising from each ganglion.

Another point to be considered here is the presence of a separate sub-intestinal ganglion in the Ampullariidae. In his first work Bouvier, from the nerve supply from the posterior part of the pleuro-pedal ganglion, was of opinion that the sub-intestinal ganglion was fused with this mass. This he upheld in his later work and as already stated criticised the faulty observations of Jhering on this head. Lloyd mentioned and described a definite sub-intestinal ganglion, and was in this followed by Ghosh. The latter author fully confirming Lloyd's work recorded in addition the occurrence of a number of sub-intestinal ganglia in a number of specimens examined by him. I have dissected a large number of specimens of *P. globosa* and can confirm the presence of such ganglionic masses, but all of them are equally developed and only represent thickenings of the nerve at the points of origin of the secondary branches. I, therefore, agree with Bouvier that the sub-intestinal ganglion in the Ampullariidae is fused with the right pedo-pleural mass. This view is confirmed by the fact that the nerves of the pallial and siphonal areas and the columellar muscle on the right side originate from this united ganglion.

Pedal Ganglion :—The area corresponding to the pedal ganglion (P.) of each side has been mentioned already. The two ganglia of the two sides are similar and are connected by two pedal commissures. The first main commissure (P.Cm. 1, text-fig. 17) arises from the anterior inner angle of the ganglion of each side and forms a transverse band nearly as broad as the pleuro-pedal mass. The second commissure (P. Cm.2, text-fig. 18) arises, as described by Burne (19) for *Ampullaria* sp. from the ventral surface of the pedal ganglion of each side below the pedal artery and connects the right with the left pedal ganglion. I agree with Burne in considering the commissure to be the anteriormost of the ladder commissures which unite the innermost main posterior pedal branches of the ganglia of the two sides. The statocyst lies attached to the pedal ganglion of each side near its posterior limit by means of a connective tissue band, which Ghosh wrongly considered to be the 'nerve of the otocyst'; this is further discussed under the account of the statocysts. The nerve supply from the pedal ganglia has only been described by Burne, but as my results differ from his in some essentials I describe it below in detail. The pedal ganglion sends a large number of nerves to the foot in the tissues of which a network-like arrangement similar to that described by Brock (14) for a number of molluscs is to be seen. The nerves will be dealt with under two heads, according as they arise from the anterior or the posterior margin of the ganglion.

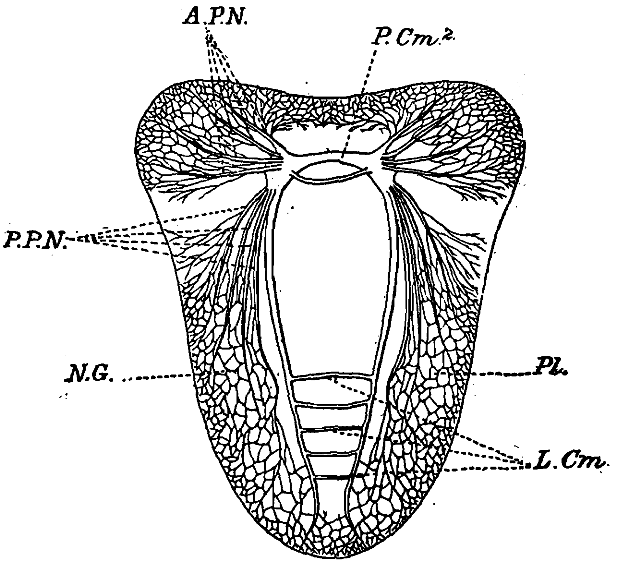

FIG. 18.—Figure illustrating the nerves of the foot of *P. globosa* as seen in a dissection from the ventral surface. *A.P.N.* Anterior pedal nerves; *L.Cm.* Ladder Commissures; *N.G.* Nerve ganglia; *P.Cm.2.* Second or lower pedal commissure; *Pl.* Nerve plexus; *P.P.N.* Posterior pedal nerves.

(*a*) Anterior Nerves :—In *P. globosa* there are 4 thick nerves (A.P.N.) and 3-4 minute nerves which arise from the anterior margin of the ganglion of each side. The three or four of the finer nerves supply only the muscles in the superficial area, while the four thicker nerves run downwards in the deeper muscular area of the foot and there running forwards spread out in a fan-shaped manner to about half an inch of the anterior margin of the foot. Here these nerves branch repeatedly sending lateral branches and have small ganglia at the points of origin of the nerves. The lateral branches unite with similar nerves from the adjacent ganglia, and form a regular plexus. In all two rows of large ganglia and a number of smaller ones between the first row and the margin of the foot are to be distinguished.

(*b*) Posterior Nerves :—From the ventral surface of the pedal ganglion of each side a thick nerve is given off on each side, this immediately after its origin gives off 4 main nerves (P.P.N.) on the outer side and these together with the main trunk run down into the substance of the foot backwards. The main trunks of the two sides are, as noted already, connected with each other by five ladder commissures (L.Cm.). The ventral commissure connecting the pedal ganglia of the two sides is probably the anteriormost connective of this series. After a short course they begin to spread outwards, and the nerves of each side supply the postero-lateral areas of the foot. Each of the nerves divides dichotomously and also sends off many lateral branches which extend to the margins. In the case of the two outer nerves of each side the plexus is not so well developed though there are ganglionic thickenings near the margins. The inner four nerves which run to the posterior edges of the foot have a less well developed but distinct plexus of the type found along the anterior border of the foot; it is formed by the lateral branches of the nerves. I could distinguish three to four transverse rows of large ganglia and a few rows of very minute ones in the marginal region.

Left Pleural Ganglion :—The position and shape of this ganglion (L.Pl. G.) have already been described in the account of the pleuro-pedal mass. It is connected with the right pleural ganglion not by a real commissure, but by the thin infra-intestinal nerve (I.I.N.) which, arising from the posterior side of this ganglion, forms a transverse band about twice as long as the pedal commissure and then continues backwards as the infra-intestinal connective to the visceral ganglion. The pleuro-cerebral connective from the left cerebral ganglion, the origin of which has already been described, is united with this ganglion somewhat to the inner side of the anterior angle of the rectangular mass. Its posterior angle is continued as a thick nerve which unites it with the supra-intestinal ganglion on the same side.

The nerves from this ganglion are as follows :—

(i) From the anterior side of the ganglion just below the pleuro-cerebral connective there is a small nerve which supplies the parietal wall.

(ii) Just next to and below the branch described above there is a fairly thick nerve supplying the inner part of the left siphon (L.S.N.).

