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MORPHOLOGY AND HISTOLOGY OF THE REPRODUCTIVE ORGANS OF *UROSALPINX CINEREA* (SAY) AND *EUPLEURA CAUDATA* (SAY)

By

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INTRODUCTION

Much of the previous work done on the common oyster drills of the Atlantic coast, *Urosalpinx cinerea* (Say) and *Eupleura caudata* (Say), has been primarily ecological in nature involving distribution, predation, and reproduction. Little was known of the morphology of the soft parts of *U. cinerea* until Carriker (1943) presented an admirable description of the structure and function of the probosis. Fretter (1941) has described the genital ducts of two closely related muricids.

Even less is known of the biology and morphology of *E. caudata* since *U. cinerea* has received the major portion of research. This is due to the far greater quantities of *U. cinerea* present on oyster beds, except for a few isolated localities.

According to Carriker (1955) *U. cinerea* was first described by Say (1922) under the name *Fusus cinereus*. Stimpson (1865) later created the genus *Urosalpinx* in the family Muricidae and included *Fusus cinereus*, calling it *Urosalpinx cinerea* (Say). Baker (1951) described a subspecies of *U. cinerea* from Eastern Shore, Virginia. *U. c. follyensis* is the large form found only in that locality while *U. c. cinerea* is the smaller form found elsewhere on the East Coast. *E. caudata* is also a member of the family Muricidae, Order Neogastropoda, Subclass Prosobranchia, Class Gastropoda (Abbott, 1954). *E. caudata* is also divided into two subspecies, *E. c. caudata* and *E. c. etterae*, which is also the large form found on the Delmarva

Peninsula (Baker, 1951). Some doubt exists as to whether E. c. etterae is a valid subspecies. Further investigations will undoubtedly settle this problem.

Since the decline in oyster production is at least partially attributable to predation by U. cinerea and E. caudata the ultimate aim is to either eradicate or greatly reduce the numbers of these carnivorous gastropods. It is hoped that this study contributed to the knowledge of the biology of these predators.

MATERIALS AND METHODS

Description of Areas

Samples of *Urosalpinx cinerea* (Say) and *Eupleura caudata* (Say) were taken from eel grass beds just offshore from the Laboratory located six miles from the mouth of York River. The large forms of both species were collected from the Wachapreague area of Eastern Shore, Virginia. Wachapreague is located near the middle portion of Eastern Shore on the eastern side, which is typically a high salinity area.

Drills were trapped using wire mesh bags filled with seed oysters, some of which had barnacles, mussels, and other fouling organisms.

Number of Specimens

A total of fourteen drills were sectioned for this study, nine *U. cinerea* and five *E. caudata*. Transverse, sagittal, and frontal sections were made from four *U. cinerea* males and five females, one of which was the large form found on Eastern Shore, Virginia. Three *E. caudata* females, and two males were also processed.

For gross studies, approximately thirty *U. cinerea*, male and females, were dissected. Only six specimens, both male and female, of *E. caudata* were dissected.

Sexing

The sex of each drill was determined before fixation using the technique developed by Hargis (1957). Individuals are sexed on the basis of presence or absence of a penis. Gonadal smears correlate well with this rapid sexing technique. Hargis (1957) stated that all of 89 male *U. cinerea* sexed by this method contained viable sperm, and 103 of 111 females had vitelline bodies while the remaining eight were immature.

Measurements

At the time of sexing total shell height measurements were taken. Probably some measure of soft parts, such as volume, would be a better index to the relative size of the animal because the shell is subjected to abrasion, dissolution and breakage. Also, a small increase in shell height is accompanied by a relatively large increase in volume of the soft parts.

