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THE MORPHOLOGY OF *POMATIOPSIS CINCINNATIENSIS* (LEA), AN AMPHIBIOUS PROSOBRANCH SNAIL*

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IN recent years field and laboratory investigations have been undertaken in the Mollusk Division of the Museum of Zoology on the biology of two local species of *Pomatiopsis (P. cincinnatiensis* and *P. lapidaria).* Both species are native in southern Michigan, and stocks are readily available for study. The distribution, ecology, and life-history of *P. cincinnatiensis* were considered by H. van der Schalie and D. S. Dundee (1955); the egg-laying habits are being reported by H. van der Schalie and H. J. Walter (in press). The following data are concerned mainly with the morphology of the organ systems of *Pomatiopsis cincinnatiensis.* Another paper, dealing with the biology of *Pomatiopsis lapidaria,* is the work of D. S. Dundee and is being issued separately.

In the course of this work reference is made to the studies of Stimpson (1865), Li (1934), Abbott (1948), and Itagaki (1955). Their papers were of interest in a comparative sense but, excepting the work of Berry (1943) describing the verge and radula, there have been no previous publications on the anatomy of *P. cincinnatiensis.* As has already been stated (van der Schalie and Dundee, 1955: 126), the similarities between the Oriental *Oncomelania* and the American *Pomatiopsis* involve an unusual number of biological relations. Although our work has been confined largely to the species of *Pomatiopsis* available to us locally, plans are being made to extend these investigations to comparative studies in which use can be made of the information published by those working with *Oncomelania.*

A great deal of detailed work remains to be done to determine the systematic relationships of *Pomatiopsis* and *Oncomelania* within the

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Rissoacea as established by Thiele (1929). The schematic arrangement presented by Krull (1935: 455, Fig. 22) to indicate the steps in the development of the reproductive systems of Neritids, Helicinids, and the Hydrobiids shows that the structural arrangements shown in Figures "E" and "F" of the diagram (Fig. 22) are essentially the systems found in *Pomatiopsis* and *Oncomelania*. Krause (1949: 141), however, in analyzing the relationship of *Lithoglyphus* within the scheme suggested by Krull, indicated that the position of the genera in relation to the larger Rissoid and Hydrobiid categories is apt to vary depending on the organ systems one considers. A better systematic understanding will be possible only when many more detailed studies of the Rissoid and Hydrobiid groups have been undertaken.

We want to take this opportunity to express our appreciation to William L. Brudon for his skillful work in the production of Plates I through VI; William Cristanelli assisted in the preparation of the photomicrographs in Plate VII. We appreciate the sponsorship of the Commission on Parasitic Diseases because without their support this project would not have been possible.

MORPHOLOGY

SHELL.—The shell of *Pomatiopsis cincinnatiensis* was adequately described by F. C. Baker (1928) and E. G. Berry (1943). The relation of the relaxed animal to the shell is shown (Pl. I), but the shell illustrated is without its characteristic mud coating. In most of the local colonies the shells are generally coated with soil to produce a rough appearance. Also, many of the shells in nature bear an algal growth producing a greenish brown color, so that the shells blend well with the soils on which these snails live. The shell also serves to reveal the sexual dimorphism (see van der Schalie and Dundee, 1955: 128), and two shell "types" are recognizable. The shell of the female is much more inflated in the region of the body whorl; it is also relatively longer so that it appears to be larger and heavier than that of the male. The males have more slender, shorter, and narrower shells. These differences are difficult to detect except among fully mature individuals.

OPERCULUM.—The operculum (figured in van der Schalie and Dundee, 1955) tends to be somewhat rounder than that of *P. lapidaria*. Its apex is much sharper and, in general, its whorls are somewhat concentric rather than paucispiral as in *P. lapidaria*. Usually, there are two and a half whorls; the nucleus is rounded, rather large, and located in the middle of the columellar side. Its texture is horny and without cal-

careous deposits. During hibernation or in adverse conditions it can be pulled quite far into the aperture.

HEAD AND TENTACLES.—The head region is set apart by its prominent tubular snout, or rostrum, and the appended tentacles. The rostrum (Pl. I) is about twice as long as the tentacles and is somewhat protrusible. It has a bilobed appearance. In live specimens the central part usually appears strikingly red, reflecting the color of the buccal mass. The rostrum is transversely wrinkled, and the anterior end is expanded to form an adherent disc. The mouth is in the middle of the anterior end of the snout and in living specimens, even when under anesthesia, the browsing movements of the mouth continue incessantly. The rostrum is also important to this animal as a means of locomotion since it is employed in the "looping" manner of progression (Stimpson, 1865) so characteristic of this group.

The tentacles are relatively short, pointed, and somewhat thickened at their bases. They are gray with a clear rim extending completely around them, as well as around the rostrum and the foot. When this snail is out of water, and during most of the active periods of its life, the tentacles appear to be incapable of erection in air, so that they remain bent and drooped down against the rostrum; they are not contractible. Structurally, the tentacles are similar to those described by Krause (1949) for *Lithoglyphus naticoides*. In both groups they are without cilia but have a cylindrical epithelium which changes to cuboidal near the base of the eyes. Internally, the tentacles (Pl. VIIA) have a loose connective tissue containing muscle fibers; lacunae of the circulatory system are scattered throughout the connective tissue, but the major lacuna does not connect directly with the large one in the head cavity.

The eyes (Pl. VIIB), at the outer side and near the base of each tentacle, are relatively complex and contain several characteristic elements, i.e., lens, iris, a pigment layer, cornea-like coat, and a prominent layer presumably of sensitive cells. In both *Pomatiopsis* and *Oncomelania* the so-called "eye-brows" are a prominent feature; they also occur in other Hydrobiid genera. In *Pomatiopsis lapidaria* they are large and yellow; in *P. cincinnatiensis* they tend to be smaller and white. Their function is unknown.

The foot is large and muscular. When crawling, the animal is capable of extending it well in advance of the rostrum. The anterior part has two lateral extensions often referred to as "auricles"; the posterior is broadly rounded. Viewed laterally the foot reveals a set of sinuses (Pl. I) adequately described by Stimpson (1865). A distinct fold separates

the foot into an anterior and a posterior segment, with the posterior about twice as long as the anterior. A second fold marks the boundary between the foot and the body; two smaller oblique creases originate at the base of the rostrum and extend postdorsally. The epithelium covering the foot is tall and cylindrical; the sole ciliated. Internally, the foot contains considerable connective tissue with many muscle fibers coursing through it. At the lower ventral edge of the operculum a heavy band of fibers can be traced as it enlarges beneath the operculum and after narrowing continues to form the well-known columellar muscle. The inner edge of this muscle, extending from the lower edge of the operculum to a point midway through the mantle cavity, consists of heavy strands of longitudinal muscle fibers that stain dark blue with Mallory's Triple Stain, whereas the outer part, the zone between the mass itself and the operculum, consists of scattered fibers interspersed with many small spaces and stains bright red. In addition to the large pedal glands at the anterior end of the foot, many mucous cells are scattered in the ventral epithelium of the foot. The pedal glands are clustered and prominent, opening in a slit running parallel to the long axis of the foot; the pedal glands are visible through the epithelium.