(iii) From the postero-external angle of the ganglion just above the connective uniting this ganglion with the supra-intestinal ganglion arises the osphradio-pallial nerve (O.P.N.). It runs with the connective to very near its junction with the supra-intestinal ganglion and then curves outwards and upwards on the ventral surface of the mantle flap in a canal throughout its course to a little to the left of the osphradium in its natural position. In dissected specimens it is visible as a transluscent line through the inner covering of the mantle. It then sends a branch which curves to the outer side of the osphradium and divides in the mantle in this area and also supplies the anterior part of the gill. The main branch runs internally to the osphradium sending three to four branches into its base and ends as a fine branch in the mantle. Bouvier (9) describes this branch as the main nerve from the supra-intestinal ganglion and calls it the "branchio-palleal" nerve. In his second paper (11) he does not refer to it specially but figures it as originating from the supra-intestinal ganglion. In the case of the sinisteral Ampullariidae, however, he figures and describes it as originating from the left pallial ganglion. *P. globosa* and other species which I have examined all have this nerve originating from the left pallial ganglion and not from the supra-intestinal.

(iv) Three stout and two or three fine branches (Pa.N.) are given off from the posterior margin of the ganglion. The three main nerves supply the collumellar muscle,, while the fine branches ramify in the parietal wall. A few more branches, usually three or four, are also given off to the parietal wall from the outer left side of this ganglion.

Right Pleural Ganglion :—This ganglion (R.Pl.G.), as has been noted already, is similar to the left ganglion except that it has the infra- or the sub-intestinal ganglion fused with it. Its connection with the left pleural ganglion through the infra-intestinal nerve has already been mentioned. It is connected with the supra-intestinal ganglion by a thin nerve—the supra-intestinal nerve (S.I.N.), which according to Bouvier is the supra-intestnal branch of the commissure referred to above as the infra-intestinal nerve.

It gives off the following nerves :—

(i) From its outer side two or three nerves are given off to the parietal wall and the epitaenia above it.

(ii) A very stout nerve, the pallial nerve (R.P.N.), issues from it below the nerves described above. It first runs backwards and then curves out to the right, and running under the epitaenia comes to supply the right nuchal lobe, the copulatory organ and its pouch, while a thick nerve curves back from it to supply the rectum and the terminal part of the genital duct. In the males the nerve supplying the copulatory organ is much thicker than in the females.

(iii) Two or three fine nerves are given off from its inner side to the parietal wall (R. Pa.N.).

(iv) The columellar muscle on the right side also receives three or four nerves.

The connective between the supra-intestinal and the left pleural ganglion also sends two or three branches to the parietal wall in the area between these two ganglia.

Supra-intestinal Ganglion :—It (S.I.G.) is a slightly swollen, somewhat fusiform body lying in a sinus about a quarter of an inch behind the pleuro-pedal mass of the left side. Its connections with the pleural ganglia of the two sides have been mentioned already, while posteriorly it is continued as the left visceral connective which unites it with the visceral ganglion.

Ghosh is wrong in describing the supra-intestinal connective as " a fine nerve from the left pleural over the anterior end of the crop to the supra-intestinal ganglion." It arises from the right pleural, and as noted already is considered by Byuvier to be the supra-intestinal branch of the secondary commissure between the two pleural ganglia. It runs without giving any branches over the oesophagus from the right to the left.

The nerves from the supra-intestinal ganglion and the left visceral connective are as follows :—

(i) A stout branch (S.I.N.1) from the ganglion on its outer left side from opposite the junction of the supra-intestinal connective with the ganglion, runs outwards and in front of the pulmonary sac. It supplies the pallium and at its termination fine branches from it supply the gill in its anterior part. Minute transverse branches from it running forwards form anastomoses with the osphradio-pallial nerve which, as described already, is the third branch from the left pleural ganglion.

(ii) A large nerve (S.I.N.2) is given off from the connective on its outer side opposite the opening of the pulmonary sac and this ramifies in the walls of this sac.

(iii) Three or four nerves (S.I.N.3) are given off near the pericardial region, all from the outer left side of the connective, and these after supplying the walls of the pulmonary sac and the pericardium arch up to the gill on the right and supply the greater part of its posterior half.
(iv) A number of fine nerves both on the inner and outer sides of the connective supply the parietal wall at various levels.

There are no real accessory supra-intestinal ganglia, only the connective at the points of origin of the bigger nerves is swollen and assumes a ganglionic appearance.

Another point which may be noted here is the formation of anastomses between the symmetrical and asymmetrical nerves of the mantle or zygoneury. This, as noted above, occurs between the branches of the osphradio-pallial nerve from the left pleural ganglion and the first branch of the supra-intestinal ganglion.

As has been noted already the infra-intestinal ganglion does not exist as a separate ganglion. The branches of the right pedo-pleural mass show that Bouvier was right in assuming that the infra-intestinal is fused with it. Lloyd and Ghosh are certainly wrong in describing a separate supra-intestinal ganglion, the swelling designated as such by these authors is only a thickening of the connective at the point of origin of the lateral nerves from it. Other such thickenings of the connectives between the supra- and the infra-intestinal ganglia and the visceral are also present in *P. globosa.*

The infra-intestinal or the right visceral connective starts from the right pleuro-intestinal part of the pedo-pleural mass and running along the right side is continued to the visceral ganglion. It gives off 3-4 large nerves on the right outer side and a number of nerves on its left inner side to the parietal wall.

Visceral Ganglion :—It (V.G.) is not, as has been described by Ghosh, a simple triangular ganglion, but is, as was stated by Bouvier, formed by the union of two spindle-shaped masses. It lies near the base of the visceral mass close to the anterior lobe of the digestive gland and to the right of the pericardium. Its connections with the other ganglia have already been described. A number of minute branches are given off from the ganglion to the surrounding area while the two main branches from it are distributed as follows :—

(i) A rather thin branch from the right side, which sends branches to the renal organ, the middle part of the genital system and the intestine.
(ii) The left larger branch from the left lobe of the ganglion after sending two or three fine branches to the pericardium is continued backwards on the inner surface of the visceral mass and supplies the stomach, the digestive gland and the generative organs.

