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The Anatomy of *Lottia gigantea* Gray.

By

Walter K. Fisher.

Leland Stanford Junior University, California.

With plates 1—4 and 13 figures in text.

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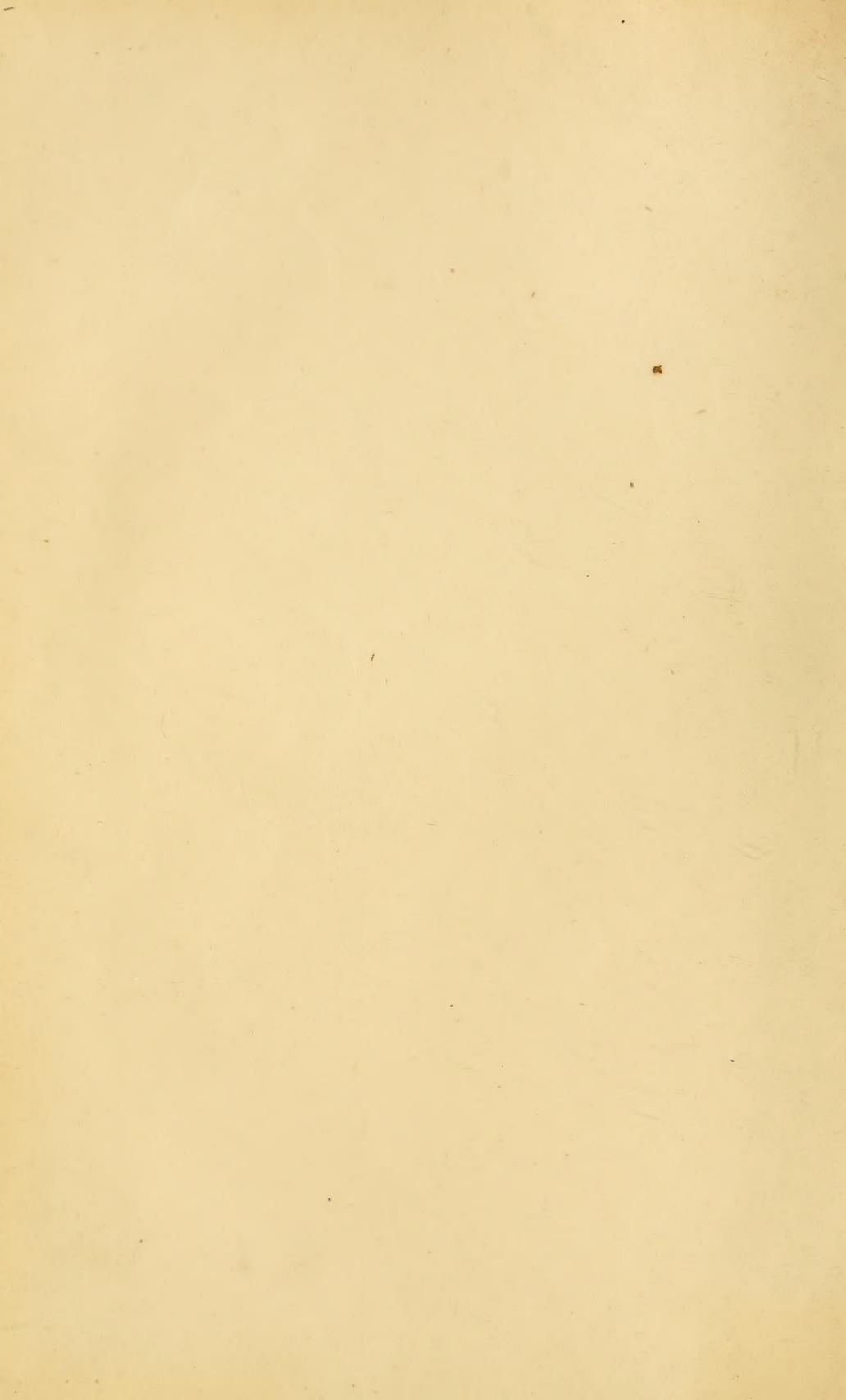
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# The Anatomy of *Lottia gigantea* Gray.

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With plates 1—4 and 13 figures in text.

Owing to the relatively large size of *Lottia gigantea* and the accessibility of fresh material, the following paper was undertaken primarily with the view of investigating the nervous system in some detail. At the same time it was deemed advisable to work out the rest of the anatomy, because for a long time many points in the organization of the *Acmaeidae* have been subject to lively controversy. It is hoped that the present contribution will aid in settling some of these questions.

The work has been carried on at the Leland Stanford Junior University, and at the Hopkins Seaside Laboratory, Monterey Bay, California. In this connection I wish to express my gratitude to Dr. HAROLD HEATH, who suggested to me the problem and who has since been ever ready with encouragement and kindly advice. For the facilities of the Hopkins Seaside Laboratory I am much indebted to the directors, Dr. C. H. GILBERT and Dr. O. P. JENKINS. I am likewise under obligations to Dr. W. H. DALL for naming a small collection of *Acmaeidae* from the coast, and to Mr. W. F. ALLEN for several times obtaining material.

**Methods.** For general dissection there is no better method than to place animals, killed in fresh water, into 70 % alcohol and then into 90. After they are thoroughly hardened they should be returned to about 70 % permanently and allowed to remain a year or two. The weak alcohol makes the tissues pliable and one can accomplish more than with freshly hardened specimens. Small individuals for sectioning should be killed in either VOM RATH's fluid, or ordinary alcohol. For the circulatory system I injected fresh

material with a gelatine mass colored by a Berlin blue solution<sup>1</sup>). This is more successful than carmine. Injections were made into the buccal sinus, and the large vein of the mantle. Ordinary ink with alcoholic specimens is often serviceable.

Material for the nervous system should be killed in fresh water to prevent contraction, and placed in a 5 to 10 % solution of nitric acid, until thoroughly hardened or until the shell comes off easily. Then it is transferred permanently into fresh 5 %, and left in a well lighted place to macerate. If specimens are to be kept for a considerable time they may be placed in a 2 or 3 % solution and laid away in a cool dark situation. In following out any of the finer nerves it is absolutely necessary to dissect in bright sunlight. By this method one can detect many minute nerves which in ordinary light are wholly invisible.

Habits. *Lottia gigantea* is common on the coast about Point Pinos, Monterey Bay, and to the southward. Most limpets are slug-gish creatures which love rough rocks and dashing air-laden waves. They are consequently found only above the level of moderately low tide, that they may be uncovered each day by the receding waters. *Lottia*, especially, shuns the sheltered coves, where the sea is still, and seeks rocky points where even during calm weather there is more or less surf from swells. It is noticeable that this species thrives best, and attains its greatest size south of Monterey Bay, where the coast is open, and exposed to the surge of the Pacific, and where on ordinary days the water, foamy and white, rushes and seethes among the rocks. Thus even at high tide the creatures are left by each receding wave, and then again engulfed by water supercharged with air. If one covers them with still water, in an aquarium, they usually attempt to crawl out, preferring the air.

It is a well known fact that limpets remain on (or at least return to) the same spot for a long time. They do, however, move about to some extent, as I was able to demonstrate with individuals near Hopkins Seaside Laboratory. About one third of those observed either merely turned around or wandered a foot or two, while the others were each day, for nearly a week, found at low tide in the same spot and position. The young of *Acmaea spectrum* (and of other species) are often found on the shell of *Lottia*, where they form

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1) MAYER, in: Mitth. zool. Stat. Neapel, V. 7, p. 310.

shallow cavities in which to rest (Fig. A). It is evident here that the creature remains in the same spot for a long time.

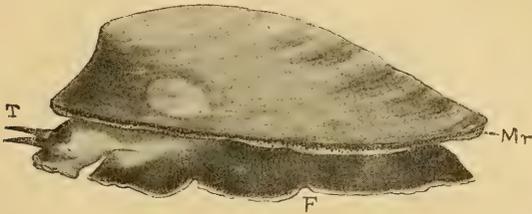


Fig. A. *Lottia gigantea*, natural size, viewed from one side. *F* foot, *Mr* mantle edge, *T* tentacle.

*Lottia* feeds by scraping the rocks, and its alimentary canal is usually gorged with diatoms. The length of the radula tube would seem to show that there is considerable wearing off of teeth.

External features. The outside of the *Acmaeidae* is almost too well known to need mention in this connection. But as *Lottia* differs in several respects from *Acmaea* a short description is here appended. The shell varies from oval to elliptical in outline and when oval is broadest toward the posterior part. In specimens of average large size the length of the shell is 55 to 60 mm, by 45 to 50 broad, and 16 or 17 high. The peak is low and is situated well forward, which enables one to recognize the young animals at a glance. The outside of the shell is usually rather uneven from growth lines and faint ridges radiating from the peak. These show more plainly about the margin. The outer surface of the shell is a light brownish, or sometimes green from algae, but the muscle scar and mantle portion of the inner surface are dark rich brown, frequently disposed in zones of different intensity, and all more or less faintly iridescent. The color of the central portion is a dull bluish white varied with brownish.

The mantle is well developed and broad, bearing a cordon of branchial lappets, which are absent however in front, opposite the opening of the pallial cavity. This recess is situated on the head as in all limpets, and is roofed by the mantle hood. There is a well developed ctenidium on the left side, attached not along one sinus as in the *Rhipidoglossa*, but by the base, something after the fashion of the chiton gill. This ctenidium, which has two series of lamellae extends diagonally across the head, and when fully relaxed the tip

protrudes from the pallial cavity. There are two osphradia, one on either side of the top of the head. The left, which is slightly the

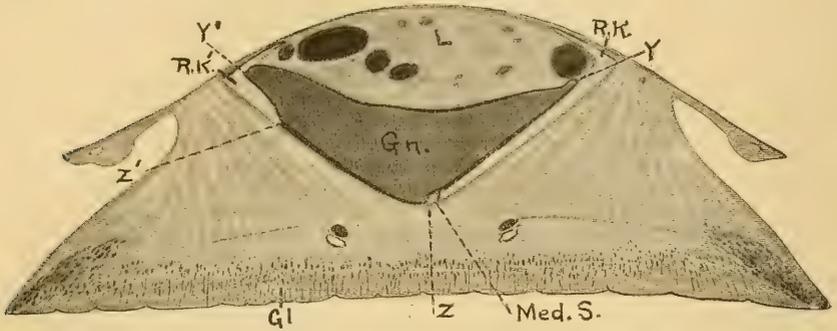


Fig. B. A cross section taken about the middle of the body to show the course of the muscle fibres of the shell muscle, and the disposition of gland cells in sole. *Gl* mucous cells in sole, *Gn* gonad, *Med. S* median blood sinus, *L* liver, *R. K* right kidney, *R. K'* that portion on left side of the body, *Y, Y'* point where blood vessels of gonad pass into membrane between gonad and right kidney, *Z, Z'* ventral line of attachment of this membrane.

larger, is in front of the base of the ctenidium, while the right occupies a similar position with respect to the anal opening. The large

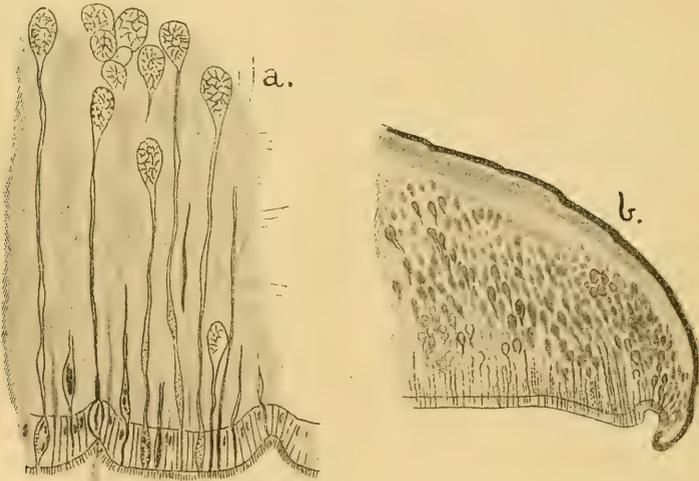


Fig. C. a) a few gland cells of foot enlarged, b) edge of anterior portion of foot showing the abundance of gland cells.

right ureter opens into the pallial cavity on the extreme right and posterior side, while the anal aperture is just to the left of it. The

left ureter is a tiny aperture on the left side of the rectum, which itself extends diagonally into the mantle cavity. The two feelers, situated on either side of the head, have slightly swollen bases, and are constantly moving when the animal is exploring. The eye is found on the outer and lower side of each tentacle. The foot is similar to that of other *Docoglossa*. There is no centralized pedal gland but individual mucous cells are very numerous throughout the sole, more especially in the anterior third, and around the margin. These gland cells are very large and are often situated deep in the tissue of the foot. They possess roundish or oval deeply staining bodies, with exceedingly long necks, by which the mucus reaches the surface (Fig. C). The epithelium of the sole is columnar, yellow, and covered with numerous short cilia. That of the sides of the foot, front of head, and distal portion of tentacles is black.

The attachment surface of the shell muscle is horse shoe-shaped, as in all limpets, and the free ends in front bound the mantle cavity on either side. The course of the muscle fibres is shown in Fig. B.

Dr. HAROLD HEATH has found specimens of *Acmaea spectrum*, and likewise of *Nacella sp.*, less than a millimeter in length, which possess a tiny nautiloid coil at the apex of the flaring shell. This larval coil is soon lost through decollation, and the familiar conical shell of the adult is left. Unfortunately at the time of writing these specimens have been temporarily mislaid, so that a figure of this interesting and important feature cannot now be published.

### Digestive System.

The mouth is nearly circular and opens ventrally when the head is held in a natural position. The lips, which form a wide wrinkled border about the aperture, are covered with an epithelium of rather high cells, and are roughly divisible into three zones. Near the margin there is a double furrow passing completely around, and the inner and deeper groove (*Sg* Figs. 7, 11, 18) is lined with cells which differ from those over the rest of the snout in being higher and staining more readily with haematoxylin. There is, moreover, a granular substance which stains densely, in the distal half of many of the cells. Between this groove, which may be more especially sensorial than the remainder of the lips, and the edge, one finds the outer smooth zone. Lastly between the sensory groove and the mouth opening the epithelium is closely beset with minute, sharp, cuticular teeth, which point inward. They are exceedingly numerous and are developed

between the epithelial cells, their bases resting on the basal membrane. But they are also bound one with another by the thin cuticle which covers the lips. In *Acmaea digitolis* THIELE<sup>1)</sup> has described similar structures but his figure (105) shows that they are simply projections or tiny spines on the cuticle, very similar to those on the palps of *Lottia gigantea* presently to be described. It is probable that these teeth in some way aid in scraping, or at least retaining small particles of food (At Figs. 7, 18).

The mouth leads directly into a spacious buccal or oral cavity. Within this the following features are to be noticed: the jaw, palps, radula, sublingual organ, subradular pouch, sublingual groove, and lateral pouches. The jaw is a rather pliable structure, and bounds

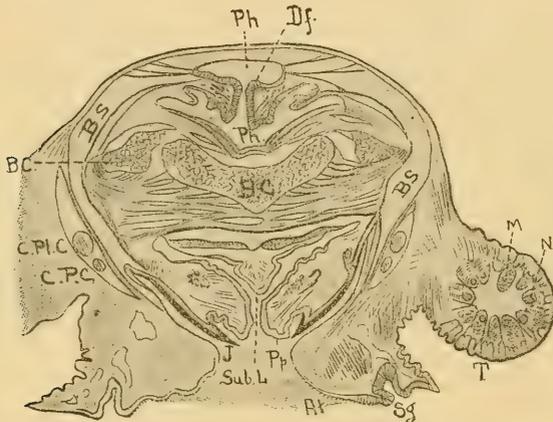


Fig. D. Cross section through head in region of mouth, to show sublingual organ and palps. *At* area of teeth on lips, *BC* buccal cartilages, *B.S* buccal sinus, *C.P.C* cerebro-pedal connective, *C.Pl.C* cerebro-pleural connective, *Df* dorsal fold of pharynx, *J* jaw, *M* muscles of tentacle, *N* nerves in tentacle, *Ph* pharynx, *Pp* palps, *Sg* sensory groove of lips, *Sub.L* sublingual organ, *T* tentacle.

the forward side of the oral cavity. It bends backward and downward at either side and forms a deep horny trough in the "upper" or forward lip. As has been suggested by THIELE this structure probably protects the lip from the radula teeth. But the heavy muscles attached to it would suggest that it also serves a more active function. It is noteworthy in this connection that the subradular furrow (Fig. 11, *Sub.L.F'*) serves the same purpose for the lower or hinder lip, and

1) Die systematische Stellung der Solenogastren und die Phylogenie der Mollusken, in: Z. wiss. Zool., V. 72, 1902, p. 338.

when seen from the outside, resembles an incipient lower "jaw". As shown in Figs. D and E the jaw is secreted by a fold of the same epithelium which lines the remainder of the buccal cavity, and in fact the inner surface of the jaw is in direct continuation with the cuticle which covers to a greater or less thickness all the interior of the mouth. The upper and outer corner of the jaw is thin and rounded (Fig. 10) and rests over the knob of each anterior lateral cartilage of the buccal mass. It has no connection with this cartilage, but is held in place by a heavy muscle (15 Figs. 4, 5, 9, 10) which passes downward under the cartilages, and partly attaches to their under surfaces, partly continues with the same muscle of the other side. Hence this muscle is a sort of anchor which tightly binds the jaw against the anterior lateral cartilages. Muscle 15 is also attached to these cartilages, and serves as a support or binder for them. Another strong muscle (16 Figs. 5 and 9) originates from the hinder end of the main cartilages and attaches on each side of the jaw below 15. Both 19 and 25 are retractors attached to the edge of the jaw and they serve to anchor it in place, as do also the small muscles (20 Fig. 3). I am unable to judge just how much these muscles, 19 and 25, are able to retract the jaw. Undoubtedly 15 holds the structure firm whenever it is used for scraping, if such is its use.

In this connection the buccal cartilages may be mentioned. Their general appearance when viewed from above can be better seen from Fig. 13 than described. The two main cartilages end posteriorly in ventrally directed divergent prolongations, which serve for the attachment of the heavy muscles working the radula. Anteriorly the blunt terminations are closely apposed and form the support of the rasp or odontophore. The two lateral cartilages are attached to the median ones only by dorsal and ventral muscles which hold them firmly in place. The median cartilages are bound together by loose tissue of the same nature as that composing the cartilages themselves, though much less firm. Small transverse muscles also aid in this binding. The cells composing the cartilage tissue are large with heavy walls and prominent nuclei. In section no cell substance is seen, only the heavy meshwork formed by the walls.