COLOR.—Externally, white flecks of three sizes appear imbedded in the epithelium in various parts of the animal. (1) Larger ones are found in abundance throughout the collar of the mantle, but in smaller amount in the lateral parts of the mantle posterior to the collar. Similar masses of pigment appear scattered throughout the rest of the body in smaller patches but without regular pattern. (2) White flecks of small size are scattered over the rostrum, the posterior part of the foot, and the median dorsal side of the tentacles to form the "eye-brows" previously mentioned. (3) Another kind of white fleck appears as white granules which are numerous and tend to follow the course of the intestine from its loop to the point where it leaves the body cavity. The head region from the tentacles and the edge of the rostrum extending around to the operculum is gray; this area is lined with a clear rim. The eyes are black.

MANTLE AND MANTLE CAVITY.—The mantle consists of three layers: the outer epithelium of flattened cells, a central layer of loose connective tissue containing lacunae presumably filled with blood, and an inner flattened epithelium differing from the outer one in that it contains widely scattered mucous cells. This inner epithelium is tall and cylindrical in the collar. No cilia are present.

At the posterior end and in the left side of the mantle cavity the inner epithelium of the mantle is folded to form the gill filaments (Pl. IIA).

The distal end of each filament is modified so that the cells again become columnar and the filament assumes a clublike appearance. The lateral cells of the filament are ciliated. Wherever the low cells change to tall ones the epithelium is modified and contains supporting rodlike structures within the gill filaments, which stain dark. In the region of the gills the outer epithelium is heavily pigmented.

Other structures within the mantle cavity include: (1) the osphradium (Pl. VIID), a small mass of epithelium, just to the left of the gill, containing a ganglion; (2) the hypobranchial gland, usually to the right of the gill but not evident as a distinct structure in any of the material examined; (3) the renal pore, posterior and on the right side of the mantle cavity behind the gill, appearing as a slit surrounded by two white, swollen lips; (4) the anal opening, an oval structure surrounded by a pair of muscular lips slightly anterior to the genital pore; and (5) the genital aperture. In the female a large pallial oviduct occupies the upper surface of the right side of the mantle cavity where it parallels the rectum; in the male the pallial oviduct is replaced by the prostate gland. In both sexes these reproductive organs are located close to the columella. The female genital pore is oval and appears at the anterior end of the pallial oviduct near the mantle collar. It is so oriented that it is slightly to the exterior side of the pallial oviduct where it serves as a common opening for both that oviduct and the spermathecal duct. In the male the penis (verge) is situated near the center line of the head about midway back in the mantle cavity. In a normal and relaxed condition it assumes a U shape and lies on the upper neck within the cavity.

Visceral sac.—The epithelium is flattened, without cilia, and highly pigmented in some regions (see under Color above). The epithelium is supported by a thin layer of loose connective tissue. If the shell is removed, some of the parts of the organ systems are visible through the sac. In the region of the mantle cavity the rectum and the large reproductive glands (pallial oviduct or prostate) are visible. In the penultimate whorl the stomach and the loop of the intestine are readily seen. When the shell is removed from a live specimen it is possible to observe heart beat through the visceral sac. The kidney usually appears as a mass of white granules just beneath the sac. In the upper whorls the digestive gland is clearly visible.

Circulatory organs.—A two-chambered heart (Pl. IIB) lies in the pericardial cavity close to the lower end of the crystalline style sac. The heart is bounded on one side by the body wall, on the other by the kidney. The auricle is smaller than the ventricle and has a thinner wall.

The heart musculature is quite thin and, consequently, the heart appears as a delicate sac. Muscle fibers project into the lumen of both the auricle and ventricle. Both chambers are connected by a short, narrow passage which appears to be without a valve. Although there is a cavernous fibrous reticulum as described by Krause (1949) in *Lithoglyphus naticoides,* the distribution in *P. cincinnatiensis* differs. In the former species it occurs only in the lumen of the ventricle; in the latter it appears to a small degree around the inner edges of both the auricle and the ventricle.

Two main vessels enter the auricle: the gill vein, entering on the side nearest the body wall; another vein entering from the kidney. Two arteries leave the short truncus arteriosus which leaves the heart on the posteroventral side. One of these main arteries brings blood to the anterior part of the body; the other supplies the posterior region. Sinuses were found in many parts of the body, but the extent of the finer vessels was not determined.

KIDNEY.—The kidney (Pl. IVA) is a large lobed sac found in the body whorl where it surrounds several other organs. In living specimens it is white; if ruptured, numerous small white granules ooze out of it. The kidney empties into the mantle cavity through a pore on its roof just posterior to the gill (see renal pore above). The portion of the kidney adjacent to the wall of the body is supported by a thick layer of connective tissue which is unusually compact and provided with numerous round nuclei; cell outlines are difficult to see. A black pigment covers this region externally.

The kidney epithelium is tall and columnar with the distal two-thirds of each cell supplied with a large vacuole. The nuclei are basal and the cytoplasm fills the cell sufficiently to surround the basal nuclei. The epithelium is folded in various places and often projects into the lumen of the kidney. Such a projection may have been called the nephridial gland by Krull (1935). However, the structure of the kidney was quite uniform in *P. cincinnatiensis,* and no special glandular tissue was observed.

NERVOUS SYSTEM.—The central nervous system (Pl. III) consists of four pairs of major ganglia: (1) the cerebral, lying posterior and dorsal to the buccal mass; (2) the pleural, just posterior to the cerebral; (3) the esophageal (sub- and supra-), posterior and connected to the pleural by rather long commissures; and (4) the pedal, lying ventral to the cerebral, found in the central area of the foot. The nervous system has the typically prosobranch arrangement in that it forms the characteristic figure eight.

Six nerves (Pl. III) originate directly from each cerebral ganglion. The optic arises from the posterolateral surface and innervates the eye; the tentacular nerve extends from the anterodorsal part of the ganglion with branches innervating the lateral surface of the proboscis and the tentacle. From the inner surface of each ganglion a nerve arises which goes to the lateral portions of the rostrum; the nerves supplying the mouth arise from the anteroventral surface of each cerebral ganglion.

The pleural ganglia are connected to the cerebral by very short commissures. One nerve from the left pleural supplies the mantle. The commissures connecting the pleural and esophageal ganglia form the middle crosspiece of the figure eight. One ganglion, the supraesophageal, as the name implies, lies dorsal to the esophagus; the other, the subesophageal, lies ventral to it. A long commissure connects each of these to a visceral ganglion lying in the body whorl near the heart. In addition to the commissure, the supraesophageal ganglion gives rise to the osphradial ganglion. Two nerves arise from the subesophageal ganglion, one supplying the mantle, the other the dorsal surface of the visceral sac.

Each pedal ganglion is connected by commissures to both the cerebral and pleural ganglia on its own side. The otocysts are found on the posterior side of the junction of each pleuropedal commissure with each pedal ganglion. They are not connected to the pedal ganglia but rather to the cerebral ganglia by means of minute nerves. The otocyst, as seen in Plate VII, is composed of a sphere of flattened epithelium. Inside this fluid-filled sphere is a hard object composed of concentric calcareous layers, the otolith. Posteriorly, each pedal ganglion gives rise to a nerve which innervates the area of the operculum. Extending ventrally from each ganglion are two small commissures; one goes to an anterior ganglion, the propodial, and the other to a posteriorly placed metapodial ganglion. Each of these in turn branches into smaller nerves, all of which supply the foot.