General :—The nervous system of the Ampullariidae was considered by Bouvier (9) to be chiastoneurous combined with a double zygoneury on both the right and the left sides. He was led to this conclusion by considering the inter-pleural commissure as a secondary one. This after uniting the two ganglia divides into two, the supra-intestinal nerve and the right visceral connective ; the sub-intestinal branch being absent owing to the fusion of the sub-intestinal ganglion with the right pedo-pleural mass. The chiastoneury is thus greatly disguised and no figure ot 8 loop between the supra-and the infra-intestinal nerves is formed. As to the zygoneury, it is normally brought about by the occurrence of anastomoses between the symmetrical and asymmetrical mantle nerves (Lang- Heschler, 48). The description of the condition in *Ampullaria* (*s.l.*) as chaistoneury with double zygoneury is not quite correct. Owing to the fusion of the infra-intestinal ganglion with the right pleural ganglion and the nerves also having a common origin no anastomoses are possible on the right side, and there is, as has been described above, only a zygoneury on the left side. The zygoneury even on the left side is somewhat disguised owing to the position of the gill.

SENSORY ORGANS.

Osphradium :—Earlier authors, in spite of the observations of Williams (86), called the Osphradium by the name of accessory or rudimentary gill. Lacaze-Duthiers was the first author to doubt the ctenidial nature of this organ in his paper on *Purpura* (45), and later (46), from its structure, came to the conclusion that the organ is of the nature of a sensory structure. Spengel (76), who gave a really good comparative account, agreed with Lacaze-Duthiers, and called the structure, which had meanwhile received the name of Lacaze-Duthiers's organ, the " Geruchsorgane " or the organ of smell. Most of the later authors, however, have designated it as Spengel's organ.

As to its function, Spengel, from the situation of the structure near the gill and from the respiratory water passing over it before reaching the gill, was of opinion that it is of use in testing both the chemical and physical qualities of the water, and probably in addition helps in the selection of the food materials. Bernard (6) who dealt at length with the comparative morphology and histology of the osphradium of various molluscs does not refer to the structure in the Ampullariidae. His conclusions regarding the Monotocardia as a whole bear out Spengel's work.

In *P. globosa*, the osphradium, as has been described already, is situated dorso-laterally on the roof of the mantle cavity, and hangs in the course of the respiratory current as a curtain. Its selective action in the case of the water-current has already been (p. 120) referred to. It may, however, be noted that the organ is a sensory one, and in spite of its position on the left side is homologous to the osphradium of other Gastropods. The osphradium in the various species of the genus *Pila* which I have examined is quite colourless and without any pigment whatsoever. Its macroscopic structure has already been described (p. 95).

The bipectinate arrangement of the leaflets on the two sides of a median axis seems to show that they are of the nature of double folds one on each side of and originating from a central axis. In a transverse section (Pl. XVIII, fig. 9) this arrangement is clearly to be seen. Here we find that the middle axis is not very distinctly marked off from the leaflets on the two sides, but appears as a little higher area in the middle. Each leaflet consists of the outer bounding layer of epithelium with the supporting and nervous tissue filling up the core with the exception of the blood spaces (B.S.). The epithelium is similar to that of the gill leaflets in being of three kinds, *viz.*, (i) sensory (S.C.), (ii) ciliated (C.C.), and (iii) glandular (G.C.). Of these three kinds the sensory epithelium occupies the greater part of the surface, and the gland cells are only distributed between the sensory and the ciliated epithelial cells, being most numerous amongst the ciliated cells. The sensory cells occupy the free margin from the middle axis outwards, while the lower margin, in its natural position which is partly attached to the middle axis and curves over to be continued with the mantle, is all lined by ciliated epithelial cells. In transverse sections one sees a narrow space between the mantle and the leaflets, and the entire lining of this cavity also consists of ciliated epithelial cells with a fair number of gland cells distributed in between them.

The epithelial cells (Pl. XVIII, fig. 10) of the sensory area are not so high as the ciliated cells, and have a fibrillar protoplasm with an oval nucleus rich in chromatin granules lying at different levels about the middle in the adjacent cells. All these cells are of the same type as the ones called the neuro-fibrillar cells by Bernard. I have failed to find any indifferent cells in between them. I have also failed to discover any connection between the neuro-epithelial cells and the multipolar ganglion cells in the nerves supplying the leaflets. The nerves branch and send delicate neurofibrillae, which branch repeatedly in all directions in between the epithelial cells and end freely near the surface. The condition is similar to that described by Dakin (24) for *Buccinum.*

The ciliated cells (Pl. XVIII, fig. 11) are of the same type as those of the gill leaflets. Their nuclei lie near the middle, and the chromatin granules of the nuclei stain deeply with iron-haematoxylin. Underneath the epithelium of the leaflets is a delicate basement membrane with the rather thin connective tissue layer consisting of the usual type of matrix and the star-shaped and rounded cells, and a few muscle fibres. Next there are a few blood spaces intercrossed by the nerves branching out from the central ganglionic mass lying in the middle. The ganglion (Pl. XVIII, fig. 9, N.T.) consists of a large central mass of neurofibrillae with the cortical ganglion cells arranged in two or three rows along the margins.

Eyes :—The eyes of *P. globosa,* as has been noted already, are two in number, and are situated on short stalks situated behind the long tentacles. They are not situated on the extreme tips of the stalks but lie slightly below and on the outer side of the tips. Seen externally they appear as deep black nearly rounded spots. The eyes of the apple-snail, as of all higer Gastopods, are closed vesicles fully cut off from the surface.

The general epithelial covering of the body, which is in continuation with that of the eye-stalks, is continued over the eyes (Pl. XVIII, fig. 12), and forms the cornea (C.) or the pellucida externa. This area consists of a single layer of rather squarish cells which are about $\frac{1}{3}$ the height of the epithelial cells covering the stalks. All the cells are uniform and there are no sensory or glandular cells in between them, as is the case with the epithelium of the body. Each cell, as has been noted already, is squarish with a nearly rounded nucleus lying near the middle and having a nucleolus lying in its centre. There is no pigment in the cells and the protoplasm is nearly homogeneous. Lying next to the outer cornea is a fairly thick layer of connective tissue (C.T.) consisting mostly of fibres with very few nuclei. The connective tissue layer is continued all round the optic vesicle and surrounds the optic nerve as it enters the eye.

The optic vesicle (O.V.) itself is a somewhat pyriform structure in horizontal longitudinal section, and has the optic nerve entering somewhat obliquely at its posterior end. The various layers which constitute the structure, enumerated from outside inwards, are :—(i) the surrounding layer of connective tissue (C.T.), (ii) pellucida interna or the internal cornea (I.C.) and the retina (R.), and (iii) the lens (L.).

The surrounding layer of connective tissue is definitely marked off from the main layer of connective tissue. It consists of circular fibres with large oval nuclei and is continued as a sheath round the optic nerve.

The pellucida interna or the inner cornea is the anterior continuation of the retinal coat, and is formed of very low cubical cells with very small nuclei. This area is in the form of a narrow arc.