The palps are two thick folds of the lateral walls of the buccal cavity, extending from each side toward the center, where they meet, and when the animal is not feeding, cover the radula and sublingual organ (*Pp* Figs. 2, 4, 5, 9, 11 etc.). Their dorsal and ventral limits are well shown in Figs. 2 and 4. The position of the palps, sub-

lingual organ, and radula, when the animal is feeding, is illustrated by Fig. 11. The portion of the palp which appears smooth in this figure, is covered by columnar epithelium (Fig. E) over which is a thin cuticle beset with tiny sharp points or spines. The wrinkled portion of the palps (in Fig. 11) does not possess these minute points. In the upper part of the palps large mucous cells are present in the muscle and connective tissue (*M. C* Fig. E). Blood from the sublingual artery has free access to the spaces within the palps, which are undoubtedly extended or swollen by this medium. Special retractor muscles (6 Fig. 9) are present. These are well developed and extend from the interior of the palps to the posterior end of the buccal cartilages. A very abundant nerve supply springs from the lingual ganglia. Without any doubt there are no structures about the mouth which are so highly sensory as these.

The radula possesses no peculiar features, and its relations are shown in Figs. 2, 4 and 11. The muscles manipulating it are described below. On either side of the area of teeth there are chitinous wing-like expansions and these seem to function chiefly for the insertion of muscles (Fig. 16). The radula tube, just behind the buccal mass, passes out of the cephalic artery in which it is encased, and enters the blood sinus of the head, or head cavity, on the left side, then plunges into the visceral mass, being surrounded by the visceral artery. It then follows a course backward between the loops of the intestine (Fig. 1), curves to the right in the lower layer of the liver, then upward, and bends forward, returning to a point just above its entrance to the visceral mass. Here it reënters the head cavity, and ends in a little knob, attached to the anterior aorta, where it divides into cephalic and pedal arteries. In Fig. 14 the arrangement of teeth is shown.

The sublingual organ hangs from under the end of the odontophore into the subradular pocket. To all appearances it is a mere fold of the epithelium, wrinkled transversely when not turgid with blood. But it is really a quite definite structure, as is now well known. In cross section it is triangular because of a slight longitudinal constriction on either side, where the organ joins the dorsal wall of the subradular pocket (Fig. E). Seen from the front, when the creature is feeding, its relations are shown by Fig. 11. Fig. 4 gives an idea of its position when viewed from the side. The organ is covered with a cylindrical epithelium which secretes a heavy cuticle, produced into sharp teeth, forwardly directed. These tiny teeth are

rather smaller than those on the lips, and are disposed in irregular transverse rows. They are larger on the posterior half of the organ and extend forward nearly to the tip, and on either side, to the longitudinal groove. They have been noted and figured by THIELE in *Acmaea digitalis*, *A. virginea* and *A. viridula*. The interior of the organ is filled with muscles except a large central space where the blood enters. This supply of blood is derived directly from the sublingual artery, a ventral branch of the cephalic, and both observation and experiment show that the organ is distended by the blood. It is retracted by special muscles lying under the radula protractors. The nerve supply, which is rather rich, springs from the subradular ganglia. These ganglia are situated on the lower side of the subradular pocket

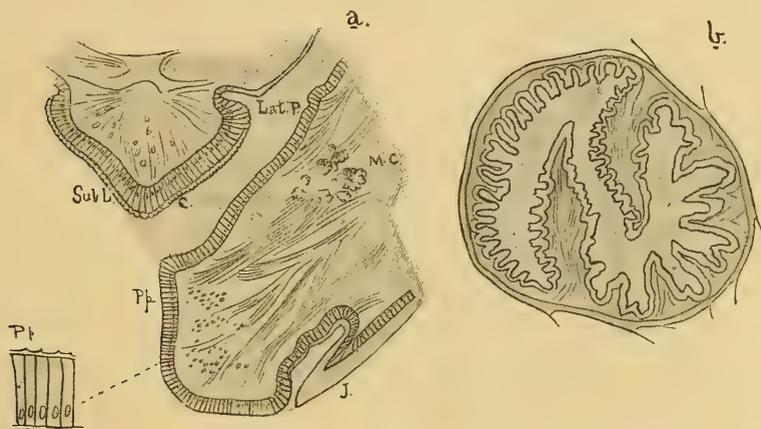


Fig. E. a) the sublingual organ and one palp from Fig. D enlarged. *c* cuticle, *Lat. P* lateral pouch, *M. C* mucous cells; b) cross section through rectum near left ureter to show folds in walls.

at its far end, and are connected by slender nerves with the lingual ganglia. Nerves are given off which pass along the dorsal wall of the subradular pocket and spread out in a network under the epithelium of the sublingual organ. One is not prepared to say definitely whether or not the sublingual organ is homologous with the subradular organ of the chitons but it is certainly a significant fact that the sublingual organ is innervated by the subradular ganglia, which I believe are homologous with those of the chitons. These ganglia will be treated more fully under the nervous system.

Extending backward under the odontophore and sublingual organ is the subradular pouch (Fig. 4). Along the middle of this is a trough-

like depression leading out onto the "lower" lip. It is lined with thick cuticle, secreted by a cylindrical epithelium. At either side the epithelium rests on a core of supporting cells resembling those which make up the buccal cartilages. This sublingual groove acts as a track on which the sublingual organ slides out and back, with the working of the odontophore, and the cuticle is probably a protection against the teeth of the sublingual organ.

The lateral pouches of the oral cavity are merely pockets on either side of the odontophore, between it and the palps.

Just above and almost in communication with the palps, on either dorso-lateral wall of the oral cavity begins a thick fold (*Df* Figs. 2, 4, 9). These two presently become the dorsal or greater folds of pharynx and oesophagus. From their commencement just above the palps, to about the beginning of the pharyngeal or posterior buccal gland, the folds are filled with mucous cells of large size, which open into the oral cavity, or pharynx, as they are forwardly or posteriorly situated. Each cell (*M. C* Fig. 25) consists of a long tube leading from the epithelium through the connective and muscular tissue, to the base of the fold where it ends in a vacuolated expansion, the cell proper. This stains deeply with haematoxylin. It is probable that the cells secrete mucus which may serve to entangle bits of food into a sort of string. In fresh specimens, yet alive, these folds are seen to be covered with a transparent glairy secretion and are of a pale yellowish color. The epithelium of the folds or ridges is columnar and ciliated, the cells being higher than those forming the remainder of the lining of the posterior portion of the buccal cavity.

The oral cavity passes into the dilated pharynx or crop. The opening of the radula tube is covered by a prominent lip. There are regular constrictions in the pharynx which form rather deep lateral pockets, but the mid-dorsal and mid-ventral regions are occupied respectively by the dorsal or greater and ventral or lesser folds of the pharynx and oesophagus. The former begin, as mentioned above, in two dorso-lateral ridges of the oral cavity. These rapidly approach each other (Fig. 2) and come to occupy the mid-dorsal line, with the beginning of the pharynx. At the posterior end of the pharynx they pass to the left, around the oesophagus (*Df* Fig. 6), come to lie on the ventral side, and finally reach the right side, where they end abruptly with the proventriculus or fore chamber of the stomach (*Pro*). The two folds are so deep that the free edges are folded back, as they hang in the narrow lumen of the oesophagus. Smaller, length-

wise plications on these greater folds are also to be seen. The lesser fold of the oesophagus begins as two ridges at either side of the opening of the radula tube (*Vf* Fig. 2). These converge, and at the posterior end of the pharyngeal cavity unite to form a single fold with two free edges, which, like those of the greater lamellae, turn back. The width of the lesser fold is scarcely a fifth that of the greater. This ventral fold follows a course exactly on the opposite side of the oesophagus from the other, and as shown by Fig. 6 comes to lie on the dorsal and finally on the right side of the oesophagus, ending like the other, after completing a turn of nearly 270 degrees. The epithelium covering both the greater and lesser folds is composed of high ciliated cells with numerous interstitial gland cells which stain deeply with haematoxylin. These cells have the same structure as the mucous cells opening into the buccal cavity, as described above, except that the long slender neck is wanting. The mucous cells pass into these interstitial cells of the oesophageal folds by degrees, from a shortening of the long tube and a gradual lessening in size. In the connective tissue between the two layers of each fold is a blood sinus, which communicates with the network of sinuses in the connective tissue and muscular covering of the oesophagus, and these in turn with a special oesophageal artery, with the visceral artery, and also with the blood sinus of the head cavity.

Between the greater and lesser folds, the lateral walls of the pharynx are thrown into pockets as before mentioned. These pockets become smaller posteriorly and with the commencement of the oesophagus proper are mere spaces between close-lying folds, whose relations with the others can be readily made out in Fig. 2. These also end with the proventriculus, and are covered with cylindrical epithelium, the gland cells being scarce or absent.

There are two paired glands in the oral region of the alimentary canal. The anterior or buccal gland is really situated behind the posterior or pharyngeal gland, but opens by a long glandular duct, into the oral cavity on a dorso-lateral fold, above the palps (Fig. 2 *Bg*, *Bg.D*, *Bg.D'*, also Figs. 1 and 6), and is hence counted first. This pair of glands might easily be overlooked in dissection because they are very inconspicuous. It is only the ducts that afford a good landmark. But in fresh unhardened specimens they appear white, and hence are easily seen. The buccal gland of the right side is spread out over the septum which separates the head cavity from the viscera, in a thin layer, and dorsally mingled with connective tissue extends

about the visceral loop. That of the left side is a trifle more elongate and has a similar position, being wedged in between the septum of the head cavity and the gonad, and posteriorly between the gonad and oesophagus. It is all but impossible to differentiate this from the wall of the oesophagus in a preserved specimen. If the septum of the head cavity on the right side be removed, however, and stained with haematoxylin, cleared and mounted, the gland is seen to consist of many tiny lobules, which, uniting, form larger ones, till a racemose structure is the result. Out of this, several collecting tubes unite into one, which passes forward beside the pharynx, as described above. Under the microscope the duct is seen to consist of a central cavity lined by small cubical cells, rather indistinct. Either in the lumen or to one side a small nerve (arising from the stomatogastric ganglia) passes along the whole length of the duct. Crowded about the small cells lining the lumen are large cells of two sorts: lesser pear-shaped cells full of heavily stained granules, and greater, more numerous, much vacuolated ones (Fig. 12). The gland itself is simply a repetition of this structure, save that the small lining cells are absent except in the collecting tubes. In many of the lobules there seems to be little or no lumen. In a whole-mount of the gland the granular cells stain heavily and can be readily detected. They are outnumbered by the larger vacuolated kind. I am unaware of the nature of the secretion.

The posterior, salivary, or pharyngeal glands (Figs. 1, 3 etc. *Ph. G*) are conspicuous, being tufted structures on either side of the pharyngeal dilation. They are composed of groups of small finger-like blind tubes opening into tiny pockets, which, in turn are divisions of the lateral sacculations of the pharynx (Fig. 8). Rarely these acini or ultimate glandules are branched once, and the tips, in preserved specimens at least, are likely to be slightly swollen. In fresh specimens the acini are very long, reaching, if turned back, quite across the pharynx. The epithelium lining the tubules is low, the cells possessing small deeply staining nuclei. In the distal part of the tubule the lumen is filled with loose tissue, apparently proliferated from the epithelium, which seems to store the secretion, for when empty only cell walls are seen. The secretion stains deeply and is found in the distal end of the glandule. In *Acmaea patina* this gland is relatively much smaller, the acini being larger and scattered, not in little bunches or tufts. Similarly the anterior or buccal gland is larger and the component parts more conspicuous. Otherwise they seem much alike in

the two species. In *Acmaea patina* the lateral walls of the pharynx are much more extensively and intricately folded than in *Lottia gigantea* and the lateral pockets are deeper. It would seem that the walls are glandular.

The oesophagus passes nearly directly backward from the pharynx, to slightly beyond the middle of the body, lying beneath the stomach and distal arm of the intestine, and being covered by a portion of the gonad. It turns to the right to enter the fore chamber of the stomach (Fig. 1). After another constriction the canal widens out into the stomach which curves around the liver and, making prominent posterior and anterior elbows, arrives again close to the proventriculus, and slightly under it. Except in the distal end where it curves downward, the stomach lies in one plane, juxtaposed to the distal arm of the alimentary canal. At the extreme anterior end of the stomach the large liver duct empties into the lumen. Along the ventral wall, and on the opposite side along the dorsal wall, there is a ribbonlike tract, running from the fore end of the stomach well into the intestine, where the epithelium is raised in little close-set crosswise plications, like an "endostyle" (Fig. 17 S). I do not know the function of these ridges. Beyond the stomach the intestine passes forward and makes a turn in the region of the subintestinal ganglion. Turning sharply backward a complete loop is executed under the forward arm of the stomach, and another forward elbow is made, in advance of the previous one, and fairly behind the septum of the head cavity and right buccal gland. From here the course is obliquely backward and to the left, under the oesophagus. After an S-shaped turn under the proventriculus the intestine curves upward and forms a final loop around the stomach passing forward and to the right, to open into the mantle cavity immediately to the left of the right nephridial papilla. The course of the canal can be much more easily understood from Fig. 1. The walls of the rectum are folded longitudinally (Fig. E) the folds completing a partial spiral. Two folds are much larger than the others, and the walls of these are in turn plicated. The epithelium is composed of high clearly defined cells with nuclei near the base, a very thin cuticle and abundant cilia, about one-third or a half as long as the cell itself.

The liver lies in the spaces between the intestine, from the gonad below to the dorsal wall above. It almost completely covers the stomach, and extends forward around the anterior bends of the canal.

Its ultimate branches are essentially tiny blind ducts or lobules, the lumen of which is surrounded by the liver cells.

From a joining of these, larger spaces or sinuses are formed, till finally the main collecting canals result, which uniting into one, open into the stomach at its anterior end. The liver cells line the duct to its union with the stomach.

### Excretory System.

The nephridia. The nephridia of the Docoglossa have given rise to considerable controversy, not only respecting their extent but also regarding the so-called reno-pericardial canals. The *Acmaeidae* have more especially been the subject of debate in recent years. As to the extent of the kidneys there can be no possible doubt, for in *Acmaea mitra*, *A. spectrum*, *A. pelta*, *A. patina*, *A. scabra* and *A. persona*, as well as in *Lottia gigantea* essentially the same relative positions are held by the right and left nephridia, and the disproportion in the size of the two also obtains in all these species. Consequently it is with considerable perplexity that one must regard the remarkable results of BÉLA HALLER's work on *Lottia viridula*<sup>1</sup>). In fig. 15 of his "Studien über Docoglosse und Rhipidoglosse Prosobranchier" the right nephridium is represented as made up of two relatively small sacs joined by a narrow neck. One of these sacs opens to the exterior, the other communicates by a remarkable passage with the pericardium. The animal which possesses such a nephridium has no place in the *Acmaeidae*. As suggested by WILLCOX (in: Zool. Anz., Jg. 1901, p. 623) HALLER has probably taken only a portion of the right kidney, calling the rest coelom. Even with this explanation, there are other incongruities in the figure which are not explained, as, for instance the wide mouth, into the right kidney, of the reno-pericardial duct. This does not accord with the condition found in every *Acmaeid* which has so far been examined by other observers, nor with the structure in the *Patellidae*. As a matter of fact the opening is excessively small.

When the shell is removed from a yet unhardened *Lottia gigantea* the extent of the large right nephridium is easily observed through the dorsal body wall, by reason of a dark green excretion which covers the renal epithelium. The nephridium is thus seen (Fig. 20 *B.K.*, in blue) to encircle almost the whole visceral mass from right

1) Studien über Docoglosse und Rhipidoglosse Prosobranchier, Leipzig 1894.

to left and to end in a cul-de-sac immediately behind the pericardium. Peripherally it is bounded by the spindle muscle, but toward the liver many finger-like pockets form a sinuous and irregular outline. Below, however, where the renal epithelium stretches over the gonad (or rather over the coelomic epithelium), there are none of these pockets. On the right side of the body the right nephridium extends, as shown by Figs. B and H to the mid-ventral line of the cavity which holds all the viscera, and from the hind wall of the buccal sinus in front, nearly to the upper edge of the spindle muscle behind. On the left side, its dorso-ventral dimension is much less, only about one third that of the right side. The remainder of the space to the mid-ventral line is taken up by the gonad surrounded by a potential secondary body cavity or coelom. A ground plan of the right kidney would be shown by Fig. K. In front, on the right side, there exists most of the free space of the kidney. The fact that the anal opening and the large right ureter extend out into the mantle cavity, as a sort of papilla, divides the forward portion of the nephridium into a ventral or subanal, and a dorsal or rectal portion (Fig. F *RK'* and *RK*). The rectal portion is thus an outpocketing into the pallial cavity and the subanal an encroachment on the buccal sinus. The two are separated by a portion of the mantle cavity, and where the rectal and anal portions fuse to form the main cavity of the kidney there is a ridge of muscular tissue as shown in Fig. 26, which is simply a fold of the body wall. From the upper or rectal part, the kidney opens to the exterior by a large ureter, with thick muscular lips. The reason for distinguishing carefully these rectal and subanal portions — purely artificial divisions I admit — is to locate more clearly the opening of the reno-pericardial canal and gonad duct. In its very forward part, the right kidney is so large that it extends practically from the mid-ventral line to the mid-dorsal, but the reader must remember that through most of its course, the cavity is largely occluded by encroachments of the visceral mass and gonad, especially during the breeding season.

The dorsal wall of the kidney from within presents a curiously fenestrated appearance, due to the intricate outsacking of the renal epithelium through all the interstices caused by several layers of innumerable veins. These veins form a net over the cavity, as described under the circulatory system. This characteristic appearance extends over all the area colored blue in Fig. 20.

In sharp contrast to the right kidney, the left is very small. It

is situated on the dorso-sinistral side of the rectum, on that part which extends freely into the pallial cavity (*L. K.*, in red) and opens like the right, abruptly to the exterior. This opening is near the anterior end of the kidney and is much smaller than the right ureter. It does not form a papilla like the right. The dorsal wall of the left kidney is also fenestrated. The extent of the cavity is best shown by Figs. 26 and F. Although the two kidneys approach each other very closely over the rectum, so close indeed that the acini seem to interdigitate in some places, I have been unable to find an actual connection between the cavities of the two.

The left nephridium, as well as the right, is actively excretory, and the epithelial linings of the two are identical. The epithelium is columnar to cubical, according apparently as it is situated over a highly vascular area, or over one with little blood, as for instance the muscular outer wall of the body (shell muscle). A large part of the epithelium is what is usually called low columnar. The cells which have roundish or oval nuclei are not very definite of outline, and are clogged with fine granular matter, and often with bodies about half as large as the nuclei. This granular matter, together with the larger transparent bodies, is found thickly packed among the fine cilia with which the epithelium is beset, in such a manner as usually to obscure the cilia. Such excreted matter, as seen in sections, is undoubtedly the decolorized greenish material which stains the kidney during the life of the animal. The epithelium of the left kidney is as active as that of the right and there is considerable of a blood supply considering the diminutive size of the organ.

The reno-pericardial canals. In *Lottia gigantea* both nephridia are in communication with the pericardium. This agrees with what GOODRICH<sup>1)</sup> and PELSENEER<sup>2)</sup> have found in other species of the Docoglossa. (Compare Fig. F with PELSENEER's fig. 100, l. c., tab. 11.)

The reno-pericardial canals are not short and to be seen in a single transverse section, but are long and lie in several planes, and are rather difficult to follow throughout their whole length. By means of an injection of ink in one specimen, and the fortunate

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1) EDWIN S. GOODRICH, On the reno-pericardial canals in *Patella*, in: Quart. J. microsc. Sc., V. 41, 1898, p. 323.