Narcotization

Carriker and Blake (1959) described a relaxation method using 1 - naphthyl N - methyl carbamate ("Sevin") and carbon dioxide. This technique has since been modified slightly (Carriker, personal communication). The modified form is:

1. 10 ppm Sevin in sea water one hour.
2. Fresh Sevin in one atmosphere of CO_2 from cylinder of CO^2 three hours.
3. Freeze snail on dry ice and leave for 24 hours.
4. Partically thaw, crack shell and remove snail.

5. Harden in ten percent formalin six hours.

6. Wash 6-12 hours.

7. Store in Owen's fluid.

Owen's fluid is 1% propylene phenoxetol, 5% glycerin, and 94% tap water.

This procedure is satisfactory for material intended for gross work, but unsuitable for histological preparations since alternate freezing and thawing ruptures the cells and generally distorts tissue relations.

Histology

Carriker's relaxation method has been further modified for our histological preparations. Instead of freezing the snail directly on dry ice, Carnoy's fixative is chilled to about -80°C in a stainless steel container surrounded by dry ice. The narcotized snail freezes instantly when dropped into the fluid. Since Carnoy's is an anhydrous fixative, ice crystals formed within the tissues are withdrawn in the vapor phase. Thus, the tissue is well-fixed with little disorganization. By this method, the structure of the foot and associated structures can be studied in the relaxed state.

Tissue fixed in this manner is somewhat more brittle and subject to mechanical damage in sectioning than tissues processed by more conventional fixatives, although this is of no great disadvantage. The shell may be removed after fixation either by cracking gently with a hammer or dissolution in 5-10% hydrochloric acid in sea water.

For histology of the reproductive tract, drills are fixed in AFA mixture of the following formula.

50% Ethyl Alcohol	200 ml
Glacial Acetic Acid	5 ml
40% Formaldehyde	13 ml

Since AFA is acid and must remain acid for proper fixation, shell removal must precede fixation. This is done by either cracking the shell or dissolution in 5-10% HCl in sea water. Drills which had their shells dissolved with acid appeared to be slightly better relaxed and took the stains more intensely than those whose shells were cracked off. Acid treatment did not hinder sectioning in any way except when they were left in the acid too long.

Stains

For serial sections Harris Hematoxylin with an eosin counterstain was used.

The dioxane method of Carsley (1938) is modified for use in dehydration and infiltration of tissues. The following schedule was used.

1. AFA fixed material
2. 70% Alcohol 1 hour
3. 1/2 70% Alcohol - 1/2 70% Dioxane 1 hour
4. 70% Dioxane 1 hour
5. 100% Dioxane 2 hours
6. 100% Dioxane 2 hour
7. 1/3 Tissuemat - 2/3 Dioxane 1 hour

8. 2/3 Tissuemat - 1/3 Dioxane 1 hour
9. Pure Tissuemat 1 hour
10. Pure Tissuemat 1 hour
11. Pure Tissuemat 1 hour
12. Embed in fresh Tissuemat

Egg Capsule

Serial sections of a freshly deposited egg capsule of *U. cinerea* were made in an effort to determine the stage of development of the enclosed embryos. These sections were cut at ten microns and stained with Chlorazol Black E.

Whole Mounts of Penes

To study the ducts of the penis, whole mounts of six penes were made and stained with Semichon's Acetocarmine and Grenacher's Alcoholic Borax Carmine, the latter giving better differentiation.

RESULTS

Morphology and Histology of the Reproductive Organs of <u>Urosalpinx</u> <u>cinerea</u> (Say)

<u>Female</u>

The following is a description, organ by organ of the reproductive system beginning with the gonad and proceeding anteriorly to the capsule gland and vaginal orifice. Figure 1 shows the gross external structure. When the shell is removed from <u>Urosalpinx</u> the ovary is seen on the right dorsolateral side of the coiled posterior end. It is a bright yellow organ with a granular appearance embedded in the gray digestive gland. A thin-walled oviduct advances along the ventral body wall under the transparent integument until it reaches the anterior edge of the digestive gland. Then, turning medially and dorsally, the oviduct enters the albumen gland which is a fairly large creamy white structure with folded walls lying between the large thin-walled renal gland on the posterior side and the small, light brown sperm ingesting gland on the anterior.