The retina (Pl. XVIII, fig. 13) is distinguished from the anteriorly lying inner cornea by its cells being much larger and deeper and containing large numbers of pigment granules It is formed of two kinds of cells :—(i) the large and broad cells (S.C.) bearing the brush of hairs—" Stiftchen "—on their outer free ends, and (ii) the more compressed slender cells (I.C.) lying in between the first kind of cells. Both types of cells have pigment in their upper or anterior half, as has been described by Dakin (24) in the case of *Buccinum*, and in other higher Gastropods (*vide* Lang-Heschler 48). I have failed to find any differences beyond the absence of " Stiftchen" and the differences in staining between these cells, which have been described as sensory and pigment cells by Meisenheimer (55). The large cells, as in the case of other higher Gastropods, bear the brush of "Stiftchen " on their free ends. They have a large elongately rounded nucleus with a nucleolus and a number of other fairly large granules, and are prolonged at their inner end near the basal membrane into a number of processes. The processes are probably continued into the optic nerve. The second kind of cells have a smaller nucleus with more densely staining nucleolus and minute granules, and also appear to be prolonged into processes on their inner ends. They do not bear any " stiftchen," but are pigmented like the other corneal cells.

The space between the inner cornea and the retina is filled by an ovoidal, structureless mass which apparently serves as the lens and has been designated as such by all observers

I have no definite observations regarding the functions of the two kinds of cells of the retina, but it appears that the " Stiftchen " bearing cells are the true visual cells and the other type are only of the nature of a supporting tissue. This view has been advocated by Dakin, who further adds that the lens is probably secreted by the supporting cells.

As to the function of the eye, the snail does not seem to rely very much on its sense of sight. In all my experiments the snails failed to respond to objects unless these were held very close to the eyes and it appears, therefore, that in spite of the highly organised eyes their sense of sight is greatly limited in its range.

Statocysts :—During recent years a very good account of these structures of the Gastropods has been published by Schmidt (68) in which and Tschachotin's paper (82) references to all earlier works will be found. These structures had formerly been called otocysts, and their nerve the auditory nerve, and they are still referred to as such in many recent works. As, however, Delage (25) had shown for invertebrates in general, and Ilyin (38) and Tschachotin for molluscs in particular, they are not the organs of hearing but of equilibrium, and regulate the exact position of the animal in space, and should, therefore, be called by the more appropriate name of statocysts. In Gastropods two such organs are found in each individual, one in the vicinity of each pedal ganglion. Each statocyst has either a large single calcareous or horny particle in its cavity—an otolith or better still a statolith—or a large number of minute particles when they are termed otoconia or statoconia. These particles float in the fluid which fills up the cavity of the capsule.

In *P. globosa* there are two somewhat pyriform statocysts of a creamy colour lying embedded in depressions slightly outwards and posterior to the pedal ganglion of each side. Each (Pl. XVIII, fig. 14) consists of a leathery outer covering of connective tissue (C.T.) with a single layered epithelium for the lining of the cavity inside. The epithelium, as seen in sections, does not show cell outlines all over and appears to be of the nature of a syncytium nuclei arranged in a single layer and corresponding to the cells and cilia which line its inner surface are, however, to be made out. In some places a few unciliated cells which do not come up to the surface and which fill up the spaces in between the syncytium are to be seen ; these appear to correspond to the " Zwischenzellen" of Butschli. In the cavity of the capsule a large number of minute elliptical statoconia (S.) are to be seen. Its connection with the cerebral ganglion has already been described (p. 138).

Tentacles :—The varying sensibility of the different parts of the skin has already been referred to, and I will here only deal with the structure and function of the two pairs of tentacles.

Labial palps or the anterior pair of tentacles, as has already been noticed, are rather short, conical prolongation of the snout on the two sides of the mouth. They correspond to the " Mundlappen " or " Lippententakel " (Meisenheimer, 55) of *Helix pomatia.* These tentacles are contractile, but can not be retracted as is the case with similar structures of some other Gastropods. These tentacles are of the same colour as the snout.

On being dissected by a vertical longitudinal slit along the middorsal line the tentacles are seen to be nearly solid, with only narrow sinuses along the margins and at the tips ; the entire core being filled up with connective tissue and muscle fibres. The nerve which arises from the cerebral ganglion of the corresponding side gives various minute branches to different parts of the tentacles, but the main trunk can be followed to very near the tip.

Sections of the palps show that they are covered externally by an epithelial layer consisting of rather elongate cells with a thick cuticular outer covering. The sensory and gland cells of the same nature as are found in the skin covering of other parts are found in between the epithelial cells. The internal structure as seen in dissections is confirmed by sections. There is first the usual thin basal membrane and then the connective tissue layer with large number of muscle fibres and the nerve branches passing through it. The vascular sinuses are distributed along the sides and extend to the tip.

True tentacles or the second pair of tentacles are much longer and much more contractile than the labial palps. They are whip-like structures much thicker at the base than at the tips. Like the labial palps they are dorsally of the same colour as the snout but are much paler ventrally.

They have essentially the same structure as the labial palps. The epithelial covering is of the same nature and the only difference in the internal structure is that the muscle-fibres are mainly restricted on the outer ventral half of the core. The rest of the area is taken up by the connective tissue, nerves and muscle fibres.

BIOLOGICAL NOTES.

Habitat :—Except for species of the genus *Turbinicola* [1] Annandale and Prashad the Indian Ampullariidae all inhabit ponds, lakes, tanks, small streams or paddy-fields. They

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[1] Prashad, *Mem. Ind. Mus.* VIII, p. 86 (1925).

prefer living in clear waters with plenty of aquatic vegetation and are most numerous in areas where the water is renewed from time to time. In still tanks or ponds with stagnant muddy water they are much less numerous. During the dry weather animals retire into the deeper parts or lie buried deep in mud or nearly dry clay with their opercula tightly closed. As noted already they sometimes make long excursions on land in quest of areas with more abundant food or with more water. At such times they crawl very slowly on dry ground and leave a definite track due to the sticky secretion of the sole of the foot. Ramanan (63) has described the locomotory habits of the Madras *Pila* in detail and I have nothing to add to his account. *P. globosa* is also able to live in salt water of low salinity and I have found specimens of it in salt water ponds at Port Canning, Calcutta.

Food :—Ampullariidae are scrupulously vegetarian and mainly feeds on leaves of succulent plants like *Vallisneria* or *Pistia*, but Annandale (*loc. cit.*) records instances of their feeding on dead animal matter. They can live in aquaria for long periods without food of any kind and are able to stand long periods of drought by aestivation.