2) PAUL PELSENEER, Recherches morphologiques et phylogénétiques sur les Mollusques archaïques, Bruxelles 1899.

presence of gas in the canal of another, I was able to follow these ducts quite to the papilla by gross dissection. The relations are shown in Fig. 26.

The canals are for the most part prolongations of the pericardium, only that exceedingly small portion within and just adjacent to the papilla (which marks the opening into each nephridium) is ciliated and possesses a high epithelium (Fig. G).

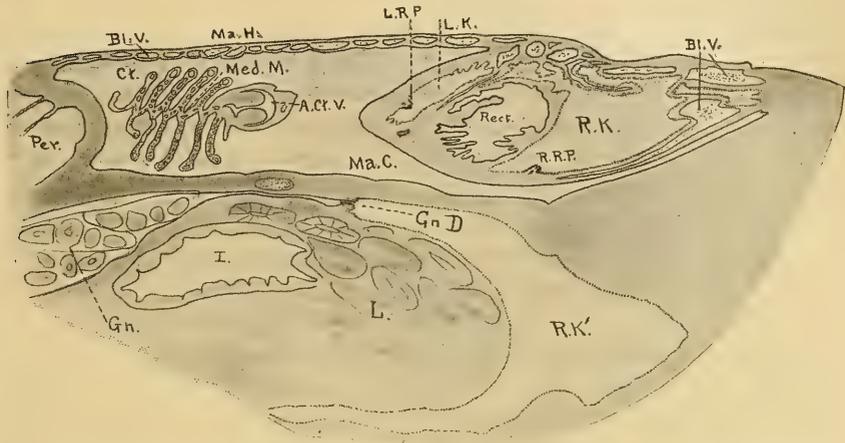


Fig. F. An oblique transverse section through portions of the right and left kidneys, mantle cavity, gonad, and visceral mass of right side to show openings of reno-pericardial canals and gonoduct. The gonoduct is actually somewhat in front of this section. *A. Ct. V.* afferent ctentidial vessel, *Bl. V.* blood vessel, *Ct.* ctentidium, *Gn.* gonad, *Gn. D.* gonoduct, *I.* intestine, *L.* liver, *L. K.* left kidney. *L. R. P.* left reno-pericardial pore, *Ma. C.* mantle cavity, *Ma. H.* mantle hood, *Med. M.* median membrane of ctentidium, *Per.* pericardium, *Rect.* rectum, *R. K.* rectal portion of right kidney, *R. K'.* sub-anal portion of right kidney, *R. R. P.* right reno-pericardial pore.

The right posterior corner of the triangular pericardium narrows down abruptly to a funnel-shaped opening directed toward the right and slightly downward. This canal on reaching the rectum divides into two branches, the left passing forward along the outer wall of the left kidney to a short distance behind the left ureter, where it opens into the nephridium by a tiny papilla, lined with high epithelial cells beset with long cilia. The other branch of the pericardial prolongation dips down under the rectum, and comes to lie close beneath the renal epithelium of the rectal, or upper, portion of the right kidney. It then turns forward, parallel to the rectum, and opens by a tiny papilla, with a ciliated lumen, near the ureter (Fig. 26).

Thus the two reno-pericardial canals open into, or are continuous with a funnel-like dextrally directed diverticulum of the pericardium, and do not open separately into the main triangular pericardial cavity.

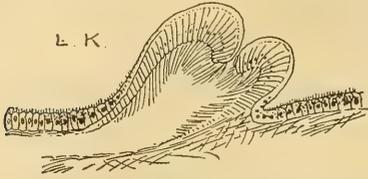


Fig. G. Aperture of left reno-pericardial canal into left kidney, very much enlarged.

Furthermore it is evident that the nephridial ends of these canals are far removed from the pericardium proper, and each opens, in relatively the same place, near each ureter.

These canals and openings I have carefully examined also in *Acmaea patina* and *A. spectrum*. In these species the reno-pericardial ducts hold the same relations as in *Lottia gigantea*, and likewise the papillae are similarly situated in each nephridium. In *Acmaea spectrum* the papillae are a trifle larger in proportion to the size of the animal, than in *Lottia*.

### The Reproductive System.

The gonad is situated beneath the alimentary canal and lies (Fig. 1) in a special compartment which is probably a portion of the secondary body cavity. During the breeding season (evidently about midwinter) it is so enlarged as to much exceed in size the other viscera. If these are stripped off, the gonad appears as in Fig. 23. It is then seen to reach from the buccal sinus in front to the end of the visceral cavity behind, and about its edge to extend upward nearly or quite to the dorsal wall of the body. Thus the alimentary canal seems to rest in a bowl-like hollow in the midst of the gonad. Forward, the gonad is produced into three divisions, two ventral, forwardly directed ones which encroach onto the head cavity, and a dorsal process extending from left to right behind and under the pericardium (Figs. 1, 20, 23). The end of this process is situated beneath the mantle cavity between the aorta and rectum and is sometimes quite extended. The portion of the gonad shown in Fig. 20 is merely the dorsal part of this process. The tip is well forward of the left nephridium. From this tip a thin-walled tube difficult of observation leads to the right and opens into the dorsal arm of the subanal portion of the right nephridium. This duct is lined with coelomic epithelium, and doubtless when the sex products are being shed could be more readily followed. The opening is more easily seen as it appears to be ciliated, and possesses prominent lips. The

muscular body wall ("neck") is above the duct and a portion of the liver below. In Fig. F (*Gn. D*) this tube is shown in the same section with the nephridial ends of the reno-pericardial canals, but in reality it would occur a trifle in front of the plane of this section, which is an oblique one.

In *Lottia gigantea* the sexes are separate, and there is no progressive change from male to female in the same individual. As soon as there is a definite gonad (when the shell is 10 to 11 mm, longest diameter) there is a sharp differentiation between the males and females. In animals 10 mm in length the ovaries and testes seem to have fully developed products, though the gonad is not relatively so large as in the adult. In fully grown examples, the females much outnumber the males.

I have found eggs free in the large right kidney sinus at Christmas, but unfortunately did not preserve those individuals to examine the state of the gonoduct.

### Secondary Body Cavity and Pericardium.

The pericardium is described in connection with the heart. It is a triangular cavity situated on the left side of the body, well in front, so that a portion overlies the head. It communicates with the lumen of the right and left nephridia (called by some investigators the "nephridial coelom") by long tubular diverticula, which pass under the renal epithelium, and open by tiny ciliated canals at the summit of minute papillae, one near each ureter. The long canals are portions of the pericardial cavity, the ciliated funnels being only that part within the papillae.

The space surrounding the gonad, scarcely more than a potential cavity in the adult with fully developed sex products, belongs to the coelom or secondary body cavity, and not to the pseudhaemal spaces or primary body cavity. One can argue of course that this cannot be logically settled till the development is thoroughly studied. The space in question, however, is lined with the thin coelomic epithelium, is not connected with the blood system in any way, and finally opens by a slender duct (the gonoduct) into the lumen of the right nephridium. The last fact seems to be conclusive evidence that the space does not belong to the pseudhaemal system, to which for instance the lacunae among the liver lobules appertain. In very small individuals, before the sex products are formed, one can see a veritable cavity beneath the intestine and liver. In this, sex cells begin

to appear, so that all trace of a lumen is early lost. But potentially the coelom is present.

### Circulatory System.

The reader is referred to the diagram of the circulation of *Lottia gigantea*, appended at the end of this account. A careful examination of this chart will place the main features of the circulation in mind, so that the following description will be easily understood.

In common with other Docoglossa the pericardium of *Lottia gigantea* is situated on the left anterior part of the dorsal side of the body. It is roughly triangular in outline and rather shallow dorso-ventrally (Fig. 22 *Per*). Its left side is formed by the anterior portion of the left limb of the U- or horseshoe-shaped shell muscle. The right side (occupied by the auricle) abuts against the mantle-hood and mantle cavity. The posterior or remaining side of the triangle lies against and over a portion of the gonad (Fig. 20). Immediately beneath the pericardium is the gonad (Fig. 1).

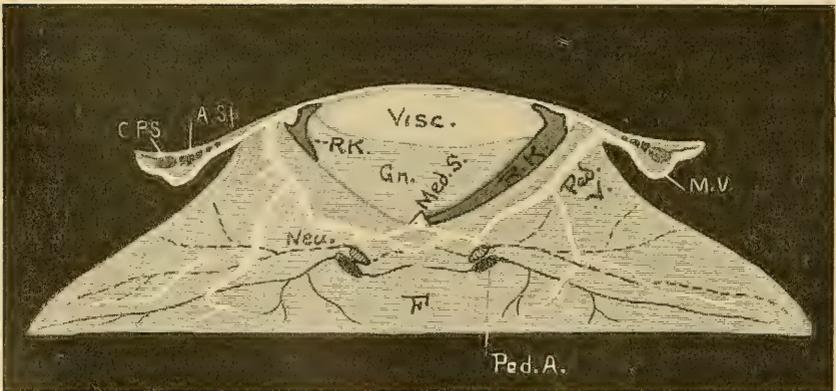


Fig. H. Conventionalized cross-section through middle of animal to show relations of arterial and venous circulation in foot and mantle. The sinuses of the foot are in white, the arteries in black. *A.Sp* arterial sinuses of mantle, *C.P.S* circumpallial sinus, *F* foot, *M.V* mantle veins, *Med.S* median sinus, *Neu.* neural arteries, *Ped. A* pedal sinuses.

The heart consists of an auricle and ventricle. The former occupies the right side of the pericardium. Anteriorly its walls are produced to meet the pallial sinus. They join the walls of the sinus near the outer edge of the spindle muscle on all sides except the right, where the blood must enter from the pallial hood (Fig. 24).

Thus boundaries of the pericardium are formed in this direction. Posteriorly the auricle extends quite to the aperture of the funnel leading toward the kidney. Along the whole of the right side, frequent and regular openings lead into the auricle from spaces in the mantle hood, into which sinus the vessel from the ctenidium opens (*Ct. V*). Blood thus enters the auricle from 1) the circum-pallial sinus; 2) from the ctenidium; 3) from the pallial hood. By far the greater amount comes from the mantle which is the chief respiratory organ.

The auricle is a rather thin sac with prominent muscular cords running lengthwise and smaller ones crossing at various angles. Its shape changes according to different degrees of contraction. Fig. 24 gives an idea of the appearance during systole.

The ventricle may be said to occupy the posterior portion of the pericardium, along that edge of which, its walls are fastened. In front, it is joined with the auricle by a fairly large opening, guarded on the ventricle side by a two-lipped valve (*Val*). From the corners of this valve prominent cord-like muscles lead off and attach to the ventricle walls. From the lower side of the ventricle a long slit-like opening with muscular lips, leads directly to the aorta. Two portions are easily distinguishable in the ventricle. The anterior half as shown in Fig. 24 has heavy muscular walls, with cords running in various directions, but mostly lengthwise and circularly. A view of the interior presents that peculiar and characteristic fenestrated appearance, seen in so many hearts, both vertebrate and invertebrate. The posterior half has thin walls, translucent and delicate, made up mostly of fibres running at right angles to the prominent cords in the anterior half. A crease leads to either corner of the ventricle from the two ends of the aorta opening, and from this crease free slender bands of muscle lead up to the dorsal wall of the ventricle. These muscle bands seem to act as stays preventing the ventricle from encroaching too much on the aorta and thus stopping a ready flow of blood.

I have noticed in live animals in captivity that the tip of the ctenidium often vibrates rhythmically, there being usually about forty of these vibrations per minute. Each vibration consists of two parts as though recording the contraction of both auricle and ventricle. A pause is succeeded by a slight moving of the tip of the ctenidium, which is followed almost at once by a strong vibration, then a pause. These animals were in a perfectly normal condition so that if the ex-

planation of the ctenidial vibrations is correct, we may suppose the heart-beats to average about forty per minute.

**Arterial System.** The ventricle opens, as stated above, directly into the aorta which lies on the floor of the pericardium, nearly parallel with the posterior boundary. The anterior (aorta) and posterior (genital artery or posterior aorta) branches or parts form essentially one continuous tube, which may be considered as simply passing under the ventricle and opening without an intermediary tube, directly into the ventricle. The anterior aorta (Figs. 1, 3, 21 and 24 *Ant. Ao*) after leaving the ventricle passes through the loop formed by the visceral commissure, to the right of the oesophagus, into the head cavity where it turns abruptly downward. Just after quitting the pericardium the aorta gives off a small artery which passes over the viscera and enters the floor of the rectal portion of the right kidney, whence it sends branches to the ureter and finally reaches the circulation of the mantle. Within the buccal sinus another small branch is given off to the oesophagus. Arriving just behind the buccal mass (Fig. 3) the aorta divides into two branches, the pedal artery (*Ped. A*) and cephalic artery (*Ceph. A*). The latter passes along the mid-dorsal portion of the buccal mass, surrounding the radula tube. Almost at once a ventral branch is given off, the sublingual artery (*Sub. L. A*) which leads directly downward between the two posterior processes of the buccal mass, through the muscular tissue, and comes to lie along the ventral side of the buccal mass embedded in muscle. Here it soon loses its walls, and passes by rather definite spaces, into the sublingual organ, palps, and a broad sinus, under the buccal cartilages, by which it is in communication with a similar sinus, above the cartilages. The cephalic artery leads into the upper lip of the radula tube thence around under the chitinous wing-like projections of the radula, into the definite sinus above the buccal cartilages, just spoken of. Hence the cephalic and sublingual arteries are ultimately again in communication. The blood now either finds its way into the buccal sinus (*B. S*) or goes directly by two small openings under the palps, into spaces in the lips, which are protruded by this medium.

We saw that the aorta bends downward and divides into a pedal and a cephalic artery within the confines of the buccal sinus or head cavity. Just at this point of division the radula tube, which has come backward inside of the cephalic artery, pierces the wall of the artery on the left side and passes out into the buccal sinus, to

enter the visceral artery (Fig. 3 *R'*). At the point where the radula tube pierces the wall of the cephalic artery there is formed an inconspicuous crescent-shaped opening, conforming to the side of the radula tube. The flap of this opening is so arranged that blood from the heart can pass out into the head cavity or buccal sinus, but the blood in the buccal sinus even omitting the greater pressure in the aorta, is unable to enter the artery.

Before considering the pedal artery and further circulation of the foot it would be well to devote a few words to the buccal sinus. By this is meant, of course, the space about the pharynx, buccal mass, and cerebral, pleural, and intestinal ganglia, with their connectives. As is well known this is a great blood sinus, a distributing center for all the circulation of the viscera (less gonad) and a large part of the foot and body wall. In Fig. 3 the reader will gain an idea of the sinus in *Lottia gigantea*, remembering of course that all the organs are more compactly fitted together, and that only when the sinus is gorged with blood are there such generous spaces between the buccal mass and pharynx. It is evident that all the structures within the sinus are bathed with blood, directly from the heart, mixed with that which has circulated to some extent in the buccal mass. The posterior wall of the sinus is definite and both dorsally and ventrally extends farther backward than in the intermediate region. In other words the viscera encroach on the head cavity bulging the septum out. But in the region of the intestinal ganglia above, and about the pedal ganglia below, there are posterior prolongations of this head cavity. Above, it does not extend farther back than the visceral ganglion as shown in Fig. 3. The cerebro-pleural and cerebro-pedal connectives lie in small side chambers of the main sinus, which are separated from the central cavity by dorso-ventral sheets of muscle and connective tissue (Figs. 1 and 3). These side cavities communicate freely with the main head cavity by openings at the front and rear, and along the sides. From the posterior part of the floor of each of these cavities a small artery or sinus leads down into the front portion of the foot (Figs. 24, 27 *Ant. P. A*) where it divides, joining branches of that of the other side, and sending twigs forward to the very margin of the foot.

From the buccal blood sinus the following vessels arise: the visceral artery; the two important neural arteries to the foot; two small arteries to the anterior part of foot (anterior pedal arteries already spoken of); two or more small arteries to lips, and to tentacles;

and a small sinus on each side, which follows the pallial nerves for a short distance and then goes directly to the mantle. These sinuses are of small calibre and lead through the tissue of the spindle muscle to the venous circulation of the mantle (Fig. 19 *x*).

The pedal artery maintains its definite walls within the buccal sinus and through its course in the foot. After leaving the anterior aorta it bends sharply backward, passes under the commissure uniting the two anterior enlargements of the pedal cords (pedal ganglia), plunges into the tissue of the foot, and immediately divides into two branches which pursue a course directly beneath the neural arteries surrounding the nerve cords (Fig. 27 *Ped. A*, in red). The dorsal wall of the pedal arteries, forms the ventral wall of the neural. The relative position of the two may be seen in Fig. H. There seems to be no direct communication between the two, notwithstanding the intimate association, because in many specimens, in which the neural arteries had been injected from the head sinus, there occurred no passage of the injection mass (which was fluid enough to follow the finest vessels to the edge of the foot) into the pedal arteries. In fact it is a difficult matter to inject the pedal arteries in the fresh animal, as most of the material follows the cephalic or escapes into the buccal sinus and injects the visceral and neural arteries. The pedal artery sends a variable number of branches toward the edge of the foot (Fig. 27, red) and also toward the center. These branches redivide and the twigs inosculate in several places. The pedal arteries and branches supply the deeper layers of the foot.

The neural arteries, of which mention has already been made, are spaces around the two great nerve cords of the foot, and are homologous apparently, with similar arteries in the chiton, and in simple Prosobranchs (*Haliotis* and *Lucapina* for instance). The neural arteries lead out directly from the buccal sinus, and are very spacious. It is probable that considerable blood circulates through this system. Abundant branches follow all the larger nerves which leave the nerve cord, both toward the edge of the foot and mesially. These inosculate in a fine network, lying in several planes, so that is difficult to represent the system adequately. Some of the branches pass directly into known venous sinuses while others become mere capillaries before losing their identity. The neural arteries with branches supply more particularly the upper layers of the foot, and the shell muscle. I could not demonstrate in the larger branches any connection with those of the pedal artery. Such a communication may occur between the smaller twigs (Fig. 27 *Neu. A*, uncolored).

The visceral artery supplies the alimentary canal, and liver. It is one of the largest vessels in the animal, being exceeded in carrying capacity only by the anterior aorta, and possibly by the genital artery. The vessel begins by a funnel-like prolongation of the buccal sinus backward into the visceral mass. Here the vessel soon divides (Fig. 21), the divisions being the two limbs of a complete loop as shown in the figure.