The albumen gland is bent abruptly upon itself giving it a characteristic square shape when viewed externally. The lumen of the albumen gland is large and the thick walls are slightly folded. The duct from the albumen gland passes anteriorly to be joined, at about 2/3 its length, by a duct from the sperm ingesting gland before entering the right ventral side of the capsule gland. A sphincter closes the duct between the sperm ingesting gland and oviduct.

Another sphincter is located in the oviduct as it enters the albumen gland. Anterior to this junction of the ducts is a large sphincter set against the ventral corner of the capsule gland. This sphincter evidently controls the flow of ova and albumen into the capsule gland and the flow of sperm from the capsule gland into the sperm ingesting gland or the albumen gland.

The capsule gland is a thick-walled structure on the dorsal side of the mantle. The anterior portion of the capsule gland is partially covered by the red, mucus-secreting rectal gland. The thickened lateral walls and thin dorsal and ventral walls of the capsule gland give its lumen the appearance of a dorsoventral slit in cross section. At both ends of the capsule gland are concave vestibules which taper sharply toward the center of this gland as the lateral walls become thicker. From the anterior vestibule the oviduct exits ventrally and passes anteriorly on the right side. The large sphincter muscle located in the oviduct anterior to the capsule gland evidently permits passage of sperm posteriorly and egg capsules anteriorly. Anterior to this sphincter the oviduct divides into two parts, one turning dorsal to the bursa copulatrix and the other passing anteriorly to the mantle, terminating at the vagina.

The bursa copulatrix is a large thick-walled sac which is used for the storage of sperm after copulation. The thick neck of this organ tapers to form a duct on the right side which is bent back upon itself and directed posteriorly and ventrally to join the oviduct. The convex posterior wall fits against the concave wall of the anterior vestibule in the capsule gland. The oviduct passes anteriorly on the right side of the bursa copulatrix and turns dorsally and laterally in the mantle, terminating in the vagina. Lying parallel to the rectum, the vaginal orifice is to the right and slightly posterior to the anus. The walls of the terminal portion of the oviduct are highly folded and capable of much distension.

In the ovary, the tubules are lined with thin germinal epithelium surrounded by rather loose connective tissue. Ova differentiate from the tubule walls and are without a follicular membrane. Associated with the ova are vitelline bodies which furnish nutrient material for developing embryos. These are eosinophilic, anucleate ellipsiods with amorphous material which appears to develop within the cytoplasm of each ovum (Figure 4). Occasional vitelline bodies appear randomly throughout the reproductive system of the female. Several hundred vitelline bodies are deposited with each ovum in the egg case. Here both vitelline bodies and embryos are enclosed by a membrane surrounded by albumen. The ovarian tubules coalesce to form tubules of larger diameter. Four or five thin-walled tubules enter the oviduct along the entire length of the ovary.

The oviduct continues anteriorly along the ventral body wall and is lined with unciliated columnar epithelium, surrounded by a thin layer of longitudinal muscle. Nuclei of the epithelial lining are oval and basal, and the cytoplasm of each cell is amorphous, lacking granules or vacuoles. At the level of the albumen gland the oviduct turns abruptly dorsad to enter the posterior side of the albumen gland.

The simple unciliated columnar epithelium of the oviduct changes to a simple columnar epithelium of greater length in the albumen gland. Clusters of secretory cells lie beneath the epithelial lining, connected to the lumen by short ducts of small caliber. Adjacent clusters of cells are separated by a thin layer of connective tissue. Globules of albuminous material line the lumen. These globules as well as spherules within the cytoplasm of the cells stain a faint pink with eosin. Nuclei of both the epithelium and subepithelial secretory clusters are oval in shape and basal. A thin layer of connective tissue separates the albumen gland from the body wall and surrounding glandular tissue, namely the renal gland and sperm ingesting gland. Passage of ova and secretions from the albumen gland through the oviduct to the capsule gland is controlled by a sphincter in the oviduct on the anterior side of the albumen gland.