The nervous system of *P. cincinnatiensis* is essentially the same as that of *P. lapidaria,* the differences being largely in the size and shape of parts. Those differences may not be significant, since there are similar variations among individuals of the same species. When the nervous systems of *Pomatiopsis* are compared with figures and published information on these systems in *Oncomelania* (Robson, 1921; Li, 1934; and Itagaki, 1955) few significant differences can be found. Detailed studies should be made to discover the relative degree of difference when these forms are compared with one another. Krause (1949: 141) considered the systematic relationships of some of the Hydrobiids and used a table based on nervous system and the verge to indicate probable relation-

ships. If *Pomatiopsis* were placed in that table it would fit between *Lartetia* and *Lithoglyphus* since *Pomatiopsis* does have a rather long pleuro-supraesophageal ganglion. As in *Lithoglyphus,* the cerebropedal and pleuropedal connectives would appear to be relatively shorter than in *Bythinella* (Bregenzer, 1915) but yet longer than in *Bythinia.* In *Pomatiopsis* the propodial and metapodial ganglia are separated by a short commissure from the pedal ganglia. The same is apparently true in *Lithoglyphus,* whereas in *Bythinella* they are widely separated and in *Bythinia* they are fused. Therefore, it appears that, solely on the basis of the nervous systems, *Pomatiopsis* would have to be placed next to *Lithoglyphus;* both of these genera would appear between *Bythinella* and *Bythinia.*

SENSE ORGANS: EYE.—Eyes are present at the outer base of the tentacles. Each eye is connected directly to the cerebral ganglion by an optic nerve. The eyes occupy a prominent space in the connective tissue. Structurally (Pl. VIIB), the eye has an anterior cornea-like layer with a lens in the fluid-filled cavity behind it. At the back of the eye a broad layer of pigmented cells lines the socket; this thick layer has an abundance of relatively large nuclei, but the borders of cells are difficult to differentiate.

SENSE ORGANS: OTOCYSTS (STATOCYSTS).—These organs of balance are paired, one appearing on the postdorsal surface of each pedal ganglion (Pls. III, VIIC); they are connected to the cerebral ganglia by fibers paralleling the cerebropedal commissures. The otocyst (Pl. VII) consists of a sphere of somewhat flattened cuboidal epithelium with nuclei round and basal, and underlain by a thick basal membrane. A round otolith, made up of concentric layers presumably of lime (see Krause, 1949), occupies the fluid-filled chamber; no tactile hairs were observed on the inner wall of the otocyst.

SENSE ORGANS: OSPHRADIUM.—In many individuals the osphradium (Pl. VIID), located to the left of the gill in the mantle chamber, is represented by two complete ridges of tissue and a third small reduced one. Considerable variation appears in the arrangement of these ridges. Usually, the osphradium is slightly less than half the length of the gill. Histologically, it represents a folding of the inner epithelium of the mantle to form ridges with the esophageal ganglion connected to one of the folds. The epithelium of the osphradium contains relatively tall cells provided with cilia. The cells in contact with the osphradial ganglion are shorter, and the ganglion is in close contact with the basal membrane of that epithelium.

ALIMENTARY TRACT.—The digestive system of this species (Pl. IV) has not been described. In1948 Abbott contributed some observations in an abbreviated way on the gross structure of the stomach and its grinding behavior in the related *Pomatiopsis lapidaria.* Although a detailed analysis has not been possible, the general aspects of the system as it was observed in gross dissection and serial sections are as follows.

The *mouth,* at the anterior end of the rostrum, in fixed specimens appears as a dorsoventral slit. A tubelike chamber leading to the buccal cavity is lined with columnar epithelium which is covered with a cuticular membrane. The jaws (Pl. VII E) are at the entrance to the buccal cavity and are attached to the cuticular membrane of the lateral walls; a muscular layer surrounds the epithelium. Each jaw consists of a series of plates (13 to 19) which project beyond the columnar epithelium into the lumen. The total width of each jaw is less than 50 microns and, consequently, the jaws are easily overlooked in gross examination.

The *pharyngeal cavity* (Pl. VII F) consists of ventrolateral extensions of the rostral tube and has the appearance of an inverted Y. Its epithelium is tall, columnar, with cilia in the upper part of the cavity; nuclei are elongate and basal. Directly beneath and on both sides of this cavity is the *odontophoral cartilage,* a conspicuous component of the buccal mass. This cartilage in living specimens is decidedly red (see J. W. Taylor) due to the haemoglobin present "in buccal muscles of species whose energetic action calls for more oxygenation than haemocyanin can accomplish." Lying still lower and between these cartilages is the *radula.* It is unique as compared with that of Amnicolids in that it has relatively few teeth, shown in E. G. Berry's excellent figure (Berry, 1943: Pl. IV, Fig. 5).

Above the buccal mass and the cerebral ganglia in the dorsal region of the head are two large *salivary glands* which open separately into lateral expansions in the dorsal walls of the buccal cavity. In gross dissections they are white and have a long and club-shaped outline. Histologically, they are composed of a tall epithelium with round basal nuclei. The lumen of each gland is small, and the secretions empty into the pharynx by separate openings previously mentioned.

The *esophagus* is a long, ciliated, flattened tube extending from the buccal cavity to the lower posterior part of the stomach. Just posterior to the buccal mass the esophagus turns downward beneath the cerebral commissure and then angles slightly toward the left side of the body as it penetrates the body wall. The anteroventral part of the esophagus has small external pouches which gradually disappear as the tubular form is assumed. The anterior part is composed of tall, ciliated, co-

lumnar cells with basal nuclei. Near the stomach the epithelial cells are lower, and the nuclei are more centrally placed. Single gland cells are sparingly scattered throughout the epithelium.

The *stomach,* an irregularly shaped sac, is contained in the half whorl above the body whorl. Projecting from its anterior end is the *style sac.* Adjacent to this sac, and to the right side of it, is the initial part of the intestine as it leaves the stomach. The lumen of the stomach is large and the walls are thin; the epithelium has tall columnar cells. Cilia occur at the anterior part near the style sac, and they are present in the region where the intestine leaves the stomach. The only other portion that has cilia is the posterior ventral region at the entrance of the esophagus; the remainder of the stomach is without cilia but lined with a cuticular layer. Opposite the entrance of the esophagus, and in the upper right region, the cuticular layer of the stomach becomes folded to form the *gastric shield* (Pl. VIIG). In live animals (Pl. IVB) a slow rotation of food particles within the stomach is often observed, and the movement is apparently due to the rotation of the *crystalline style,* a clear gelatinous rod found within the style sac. The head of the style rotates against the gastric shield in the portion of the stomach just anterior to the point of entrance of the esophagus. The fold of the stomach at this point is so large that it nearly divides the ventral wall into two parts.

All of the style sac is lined with very long and prominent cilia which rotate the style. A very distinctive epithelium lies beneath these cilia; it has tall, columnar cells supported on several layers of muscle. At the junction of the intestine and the style sac a ridge of epithelium enters the intestine to form the *typhlosole* found in the intestine as far down as the posterior end of the gill.

The *digestive gland,* with its anterior part adjacent to the posterior end of the stomach, opens into the posterior ventral part of the stomach close to the entrance of the esophagus. The opening of the digestive gland into the stomach is very short and tubular and it contains short, cylindrical cells. The junction is continuous with the lumen of the digestive gland which is large, compound, and occupies most of the upper whorls. The epithelium of the digestive gland contains two cellular elements: relatively short, triangular cells with basal nuclei; and taller club-shaped cells also with basal nuclei but containing a highly vacuolated cytoplasm. As in *Bythinella* (Bregenzer, 1915) the two cell groups seem to be about equal in number. The brownish color of the digestive gland is produced by large, brown masses present in the vacuoles of the cytoplasm. The masses may occur in either type of epithelial cell or they may appear between the cells.