Within the visceral artery is the radula tube which thus curves around and reenters the buccal sinus to become attached to the anterior aorta by the end of the sheath. Starting with the left limb, which is the chief blood channel, we will find that the artery dips slightly downward into the lower layers of the liver, under all the alimentary tract, then curves to the left and lies next to the oesophagus to which numerous branches are given off. Now rising slightly, the artery makes a complete curve, just in front of the proximal end of the stomach and fore-chamber. To the left

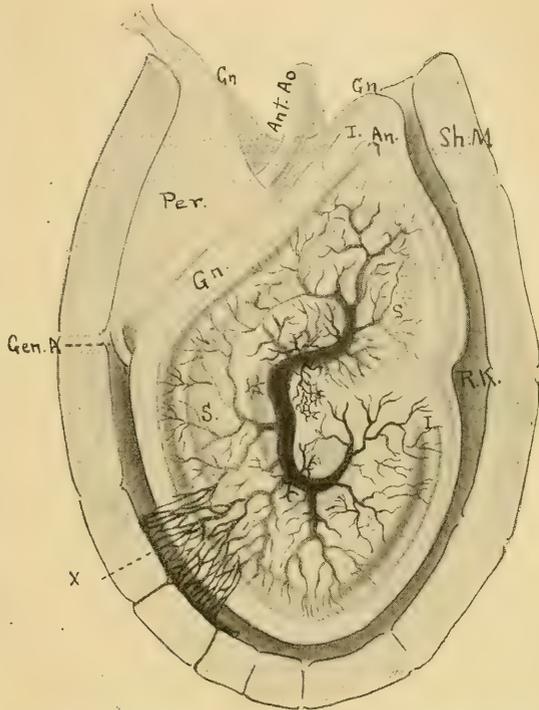


Fig. I. Dorsal view of visceral mass showing the dorsal branch of visceral artery (Fig. 21 *Dors.Br*) which spreads over the upper layers of the liver and over the stomach. *Ant. Ao* anterior aorta, *S* stomach, *X* portion of vein-net of right kidney (*R. K.*) to show manner of formation from the branches of visceral artery.

of the proventriculus a very large branch is given off to the hind portion of the viscera. This immediately divides into a dorsal and a ventral part. The former (Figs. 1 and 21 *Dors.Br*) passes directly upward and divides sometimes into three, but usually into two (anterior and posterior) branches. The smaller branches redivide excessively and form a fine network through the upper layers of the

liver and over the stomach and rectum. All the blood passes into vessels of the right kidney, to be detailed more fully under the venous circulation. The ventral branch (*V.Br*) also divides into numerous branches which course backward, anteriorly, upward and downward. The main posterior branch supplies chiefly the under side of the stomach, intestine, and liver. Certain branches pass under the stomach and over the distal limb of the intestine directly into the kidney network. Anterior branches supply the several coils of the intestine in that portion of the visceral mass and are better understood from the figure than from descriptions. The dorsal branch shown in this figure in deep red, arises from the anterior portion of the visceral artery and courses directly upward to supply the under surface of the anterior loop of the stomach and a loop of the intestine (Fig. 1, blue) lying under the stomach and rectum. From the curvature in front of the proventriculus the main artery turns directly forward and rises so that it comes to lie considerably above the level of the left portion. Just before joining the funnel-shaped opening from the head cavity the artery bends sharply downward. Putting the same fact conversely, the right limb of the visceral artery on leaving the common opening from the buccal sinus turns sharply upward, then backward.

The genital artery or posterior aorta, whichever one may choose to call it, passes from the outer posterior corner of the pericardium, turns downward and enters the gonad (Figs. 1 and *J Gen. A*). Here a division into anterior and posterior portions takes place, and each of these divides into a varying number of branches. The ultimate ramification results in very fine vessels, permeating every part of the gonad, and forming an intricate network, in and about the lobes and lobules of the gland, which would be difficult to show in a drawing. All the blood reaches the mantle circulation but by two different routes. A very small portion passes through slender vessels, the final branches of those lying nearest the upper surface of the gonad (Fig. *J XX*), directly into the venous meshwork of the kidney. To understand the course of the remainder it will be necessary to turn aside for a moment. The cavity of the coelom, or secondary body cavity, in which the gonad lies is separated from the large right kidney space by a prominent membrane. This is attached to the muscles of the floor of the hollow in which all the organs lie, along the median line (*Z* Figs. *B* and *K*), from the boundary of the buccal sinus in front nearly to the attachment surface of the spindle muscle

behind. From here the line of attachment turns again forward and parallel to the curvature of the spindle muscle, to the corner of the pericardium, following a course about one-third of the distance from the upper edge of the shell muscle to the median line of attachment (Z). It is obvious that the space between the membrane and the muscular wall is the right kidney: that centrally between the two parts of the membrane, occupied mostly by the gonad, is the coelom. Vessels which reach the edge of the gonad (Y Figs. J, K and B), and these include the greater number, pass directly into this membrane just described (X Fig. K), where they intercommunicate and course ventrad. Those

of the right side reach a median venous sinus, which follows the line of attachment of the membrane along its whole length, and opens posteriorly into a vessel leading through the spindle muscle, directly to the mantle circulation (*Med. S*). The blood in the small portion of the mem-

brane on the left side of the body (X') enters mostly spaces lying directly under the superficial layer of muscle on the floor of the coelom, whence it reaches the median sinus. Some, however, works backward through the inosculation of these veins in the membrane, and reaches the median sinus near where it passes through the spindle muscle. From these remarks it is evident that the greater part of the blood from the gonad reaches the mantle circulation without entering the vascular network over the dorsum of the nephridium,

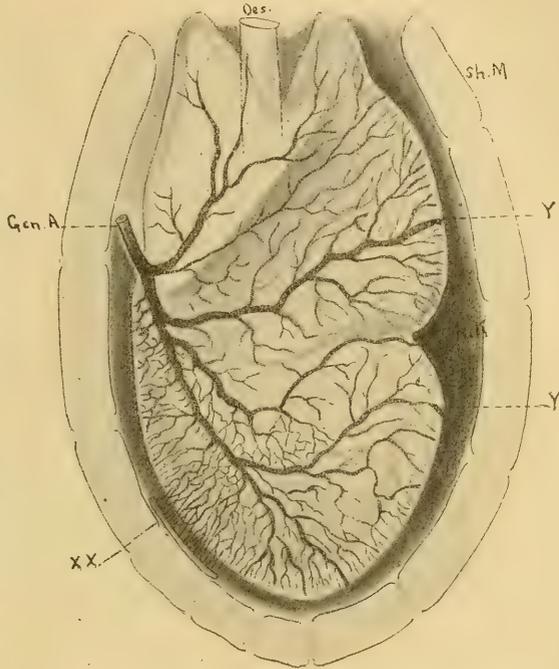


Fig. J. Gonad, with alimentary system removed, viewed from above to show branching of genital artery (*Gen. A*). XX showing a few vessels passing into vein-net of kidney, Y, Y place where vessels leave gonad and pass into membranes (Fig. K) separating gonad from right kidney.

presently to be described. However, the blood, circulating through the membrane between kidney and gonad, is directly under the renal epithelium, and is thus subject to its action. A very small portion does pass into the dorsal vascular network, direct from the gonad, while some may reach the vessels of the visceral circulation and thence arrive at the kidney. I have not been able to demonstrate

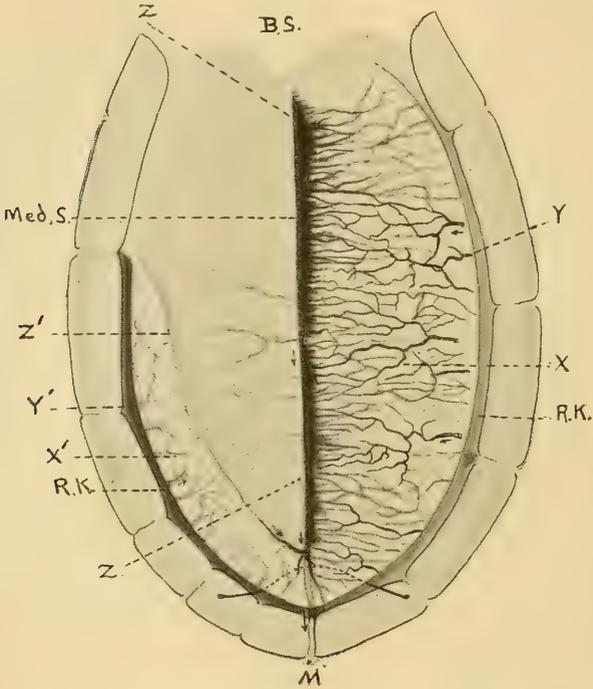


Fig. K. The gonad has been removed from Fig. J, to show the manner in which blood from gonad reaches median sinus and mantle. *B.S.* buccal sinus, *Med.S.* median sinus emptying posteriorly into mantle circulation at *M*, *R.K.* cavity of right kidney, *X, X'* membrane separating gonad from right kidney, composed of coelomic epithelium and renal epithelium fused, the blood sinuses including the median sinus, occupying space between these two epithelia, *Z, Z'* line of attachment of above membrane to muscular body wall, *Y, Y'* point where vessels leave gonad to enter membrane.

this, however, as it is beset with considerable difficulty. In conclusion it might be well to state that the entire circulation of the gonad is closed, and that the space about the gonad is not a primary body-cavity or pseud-haemal sinus as Miss WILLCOX believed to be the case in *Acmaea fragilis*, but almost without doubt appertains to the secondary body cavity or coelom.

The great circumpallial blood sinus which conducts the aerated blood to the auricle is best considered with the venous circulation.

**Venous circulation.** The blood which is collected from the various organs of the body reaches for aeration, the ctenidium and mantle, the latter being the most important respiratory organ. From these two structures it is carried to the heart. Blood to the pallium may either come directly, as is the case with the greater part of that of the foot and gonad, or it may pass through the meshwork of vessels of the kidney, as happens with the blood from the visceral artery.

The venous sinuses of the foot are shown in Figs. 19 and H. They are greater in calibre than any of the arteries of the foot, with the exception of the pedal arteries. Their course, which is somewhat devious, and in several planes, is best understood by a comparison of the two figures. About twelve of these vessels are present corresponding to the rather constant number of veins piercing the shell muscle and leading from the kidney blood sinus to the mantle. A prominent branch results from the anastomosing of numerous sinuses in the lower parts of the foot. This passes upward and joins another branch or branches which come from the central portion. These divisions in the central part of the foot lie above the neural artery (Fig. H, in white) and communicate with each other by rather irregular and fairly large sinuses, and also by much smaller ones. Into these sinuses many small arteries open directly. Transverse venous sinuses are also in communication with the median longitudinal sinus already spoken of under the circulation of the gonad. Each vessel which results from the union of branches from the lower parts of the foot, and those from the median portion, courses upward and outward, to open into the transverse vessel leading from the kidney vein to the mantle (19). The median sinus, though classed with the pedal circulation by reason of its connection with very numerous cross sinuses lying within the muscular tissue of the foot, itself, of course, lies at the base of the membrane separating the coelom from the right kidney, and along with the other vessels in this membrane, may be said to be a definite lacunar space between the exceedingly thin epithelium lining the coelom, and the thicker epithelium lining the kidney cavity. The two epithelial linings are hence fused to form one membrane. In the diagram of the venous circulation of the foot only the more prominent vessels have been shown.

So far as I have been able to observe, all the blood from the visceral artery reaches either the mantle or the gill by way of the

vein-net of the kidney. The final peripheral ramifications of the visceral artery pass into the dorsal wall of the kidney, where there are several layers of these vessels, among which the kidney spaces, lined with ciliated epithelium, form an intricately fenestrated structure. The limits of this excreting portion of the right kidney are shown in Figs. 20 and 22. These vessels then open into the kidney vein (*K.S*) which nearly encircles the body, on the inner side of the spindle muscle, at its upper edge. From the kidney sinus, ten vessels, five on each side, pierce the spindle muscle just under the shell and on reaching the mantle divide into many branches (Fig. 19) which distribute the blood for aeration close under the epithelium.

As shown in this figure the mantle hood covering the mantle cavity over the head, is highly vascular. Vessels are distributed to it directly from the anterior (right) portion of the kidney mesh, and also from a forward prolongation of the kidney vein. On the left side this blood flows directly into the circumpallial sinus as it turns toward the heart, but in front, the joining with the sinus takes place less directly, in a manner to be described shortly in connection with the mantle circulation.

In Fig. 21 a portion of the stomach and intestine is shown with some of the branches of the visceral artery passing directly into the vein-net of the kidney. Finer twigs of both the dorsal and ventral branches of the visceral artery are drawn together, so as to show the relation of the two (see also Fig. 1). Not all the blood from the visceral mass reaches the kidney so directly. Many of the smaller arteries branch and rebranch to capillary fineness, particularly those of the upper layer of the liver, and the blood passes into minute spaces or capillary lacunae between the lobules of the liver. It finally collects in more or less definite spaces between the dorsal surface of the liver and the dorsal epithelium of the body, and thence passes into the vein-net of the kidney. Hence the space or cavity in which the alimentary canal and liver lie, must be regarded from an anatomical standpoint at least, as a blood space, homologous with the visceral cavity of the chitons. It should be remembered in this connection that the cavity is so completely packed with liver tissue and alimentary canal that only the minutest lacunae survive, and that in point of fact, no sinus as such now exists. This primary body cavity or pseudohaemal space is separated from the coelom, or secondary body cavity below, in which is the gonad, by a thin epithelium, which

is, however, of sufficient thickness to be seen in gross dissection, if sufficient care be taken.

The blood, on reaching the mantle, courses through a rather intricate system on the lower surface, as shown in Fig. 19, and is distributed to the many lamellae. Around the free edge of each of these runs a vein, which proceeds thence to the edge of the mantle after dividing and subdividing many times. These minute vessels are found close under the epithelium, which here consists of rather low cylindrical cells. From the edge of each lamella or lappet very many tiny veinlets pass dorsad on either surface just beneath the low epithelium, whence the blood finds its way into numerous venous spaces on the lower surface of the mantle. Thence it either courses toward the edge of the mantle, some of it entering the circumpallial sinus by minute openings in the floor, the rest probably following the other surface blood to the mantle edge, or it passes almost immediately upward through rather indefinite tiny sinuses and enters the arterial spaces (*A. Sp*) through small and inconspicuous openings. The blood which circulates in the border of the mantle through the fine veinlets, is carried to the large circumpallial sinus by dorsally situated sinuses, some of which open into the main vessel on the outer side, others on the dorso-lateral. Between the circumpallial sinus (which conveys the purified blood to the heart) and the inner edge of the mantle there are very definite spaces, situated above those veins which carry blood to the mantle from the kidney sinus. These arterial sinuses are quite distinct from the veins, which when injected can be seen below them, if one removes the dorsal wall of the mantle. When this is done it is easy to demonstrate that no direct connection, unless of the very minutest sort, exists between the vessels below and the sinuses above. Such a connection exists, however, with the capillary spaces of the lappets. These sinuses communicate with the circumpallial vessel, by frequent openings. If the reader will imagine the dorsal and ventral sheets of muscle which cross the mantle from inner to outer edge, as being separated by a definite cavity extending from the circumpallial vein to the inner edge of the mantle, and if he will further imagine these two sheets bound together by frequent dorso-ventral trabeculae of muscle and connective tissue, he will gain an idea of the structure of the lacunae.

In conclusion I might repeat by way of emphasis that venous blood reaches the circumpallial sinus only by very fine vessels, after



along the whole of the right side of the pericardium. The afferent ctenidial vessel leaves a short sinus above the left kidney and is much less roomy than the efferent vessel. Two stout muscles pass along its dorsal and ventral sides, and a nerve along its outer, buried in the muscular wall. This vein drains blood from the left nephridium and the fore part of the vein-net of the right.

The vein leading from the ctenidium opens into a sinus of the mantle hood, whence the blood reaches the auricle through numerous openings. This vessel also possesses two muscles and a double nerve. The leaves of the gill are arranged in a double, or dorsal and ventral, series and are attached at their bases to a median membrane, through which the blood can pass from one vessel to the other. About the edges of each gill-leaf is a rather prominent space through which the main stream of blood passes, and from which it seeps, by lesser spaces toward the base of the lamella. The histology has been described by HALLER (l. c.).

There is little foundation for THIELE's dictum<sup>1)</sup> that the single ctenidium of the monobranchiate *Docoglossa* is a secondary structure and that the primary gill has degenerated. As a matter of fact nothing is known of the development of these forms, while everything about the structure points to the fact that the existing ctenidium is not secondary. The nervous supply is very abundant and springs from the selfsame ganglion as does that of the corresponding gill of *Haliotis*, which this investigator is so anxious to prove primitive and in a direct line of descent. Furthermore the attachment of the gill by its base in the *Acmaeidae* is much more similar to the condition in the chitons, than is that of *Haliotis*, where the gill is fastened along the side of the efferent vein. The passage of the blood in *Lottia* from the ctenidium into a pallial sinus, and thence into the heart is more primitive than the direct connection found in *Haliotis*, and again agrees more closely with the condition of affairs found in chitons. Here both the vessel distributing blood to the gills, and that bearing it to the heart are no more than pallial spaces, into which the two main vessels of each ctenidium communicate. Consequently it would seem ill-advised to insist very strongly on the secondary nature of the *Acmaeid* gill, until something definite is known of the development of these forms. The structure and relations of the organ can just as readily lead to the opposite conclusion.

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1) THIELE, l. c. p. 332 and 356.

### The Mantle.

In all the *Acmaeidae* the mantle has become a most important auxiliary organ of respiration, and in such forms as *Scurria* and *Lottia* may be said to have reached its acme in this respect.

For the sake of discussion the mantle may be divided into an outer or glandular zone and an inner or branchial zone. As shown in Fig. 19 the inner zone is taken up by the so-called branchial cordon which extends completely around the animal, with the exception of a small space in front. This cordon consists of lappets, roughly semicircular in outline which hang from the lower side of the mantle and afford an increased surface for the aeration of blood. Each lamella consists of a plate of muscle and connective tissue, between which and the cubical epithelium are very many blood spaces as shown in Fig. M. These lappets appear late in the development of the animal. Small individuals do not possess them, the mantle appearing in all respects like that of an *Acmaea*. In an example with a shell 17.5 mm long, the branchial cordon is in the process of development. The lappets appear as buds and although the cordon is as complete as in the adult the lappets in the anterior part of the pallium are slightly larger and more numerous than those posteriorly, showing perhaps the locality of first appearance. Occasional examples occur as large as 22 mm, in which there is no trace of the cordon, but 20 mm is the usual length at which it appears. I have one specimen as small as 19 mm in which the cordon is like that of the adult. By the time the creature has reached the length of 23 to 24 mm the lamellae are always fully developed. Consequently when under 20 mm in length, *Lottia gigantea* does not possess its generic character!

The circulation of the mantle is considered under the circulatory system, and the complex innervation under the nervous system.