Breeding :—As noted in the general description of the species (p. 92) *P. globosa* breeds in Bengal during May and June and the eggs are laid about this time. In some cases, however, eggs may be laid even later. No observations have hitherto been published regarding the copulation or oviposition of any Ampullarid and I have not been able to observe these phenomena myself. I found the following note on the peculiar method of oviposition of the Madras species by Mr. V. V. Ramanan in a manuscript on the habits, etc., of some non-marine molluscs of Madras and now preserved in the Connemara Library, Madras.

" The *Ampullaria globosa* [1] Swainson invariably goes to the banks of the pond, puddle or river in which she lives for the purpose of spawning. She selects a place a few inches above the water margin, burrows underground till her shell is just visible above the mud and deposits her ova. So to speak, she incubates, after gathering the bunch of eggs within the folds of her mantle and foot and till the rather soft and transparent jelly-like substance of her spawn turns in a few hours considerably thicker, and each egg becomes invested with a pure white calcareous shell. After the operation is over, she returns to the water."

Eggs of *P. globosa* are laid in masses of two to three hundred. The eggs are firmly attached to one another and the egg-masses are found in rice-fields or along the banks of tanks or ponds above water level.

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[1] This species should be called *P. virens* (Lam.), see Prashad, *Mem. Ind. Mus.* VIII, p. 75, pl. xiv, figs. 1-3 (1925).

[2] Unfortunately Karl Hagler's paper entitled " Über neure Untersuchungen an Ampullariiden " published in *Vierteljahrsschr. Naturfor. Ges. Zurich*, LXVIII, pp. 360-379 (1923) was received in Calcutta after the present paper was ready for the press, and I have not been able to refer to it in my work.

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[1] I have to thank Prof. Karl Heschler of the Zoological Department of Zurich, Switzerland, for sending me a copy of this work. (*B. Prashad.*)

EXPLANATION OF PLATE XVI.

Fig. 1. Living animal of *P. globosa* with the elongate siphon formed by the left pseud-epipodium. × 1.

Fig. 2. Side view of living animal of *P. globosa* in water showing the broad funnel-shaped aperture formed by the left pseud-epipodium when the animal is respiring air near the surface. × 1.

Fig. 3. Egg mass of *P. globosa.* × 1.

Fig. 4. Operculum of *P. globosa* ; external surface. × 1½.

Fig. 4*a*. Operculum of *P. globosa* ; inner surface. × 1½.

Figs. 5, 5*a*. Ventral and dorsal views of the shell of freshly born young of *P. globosa.* × 6.

Fig. 6. Animal of *P. globosa* as seen from in front after the removal of the shell. × 1.

Fig. 7. Part of shell of *P. globosa* showing the region of attachment of the columellar muscle. × 1½.

Fig. 8. Dissected view of a female individual of *P. globosa* to show the organs of the pallial cavity. × 1.

Fig. 9. Surface view of a gill lamella. × 8.

Fig. 10. Osphradium of *P. globosa.* × 8.

Fig. 11. Surface view of the copulatory organ of a male of *P. globosa.* × 8.

Fig. 12. Ventral view of the penis-sheath slightly displaced to show the penis. × 8.

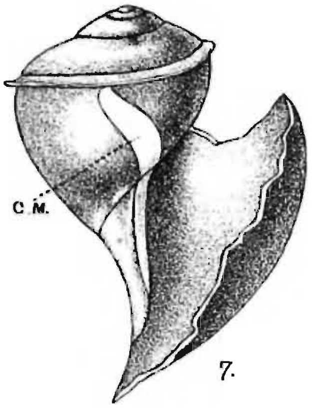
Fig. 13. Surface view of the rudimentary copulatory organ of a female of *P. globosa.* × 8.

Fig. 14. Ventral view of the dissected copulatory organ of a female of *P. globosa* to show the rudimentary penis. × 8.

Fig. 15. Jaws of *P. globosa* seen from above.

REFERENCE LETTERING.

B. Branchia or Ctenidium ; *C.E.* Cutting edge of jaw ; *C.M.* Columellar muscle ; *E.* eye ; *Ep.* Epitaenia ; *F.* Foot ; *H.G.* Hypobranchial gland ; *L.P.E.* Left pseudepipodium ; *M.* Mouth opening ; *M.A.* Ridge for the attachment of the sphincter muscle ; *Mt.* Mantle ; *M.P.* Membranous part of jaw ; *M.V.* Visceral mass ; *O.* Operculum ; *Os.* Osphradium ; *P.* Penis of the male ; *P.*^{1} Rudimentary penis of the female ; *P.C.* Pulmonary sac ; *P.C.O.* Opening of the pulmonary sac ; *P.S.* Penis sheath ; *R.* Rectum ; *R.P E.* Right pseudepipodium ; *S.* Siphon ; *Sh.* Shell ; *T1.* 1st pair of tentacles or labial palps ; *T2.* Second or true pair of tentacles ; *V.* Vagina.



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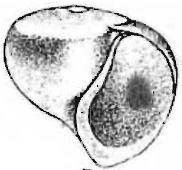

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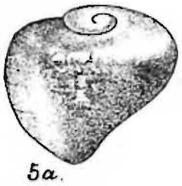

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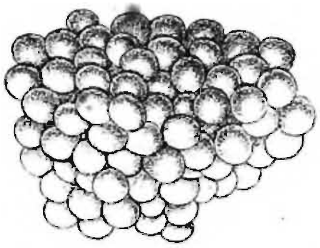

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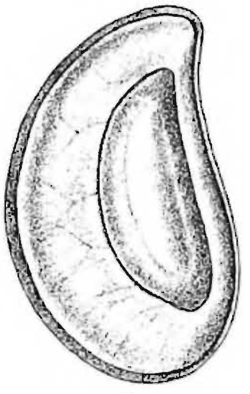

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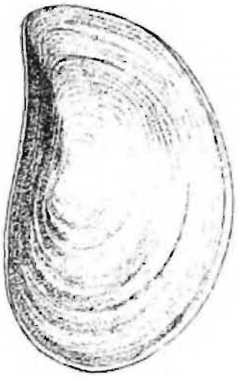