Although it has not been possible to study the food and digestion in *Pomatiopsis,* Graham (1939) has summarized information bearing on a number of style-bearing prosobranchs. These studies are of interest in connection with the anatomical information observed in *P. cincinnatiensis.* Both Yonge (1930) and Graham (1939: 105) emphasized that two generalizations are possible for style-bearing mollusks: "The first of these is that all molluscs which possess a style are microphagous herbivores without free proteolytic enzymes in their gut, and the second is that all these animals feed either by cilia or radula in such a way as to maintain an almost constant stream of food along the alimentary tract." Graham also indicated that the salivary glands produce mucus to lubricate the radula and to cement the food particles it collects; the digestive gland in turn appears to function not as an organ of secretion, but to ingest minute particles for intracellular digestion. Graham (1939: 108) emphasized the fundamental role of the stomach, as follows:

> In those with styles, on the other hand, the stomach becomes an important part of the alimentary tract, where the food particles are mixed with style substance, where those which can be manipulated by the cells of the digestive diverticula are separated from those which cannot, and where the indigestible matter from the diverticula is directed away from the incoming food and passed to the intestine for defecation. As the animals are more or less continuous feeders all these processes must be capable of going on simultaneously, a fact which has transformed the stomach into a complex ciliated structure upon the successful functioning of which that of the rest of the alimentary canal depends.

The style is credited with assisting the passage of food through the stomach and Graham stated: "At some point on the wall near the base of the intestine is an area which sorts particles on the basis of size, the larger ones being passed directly into the intestine as not adapted for ingestion by the cells of the digestive diverticula, the smaller ones being passed into the ducts of the digestive diverticula, although the details of this are not usually decipherable." Evidently, *Pomatiopsis* and *Oncomelania* are similar functionally to the groups studied by Graham; their feeding mechanism and process would constitute an interesting problem. If these snails are at all similar to *Lithoglyphus naticoides* as described by Krause (1949), their food is primarily vegetative, which would account for the presence of empty diatom shells found in the stomach.

The intestine of *P. cincinnatiensis* leaves the anterior end of the stomach and bends posteriorly a short distance along the dorsal surface of the stomach to form a U-shaped loop, and then continues through the lower body whorls along the lower surface of the mantle to the anus which is located within the right side of the mantle cavity and near the

mantle collar. The whole inner surface of the intestine has an epithelium composed of tall, ciliated columnar cells; no muscle layers were found beneath it. The typically oval fecal pellets are usually present and are already well formed at the pyloric end of the intestine.

MALE REPRODUCTIVE SYSTEM (Pl. V).—In live specimens the testis is found in the upper whorls and, like the ovary, has a characteristic yellow color which is in marked contrast to the gray-brown of the digestive gland where it is embedded. The ovary has a finger-like appearance, and the testis resembles a large cluster of grapes. The sperm (Pl. VC) is rodlike and tapers toward the tail end; the threadlike tail is spirally coiled about the body region, thus giving the sperm a corkscrew appearance.

The renal vas deferens is a long (about 6 mm.), white, coiled tubule, most of which is massed just below the testis. The upper portion of the vas is enlarged and during the reproductive period is packed with sperm. This obvious storage function indicates that it should be designated the seminal vesicle. Some sperm are found there during all seasons of the year. Structurally, the seminal vesicle is composed of short, nonciliated, columnar epithelial cells with scattered circular muscle fibers surrounding it.

The smaller or renal portion of the vas deferens extends from the seminal vesicle down along the columella and into the prostate gland. It has the same basic structure as has the seminal vesicle.

The prostate gland is a light-colored, kidney-shaped mass on the right side of the body whorl and paralleling the rectum. Its appearance and position make it comparable to the pallial oviduct of the female. At first, the prostate appeared to be composed of tall, columnar cells with nuclei at both the proximal and distal ends. However, by staining with Safranin O and Fast Green, it was observed that the arrangement is somewhat the same as that in *Buccinum* (Fretter, 1941), in which the tall, ciliated, columnar epithelial cells contained nuclei occupying a median position. Beneath that epithelium the gland cells with more basal nuclei tended to produce the scattered pattern described above. The epithelium of the whole prostate is thrown into deep longitudinal folds. The secretions from this gland empty into the pallial portion of the vas deferens near the middle of the columellar side of the gland. This part of the vas deferens continues as a smaller, wavy tubule which, as it proceeds anteriorly, has a much thicker circular muscle layer surrounding it. Just before it enters the verge on the median dorsal surface of the head its cells are short, ciliated, columnar with large basal nuclei.

The verge is a dorsoventrally flattened organ which, when not extended, lies completely within the mantle cavity and at rest in a curved position against the dorsal surface of the head. Its outer epithelium is composed of cubical cells with basal nuclei. The dorsal surface of the verge is ciliated. Underlying the epithelium is a circular muscle layer; distally, longitudinal fibers become apparent. Inside the verge there is a network of loose connective tissue with circulatory lacunae running through it. The centrally placed vas deferens continues through the entire length of the verge and is surrounded by a heavy layer of circular muscle. Its epithelium within the verge is composed of ciliated, cubical cells with large basal nuclei. At the end of the verge of *P. cincinnatiensis* there is a very characteristic filament which is half as long as the verge itself; the vas deferens continues to the very end of this filament.

FEMALE REPRODUCTIVE SYSTEM (Pl. VI).—In the living condition the bright yellow ovary lies embedded in the digestive gland on the columellar side of the second whorl. It has a variable number of finger-like branches (often five). The germinal epithelium consists of short, irregularly shaped cells with elliptical nuclei. Ova in various stages of development extend from the base of the germinal epithelium into the lumen of the ovary.

The oviduct, which follows a course down the body whorl parallel to the columella, may also appear yellow, especially when it contains ova. This yellow coloration is due to substance within the lumen rather than to granules within the epithelium as described in *Pomatias elegans* (Creek, 1951). This pigment always ends at a point just at the level of the heart and near the visceral ganglion. Here the oviduct (renal oviduct) becomes extremely convoluted and forms a compact mass which is partially surrounded by the kidney. The nonconvoluted part of the oviduct is covered by a thin layer of connective tissue interspersed with occasional circular muscle fibers. Its epithelium is nonciliated, cuboidal, and often vacuolated, whereas the epithelium of the convoluted part is ciliated and columnar.

Attached to the renal oviduct and lying close to the posterior end or top of the pallial oviduct are two blind sacs. One, the bursa, is approximately four times the size of the other, has yellowish or orange color, and often contains a mass of unoriented sperm. The wall of the bursa has a nonciliated columnar epithelium with basal nuclei, and its epithelium appears to be glandular. The ends of cells nearest the lumen seem to slough off when sperm are concentrated in the bursa and, consequently, the inner lining of the bursa often has a ragged appearance.

According to Krause (1949) excessive amounts of sperm may break down in the bursa.

The other blind sac, the seminal receptacle, lies beneath the base of the larger bursa and is always white. Some of the sperm in it were found to be oriented perpendicular to the wall of the sac, whereas others may form a dense ball in the center. The wall of the seminal receptacle contains circular muscle, and its epithelium has tall columnar cells with basal nuclei. Cilia are absent.

Each of these blind sacs opens separately into the oviduct; however, in addition to the one opening from the oviduct into the bursa, it also connects with another tubule, the spermathecal duct. This long, slender duct extends from an opening immediately behind the collar of the mantle on the right side and parallels the columella posteriorly to the point where the tubule enters the bursa. Histologically, the spermathecal duct is composed of columnar epithelial cells with elongate, eosinophilic nuclei and extremely long cilia; a layer of circular muscle surrounds the epithelium.