In the outer zone of the mantle, between the circumpallial vein and the free border is the glandular portion. At the margin empty three separate glands which by reason of their relative position have here been designated merely as dorsal, middle and ventral pallial glands (Fig. L). Running around the edge of the mantle is a shallow groove. Into this the median gland opens, while the dorsal and ventral empty respectively above and below it, as shown in the figure. The dorsal gland (*Dors. Gl*) consists of several layers of pear-shaped cells with large nuclei, and long necks which pass between the epi-

thelial cells. This gland is rather inconspicuous because it usually does not stain deeply. The middle gland seems to consist of a long string of cells, lying over the ventral gland. It is probably branched

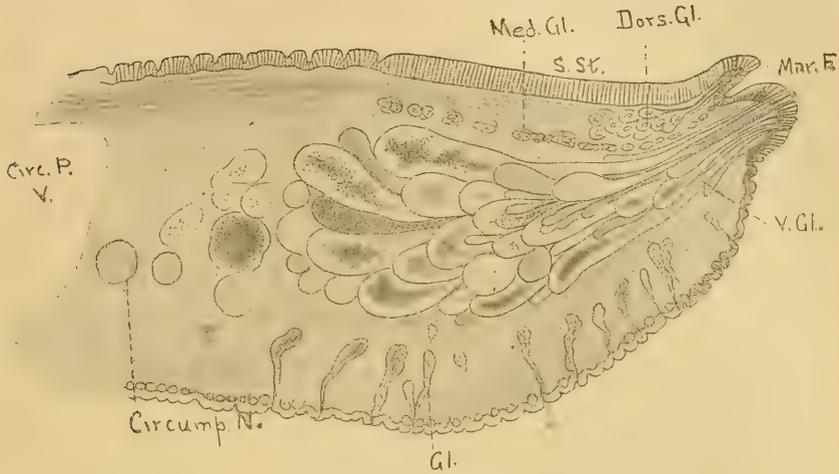


Fig. L. Cross section through glandular margin of mantle, left side, much enlarged. *Circump. N* circumpallial nerve, *Circ. P. V* circumpallial vein, *Dors. Gl* dorsal pallial gland, *Gl* glands emptying onto lower surface of mantle, *Mar. F* marginal furrow, *Med. Gl* median gland, *S. St* sense stripe of mantle, *V. Gl* ventral gland.

in a horizontal plane as portions appear detached through several sections. The cells are smaller than those of the upper gland and

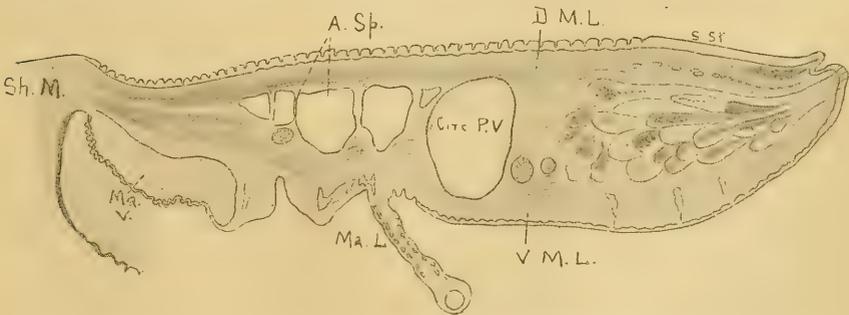


Fig. M. Cross section through whole of mantle to show relation of vascular to glandular area. *A. Sp* arterial spaces, *D. M. L* dorsal muscle layer, *Ma. L* mantle lappet, *Ma. V* mantle veins, distinct from arterial spaces, *V. M. L* ventral muscle layer.

contain granules. The ventral gland (*V. Gl*) is conspicuous as it consists of gigantic cells, of various sizes. These cells possess very definite walls and narrow down from a pouch-like form to a narrow neck

which becomes very slender before piercing the epithelium. Most of the cells contain a finely granular secretion which tends to harden in the center of the lumen, leaving a clear space next to the walls. Sometimes the cells are quite empty. In the fully grown animal these glands occur at frequent intervals with glandular spaces between them, but in very young individuals the glands are relatively much enlarged so that there is a continuous cordon of them around the mantle. As the animal increases in size, they tend to withdraw from each other and become segregated as definite bundles of cells. It is probable these glands are concerned with the secretion of material of the shell which consists of several layers. Along the ventral side of the mantle, large gland cells occur at frequent intervals (Fig. L *Gl*).

The muscular system of the mantle consists of a dorsal and a ventral transverse, or edge to edge, layer with dorso-ventral bundles at frequent intervals. There are also many oblique fibres, but not disposed in any definite bundles. The strong dorsal and ventral layers serve to contract the mantle toward the spindle muscle whenever the animal is irritated.

The epithelium of the dorsal side is much higher than that of the ventral side and is pigmented. On the left side of the animal the outer fourth of mantle has a zone of rather thicker epithelium on the dorsal side. This epithelium is not thrown into lengthwise wrinkles as is the rest, and contains little pigment. It has been called the mantle sense organ by HALLER, who found ganglion cells under the epithelium.

Along the edge of the mantle are many little sense papillae, sunk in shallow pits lined with pigmented epithelium. Fine branches of the mantle nerves terminate in these papillae.

### Muscular System.

In this connection only the muscles of the buccal mass will be considered. In life they are bright pink in color, and one can see the reddish tinge through the dorsal wall of the head. This color is in sharp contrast to that of the other muscles of the body, namely the foot, spindle muscle, heart, mantle, et cetera, which, as is well known, are whitish.

On account of the very definite and rather rapid set of movements in connection with the radula, when the creature is feeding, we find developed in the buccal mass clear cut groups of muscles. In the accompanying figures each muscle has been numbered so that it can

be seen from several points of view. In each succeeding figure taken in the order of 3, 10, 9, 4, 5, 16 and 13, a few muscles have been removed so as to uncover deeper-lying ones. In this manner it is believed the relationships of the several groups can be clearly seen. Bilateral symmetry is observed in all the muscles, or groups of muscles. The retractors of the buccal mass (3) are attached to the posterior processes of the cartilage and originate on the floor of the head cavity between, and just in front of the pedal ganglia. Auxiliary oblique muscles (13) are found in connection, which act as depressors, and permit of a lateral movement of the mass. The protractors are much heavier than the retractors and there are two sets of them on each side, namely the lateral (7) and right and left inferior protractors (8). The latter originate just behind the mouth on the floor of the head cavity and are inserted near the retractors on the posterior processes of the cartilage. It is probable that muscles 10 and 12, especially 12 which passes from the lateral processes or knobs of the cartilage to the dorsal wall of the head cavity, may act in manipulating the buccal mass as a whole. Two very well developed sets of muscles work the radula. The major retractor of the radula (1) is very conspicuous, being disposed in cord-like bundles, which, originating on the latero-ventral surface of the cartilage, pass up over the top and are inserted along the edge of a horny wing-like expansion of the forward end of the radula (Figs. 4 and 16 1). Under this, next to the cartilage, is a tendinous sheet, the minor retractor of the radula (Fig. 16 2), which originates on the posterior process, and ventral side of the cartilage, and is inserted along the under side of the wing-like expansion of the radula (stippled 2'). This muscle must have a splendid purchase on the whole expanded portion of the radula. The protractor of the radula (9), in texture resembles the major protractor, and originates on the posterior knob or process of the cartilage, passes along its ventral surface and is inserted on the horny wing of the radula, below the major retractor. Fig. 4 shows the relation between these two. Muscles 10 and 11 (Fig. 10) also probably act as protractors of the radula tube. Muscle 4 seems to act as a retractor of the dorsal lip of the radula tube. Contractions of the set marked 5 (Figs. 9 and 10) would widen the oral cavity. They are inserted along the heavy lateral folds of the buccal cavity. The retractors of the palps (6) originate on the posterior knobs of the cartilage and pass directly forward to be inserted all along the interior of the

"inner lips", which as pointed out in another connection are so abundantly supplied with nerves that they almost certainly subserve the function of taste, or something allied thereto. The presence of a strong retractor is a necessity to withdraw such highly sensitive structures. Muscle 14 (Figs. 9 and 10) is small. It probably retracts the forward portion of the pharynx. Its origin is on the radula tube, and insertion along with muscle 5. Muscle 15 is a stout bundle which passes from the dorso-lateral wing of the jaw (inner surface) and lateral knob of the buccal cartilage of each side, underneath the cartilage, where a portion may be said to have its origin. But a goodly part of the muscle appears to simply continue from the insertion on the jaw and knob of one side, under the cartilages, to a similar insertion on the other. As will be seen by Fig. 13, the "lateral knobs" of the radula supports are in reality separate pieces of cartilage which are anchored to the main radula support by muscles (23). Consequently 15, which is probably a mixed muscle, acts as an anchor for these cartilages and a depressor of the jaw (?). It also acts as a strengthener of the whole cartilage, which would tend (from a longitudinal line of weakness along the middle) to fold together. 15 acts in exact opposition to any such strain. Muscle 16 (Figs. 5, 9 and 10) is inserted on the jaw and originates on the posterior knob of the cartilage. Its contraction would tend to draw the jaw inward and downward. Muscle 25 is similarly situated, though it is outside of all of the buccal muscles, and is attached to the upper and outer edge of the jaw. The sheet of muscle 17 is thin and passes from side to side connecting the two lateral knobs of cartilage, and the major portion ends in an aponeurosis of connective tissue fibres in connection with muscles 16 and 8, and the sheet lies between the two, above 8 and below 16. A thin sheet of muscle (19 Fig. 3) extends over the dorsal half of each side of the buccal mass, covering the retractor major of the radula. Its origin is on the posterior knobs of the cartilage. It is inserted partly on the jaw (upper edge) and extends partly as muscle 22, to the outer lip, or proboscis. The contraction of this muscle would tend to lift the jaw and fore part of proboscis. Small muscles (20) pass from the jaw to the head wall, while others (21) anchor the pharynx and pharyngeal pockets to the wall. Muscle 22 is partially a continuation of 19, but the greater part of the thin sheet attaches along the upper edge of the jaw. Bands in connection with this pass through muscles 20 like basket-work. Muscle 18 (Figs. 3 and 10) properly not belonging to the

buccal mass but to the side of the head cavity, is a thin sheet of white muscle and connective tissue, often interrupted or divided into several bands, segregating the cerebro-pleural and cerebro-pedal connectives into side pouches of the head cavity. In Fig. 13, showing the dorsal view of the buccal cartilages, a muscle (23) is shown, which anchors the lateral cartilages to the main radula support. Another muscle (24) passes between the two halves of the support, and binds them closely. The tissue between these two halves is rather soft and not rigid enough to form a firm connection.

### Nervous System.

Cerebral ganglia and nerves arising therefrom (Fig. 33). The cerebral ganglia are situated on either side of the buccal mass at the base of the tentacles, and are connected one with the other by a long ribbon-like commissure, which embraces the front of the buccal mass. Each ganglion, as well as the cerebro-pleural and cerebro-pedal commissures, is situated in a sort of incomplete side chamber of the head sinus, formed by thin dorso-ventral sheets of muscle (18 Fig. 3). From each ganglion the following commissures and nerves arise: the cerebral commissure, labial commissure, cerebro-pleural and cerebro-pedal commissures, two prominent nerves to the lips (*ul*, *ul'*), a strong tentacle nerve (*tn*), a very slender nerve to the eye (*op*), several minute nerves to the base of the tentacle (*tn'*), a fine nerve to the otocyst and two small nerves to the dorsal wall of the head cavity (*hw*).

The cerebral commissure lies perfectly free in the head cavity, but is held in place to a certain extent by slender muscle bands which anchor the buccal mass to the front wall of the head sinus (Fig. 3). From the upper edge of the commissure three or four, probably more, very fine nerves are given off to the head wall. Below the cerebral commissure, and from the anterior ventral portion of each ganglion two important nerves (*ul*, *ul'*) pass downward and forward into the musculature of the lips, particularly the portion in front. These two nerves soon anastomose and also send a branch or two backward to join nerves from the labial ganglia. As shown by the figure (Fig. 34) the system not only supplies the lips but also, by dorsal branches, the whole front of the head.

From the outer face of each ganglion three sets of nerves pass into the tentacle of that side. Counting from the front the first, as already mentioned, is the tentacle nerve (*tn*). This soon divides into

a number of branches, which distribute themselves radially and proceed to the tip of the tentacle. Next is the fine optic nerve, which runs parallel and close to the tentacle nerve, straight to the eye, which is situated beneath the integument near the base of the tentacle. The third set arises just back of the optic nerve and consists of a variable number of minute fibres which pass outward to the outer side of the base of each tentacle.

From the hinder end of each cerebral ganglion the cerebro-pleural and cerebro-pedal commissures pass backward and slightly inward. The former, which is considerably the larger of the two, rises outermost. Between them and closely appressed to the cerebro-pleural connective the otocyst nerve is seen to originate. This passes backward still close to the connective, to the otocyst (*ot*) which is situated on the ventral surface of each pleural ganglion. As the two commissures proceed backward they diverge more and more, the pedal bending inward to join the pedal ganglionic mass. From the cerebro-pedal connective of each side there are given off two, sometimes three, nerves to the ventral and lateral walls of the head (*p'*). These branch and some of the twigs anastomose. One or two fine nerves are also given off from the cerebro-pleural connective. It would appear that the septa separating, from the main buccal sinus, the chambers in which lie the connectives, serve in a measure to protect the commissures during the vigorous movements of the buccal mass. Several fine nerves are given off to these septa from the cerebro-pedal connective (see Fig. 3).

The labial ganglia and subradular ganglia (Figs. 37 and 38). The two labial ganglia are found imbedded in the protractors of the buccal mass, each one beneath and a little to the side of the subradular pocket. The cerebro-labial commissure departs from the inner and lower side of each cerebral ganglion which is produced or extended toward the labial ganglion of that side. Ganglion cells extend wholly across the connective, though scarce in the middle portion of the commissure. This is also true of the rather more slender commissure uniting the two labial ganglia. From the anterior face of each labial ganglion three strong nerves (*Ppn*) are given off to the palps (*Pp*). These branch freely and anastomose in such a manner as to form an astonishingly complicated network of nerves, passing upward to the uppermost parts of each palp, and also downward to the lower border. A small cross nerve connects the innermost palp nerves of each side. From the anterior and lower side of

each ganglion there also arise two nerves (*il*, *il'*) which innervate the lower lips (or posterior, if the head is held in a natural position). The outermost of these nerves seems to anastomose in several places with branches of the labial nerves (*ul'*), from the cerebral ganglia. Nerves from the labial ganglia may therefore be said to innervate primarily the palps, and lower lip. From the outer end of each labial ganglion arises the stomatogastric or buccal commissure (*StgC*). This commissure passes upward around the buccal mass to the stomatogastric, or buccal, ganglion of its respective side. In its lower portion the commissure is rather flat and ribbon-like, but above becomes constricted. A description of the stomatogastric ganglia will be given later. From the lower part of each stomatogastric commissure a fine nerve (*bn''''*) passes downward and backward through the protractor muscles and was lost near the origin of these muscles on the posterior processes of the buccal cartilages.

BÉLA HALLER has rightly contended that subradular ganglia are present in the *Docoglossa*, but the statement has been denied by various other observers.

In *Lottia gigantea* I have found what I believe to be the subradular ganglia. They are small, and are connected by very definite nerves with the labial ganglia. They are most certainly not connected, as HALLER believes, with the pedal ganglia. At the base of the stomatogastric commissure of each side a slender nerve (*Sub. R. C*) is seen to depart into the protractor muscle, having a course backward and upward. When about opposite the hinder end of the subradular pouch, this nerve divides into two branches, one passing backward, the other inward and forward. This inner branch goes directly to the subradular ganglion of its side. The subradular ganglia (*Sub. R. G*) are situated on the under surface of the lower wall of the subradular pouch near its hinder end (see also Fig. 4), and sometimes right at the end. Each ganglion lies obliquely, from a direct transverse line, pointing forward. In one or two specimens there seemed to be a very slender commissure uniting the two. To find them it is only necessary to remove the ventral wall of the buccal sinus, working from below, then to remove the protractors and to part the muscles lying above these. The ventral wall of the subradular pouch is then seen, and near the hinder end the two small ganglia.

Running forward along the ventral wall of the subradular pouch is a very delicate nerve from the inner end of each subradular ganglion.

Opposite this from the posterior end of each ganglion there also departs a much more prominent, though delicate nerve, which passes around the hind end of the subradular pouch, and then proceeds forward. Almost at once each divides into three branches, as shown by Fig. 38. The outermost ones turn directly at right angles and proceed outward over the dorsal wall of the pouch. The others (*Sub. R. N*) go forward and anastomose, branch, and form a delicate network over the whole sublingual (or subradular) organ, and anterior portion of the dorsal wall of the subradular pouch. These nerves can be made out only in a carefully macerated specimen, as they are extremely delicate. Their position seems to be in a thin connective tissue basis, beneath the epithelium.

From the subradular commissure a long slender nerve (*Ppn'*) is given off on each side, forward to the palps, and can be traced as far as indicated in the figure. Another very tiny nerve is given off to the subradular pouch from the point where the commissure turns forward. From this point also, as already indicated, a long nerve (*bn*) passes backward in the radula protractors to the hind end of the buccal mass, whence it proceeds to the sublingual artery and becomes too small to follow further. From this nerve, about half way from its origin to the end of the buccal mass, two other nerves are given off into the heavy muscles. One (*bn'*) passes forward above the subradular pouch (innervating the forward portion of the radula protractors) and the outer (*bn''*) goes forward and outward. I am unaware of the final distribution.

The subradular ganglia were also found in *Acmaea patina* and the main connections and nerves followed out. These were identical with those of *Lottia gigantea*. I have no hesitation in saying that the ganglia are characteristic of the *Acmaeidae* in general. The theoretical bearings of the presence of these ganglia on the relationships of the *Docoglossa* are most important and it would be entirely superfluous to detail them in this connection.

Pedal ganglia and nerves (Figs. 30 and 33). The pedal ganglia are the largest in the animal, and consist essentially of an anterior thickened portion on each side, two long pedal cords, and three distinct commissures (*Pc, Pc', Pc''*). The pedal cords (*Ped. G'*) are really elongated ganglia. In front, the main thickened pedal ganglia (*Ped. G*) are connected by a heavy commissure (*Pc*), in which are numerous ganglion cells. The cerebral and pleural connectives enter each ganglion on the anterior face, which is produced forward

and outward they meet them. Practically the whole of the pleuro-pedal connective is ganglionic. The pedal cords pass directly backward and outward in the cavity of the neural arteries and form with the posterior commissure (*Pc''*) a rude ellipse. Just back of the anterior commissure (*Pc*) is a small and very distinct secondary commissure (*Pc'*) uniting the two cords. Ganglion cells extend part way across the posterior commissure (*Pc''*). Back of this connective the pedal cords (*Ped. G''*) are still ganglionic, and remain so till the branching takes place.

Three sets of nerves are given off from the pedal ganglia and cords: 1) those innervating the foot proper, 2) small nerves supplying the spindle muscle, 3) fine nerves given off on the inner side of the cords to the central portion of the foot. The foot nerves (*Ped. N*) are by far the largest, and they leave the pedal cords on the outer and lower aspect. Usually there are about sixteen nerves to each side, but the number varies, and an exact bilateral symmetry of number is by no means constant. The nerves pass downward and outward in a slanting plane, and very soon begin to branch, and anastomose with those next to them, the net becoming finer and finer as the edge of the foot is approached. Not only is there a branching in this single plane but also, to a more limited extent, in dorsal and ventral directions. Usually about half way from the pedal cord to the edge of the foot rather prominent ventral branches depart from the main pedal nerves, and these in turn ramify over the sole of the foot. So many nerves end in the edge of the foot it is not surprising that the margin is one of the most sensitive portions of the whole animal. In watching the creatures crawl one sees at once that they depend largely on this restless margin for orientation, and that as they move along it responds to any irregularity or roughness of the surface quite as quickly as do the tentacles. The pedal cord beyond the posterior commissure loses its ganglion cells and divides, just as do the ordinary foot nerves, the branches anastomosing freely with those of the nearest pedal nerves. In front, also, there is a continuous network in the anterior portion of the foot, as indicated in Fig. 36.