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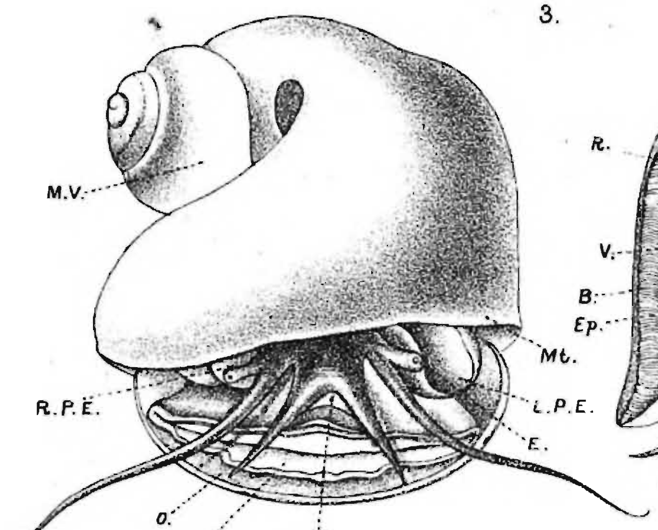

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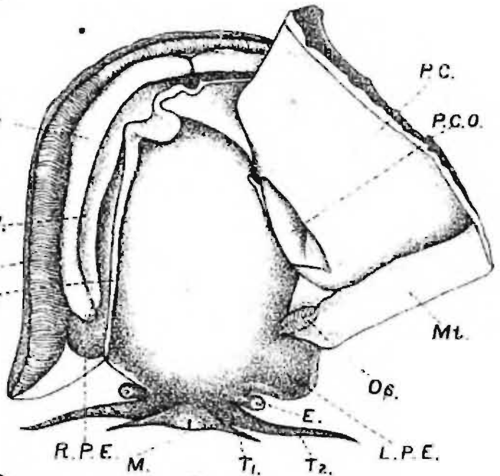

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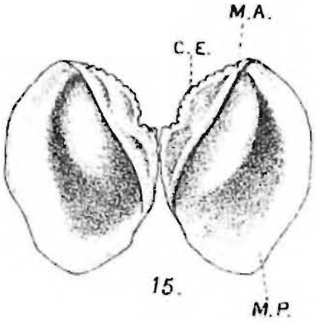

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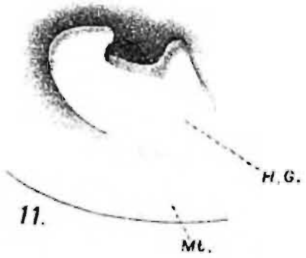

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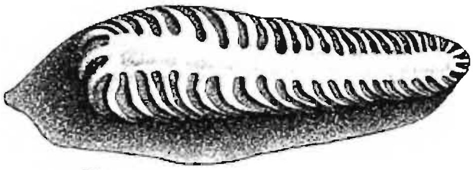

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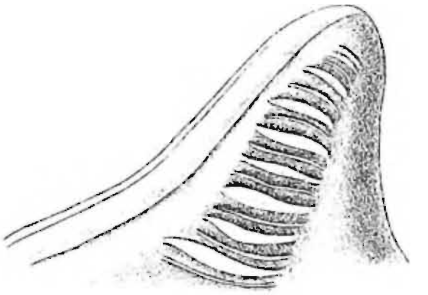

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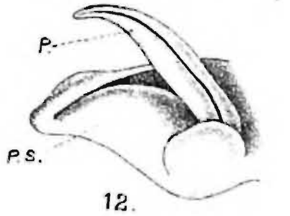

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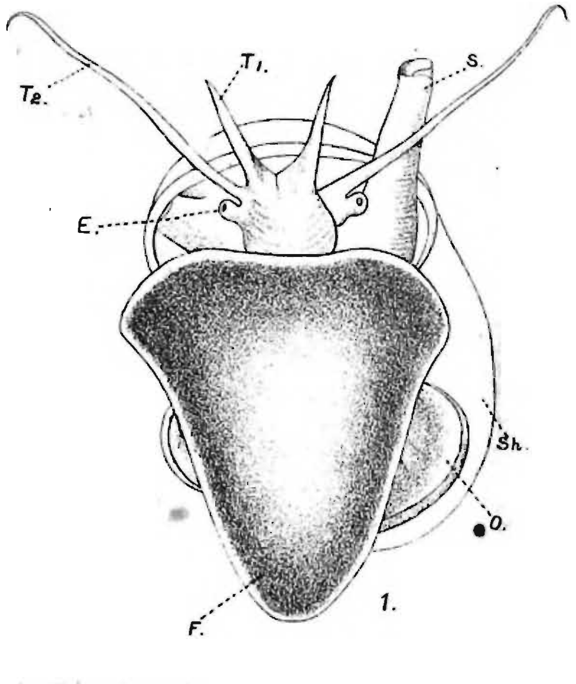

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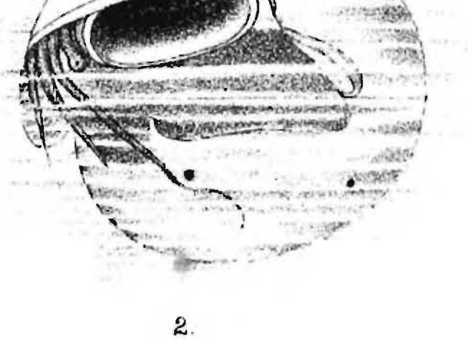

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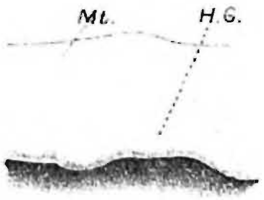

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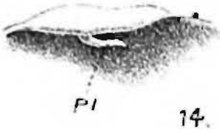


14.

A. Chowdhary del.

ANATOMY OF PILA GLOBOSA.

EXPLANATION OF PLATE XVII.

Fig. 1. Surface view of a portion of the pulmonary wall as seen with the high power of the microscope. × 250.
B.S. Blood spaces; *C.G.* Calcareous granules; *C.T.C.* Connective tissue cells; ***M.F.*** **Muscle fibres**; *P.G.* Pigment granules.

Fig. 2. Transverse section of a portion of the outer wall of the pulmonary sac. × 75.
B.S. Blood space; *C.T.* Connective tissue; *E.* Epithelium; *M.F.* Muscle fibres.

Fig. 3. A portion of the transverse section in fig. 2 more highly magnified. × 250.
Reference lettering same as in figs. 1, 2.

Fig. 4. Transverse section of two branchial leaflets with a portion of the mantle. × 75.
B.M. Basement membrane; *C.E.* Ciliated epithelium; *C.T.* Connective tissue of the mantle; *E.* Non-ciliated epithelial cells; *M.F.* Muscle fibres; *P.E.* Pallial epithelium; *S.* Space between the lamellae of leaflets.