The most conspicuous element of the female reproductive system is the large pallial oviduct which may be seen through the mantle as an opaque, white, kidney-shaped mass adjacent to the rectum in the body whorl. At times during the reproductive season the upper part of this gland may be light yellow and hard to the touch.

The pallial oviduct is divided into two parts, an upper (posterior) glandular mass, the albumen gland, producing dense secretions, and a lower (anterior), less glandular portion, the capsule gland (Pl. VIIH). The albumen gland has a very tall columnar epithelium with large basal nuclei and a muscle surrounding the entire gland. The secretions from this gland occur as droplets of various size which stain dark blue with hematoxylin. In sections these droplets tend to obscure the epithelium. Deep longitudinal folds in the epithelium give this gland an irregular lumen. The lower or capsule part of the mass likewise has tall columnar cells, but the nuclei are elongate, and the secretions appear as smaller droplets and generally are within the boundaries of the cells so that they do not obscure the cellular detail as in the albumen gland.

There appears to be a connection (Pl. VI C, D) between the renal and pallial parts of the oviduct on the columellar side at a point approximately one-third of the way from the posterior end of the pallial oviduct. This connection was extremely difficult to find in gross dissection. Unless the knife passed directly through it in serial section, it was impossible to find on slide material. However, it appears that this connection may be of the nature of a minute tubule extending from the coiled

portion of the renal oviduct and entering into a slitlike opening in the pallial oviduct. Additional studies of the function of the genital tract to determine the relationship of these structural elements are now underway.

The appearance of the egg with its characteristic husk was described by van der Schalie and Dundee (1955), and the egg-laying habits by van der Schalie and Walter (in press). The specimen shown here (Pl. VIE) represents a laboratory-laid egg at near hatching after about three weeks at 80°C.

SUMMARY

The general anatomical aspects of the major organ systems of *Pomatiopsis cincinnatiensis* are in many ways similar to those of *Pomatiopsis lapidaria* as reported by D. Saunders Dundee (in press). Although the structure and the topography of the organs of both species are alike, the names applied to some organs, especially in the reproductive system, must be considered tentative because their functions are not well enough known, and hence the names applied to them have little meaning.

Some of the features that appear to have important systematic relations are as follows:

1. These animals are without a gonopericardial duct as found in stenoglossan prosobranchs (Fretter, 1941).
2. Although Johannson (1939) found a renopericardial duct in a Hydrobiid *(Hydrobia ulvae),* our observations agree with Bregenzer (1915) and Robson (1921), who did not find such a duct in the species they studied.
3. The otocyst was found to contain but a single otolith.
4. The digestive tract belongs to the second type according to the system of Mackintosh (1925: 334) with "style-sac in restricted communication with the intestine."
5. In the female reproductive tract the eggs were observed in the ovary and as far down as the pallial oviduct; they were never seen in the pallial oviduct itself in any of the sectioned animals.
6. The heart appears to be without an atrioventricular valve.
7. The nervous system has a concentration of ganglia somewhat like that of other Hydrobiids.

The anatomy of *P. cincinnatiensis* and *P. lapidaria,* although sharing many features with Hydrobiids, may prove sufficiently distinctive to support the recommendations of Berry (1943) and others that *Poma-*

tiopsis be placed in a family by itself. There are indications, however, that studies are needed to discover whether *Oncomelania,* which is so similar in structure, ecology, and life-history, may belong not only to the same family as *Pomatiopsis* but perhaps even in the same genus.

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PLATE I

General external view of the animal of *Pomatiopsis cincinnatiensis* (Lea). Insert shows ventral surface of foot.