The nerves supplying the spindle muscle (*Sh. M. N*) are small and are imbedded in the superficial muscles of the body wall. Like the pedal nerves, they vary, apparently, in number. The anterior most of these nerves are the largest and they are also more easy to follow. An anastomosis takes place between them and this apparently occurs throughout the length of the animal. The posterior nerves are quite

delicate, and are difficult to make out for any great distance in the muscle, even in well macerated specimens. All these nerves pass nearly to the upper edge of the spindle muscle, where it joins the shell, but in dissection were invariably lost here.

The median pedal nerves (*Ped. N'*) are also very slender. There are from fifteen to twenty of them to each cord, and they anastomose with each other and also to a limited extent with those of the opposite side. They are so delicate that one finds great difficulty in following them in the tough muscle of the body wall.

Pleural ganglia and mantle nerves (Fig. 30). The pleural ganglia are connected with the pedal ganglia each by a short, thick ganglionic cord. The ganglia are not precisely alike in shape by reason of a slightly different arrangement of the nerves which are given off. Each is produced for some distance dorsally, being, as it were, drawn out by the visceral commissure. In the right this prolongation is more nearly vertical than in the left, because the visceral loop lies to the right of a sagittal plane. By a comparison of the several figures, the reader will have no difficulty in making out the shape of the ganglia and the origin of the nerves.

From each ganglion the following sets of nerves arise: mantle nerves, the visceral commissure or loop, several nerves to the alimentary canal and viscera, on the left side a nerve connecting the left pleural ganglion with the osphradial or ctenidial nerve, and an unimportant nerve to the body wall.

Each pleural ganglion gives rise to a pair of prominent nerves to the mantle, the anterior pallial (*A. P. N*) and posterior (*P. P. N*) pallial nerves. Those of the right side will be considered first. After leaving the right pleural ganglion they diverge slightly, both however passing outward. Before reaching the upper edge of the spindle muscle the posterior pallial turns backward and soon enters the body wall a short distance below the attachment surface of the spindle muscle. The right anterior pallial, having divided into two branches, turns a little forward and plunges into the shell muscle. These pallial nerves like their fellows of the left side are free from ganglion cells. They are white glistening bands, somewhat flattened and ribbon-like near their origins, but soon round like other nerves, and become constantly smaller. Immediately after entering the tough spindle muscle the anterior branch of the right pallial divides into two parts. At the inner edge of the pallium these two branches diverge, one passing forward in the mantle, the other backward. Each again divides

into smaller branches which pass toward the periphery of the mantle and join the circumpallial nerve (*C.P.N.*). This nerve completely encircles the animal. It lies at a constant distance from the mantle edge, and on the outer border of the circumpallial blood sinus. All the pallial nerves and their branches ultimately reach and join it. A description of the nerve will be deferred till later. Occasionally the tertiary branches of the pallial nerves again divide before reaching the circumpallial. The hinder branch of the anterior pallial (right), after entering the spindle muscle, turns sharply backward and pursuing this general direction divides into two branches which join the circumpallial at about the middle of the animal. While still within the muscle this posterior branch of the right anterior pallial is joined by a slender nerve (*R.Par*) given off by the right osphradial nerve. I have called it for convenience of description the right posterior parietal nerve. That of the left side has very similar connections. The anterior prolongation of the right osphradial (*R.Par'*) joins, in the mantle, the right anterior pallial nerve. Consequently the osphradial nerve may be considered to divide into two terminal branches, both of which unite with the pallials. This is true of the left side also, as will be seen later.

The right posterior pallial passes directly backward conforming somewhat to the trend of the spindle muscle, which it soon enters and follows nearly to the hind end of the animal, giving off enroute three main branches, which reach the circumpallial after again dividing. As it nears the hind end of the animal the posterior pallial (right), now very much attenuated, passes out onto the mantle and near the median line turns abruptly toward the circumpallial which it joins. A very much slenderer nerve, in fact quite the smallest in that vicinity (*P.P.N'*), leaves the posterior pallial just as it turns to join the circumpallial and running a short distance parallel with the last, joins the attenuate, final branch of the left posterior pallial. Thus the ends of the two posterior pallials are joined by a short, fine nerve, which completes an inner ring as it were. It does not need but a glance however to show that this inner ring does not at all resemble HALLER'S<sup>1</sup>) "Mantelrandnerv" which is figured as of the same calibre throughout, and with scattered ganglion cells, which the posterior pallials do not possess.

As on the right side, there are two main pallial nerves issuing

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1) HALLER, l. c., fig. 1.

from the left pleural ganglion. They pursue likewise the same relative directions. But while it is the anterior right pallial that branches near the ganglion, on the left side it is the posterior. The left anterior pallial does not branch till after it has passed into the thick tough tissue of the spindle muscle. Here three branches are given off, which, pursuing different directions, redivide on reaching the pallium, and ultimately join the circumpallial nerve. The left posterior pallial divides into two branches very soon after leaving the ganglion, and both enter the spindle muscle sooner than the corresponding nerve of the right side. The anterior branch presently leaves the other, to which it has been running parallel for a short way, and turning outward passes under the left side of the pericardium, and on reaching the spindle muscle turns backward. Here it receives the posterior left parietal (*L. Par*) which, like the right, is a terminal branch of the osphradial nerve. The pallial nerve then divides, on reaching the mantle, and joins the circumpallial. The course of the other branch of the posterior pallial is much like that of the posterior pallial of the right side. As noted above a slender nerve joins the two near their ends (*P. P. N<sup>u</sup>*).

The circumpallial nerve. As has already been indicated the circumpallial nerve (*C. P. N*) forms a complete circle around the animal, near the mantle edge. It lies on the inner border of what has been called the gland zone, and just outside the circumpallial blood sinus, about midway between the dorsal and ventral surfaces of the pallium.

The branches of the pallial nerves join the circumpallial from below, passing under the circumpallial sinus. Throughout this nerve ring there are ganglionic cells scattered in the form of frequent nodes, particularly where the large pallial nerves join, and where the more prominent branches to the margin depart. The appearance of the circumpallial with its frequent loops can best be gained from the figure. The nerves which depart to the margin of the mantle vary considerably in size. They anastomose in a very intricate way, and where the more prominent join each other there are tiny ganglionic swellings. The final branches of these nerves reach the mantle border and most of them enter the little sense papillae which are here very numerous. This point can be determined by dissection. Other branches pass downward.

Another system of branching is present, though not developed to the degree that the nerves to the mantle edge are (Fig. 31). These

nerves usually leave the pallial nerves just as they pass under the circumpallial sinus, before joining the ring nerve. They pass upward over the sinus and branch out under the epithelium of the dorsal surface of the pallium, branches passing both inward and outward (*M.N'*). They lie above the main marginal system.

There is still another set of nerves in the mantle, which are very difficult to demonstrate, and can be seen only in particularly favorable specimens. It so happens sometimes that in specimens macerating in weak nitric acid, a stage arrives where all the muscular and connective tissue becomes semi-transparent or translucent, but the nerves are not affected at all and remain opaque and whitish. If one secures such a favorable specimen he will be able to see these nerves under bright sunlight. They are exceedingly fine and branch over the floor of the sinus and arterial spaces of the mantle in such a way that if the dorsal sheet of muscle is stripped off the mantle, no further dissection is necessary to show them (*M.N''*). They are apparently given off from the circumpallial, or some of its branches, because they are more prominent in the region of this nerve, and fade out toward the inner edge of the mantle. No direct connection with the circumpallial could be demonstrated, because so soon as one would try to lift it up, the very delicate connections would be broken, if they really existed. From the nature of the anastomosing I have no hesitation in saying that these are nerves. They have been drawn in for only a small portion of the mantle, in the figure, but were seen on the opposite side, in front, and in the rear.

The pleuro-osphradial connective. A rather remarkable nerve (*P.O.C*) is that which joins the left pleural ganglion with the osphradial nerve. I have been able to demonstrate this only on the left side of the body. This connective issues from the left pleural between the two pallial nerves, and pursues a course to the spindle muscle close beside the left anterior pallial. Soon it enters the muscular tissue and turns abruptly upward, piercing the thick muscles forming the floor of the anterior angle of the pericardium. Just below the surface, however, it is joined by the osphradial nerve, and at the junction the osphradial nerve turns forward as the ctenidial nerve (*Ct.N*). Usually, but not always, the left posterior parietal nerve leaves at this point also, and passes back to join, as already pointed out, the posterior pallial. Consequently on the left side the osphradial nerve is connected with the pallial nerves in two different

places, and by two nerves and also with the pleural ganglion direct, by a third, the pleuro-osphradial connective.

The osphradial, ctenidial, and parietal nerves. The logical method perhaps would be the description of the visceral commissure and its ganglia before mentioning the osphradial nerves, which arise from ganglia in this commissure — namely from the supra- and sub-intestinal. It seems desirable, however, to finish all those nerves which have any connection with the mantle, or other portions of the body wall, and defer the description of the visceral commissure and its ganglia until the visceral nerves are considered.

The right osphradial nerve arises from the subintestinal ganglion, and is considerably smaller than that of the left side. It passes outward and usually slightly forward (depending largely on whether the gonad is very large and encroaches on the head cavity). A tiny nerve accompanies it, in front, and apparently joins the complex of nerves under the osphradium. For a short distance the right osphradial nerve is free, but sooner or later enters the dorsal wall of the head cavity, and just before reaching the osphradium sends a prominent branch backward, the posterior right parietal (*R. Par*). This nerve lies in the muscular floor of the rectal portion of the right kidney, and as already described joins the posterior branch of the right anterior pallial, within the spindle muscle. Just after leaving the osphradial nerve it gives off one or two fine branches ventrally into the muscular wall of the body. I have been unable to trace either of these to the pleural ganglion, so that, on the right side, the pleuro-osphradial connective does not seem to exist.

Before entering the spindle muscle to join the pallial nerve, the right posterior parietal gives off a delicate branch (*Nph. N*) which lies in the wall of the nephridial blood sinus, and follows this sinus back, close beside the inner edge of the attachment surface of the spindle muscle, nearly to the hind end of the animal. Here it is seen to leave the sinus and pass into the vein-net of the right kidney, nearly to the median line. It may or may not join that (*Nph. N'*) of the left side. The nerve is so fine that it has been impossible to tell whether branches are given off, along its length, to the vein-net, or into the spindle muscle.

The main osphradial nerve of the right side then passes behind the osphradium and is here strongly ganglionic. On reaching the spindle muscle it turns abruptly forward (*R. Par'*), follows the edge around, being imbedded in the pallial hood, and joins the anterior-

most branch of the anterior pallial nerve, close to its point of departure from the spindle muscle. The nerves to the right osphradium are numerous and depart from the osphradial ganglion. They are best understood from the figure.

Just at the inner edge of the mantle where the forward branch of the osphradial nerve (*R. Par'*) joins the anterior pallial, in the forward angle between the two, there is present a very curious ring nerve (*Rg. N*), lying in the upper wall of the pallial hood. (The hood consists of a dorsal and a ventral wall joined by numerous trabeculae. Through the spaces thus formed, blood circulates and is aerated.) The shape of this remarkable nerve is best shown by the drawing. Small nerves from the right anterior parietal (*R. Par'*), which is merely a prolongation of the osphradial, supply the ring, which also gives off extremely fine nerves. A second nerve ring (*Rg. N'*) much smaller than the first was found near the median line, in a similar position with reference to the mantle and mantle hood. This median ring is connected with the lateral one by a very fine nerve. Slender nerves are given off from it to the mantle hood, and mesially from the central ring a few faint branches can be seen going toward the circumpallial (which they doubtless either directly or indirectly ultimately join). The lateral ring is larger in smaller specimens than in large ones, and the median ring (*Rg. N'*) could be found only in specimens about two-thirds adult size. Is it probable that we have here a sense organ characteristic of the younger stages of the adult animal?

By way of emphasizing the fact it may be repeated that the osphradial nerve of the right side is connected with the pallial nerves in two places and by two nerves — namely the anterior and posterior right parietals (*R. Par'* and *R. Par*).

The left osphradial nerve arises from the supra-intestinal ganglion of the visceral commissure (*Sup. I*) and follows a course on the left side similar to that of the right osphradial nerve on the right. It is much stouter than the right osphradial, and is at first free, but enters the dorsal head wall just before reaching the osphradium. Like the right, the left osphradial nerve does not go directly under the osphradium, but behind it, and gives off branches to the organ. These are necessarily small and the figure does not do justice to the finer branches, either in extent or numbers. Where these nervelets are given off there is a ganglion in the osphradial nerve, just as is the case on the right side. After leaving the osphradial ganglion the main nerve enters the thick muscles of the dorso-lateral portion of

the head cavity, thence passes upward to the floor of the anterior angle of the pericardial cavity. Here, just beneath the surface, a junction is formed with the pleuro-osphradial connective, and usually also, the posterior left parietal (*L. Par*) departs from this point. From this junction point the main nerve now turns abruptly forward, on the floor of the pericardium, and parallel to the inner edge of the spindle muscle (*Ct. N*). Sometimes, but not always, this portion of the nerve divides and then rejoins, to form an elliptical loop, as it were. Upon reaching the base of the efferent branchial vein the nerve turns sharply to the right, and at this point there is a ganglion (*Ct. G*). The ctenidial nerve (*Ct. N'*) enters the efferent sinus of the gill, and from the ganglion there are also given off two anterior left parietals (*L. Par'*). The exact details of the ganglion, and the arrangement of the two parietals which leave it are subject to considerable variation. The figures are fairly typical. On entering the efferent sinus the ctenidial nerve divides into two, one quite small (*Ct. N''*), the other more prominent (*Ct. N'*), which run parallel in the tissue of the outer wall of the vein. Fine nerves are given off at frequent intervals, dorsally and ventrally (*ctn*). The ventral ones are more easily seen, the dorsal ones being difficult to make out. The former pass along the bases of the gill leaves, and are soon lost. The main ctenidial nerve runs to the tip of the gill.

The two anterior parietal nerves (*L. Par'*) start out from the branchial ganglion and soon diverge. The inner one is very delicate and spreads out over the central portion of the hood. The other joins the anteriormost branch of the left anterior pallial, just as the corresponding nerve does on the right side.

Just posterior to the branchial ganglion there are usually two small nerves which pass outward into the spindle muscle.

The posterior parietal of the left side (*L. Par*) leaves the osphradial nerve at two different points, in different individuals. The most usual point of departure as already described is at the junction of the pleuro-osphradial connective with the osphradial. In others the osphradial ganglion is the point. In both cases, however, the nerve goes outward and backward in the floor of the pericardium, one branch joining the posterior pallial, the other (*Nph. N'*) following a course exactly like the same branch of the other side. As mentioned above, a direct inter-connection of these two nephridial nerves has not been made out.

This finishes the principal nerves to the body wall, mantle and foot.

Innervation of the viscera. The nerve supply of the viscera — pharynx, oesophagus, intestine, glands, circulatory system, nephridia and gonad — is derived from the following ganglia: the stomatogastric (buccal), the pleural and visceral (sub-anal, or abdominal). The nerves will be taken up in this order.

Stomatogastric system (buccal or sympathetic, Figs. 33, 35, 39, 42, 43). The two stomatogastric ganglia (*Stg. G*) and the commissure uniting them are situated on top of the buccal mass in the angle between the pharynx and radula tube, or at that point where the pharynx seems to leave the buccal mass. The ganglia are placed obliquely, each nearing the other posteriorly, where they are joined by a transverse commissure. From the forward end of each ganglion the stomatogastric commissure passes outward around the buccal mass, then downward imbedded in muscle, to join the labial ganglion of that side. On the way, a long nerve is given off into the muscles as already described. From the posterior end of each ganglion a nerve passes outward into the muscles of the buccal mass, and here branches. Another fine nerve starts from the same place and passes into a cord-like muscle on the top of the radula tube, which it follows backward.

From the posterior end of each ganglion (Fig. 43) a slender nerve passes forward on each side, into what might be termed the upper lip of the radula tube, which serves undoubtedly as a valve to close the mouth of the radula tube. These nerves diverge slightly and on reaching the front of the lip they branch. A cross nerve passing through the thick tissue of the flap, unites at this point the nerves of the two sides. One branch passes inward and backward along the side of the radula tube; another goes forward and outward around the buccal cartilages; two others pass forward and downward into the buccal mass, and a fifth inward to the front of the lip.

At about the middle of each stomatogastric ganglion, a small nerve (*ipn*) is given off to the ventral wall of the pharynx. At this point the sacculate pharynx narrows, and the ventral wall which is thin, turns downward over what has been called the upper lip of the radula tube. These smaller nerves (one on each side) pass at first forward, then upward and backward under the lesser or ventral folds of the pharynx. The nerves anastomose with each other and also give off very fine branches which cannot be followed. The two main nerves follow the course of the folds, spirally around the oesophagus, and enter the proventriculus, along with numerous others, and are

then lost in the maze of fine nerves, forming a network over the walls of this fore-chamber of the stomach.

It is from the anterior end of each ganglion that one of the principal visceral nerves originates. This passes directly upward and inward on either side of the dorsal wall of the buccal cavity. It immediately divides into two branches. One of these passes forward and enters the duct of the buccal gland, which it follows back, on each side as the stomatogastric nerve (*Stg. N*, *Stg. N'*), to be spoken of presently. The other branch passes into the dorsal fold of the pharynx, on each side, where it divides into a forward (*spn'*) and a posterior (*spn*) branch. The forward branches follow the two folds forward and downward, while the posterior branches, in a similar way, follow along the base of each fold to the proventriculus. In the pharynx, fine branches (*spn''*) are given off laterally along the septa constricting the crop into lateral pockets. These probably continue, in the oesophagus, but could not be determined.

The nerve which passes forward after the branching of the main stomatogastric nerve from the forward end of the ganglion, itself branches. One division follows each duct of the buccal gland, backward, while the other continues forward in the folds of the dorsal wall of the pharynx, nearly to the palps.

The posterior or stomatogastric nerves have a different distribution on either side of the body so that they will have to be considered separately. Each lies either free in the lumen of the salivary duct (*Bg. D*) or just to one side of the lumen. The right stomatogastric nerve (*Stg. N*) enters the posterior septum of the head cavity at about the level of the ventral wall of the pharyngeal pouch. A prominent branch is given off from the nerve to the anteriormost bend of the alimentary canal, where it divides, one division going to the liver, the other to the intestine (*a*). The nerve in the septum now branches several times. One division (*b*) passes through the visceral loop and runs backward toward the heart, in the wall of the aorta. The other main branch passes backward out of the septum through the visceral loop, under the aorta, pursuing a course to the left between the oesophagus and the intestine. A small branch (*b'*) is given off to the lateral wall of the aorta, and then the main nerve divides into two branches. One (*c*) passes ventrally to the dorsal wall of the visceral artery, along which it can be followed for some distance. The dorsal branch follows the ventral wall of the first anterior loop of the intestine, backward, dividing into two branches (*Stg. N*

and *d*). One of these branches (*d*) supplies the ventral wall, while the other (*Stg. N*) curves around to the dorsal wall, keeping quite distinct from branches of the left stomatogastric (*Stg. N'*).