Fig. 5. Non-ciliated columnar epithelium of the branchial leaflets. × 250.

Fig. 6. Ciliated epithelial cells of the branchial leaflets. × 250.

Fig. 7. Stomach of *P. globosa* with its upper wall removed. *A.C.* Anterior chamber; *C.O.* Coecal opening; *D.G.O.* Opening of the united ducts of the digestive gland; *O.* Oesophagus; *P.C.* Posterior chamber; *R.* Transverse ridge of the stomach.

Fig. 8. A portion of the inner cell lining of the Oesophagus. × 500.
E. Rodlet epithelial cell; *E.C.* Eosinophil cell; *G.C.* Gland cell.

Fig. 9. Outline of a transverse section of the intestine. × 50.

Fig. 10. Outline of a transverse section of the rectum showing the ridge (*R*) arising from the ventral surface. × 50.

Fig. 11. Surface view of the subradular organ. × 10.

Fig. 12. Transverse section of the subradular organ. × 250.
C.T. Connective tissue; *E.* Epithelial cells; *G.C.* Gland Cells; *M.F.* Muscle fibres.

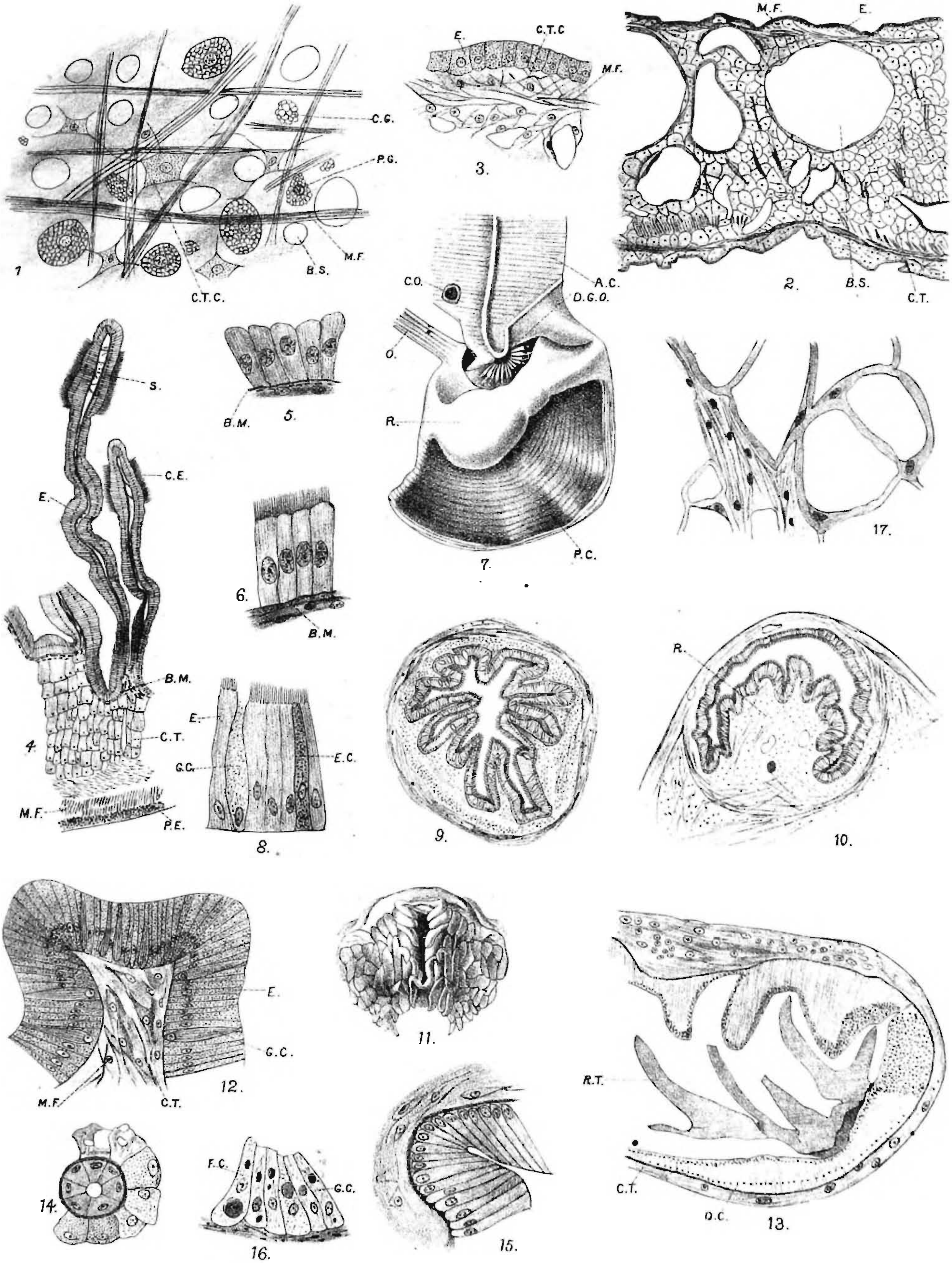
Fig. 13. Ventral longitudinal section of radular sac. × 500.
C.T. Connective tissue; *O.C.* Odontoblast cells; *R.T.* Radular teeth.

Fig. 14. Transverse section of one of the tubules of the salivary gland. × 300.

Fig. 15. Part of a transverse section of the Oesophageal pouch. × 300.

Fig. 16. Part of a transverse section of a tube of the digestive gland. × 300.
F.C. Ferment cells; *G.C.* Gland cells.

Fig. 17. Drawing of a transverse section of a part of the lateral cartilage. × 500.



B.P. del.

ANATOMY OF PILA GLOBOSA.

EXPLANATION OF PLATE XVIII.

Fig. 1. Heart of *P. globosa.* × *ca.* 10.

A. Auricle ; *A.A.* Aortic ampulla ; *C.A.* Cephalic aorta ; *E.C.V.* Efferent ctenidial sinus or vein ; *E.R.V.* Efferent renal vein ; *P.V.* Pulmonary vein ; *V.* Ventricle ; *V.A.* Visceral aorta.

Fig. 2. Longitudinal section of the anterior renal chamber. × 250.

C.T. Connective tissue ; *E.* Epithelial covering of the roof ; *E.S.* Efferent sinus ; *L.* Section of lamellae ; *M.* Muscles ; *R.E.* Renal epithelium.

Fig. 3. Transverse section of the roof of the posterior renal chamber ; the epithelial and connective covering of the roof is not shown. × 250.

A. 1st type of renal epithelial cells lining the chanels ; *B.* Second type of renal cells ; *C.* Channels of the posterior chamber ; *T.C.* Connective tissue.