PLATE I

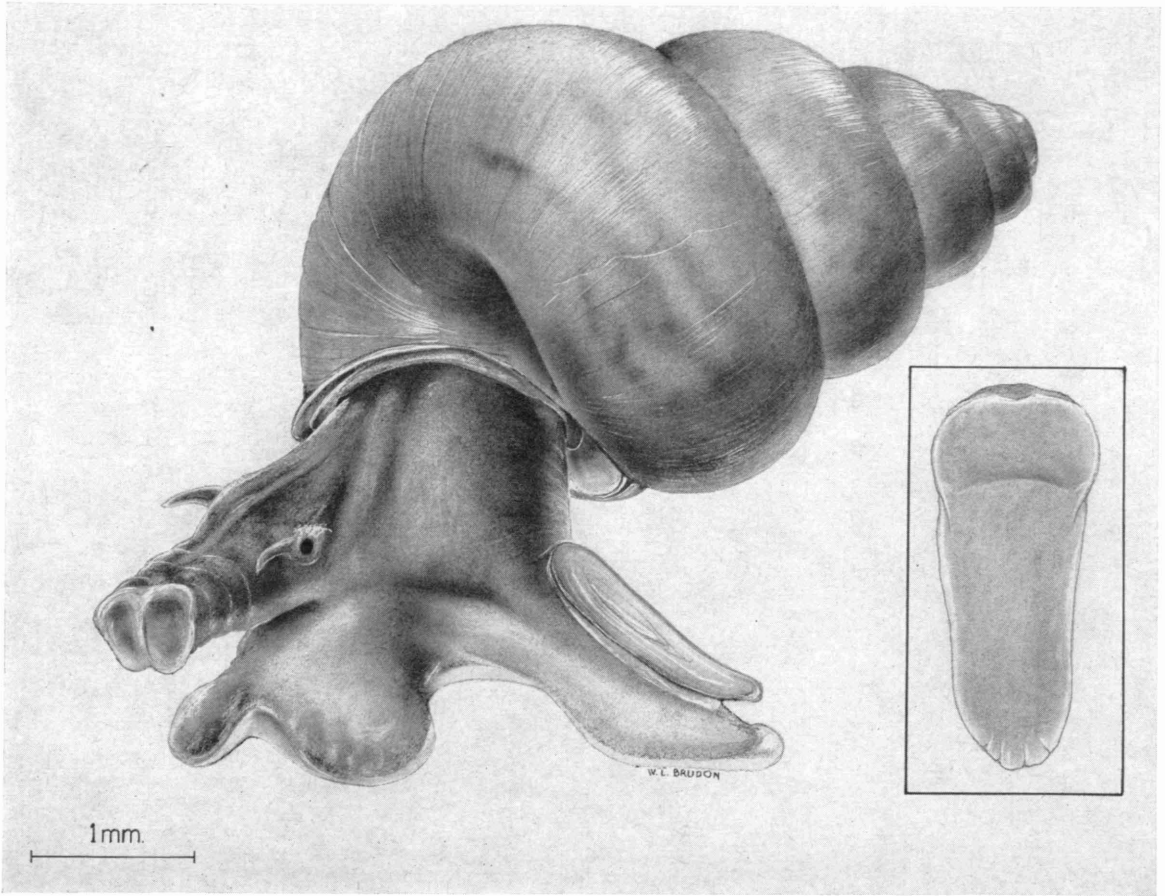


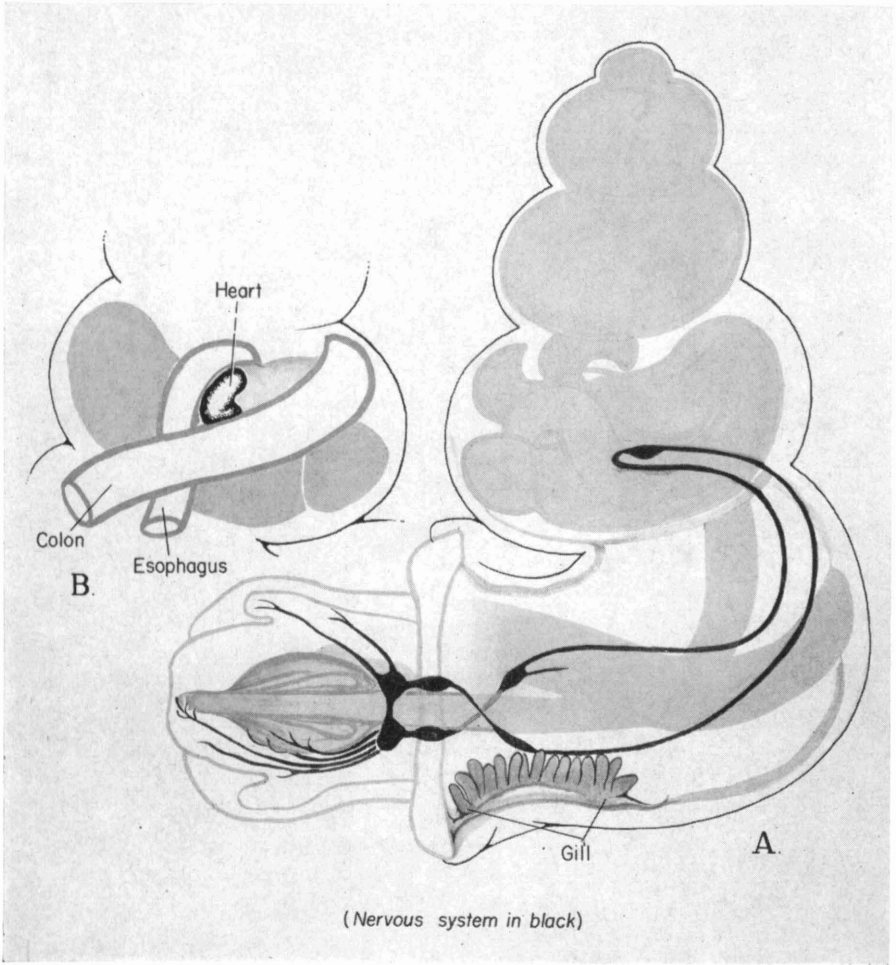
PLATE II

The more conspicuous parts of the circulatory, respiratory, and nervous systems of *Pomatiopsis cincinnatiensis* (Lea).

A. Gills and the streptoneurous arrangement of the nervous system in relation to the shell, the animal, and the digestive tract.

B. Position of the heart within the framework of parts of the digestive tract as seen in posterior view.

PLATE II



(*Nervous system in black*)

PLATE III

Dissection of anterior part of *Pomatiopsis cincinnatiensis* (Lea) showing a major part of the nervous system and its relation to the buccal mass and alimentary tract, the pedal glands, and the otocyst.

PLATE III

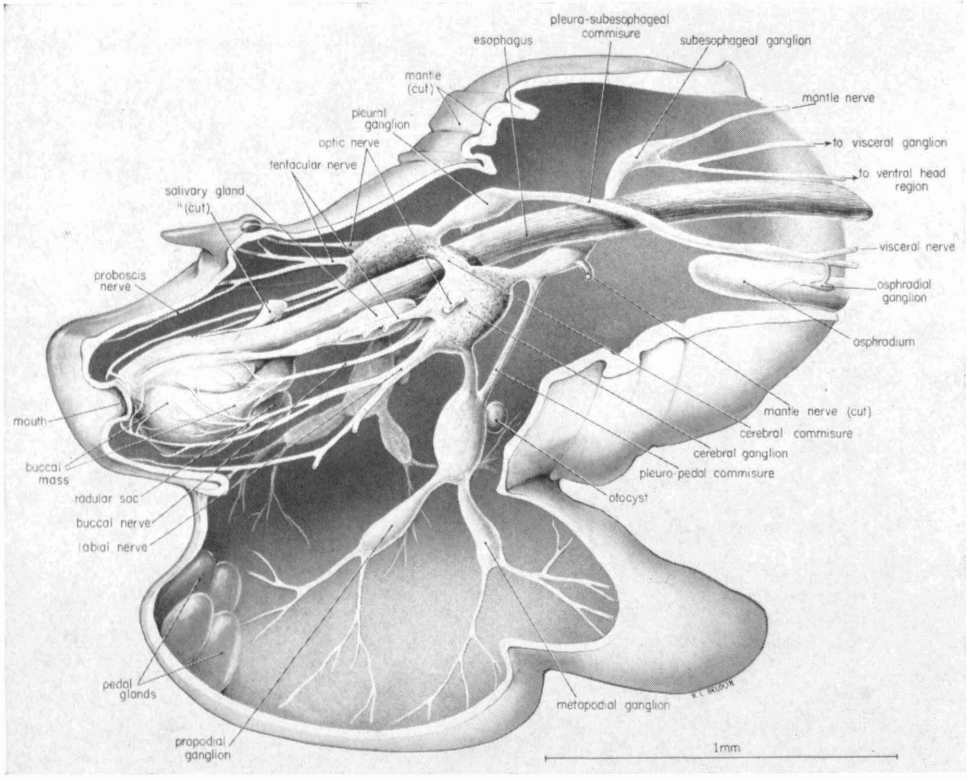

pleuro-subesophageal commisure
esophagus
subesophageal ganglion
mantle (cut)
mantle nerve
pleural ganglion
optic nerve
to visceral ganglion
tentacular nerve
to ventral head region
salivary gland (cut)
visceral nerve
proboscis nerve
osphradial ganglion
osphradium
mantle nerve (cut)
mouth
cerebral commisure
cerebral ganglion
buccal mass
pleuro-pedal commisure
otocyst
radular sac
buccal nerve
labial nerve
pedal glands
metapodial ganglion
propodial ganglion
1mm

PLATE IV

The digestive system and kidney of *Pomatiopsis cincinnatiensis* (Lea).

A. The tract in its natural position in the animal.

B. Relation of the esophagus, stomach, crystalline style, and the intestine. Arrows indicate the direction that food travels through the somach.