The left stomatogastric nerve, like the right follows the salivary duct to the posterior septum of the head cavity, and here divides into at least two parts. The smaller (*e*) supplies the ventral wall of the oesophagus. The main branch passes backward, between the gonad and the oesophagus, to both of which fine branches are given off. It here lies in the thin buccal gland. A fine branch (*f*) is given off to the genital artery, and follows the vessel, along its ventral floor, into the pericardium. From this point the main nerve passes diagonally across the dorsal wall of the oesophagus, and reaches the left limb of the first anterior loop of the intestine (Fig. 39). Here it divides, on the lateral wall, into two branches, one going forward to supply the lateral and dorsal walls of this portion of the intestine, keeping distinct apparently from branches of the right stomatogastric. The other, or posterior, branch (*Stg. N'*) runs along the lateral wall, where it divides. One division (*g*) keeps on the lateral wall while the other passes to the dorsal.

Visceral nerves arising from the pleural ganglia (Figs. 39 and 41).

Each pleural ganglion is prolonged dorsally into a sort of horn from the summit of which the visceral commissure or loop arises. It is from this dorsal or visceral tract of each pleural ganglion that the visceral nerves arise.

From the right pleural ganglion fine nerves reach the pharynx, oesophagus, visceral artery and dorsal aorta. There are two nerves which ultimately reach the oesophagus. The largest (*y*, see also Fig. 3) leaves the ganglion near its upper end, and passes through the visceral loop, over the little knob-like distal end of the radula tube, pierces the septum of the buccal sinus, after following it for some distance to the side of the oesophagus. Then the nerve goes backward diagonally across the dorsal wall of the oesophagus, reaching the left side about where the left stomatogastric crosses obliquely to the intestine. Thence the nerve passes backward along the lateral wall of the oesophagus to the proventriculus, where it is lost. On the way it anastomoses with other nerves near the hind end of the oesophagus. Before this nerve reaches the oesophagus it gives off at least one branch (*y'*) which following the right side of the oesophagus innervates that portion of the intestine of a bluish tint in Fig. 1. This

part lies under the oesophagus, and the nerve can be seen to join the network of nerves which covers the intestine at this point.

The other nerve (*x*) to the oesophagus leaves the ganglion at its uppermost end, and passes directly to the oesophagus, which it follows along the right wall, to the proventriculus.

From the right pleural ganglion a small nerve (*z*) departs near the two others already referred to and passes through the visceral loop, whence its course is backward in the dorsal wall of the funnel-shaped mouth of the visceral artery. It then follows the visceral artery backward, lodged in the dorsal wall, and close beside branch *c* of the right stomatogastric. All these nerves on the visceral artery may finally reach the intestine, but are too small to follow unless lodged in some resistant tissue.

Two other nerves leave the right pleural ganglion. A dorsal one (Fig. 3 *v*) innervates the aorta and posterior portion of the pharyngeal pouch. The ventral nerve (*v'*) passes forward along the floor of the pharyngeal pouch which is here thin-walled.

There are three nerves from the left pleural ganglion which have been found to innervate the viscera, principally the oesophagus (Fig. 41 *l, m, n*). The innermost (*l*) is the largest. It goes directly upward to the oesophagus and divides into several branches, which pass backward along the ventral, dextral, and dorsal walls of the oesophagus, anastomosing freely. These nerves form part of the general supply for stomach and intestine. The next nerve (*m*) is smaller and usually divides only a few times. Its branches pass backward along the ventral wall of the oesophagus. The third nerve (*n*) has a similar course. A branch of the nerve *m* passes to the right and follows the visceral artery along with the other nerves already described (*m'*). Branches of the nerve *l* not alone supply the oesophagus, but also that portion of the intestine to which the nerve *y'* goes.

The visceral commissure and nerves from its ganglia (Figs. 35 and 39). The visceral commissure as will be seen from the figure is not extensive, and is situated to the right of the pharynx. The upper loop of the "Fig. 8" encircles the aorta. The three ganglia are rather small and are close together, there being little or no commissural connective between them. The left or supra-intestinal ganglion is situated on the left side of the aorta, and in life is covered by the acini of the pharyngeal or posterior salivary glands. As already described the left osphradial nerve arises from this ganglion. On the right side of the aorta, in that portion of the loop arising

from the left pleural ganglion is the subintestinal ganglion. This gives rise to the right osphradial nerves. Between the above two ganglia is the visceral ganglion (abdominal or subanal) which supplies several very important nerves to the alimentary canal, nephridia, and heart.

Three main nerves can be distinguished. These supply (first nerve) heart (presumably) and pericardium; (second nerve) the ureters, nephridia, rectum, afferent ctenidial vessel, and visceral mass; (third nerve) visceral mass. The nerves to the heart and pericardium (*Cd. N*, *Cd. N'*) lie along the dorsal wall of the aorta. The larger nerve arises from the visceral ganglion close to the main visceral nerve but the smaller one usually about midway between the left stomatogastric and the larger nerve. As the aorta is about to enter the pericardium the two nerves join. Then an immediate division takes place (*Pd. N'* and *Pd. N''*) passing into the dorsal wall of the pericardium, while *Cd. N''* continues along the aorta, but was not traced onto the ventricle. Another branch (*Pd. N*) passes backward and to the right, thence turns again to the left and lies along nearly the whole length of the ventral wall of pericardium, giving off a branch or two into the dorsal wall of the right kidney (cul-de-sac). This nerve is joined to a branch of the main visceral-nephridial nerve by a short cross nerve (*j*). It will be seen from the foregoing that no nerve was actually traced into the heart.

The visceral nerve (*Vn*) is the largest arising from the visceral ganglion. It passes backward and slightly to the right, over a loop of the intestine, and soon gives off two branches (*Vn'* and *Vn''*) to either side. The latter passes to the left where it is joined by the cross nerve *j* from the heart nerve (*Cd. N*), then turns backward under the rectum, and divides into three branches, two of which spread out in the membrane covering the visceral mass while the third reaches the cul-de-sac of the right kidney, on the left side of the body. The other (*Vn'*) of these two branches of the visceral nerve has a course backward over a portion of the intestine best shown in Fig. 39. A branch is given off to the liver, and the main nerve supplies not only the portion of the intestine alluded to, but likewise the anterior half of the stomach.

From the origin of these two divisions, the main visceral nerve (*Vn*) passes backward then turns upward and forward around the inner side of the body wall, bounding the pallial cavity at the rear (Fig. 40). In other words the nerve passes onto the floor of the

upper or rectal portion of the right nephridium, near the ureter. In this connection it should be remembered that the rectal portion of the kidney extends out into the pallial cavity, bounded on the forward side by the rectum. Just before passing under the rectum, on its course forward, the visceral nerve divides into two branches, one of which supplies the right ureter. The other division, somewhat smaller, keeps on forward under the rectum to the outer wall of the left kidney, where another division into two nerves takes place. The left one of these (*act. n*) leaves the wall of the kidney and enters the afferent vein of the ctenidium which it follows, imbedded in the muscles of the outer wall. This nerve is considerably smaller than the main ctenidial nerve (*Ct. N'*). Just before entering the sinus the nerve splits and then joins again, forming a sort of loop.

The right branch (*lu. n*) supplying the left kidney and its ureters follows close under the left reno-pericardial canal, nearly to the ureter, where it divides into two, one passing to either side of the ureter. The lower of these branches then passes upward into the vein-net over the kidney, and thence backward where it was soon lost.

The prominent branch (*ru. n*) which innervates the right ureter lies just under a thin layer of muscle in the floor of the rectal portion of the kidney, and pursues a course almost direct to the ureter. The branchings can be better understood from figure than by description. Two divisions at the end of this nerve surround the opening of the ureter and form a plexus. A prominent anterior division (*ru. n'*) passes upward, and enters the vein-net of the kidney.

The third nerve from the visceral ganglion (*Int. N*) is smaller in caliber than either of the others. Occasionally it arises by two roots, one of which anastomoses with nerve  $\bar{V}n$ . It then passes backward and to the right over the anterior-most loop of the intestine, branching a number of times. The distribution of these divisions can best be seen in Fig. 39. The nerve supplies, then, the right anterior portion of the visceral mass.

Resumé of nerve supply of alimentary canal. It has become evident from the foregoing account that the alimentary canal is very plentifully supplied with nerves, arising from three centers: the stomatogastric, visceral, and pleural ganglia. All the nerves of the alimentary canal, particularly those of the stomach, anastomose in a very intricate way, which can be better judged from the figure than from the description. In working out these nerves it must again be stated that only fresh specimens, carefully macerated, are of any

service. Usually only one specimen in ten shows the network on the stomach satisfactorily.

The nerve supply to the oesopagus and stomach is derived from all three centers mentioned. From the stomatogastric ganglia there are two nerves (*ipn*) following the base of the lesser folds of the oesopagus, and two others (*spn*) pursuing a similar course under the dorsal or greater folds. These nerves reach the proventriculus. The left stomatogastric (*Stg. N'*) nerve supplies the left side of the oesopagus, but I was unable to find any branches reaching the stomach. From the left pleural ganglion there are three nerves (*l, m, n*), which branch profusely, spreading over the ventral, lateral, and dorsal walls. From the right pleural ganglion there are two nerves (*x, y*) to the oesopagus. All these reach the proventriculus, where the mesh work of nerves first clearly becomes evident (because the lining is smooth), and thence they continue out onto the stomach. The forward curve of the stomach receives nerves (*Vn', Int. N*) from the visceral ganglion, but no nerves from the visceral ganglion appear to reach the oesopagus.

The intestine just beyond the stomach is supplied from continuations of the stomach nerves, besides the following, the nerve *y'*, a branch of *y*, from the right pleural ganglion, and branches of the nerve *l* from the left pleural ganglion. The loops on the anterior and right side of the body are supplied principally by the nerves *Vn'* and *Int. N* from the visceral ganglion, and by nerve *a*, a branch of the right stomatogastric (*Stg. N*). That portion of the intestine on the left side of the body, lying under the stomach and over the oesopagus (Fig. 39), is plentifully supplied by the left stomatogastric (*Stg. N', g, h*), by the right stomatogastric and its branches (*Stg. N, d*), and by the nerve *y* which lies along the ventral wall, when the intestine is in the natural position. It is wholly probable that the nerves *m', c* and *z*, lying in the wall of the visceral artery, all contribute to the supply of the lower layers of the intestine. Nerves supplying the rectum arise from the main visceral nerve (*Vn*). There is no portion of the alimentary canal on which at least a few nerves cannot be made out, either running parallel, as on the rectum, or forming a net, as on the stomach and on the greater part of the intestine.

Special sense organs. The organs of special sense are the osphradia (SPENGLER's organs), the otocysts, and eyes. The innervation and position of these structures have already been described.

The left osphradium is somewhat larger than the right, and both appear as mere yellowish, elongate lumps on the "neck". In cross section these are seen to be produced forward, and the substance of the organ is made up of a curious spongy connective tissue sharply defined from the muscle layer of the body wall, beneath. In this meshy tissue are seen blood cells, ganglion cells and nerves. The epithelium is low, almost cubical and seems to differ little from that covering the surrounding head wall, except in the clearer more brightly staining nuclei.

The eye is a pear-shaped pit near the base of the tentacle (Fig. 29) and opens to the exterior by a very narrow pore. Undifferentiated epithelium lines the portion nearest the opening, and extends farther down on one side of the cavity than on the other. The "retinal" epithelium is high and very heavily pigmented. The lumen of the eye-pit is filled with congealed humor, which tends to form a definite columnar layer next to the pigmented epithelium.

I have not followed out the finer structure of the otocysts. In sections one can readily see the minute granules which are found inside. As shown by Fig. 28 each is shaped like a little apple seed, and is imbedded in connective tissue, beneath the pleural ganglion. Three connective tissue stays or ligaments hold the structure firmly in place. One (*Lig.* Fig. 28) connects the two otocysts, while two others bind each to the pleural and to the pedal ganglion of that side.

### Summary.

A summary of the more important points in the anatomy of *Lottia* are here given, following the order of the preceding text.

- 1) The *Acmaeidæ* possess a larval nautiloid shell.
- 2) The lips are armed with tiny teeth.
- 3) Within the oral cavity there are two well-developed palps, which receive an abundant supply of nerves from the labial ganglia, and function probably as taste organs.
- 4) A sublingual or subradular organ innervated from the subradular ganglia is present, situated under the tip of radula.
- 5) There are two pairs of buccal glands, the anterior opening by long glandular ducts into the oral cavity, the posterior by the separate acini into the swollen pharyngeal sac.
- 6) The pharynx is thin-walled and dilated, and divided into lateral pockets by frequent constrictions. Into these the posterior salivary glands empty.

7) There is a small forechamber or proventriculus to the stomach.

8) The liver empties by a single large hepatic duct into the proximal end of the stomach.

9) The nephridia are very unequal in size, the left being a tiny sac on the left side of the rectum. The right is large, surrounds the visceral mass, and ends in a cul-de-sac behind the pericardium.

10) Both nephridia are in communication with the pericardium by long canals, which are really diverticula of the pericardium. Only that small portion within the papillae, at the nephridial ends of the ducts, is ciliated.

11) The gonad is large and occupies the ventral portion of the cavity containing the viscera. It lies within the coelom or secondary body cavity and is in communication with the anterior part of the right nephridium by a slender duct.

12) The heart consists of an auricle and ventricle, with a two-lipped valve between them.

13) The circulation is for the most part closed. Sinuses, however, collect the blood in the foot, and there are also open lacunae of minute size in the liver. The arterial system is extensive. The mantle circulation is very well developed, and receives blood from the kidneys, foot and gonad. Over the nephridia there is present a highly developed vein-net. The mantle discharges its blood directly into the auricle.

14) There is a simple ctenidium, on the left side, which receives blood from the right kidney.

15) The mantle is an important auxiliary respiratory organ. It is provided with a cordon of lappets (interrupted in front) which first appear when the animal is about 20 mm in length. The mantle edge contains three sets of glands.

16) In connection with the radula, there has been developed a complicated system of buccal and radular muscles.

17) The cerebral ganglia supply nerves chiefly to the tentacles, eyes, otocysts and lips.

18) Two well developed labial ganglia are present, and supply the palps with nerves, besides giving rise to the stomatogastric and subradular commissures.

19) There are two small subradular ganglia, situated behind the labial ganglia on the subradular pocket of the oral cavity. These ganglia send nerves primarily to the subradular organ. They are united

by slender commissures with the labial ganglia and have no connection whatever with the pedal.

20) There are two long thick pedal cords, continuations of the pedal ganglia. These are united by three direct commissures, and supply the foot and spindle muscles.

21) The innervation of the mantle is complex and wholly typical of the *Acmaeidae*. From each pleural ganglion, there are two principal pallial nerves, which reach a circumpallial nerve completely encircling the animal near the mantle edge. This nerve is ganglionic to a slight degree, and supplies the finer nerves to the mantle.

22) On the left side there is a pleuro-osphradial connective, joining the left pleural ganglion directly with the osphradial nerve.

23) The osphradial nerves arise from the intestinal (or parietal) ganglia of the visceral loop. In the course of each of these nerves there is a ganglion which sends nerves to the osphradium of that side.

24) A continuation of the left osphradial nerve becomes the ctenidial nerve, at the beginning of which there is a small ganglion.

25) Each osphradial nerve by two terminal branches, the parietal nerves, is joined to the pallial nerves, posteriorly in the spindle muscle and anteriorly in the mantle.

26) The nephridial nerves are branches of the posterior parietals, one on each side, and follow the kidney blood collector to the hind end of the animal.

27) In the mantle hood on the right side there is a curious nerve in the form of a small ring, and another in the median line. These are connected with the anterior parietal of the right side. Their significance is not known.

28) The nerve supply of the viscera is derived from the stomatogastric ganglia, the visceral ganglion, and the pleural ganglia. The stomatogastric may be considered the most important center for the alimentary canal.

Palo Alto, California, May 1, 1903.

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## Explanation of the Plates.

Plates 1—4.

The following abbreviations have been used :

- |  |   |
|--|---|
| <i>A</i> auricle   | <i>Coe</i> coelom, secondary body cavity                    |
| <i>a</i> branch of right stomatogastric nerve                                | <i>C. Ped. C</i> cerebro-pedal commissure                   |
| <i>an</i> anal opening   | <i>C. Pl. C</i> cerebro-pleural commissure                  |
| <i>act. n</i> nerve to afferent sinus of ctenidium                           | <i>C. P. N</i> circumpallial nerve                          |
| <i>Ant. Ao</i> anterior aorta  | <i>C. P. S</i> circumpallial sinus or vein                  |
| <i>Ant. P. A</i> anterior pedal arteries                                     | <i>Ct. G</i> ctenidial ganglion                             |
| <i>A. P. N, A. P. N'</i> right and left anterior pallial nerves              | <i>Ct. N, Ct. N', Ct. N''</i> ctenidial nerves              |
| <i>A. Sp</i> arterial spaces of mantle                                       | <i>ctn</i> branches of ctenidial nerves                     |
| <i>At</i> area of teeth on lips  | <i>Ct. V</i> efferent ctenidial vein                        |
| <i>b, b'</i> branches of right stomatogastric to aorta                       | <i>d</i> branch of right stomatogastric nerve               |
| <i>B. C</i> buccal cartilages  | <i>Df</i> dorsal or greater folds of oesophagus and pharynx |
| <i>Bg</i> buccal, or anterior, salivary gland                                | <i>Dors. Br</i> dorsal branch of visceral artery            |
| <i>Bg. D</i> duct of buccal gland  | <i>E</i> eye  |
| <i>Bg. D'</i> aperture of duct of buccal gland                               | <i>e</i> branch of left stomatogastric to oesophagus        |
| <i>Bl. C</i> blood corpuscles  | <i>f</i> branch of left stomatogastric in genital artery    |
| <i>Bl. S</i> blood sinus   | <i>g</i> branch of left stomatogastric to intestine         |
| <i>Bm</i> buccal mass  | <i>Gen. A</i> genital artery                                |
| <i>bn, bn', bn'', bn'''</i> nerves to buccal mass from subradular connective | <i>Gn</i> gonad   |
| <i>B. S</i> buccal sinus   | <i>Gn. D</i> gonoduct (Fig. 23)                             |
| <i>C. c</i> cerebral commissure  | <i>h</i> branch of left stomatogastric nerve                |
| <i>c</i> branch of right stomatogastric nerve to visceral artery             | <i>hw</i> nerves from cerebral ganglia to head wall         |
| <i>Cd. N, Cd. N', Cd. N''</i> nerves to heart                                | <i>il, il'</i> nerves to lips                               |
| <i>Ceph. A</i> cephalic artery   | <i>Int. N</i> nerve from visceral ganglion                  |
| <i>C. G</i> cerebral ganglion  | <i>ipn</i> inferior pharyngeal nerves                       |