Immediately before entering the posterior end of the capsule gland, the oviduct is joined by a duct from the sperm ingesting gland. The dorsal branch of the oviduct as well as the posterior branch to the albumen gland are lined with simple ciliated columnar epithelium. A small sphincter is present at the base of the sperm ingesting gland. At the orifice of the sperm ingesting gland, the epithelial lining changes to a very tall (100 u) unciliated columnar type. The walls of the sperm ingesting gland are only one cell thick and all the cells are of this same tall type. Nuclei of these cells are oval and set deep within the cell, and the cytoplasm is vacuolated and also contains small amorphous non-staining spherules which are presumably the breakdown products of ingested sperm. Intact sperm are distributed throughout the cytoplasm of the cells, but these may be artifacts introduced in the sectioning process. Though this is unlikely due to the number and location of these sperm and sperm fragments. Sperm are also distributed in a disorganized manner throughout the lumen of the sperm ingesting gland, and occasional sperm are attached to the cell walls, tails projecting into the lumen.

The suggested function of the sperm ingesting gland in other gastropods, such as _Nucella lapillus_, is to rid the female of excess sperm, at the same time possibly the animal extracts some nutrients from the ingested sperm. Presumably the sperm ingesting gland of _U. cinerea_ would have an homologous function. The sperm ingesting gland may also serve partially as a seminal receptacle, since Hargis (personal communication) has found motile sperm in the sperm ingesting gland throughout the year. It has been suggested that in other gastropods the duct leading to the sperm ingesting gland may function as a seminal receptacle since sperm appear closely packed and oriented in this segment (Fretter, 1941). It is rather doubtful that the duct from the sperm ingesting gland in _U. cinerea_ serves an homologous function. Sperm have never been observed in this segment, not even in the lumen of the duct.

Entering the capsule gland near the base, the U-shaped ciliated duct connects the posterior vestibule of the capsule gland with the oviduct. A rather larger sphincter which probably controls the passage of both sperm and ova and albuminous substance through this duct is immediately adjacent to the ventral side of the capsule gland. The lumen of this duct is highly folded and lined with short simple ciliated columnar epithelium which changes abruptly just inside the capsule gland to a taller simple columnar epithelium with shorter cilia. The cilia of the epithelial lining of the duct are equal in length to the cell to which they are attached. On the ventral side of the duct, the short ciliated columnar epithelium continues anteriorly as the lining of the ventral channel of the capsule gland, becoming shorter with shorter cilia. Cells lining the duct rest on a basement membrane over a thin layer of longitudinal muscles.

In transverse section the capsule gland is divided into three distinct histological regions, a dorsal basophilic, medial eosinophilic, and ventral basophilic section. All three regions have secretory cells under the simple ciliated columnar epithelium. The medial eosinophilic segment of the capsule gland has clusters of subepithelial secretory cells connected with the lumen by small thin-walled ducts. A thin layer of connective tissue separates adjacent clusters of these protein secreting cells. Within these cells large oval nuclei are embedded in a granular cytoplasm. Morphologically these cell clusters are the same as found in the albumen gland. Fretter (1941) describes the same type of cell clusters in _Nucella lapillus_. However the cell cluster of _N. lapillus_ appears to have a basement membrane which has not been observed in

U. cinerea. These cells are described by Fretter as having the function of secreting the fibrous protein layer of the egg case of *N. lapillus* and probably have a similar function in *U. cinerea*. The basophilic dorsal and ventral segments of the capsule gland probably secrete mucoid materials.

At either end of the capsule gland, in the region of the anterior and posterior vestibules, strongly basophilic cellular areas occur in which the cells contain large vacuoles in the cytoplasm. These cells probably secrete the mucus plug which is said to precede formation of the egg capsule (Fretter, 1941).