PLATE IV

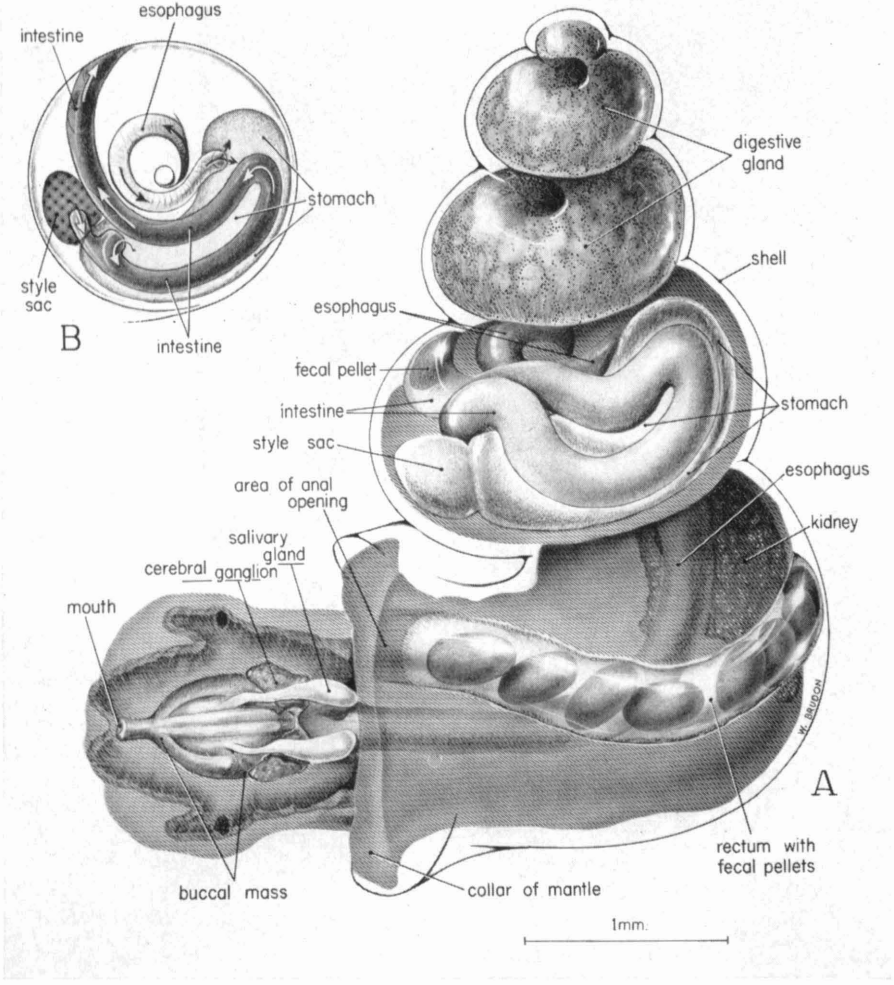

esophagus
intestine
stomach
style sac
B
intestine
digestive gland
shell
esophagus
fecal pellet
intestine
stomach
style sac
area of anal opening
esophagus
kidney
salivary gland
cerebral ganglion
mouth
W. BRUNDIN
A
rectum with fecal pellets
buccal mass
collar of mantle
1mm.

PLATE V

The male reproductive system of *Pomatiopsis cincinnatiensis* (Lea).

A. Position of the male reproductive organs with relation to the other systems of the animal.

B. Organs of the male reproductive system.

C. Enlarged sperm.

PLATE V

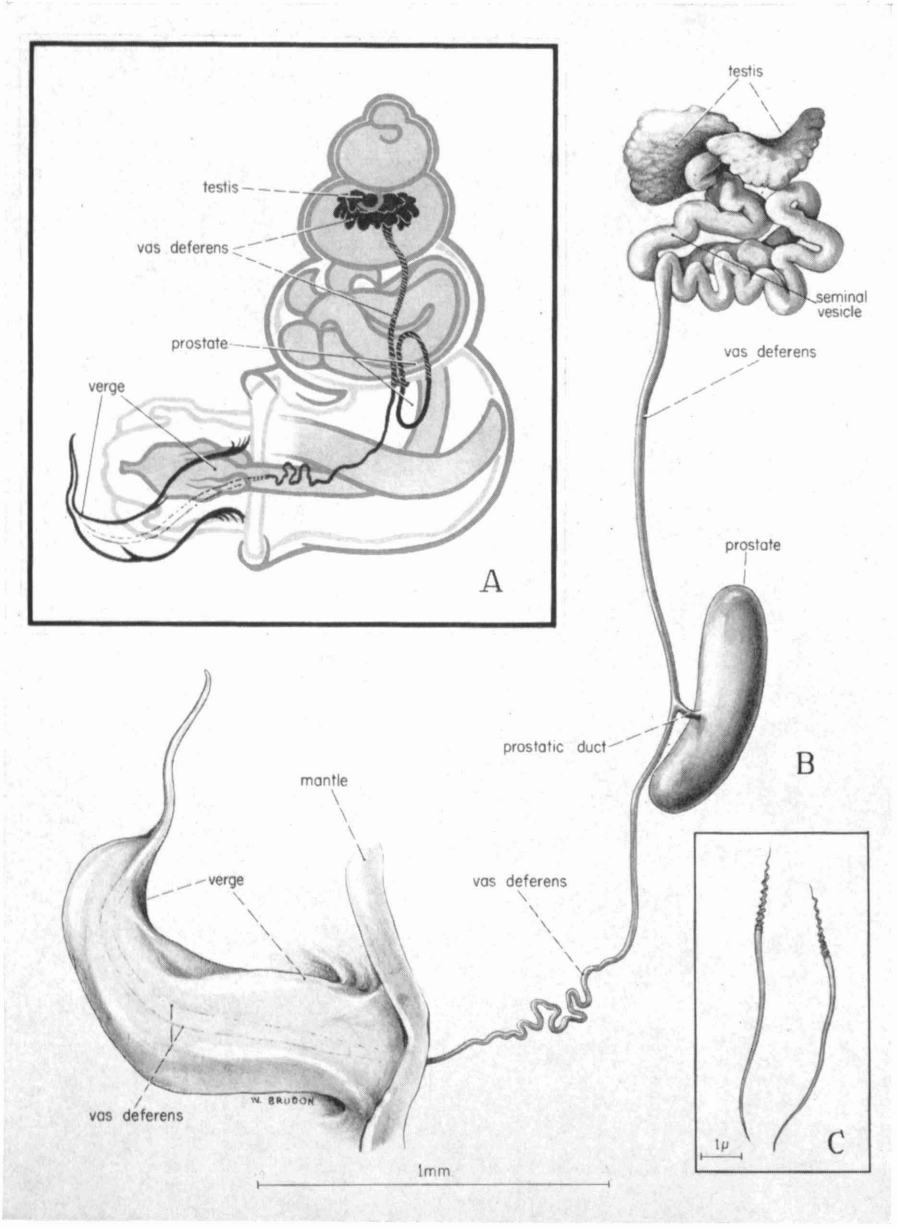

testis
vas deferens
prostate
verge
A
testis
seminal vesicle
vas deferens
prostate
prostatic duct
B
mantle
verge
vas deferens
vas deferens
W. BRUBON
1mm
1μ
C

PLATE VI

The female reproductive system of *Pomatiopsis cincinnatiensis* (Lea).