- J* jaw  
*j* nerve connecting heart nerve with visceral  
*K.M* vein-net over kidney  
*K.S* kidney vein, or collector from vein-net (*K.M*)  
*L* lips  
*l* nerve to oesophagus from left pleural ganglion  
*Lat.P* lateral pouches of oral cavity  
*Lc, Lc'* labial commissures  
*Lig* ligament connecting two otocysts  
*L.K* left kidney  
*L.G* labial ganglion  
*L.Osph.N* left osphradial nerve  
*L.Par, L.Par'* posterior and anterior left parietal nerves  
*L.U* left ureter  
*lu.n* nerve to left ureter  
*Lv* liver  
*Lv.D* liver duct  
*M* muscular tissue  
*m, m'* nerves to oesophagus from left pleural ganglion  
*Ma* mantle  
*M.C* mucous cells  
*Med.S* median blood sinus of foot  
*M.N, M.N', M.N''* mantle nerves  
*Mth* mouth  
*M.V* mantle veins  
*n* visceral nerve from left pleural ganglion  
*Neu.A* neural artery  
*Nph.N, Nph.N'* nephridial nerves  
*Oc* oral cavity  
*Oe* oesophagus  
*op* optic nerve  
*Osph.G* osphradial ganglion  
*ot* otocyst  
*ot'* otocyst nerve  
*Ov* ovary  
*p* nerves from cerebro-pedal connective  
*Pc, Pc', Pc''* pedal commissures  
*Pd.N, Pd.N', Pd.N''* nerves to pericardium  
*Ped.A* pedal artery  
*Ped.G* pedal ganglion  
*Ped.G'* pedal cords  
*Ped.N, Ped.N'* pedal nerves  
*Per* pericardium  
*Per'* pericardial wall  
*Ph* pharynx  
*Ph.G* posterior or pharyngeal glands  
*Pl.G* pleural ganglia  
*Pp* palps  
*P.P.N, P.P.N'* right and left posterior pallial nerves  
*P.P.N''* nerve joining the above  
*Ppn, Ppn'* palp nerves  
*Pro* proventriculus  
*P.S* pedal sinuses  
*R* radula  
*Ren.P.C, Ren.P.C'* right and left reno-pericardial canals  
*Rg.N, Rg.N'* ring nerves in mantle  
*R.K* right kidney  
*R.Osph.N* right osphradial nerve  
*R.Par, R.Par'* posterior and anterior right parietal nerves  
*Rt* radula tube  
*Rt'* point where radula tube quits aorta  
*Rt''* distal knob of radula tube  
*R.U* right ureter  
*ru.n, ru.n'* nerves to right ureter  
*S* stomach  
*Sac* lateral sacculation of pharynx  
*Sg* sensory groove of lips  
*Sh.M* shell muscle  
*Sh.M.N* nerves to shell muscle  
*spn, spn', spn''* superior pharyngeal nerves  
*Stg.C* stomatogastric commissure  
*Stg.G* stomatogastric ganglion  
*Stg.N, Stg.N'* right and left stomatogastric nerves  
*Sub.I* subintestinal ganglion  
*Sub.L* sublingual or subradular organ  
*Sub.L.A* sublingual artery  
*Sub.L.F* sublingual furrow  
*Sub.R.C* subradular commissure  
*Sub.R.G* subradular ganglion  
*Sub.R.N* subradular nerves

<i>Sup.</i> <i>I</i> supra-intestinal ganglion	<i>Vg</i> visceral ganglion
<i>t</i> tentacle	<i>Vn</i> , <i>Vn'</i> , <i>Vn''</i> visceral nerves
<i>tn</i> , <i>tn'</i> tentacle nerves	<i>Vis. A</i> visceral artery
<i>ul</i> , <i>ul'</i> nerves to lips	<i>X</i> vein from buccal sinus to mantle
<i>V</i> ventricle	<i>x</i> , <i>y</i> , <i>z</i> nerves from right pleural ganglion to intestine and visceral artery
<i>Val</i> auriculo-ventricular valve	<i>1</i> to <i>25</i> muscles of buccal mass, described in text.
<i>V.Br</i> ventral branch of visceral artery	
<i>Vf</i> ventral or lesser fold of pharynx and oesophagus	

All figures are of *Lottia gigantea*.

#### Plate 1.

Fig. 1. General view of the alimentary canal and gonad. The dorsal wall of the body, pericardium, heart, and all the liver etc., have been removed. The buccal sinus is opened to show pharynx and pharyngeal glands. 2 : 1.

Fig. 2. Oral cavity, pharynx and portion of oesophagus seen from above. The dorsal wall has been slit open longitudinally just to the right of the median line, so that the greater part of the dorsal wall is turned to the left. 6 : 1.

Fig. 3. Dissection of head, viewed from the right side, to show relation of buccal mass, pharynx, arteries and nerves to each other. The space between the buccal mass and pharynx is greater than is usual in life. Cerebro-pleural and -pedal connectives are shown in side chamber. 8 : 1.

Fig. 4. Side view of buccal mass and oral cavity to show relations of radula, subradular ganglia, and also certain muscles which operate the radula. 4 : 1.

Fig. 5. Ventral view of buccal mass to demonstrate muscles described in text. 4 : 1.

Fig. 6. Oesophagus isolated to show spiral course of the folds on its inner wall, and the two pairs of salivary glands. 2 : 1.

Fig. 7. Section showing three zones on lips, especially the area of small teeth (*At*). 100 : 1 (from small specimen).

Fig. 8. A bunch of acini or glandules of the pharyngeal or posterior salivary gland, much enlarged.

Fig. 9. Side view of buccal mass to show arrangement of muscles described in text. 4 : 1.

Fig. 10. The buccal mass seen from above, the pharynx having been removed, and the right half of jaw (*J*) also. Drawn to show the muscles. 4 : 1.

Fig. 11. Drawn to show the radula (*R*), palps and sublingual or subradular organ (seen between them) in position when animal is feeding. 3—4 : 1.

Fig. 12. Cross section of duct of buccal or anterior salivary gland, much enlarged.

Fig. 13. Buccal cartilages, showing muscles which fasten lateral cartilages (*lat. c.*) to the pair of fused median ones (*med. c.*). 4 : 1.

Fig. 14. Radula teeth, much enlarged.

Fig. 15. Section of epithelium from subradular organ, showing teeth, pointing forward; much enlarged.

Fig. 16. Dorsal view of buccal mass to show retractors of radula (see text). 4 : 1.

Fig. 17. Stomach: most of the dorsal wall has been taken off to show raised stripe of epithelium, and opening of the liver duct.  $1\frac{1}{2}$  : 1.

Fig. 18. Lips, seen from below. Enlarged three times (3 : 1).

### Plate 2.

Fig. 19. Drawn to show circulation in mantle, and venous circulation of foot, seen from below. The head has been removed to show the mantle hood. The circumpallial vessel is red, while the veins emerging from the foot and spreading out on the mantle are in blue. Enlarged slightly over. 2 : 1.

Fig. 20. Dorsal view of animal with shell, and portion of mantle hood (*Ma'*) removed. The right nephridium is in blue, and the small left one in red. That portion of the right nephridium in blue also includes the area of the vein-net of blood vessels. The arm of the gonad, which leads to the gonoduct is shown behind the pericardium. Natural size, large individual.

Fig. 21. Dorsal view, with sections of the stomach and intestine removed to show the arterial circulation in visceral mass. (The branches of the genital artery lie beneath these and are not shown.) The whole anterior loop of the stomach, the rectum, and a bend of the alimentary canal just beyond stomach have been taken out. The dorsal branch (*Dors. Br*) of the visceral artery is not shown. A section of the kidney vein-net, and kidney collector (blue) are drawn in on the left. 2 : 1.

Fig. 22. Dorsal view to show venous circulation in vein-net of kidney. The outline of the right nephridium is shown. Centrally the blood channels over liver are drawn, and a portion of the mantle hood is removed to show the ctenidium and its two vessels. The dorsal wall of pericardium is removed to show heart.  $1\frac{3}{4}$  : 1.

Fig. 23. The gonad. All the alimentary canal, liver and head have been removed. The gonoduct is shown emptying into the forward (sub-anal) portion of the right nephridium. The edge of the muscle separating the sub-anal from the rectal portion of the right nephridium is dotted. Natural size.

Fig. 24. The pericardium and heart. All the dorsal wall of the pericardium has been removed, and most of that of the ventricle. The

aorta is shown in red. The muscular portion of the ventricle is shown differentiated from the thin-walled portion next to the aorta. A small section has been cut out of the dorsal wall of the auricle to show the interior and the connection with mantle spaces and efferent ctenidial vessel. 5 : 1.

Fig. 25. A section through a dorsal fold of the oral cavity, showing large mucous cells. Much enlarged.

Fig. 26. A portion of the pericardium, and right and left nephridia to demonstrate the two reno-pericardial canals. Both right and left nephridia have been opened; the left drawn semi-diagrammatic. A portion of the wall of the forward part of the right nephridium is turned back to give an idea of the actual appearance of the fenestrated dorsal wall. The reno-pericardial canals are shown in red. Much enlarged.

Fig. 27. Arterial circulation of foot, seen from above; semi-diagrammatic. The pedal arteries are drawn in red, the anterior pedal arteries in black, and the neural arteries in gray. Posterior portion of buccal sinus is shown in black dashes and the anterior part of the pedal nerve cords is drawn in to give a further idea of relations.  $1\frac{1}{2} : 1$ .

### Plate 3.

Fig. 28. Left pleural ganglion, much enlarged to show the otocyst. *Lig* ligament uniting the two otocysts; *Lig'* that binding otocyst to pedal ganglion; *Lig''* that binding the otocyst to the pleural ganglion.

Fig. 29. Section through eye, much enlarged, to show the heavily pigmented "retina".

Fig. 30. A general view of the nerves to foot and mantle, with special reference to the pallial nerves, which supply the circumpallial. 5 : 1.

Fig. 31. Detail of nerves leaving left osphradial ganglion to innervate the left osphradium, seen from above. Much enlarged.

Fig. 32. Detail of a portion of mantle to show nerves (*M. N'*) lying in dorsal wall.

### Plate 4.

Fig. 33. General view of cerebral, pleural, pedal, labial, subradular and stomatogastric ganglia with connectives, to show relations one with another. All the nerves given off by the cerebral ganglia are shown in this figure. 5 : 1.

Fig. 34. Front view of head and lips, showing nerves and their branches given off to lips from cerebral ganglia. Enlarged like last.

Fig. 35. A general view of the visceral loop, with supra- and subintestinal ganglia, visceral ganglion, and their nerves, together with the pharynx and a portion of the stomatogastric system. The dorsal body wall and pericardium have been removed. 4 : 1.

Fig. 36. Showing the principal pedal nerves to the foot, drawn only on one side, in front and rear.  $1\frac{1}{2} : 1$ .

Fig. 37. Dissection to show labial ganglia, and subradular ganglia, with their principal nerves, viewed from below. The buccal mass and a portion of the lips, and palp are shown. The large protractors of the buccal mass have been removed. 6 : 1.

Fig. 38. A detail to show nerves to subradular organ from subradular ganglia. The subradular organ and dorsal wall of subradular pouch are drawn in. Viewed from below. 7 : 1.

Fig. 39. A general view of the nerves supplying the alimentary canal. The forward bend of the stomach has been removed, also the rectum, and a section beyond the stomach. The remaining portions have been slightly moved to give a better idea of the course of each nerve. Fig. 1 will give the exact position of the loops of the canal. 3 : 1.

Fig. 40. Detail of nerves to ctenidium, and those to the ureters. The nerves to right ureter lie in the floor of the rectal portion of the right nephridium, shown in Fig. 26. Much enlarged.

Fig. 41. Oesophagus seen from right side, to show the nerves, arising from left pleural ganglion, which supply oesophagus and a portion of intestine.

Fig. 42. A detail of ventral wall of pharynx to show the inferior pharyngeal nerves, from stomatogastric ganglia. Much enlarged.

Fig. 43. Detail of nerves to the upper lip of radula tube. This lip acts as a valve closing the mouth of the radula tube. Much enlarged.

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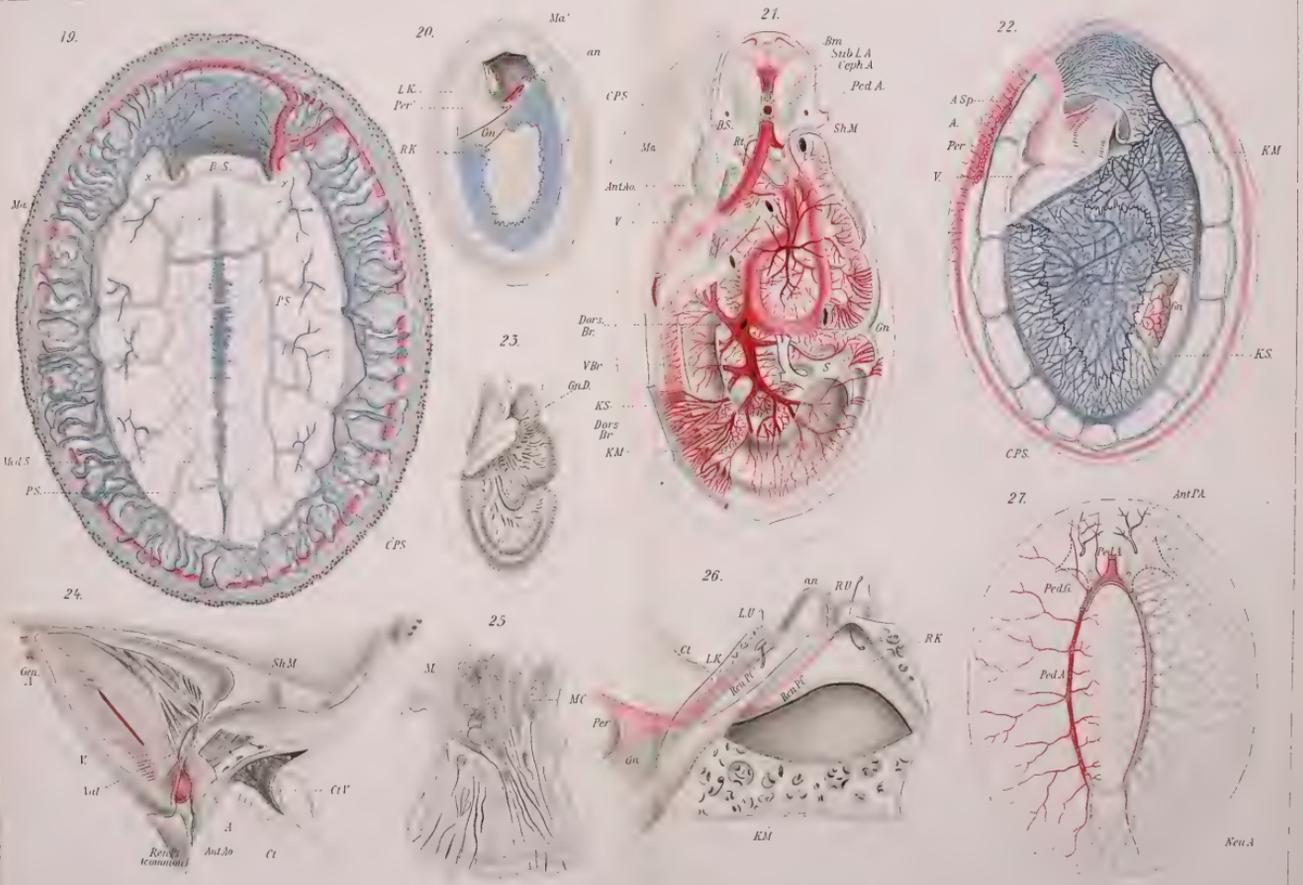












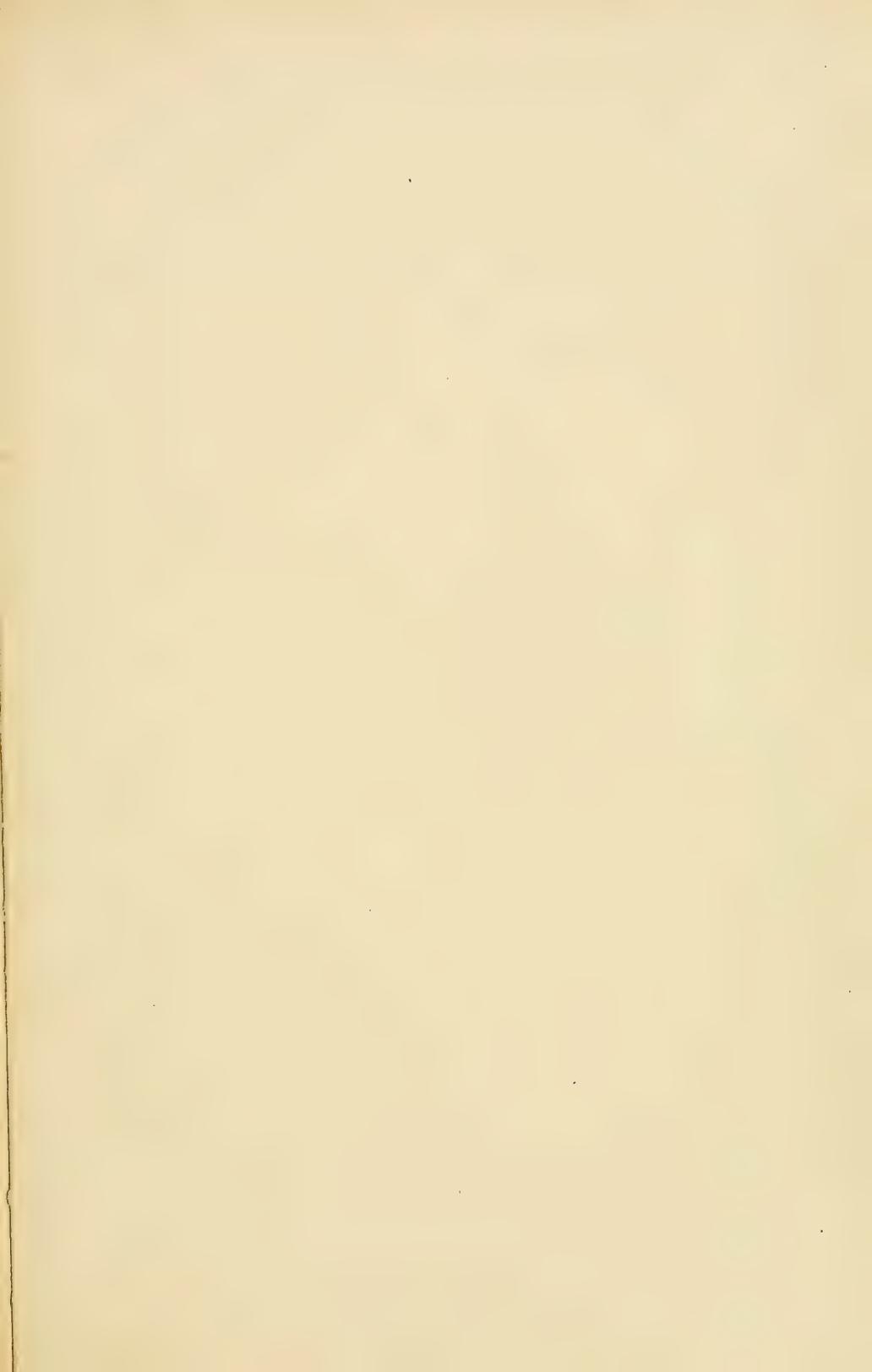




















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