The ventral channel is a fold of ciliated columnar epithelium, which forms a functionally closed duct traversing the length of the capsule gland, and terminating in the anterior vestibule of the capsule gland near the anterior segment of the oviduct. Apparently sperm travel from the oviduct to the sperm ingesting gland in this channel.

Passing anteriorly from the right side of the capsule gland, the oviduct is joined by a duct from the bursa copulatrix. In this segment which lies between the capsule gland and the junction with the duct of the bursa copulatrix, there is a prominent sphincter. The epithelial lining of the oviduct is the same simple ciliated columnar cells found elsewhere in the anterior part of the reproductive system of *U. cinerea*. A layer of longitudinal muscle fibers surrounds the epithelial layer, and circular muscle fibers may also be present but have not been observed.

The bursa copulatrix is a large kidney-shaped structure with a thick tapering neck which forms a duct connecting with the oviduct. The lumen of the bursa copulatrix is lined with unciliated stratified squamous epithelium. Some of the sperm are oriented with their heads embedded in the cytoplasm of the epithelium and tails projecting into the lumen. In the lumen proper, sperm appear to be in disoriented closely packed masses.

In the region of the sphincter in the duct of the bursa copulatrix, which probably controls the passage of sperm to and from the bursa copulatrix, the epithelial lining is transitional between stratified squamous epithelium of the lumen and simple ciliated columnar with circular muscle fibers interspersed.

The epithelial lining of the bursa copulatrix has more or less cuboidal cells lining the lumen and irregularly shaped polyhedral cells in the subepithelial layer. The number of cells varies in depth giving a corresponding variation in thickness of the bursa wall. Large nuclei occupy the center of each cell and the cytoplasm is not vacuolated, but appears somewhat granular, the granules being extremely small and indistinct.

A narrow band (11 u) of longitudinal muscle surrounds the entire bursa and increases in depth in the neck approaching the sphincter. As in the terminal segment of the oviduct, circular muscle fibers are apparently lacking in the bursa copulatrix.

A layer of longitudinal muscle surrounds the oviduct. A layer of circular muscle is probably also present, but was not clearly seen in our preparations. Toward the vaginal opening, the number and size of mucus cells increases. The mucus cells probably aid the movement of the egg case through the oviduct by supplying mucus which acts as a lubricating agent, thus reducing friction.

No sphincter muscle has been observed in the oviduct anterior to the junction with the duct from the bursa copulatrix. However, since this part of the oviduct is distensible and well supplied with longitudinal muscle fibers, the whole segment may act as a sphincter.

The Pedal Glands

The next components to be described are located on the ventral surface of the foot. Only one, the pedal gland, is connected functionally but not physically with the sexual apparatus described above. Carriker (1943) and Fretter (1946b) independently describe the pedal sucker of Urosalpinx cinerea which is a concave ciliated plate present in both sexes. Carriker (1943) calls this structure the accessory probosis. Immediately posterior to the pedal sucker is a blind sac, the pedal gland, present only in the female (Figure 3). The gland is lined with pseudostratified columnar epithelium with elongate nuclei. Occasional mucus cells are interspersed among the epithelial layer. A thick layer of circular muscle fibers surrounds the epithelium. Rather dense connective tissue and muscles of the foot lie around the whole gland. The reported function of this pedal gland is to secrete the outer layer of the egg case, which hardens to a definitive shape, and to cement the egg case to the substratum. It is rather doubtful that the outer layer is actually secreted by this gland because of the paucity of secretory cells in the epithelial lining. Before the egg case is passed to the pedal gland, the walls are soft, pliable, and slightly wrinkled.