A. Position of the organs in relation to other parts of the animal.

B. Organs of the female reproductive system.

C. Relation of renal oviduct to the pallial oviduct as seen in gross dissection.

D. Proper relation as indicated by serial section.

E. Egg, with husk, at well-developed stage.

PLATE VI

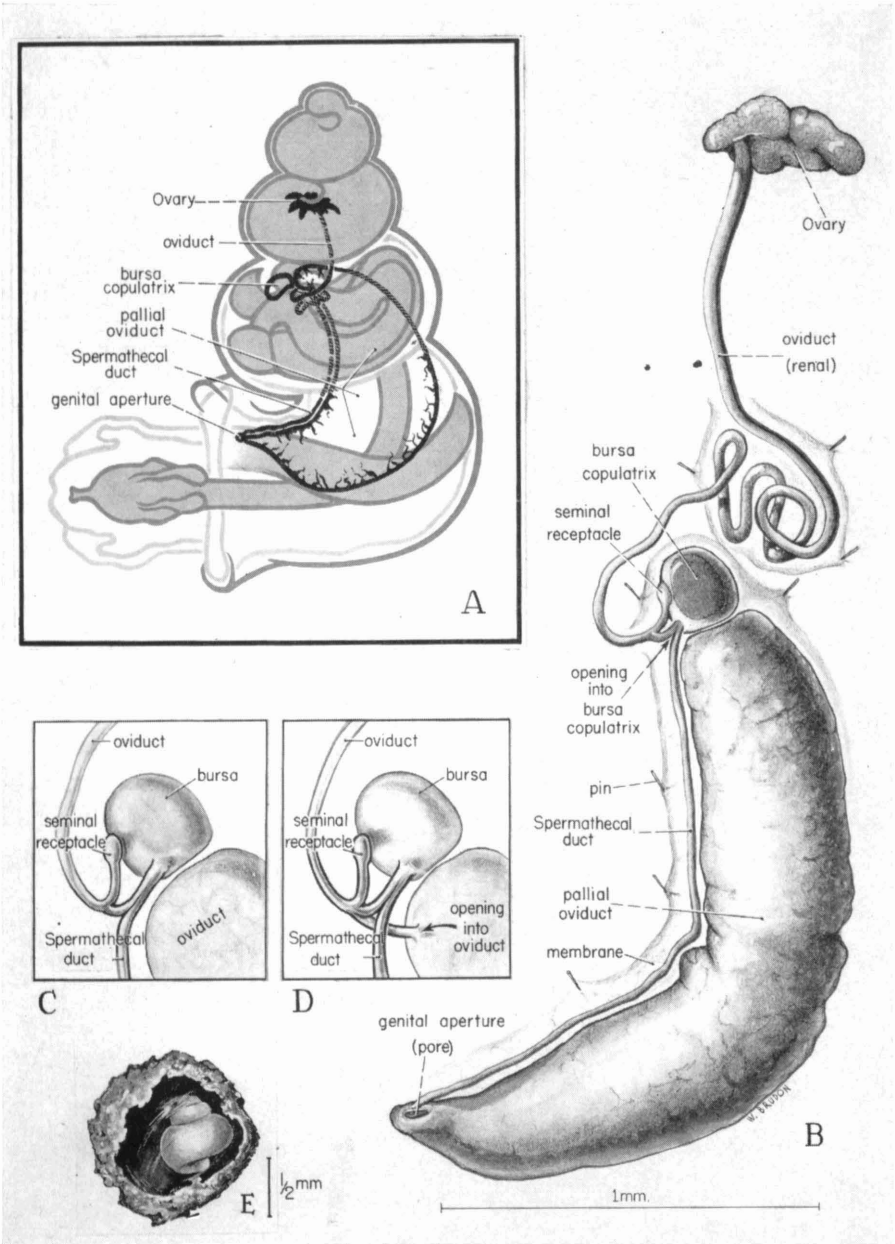

Ovary
oviduct
bursa copulatrix
pallial oviduct
Spermathecal duct
genital aperture
A
Ovary
oviduct (renal)
bursa copulatrix
seminal receptacle
opening into bursa copulatrix
pin
Spermathecal duct
pallial oviduct
membrane
genital aperture (pore)
B
1mm.
oviduct
bursa
seminal receptacle
Spermathecal duct
oviduct
C
oviduct
bursa
seminal receptacle
Spermathecal duct
opening into oviduct
D
E
½mm

PLATE VII

Photomicrographs of certain organs in *Pomatiopsis cincinnatiensis* (Lea).

A. Cross section of tentacle.

B. Cross section of eye.

C. Cross section of otocyst with otolith.

D. Section showing osphradium in relation to circulatory sinus and gill filaments.

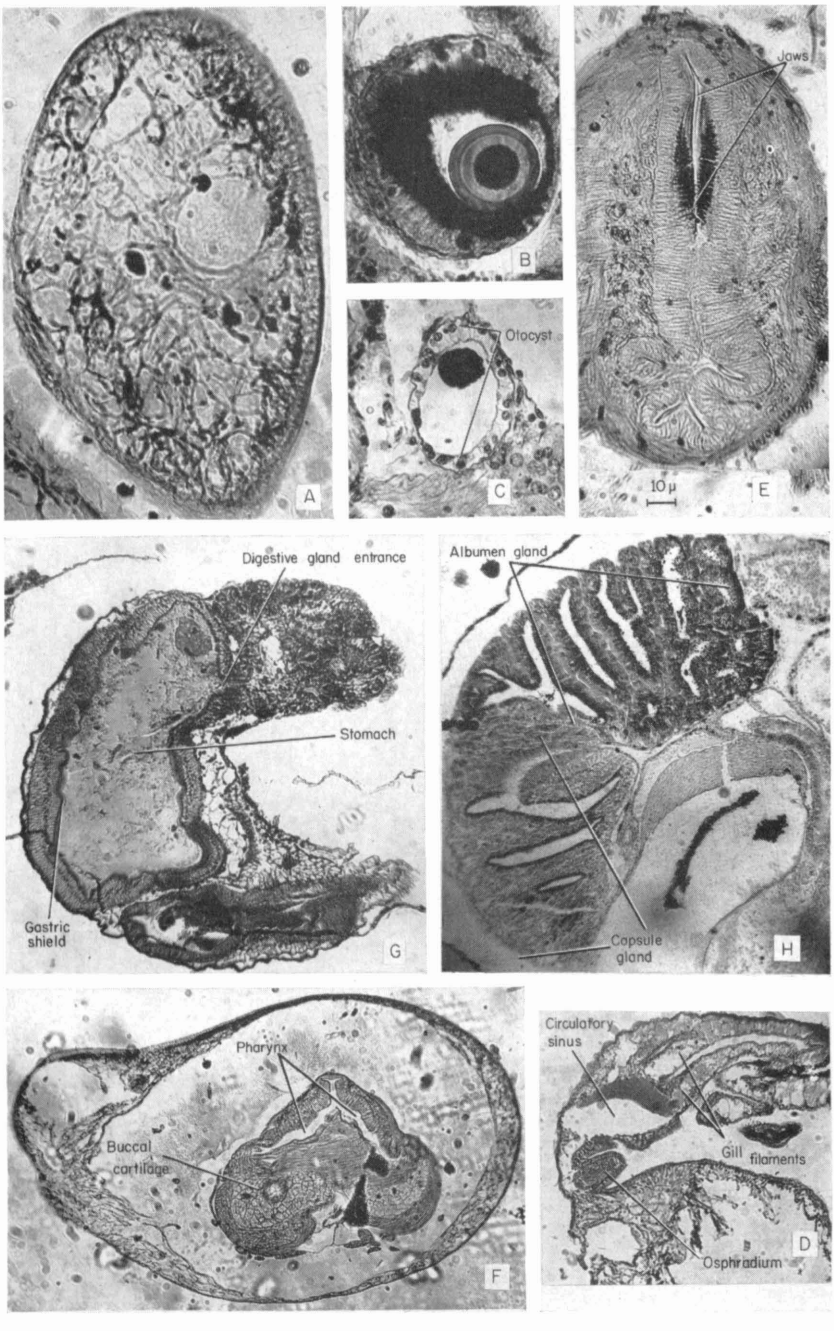
E. Cross section of pharynx showing the jaws.

F. Cross section of buccal mass at level of pharynx and indicating the buccal cartilage.

G. Sagittal section of stomach showing gastric shield and entrance of digestive gland.

H. Sagittal section of pallial oviduct indicating the structural differences in albumen and capsule glands.

PLATE VII


A
B
Otocyst
C
Jaws
10 μ
E
Digestive gland entrance
Stomach
Gastric shield
G
Albumen gland
Capsule gland
H
Pharynx
Buccal cartilage
F
Circulatory sinus
Gill filaments
Osphradium
D