Fig. 4. Transverse section of the penis of the male. × 50.

B.S. Blood spaces ; *C.M.* Circular muscle fibres ; *C.T.* Connective tissue ; *E.* Epithelium ; *G.* Penial groove ; *L.M.* Longitudinal muscle fibres.

Fig. 5. Eupyrene sperms of *P. globosa.* × *ca.* 1000.

Fig. 6. Oligopyrene sperms of *P. globosa.* × *ca.* 1000.

Fig. 7. Receptaculum seminis of *P. globosa* cleared in clove oil. × *ca.* 10.

Fig. 8. Dissection of *P. globosa* to show the position of the main nerve ganglia and nerves. The buccal mass and oesophagus are turned forwards and the greater part of the oesophagus is removed.

F. Foot curled forwards ; *L.B.G.* Left buccal ganglion ; *L.C.G.* Left cerebral ganglion ; *L.P.G.* Left pedal ganglion ; *L.Pl.G.* Left pleural ganglion ; *O.* Oesophagus ; *Os.* Osphradium ; *P.C.O.* Opening of the pulmonary sac ; *R.S.* Radular sac ; *S.I.G.* Supraintestinal ganglion ; *V.G.* Visceral ganglion ; *V.M.* Visceral mass.

Fig. 9. Transverse section of the osphradium. × 50.

B.S. Blood spaces ; *C.C.* Ciliated epithelial cells ; *C.T.* Connective tissue ; *G.C.* Gland cells ; *N.* Nerve ; *N.T.* Nervous mass ; *S.C.* Sensory cells.

Fig. 10. Sensory epithelial cells of the Osphradium. × 250.

B.M. Basement membrane ; *N.C.* Multipolar nerve ganglion cells ; *S.C.* Sensory cells.

Fig. 11. Ciliated and ganglion cells of the Osphradium. × 250.

C.C. Ciliated cells ; *G.C.* Gland cells.

Fig. 12. Horizontal longitudinal section of the eye. × 50.

C. Outer cornea ; *C.T.* Connective tissue ; *I.C.* Inner cornea; *L.* Lens ; *O.N.* Optic nerve ; *O.V.* Optic vesicle ; *R.* Retina.

Fig. 13. Retinal cells enlarged. × 250.

I.C. Intermediate cells lying between the Stiftchen ' cells ; *P.* Pigment ; *S.C.* ' Stiftchen ' cells.

Fig. 14. Statocyst of *P. globosa* cleared and mounted in Canada balsam. × 50.

C.T. Connective tissue ; *N.* Nerve ; *S.* Statoconia ; *S.C.* Capsule of the statocyst.

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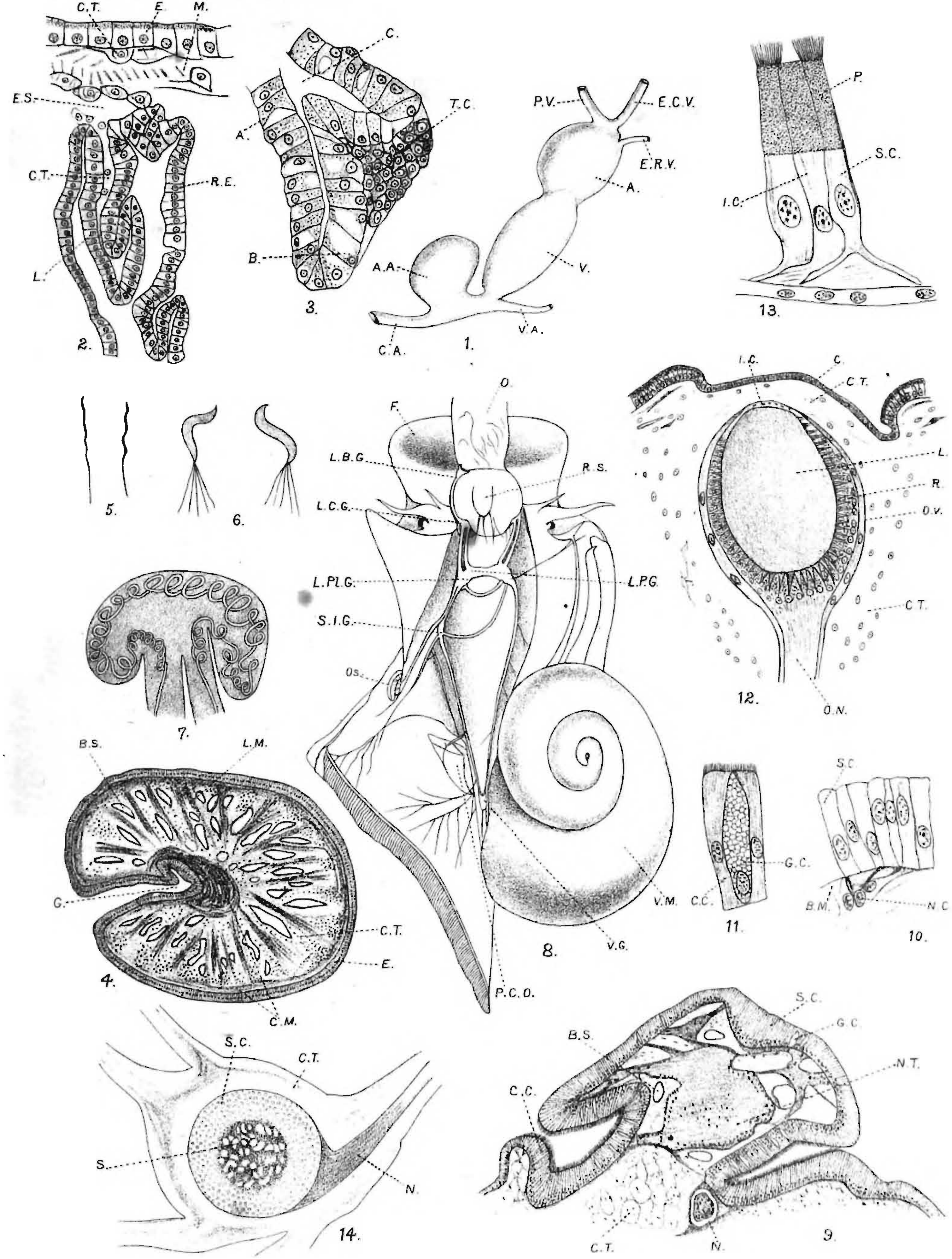

A Chowdhary, del.

ANATOMY OF PILA GLOBOSA.