Opening at the anterior edge on the ventral side of the foot between the propodia is the pedal mucus gland. Its lumen is lined with simple ciliated columnar epithelium with a heavy concentration of mucus cells interspersed. Nuclei of the epithelial cells are oval and basal. Ducts of subepithelial secretory cells open between the ciliated columnar epithelial cells. In the connective tissue layer surrounding the lumen, dense concentrations of granular eosinophilic and basophilic secretory cells are present. These cells appear to empty into the lumen of the pedal mucus gland by way of thin-walled ducts. Muscle fibers and nerves of the foot pass among the cluster of secretory cells.

This gland is present in both sexes and is probably associated with the specialized method of feeding found among carivorous gastropods. During the drilling operation the propodia close around the extended probosis to guide it. It is also possible that the pedal mucus gland secretes a lubricating agent near the probosis to aid the drilling operation, since during this period the probosis and orifice of the pedal mucus gland are in close proximity.

Male

The reproductive system of the male *U. cinerea* is less complex than that of the female. The male is easily distinguished from the female by the presence of a broad-based, tapering, C-shaped penis which lies under the mantle on the right side of the neck (Figure 2). Normally the flattened penis lies in a curved position.

In the excited state the penis is considerably elongated and straightened, then protruding from the mantle cavity. The distal end of the vas deferens opens at the apex of the penis, and from this position, proceeds posteriorly as a straight tube to about the mid-point of the penis where it becomes highly coiled and continues as a coiled duct lying on the left side of the penis (Figure 7A). Near the base of the penis the vas deferens again becomes a straight tube, still lying on the extreme left side of the penis, and turns medially into the base of the penis. The vas deferens again turns posteriorly at this point and continues as a straight tube just under the integument of the cephalic mass. At the posterior margin of the mantle cavity the vas deferens enters the prostate gland, a thick-walled elongate structure. The prostate gland lies obliquely just under the right lateral body wall with its long axis running diagonally to meet the vas deferens on the ventral side of the body posteriorly. The vas deferens continues caudad to the testis as a thin-walled transparent tube immediately under the integument. On the ventral side of the testis, the vas deferens gives off four or five thin-walled branches which further divide until the testis is a highly diverticulated tubular structure embedded in the digestive gland.

In a living or freshly preserved U. cinerea male the testis is a yellow granular body on the right dorsolateral side of the gray digestive gland. The color of the testis and ovary is variable, ranging from white to orange. Gonadal color has been used to differentiate sexes (Federighi, 1931; Cole, 1941) but is unsuitable for this purpose due to the color overlap of both male and female testes (Hargis, 1957). The testis was bright yellow in all the specimens examined for this study, further confirming the unreliability of gonad color as an indicator of sex.

The testis is lined with thin germinal epithelium from which spermatazoa are differentiated. A thin layer of connective tissue separates the testis tubules from digestive gland. At the base of the testis the tubules, which coalesce to form the vas deferens, are lined with simple columnar epithelium. The vas deferens becomes ciliated at the level of the anterior end of the testis. Cilia are at first short in the transitional zone between the non-ciliated and ciliated columnar epithelium, and increase in length until they are equal to the cell height. Nuclei of the ciliated cells are large, oval and basal. A thin layer of longitudinal muscle encloses the epithelial lining of the vas deferens. Circular muscle fibers are not present in this segment of the vas deferens.

Near the base of the renal gland, on the right ventral side of the body, the vas deferens turns dorsad to enter the posterior end of the prostate gland. The lumen of the prostate gland is lined with pseudostratified ciliated columnar epithelium (Figure 7B). A basement membrane cannot be seen. Nuclei of the epithelial lining are long, and about two-thirds the total cell height. Walls of the prostate gland are of uniform thickness and compressed laterally. At the anterodorsal end of the prostate gland, a vent lined with a thin fold of ciliated epithelium opens into the right posterolateral corner of the mantle cavity, and is closed by a mucus plug. It is possible that the mucus plug observed is an artifact of fixation rather than a natural condition. Excess sperm may be voided into the mantle cavity through this vent, but sperm were not observed in either the prostate lumen or mantle cavity near the vent.

A strong sphincter in the vas deferens, which probably controls the flow of sperm and prostatic secretions to the anterior segment of the vas deferens is present on the anterodorsal side of the prostate gland. The vas deferens is constricted in the area immediately preceding the sphincter.

Turning dorsad, the vas deferens follows an anterodorsal course along the right side of the cephalic hump. Histologically this segment is the same as the segment preceding the prostate gland. It forms a ridge beneath the integument which is easily visible without magnification.

At the base of the penis the vas deferens makes an S-shaped turn to enter the lateral side of the penis. A thick layer of circular muscle surrounds the vas deferens in the proximal end of the penis. The lumen of the vas deferens is lined with simple ciliated columnar epithelium. The diameter of the lumen decreases, accompanied by a corresponding decrease in the circular musculature, proceeding from the proximal to distal end of the penis.

Two large blood sinuses, a smaller medial one and larger lateral sinus, traverse most of the length of the penis and give off branches at intervals along most of their length. These probably serve to distend the penis.

The epithelial covering of the penis is ciliated and appears to be almost cuboidal. Mucus secreting cells are interspersed among the ciliated epithelial cells for most of the length of the penis.

No trace of a pedal gland exists in the male U. cinerea. However, the pedal sucker and pedal mucus gland are present in the male and are probably homologous to those of the female oyster drill.

Morphology and Histology of the Reproductive System of Eupleura caudata (Say)

Female

In gross aspect the most conspicuous organ of the reproductive system is the ovary which is located on the right dorsolateral side of the coiled posterior end. This bright yellow organ stands out against the grey to black color of the digestive gland. From the base of the ovary the thin-walled oviduct advances along the ventral body wall under the transparent integument until it reaches the anterior edge of the digestive gland. At this point, turning medially and dorsally, the oviduct enters the albumen gland.

The albumen gland is a small thick-walled structure lying between the digestive gland and sperm ingesting gland and partially under the renal gland so that only the right side is exposed to view. The kidney or renal gland is located on the left side of the trunk adjacent to the digestive gland and is easily recognized by its white, thin-walled appearance. The large lobe of the kidney on the left side becomes smaller as it progresses obliquely from left dorsal to right ventral where it enters the renal duct.

The sperm ingesting gland, which is four or five times as large as the albumen gland, lies anterior and dorsal to the smaller albumen gland. It is a moderately thick-walled structure with a lobed appearance due to the slightly folded walls. The sperm ingesting gland is not a continuation of the oviduct as is the case of the albumen gland but a blind sac opening into the right posterior corner of the capsule gland by a separate duct.

The oviduct proceeds ventrally from the albumen gland to the capsule gland as a U-shaped duct. The large thick-walled capsule gland lies anterior to the sperm ingesting gland and lateral to the large red hypobranchial gland. The lateral walls of the capsule gland are thick while the dorsal and ventral walls are thin, corresponding to the sutures of the egg capsules. In the ventral wall a fold of epithelium forms a functionally closed channel. The ventral channel is present almost the entire length of the capsule gland, terminating near the points of entry of both the albumen and sperm ingesting glands.

The terminal portion of the oviduct passes anteriorly from the right side of the capsule gland and terminates just posterior to the rectum. Both the oviduct and rectum are embedded in the mantle on the right dorsal side of the drill above the hypobranchial gland.

Structurally and histologically the ovary is a thin-walled highly branched tubular structure with öocytes developing from the walls. A transparent cuboidal epithelium (5-6 u thick) covers both the ovary and digestive gland. Nuclei of the germinal epithelium are irregularly spaced and embedded in the tubule wall. Immature ova are found in the largest concentration in the distal portion of the ovary. Maturing and mature ova appear to be found in higher concentrations closest to the oviduct.

Vitelline bodies are mixed in varying concentrations with ova in the ovarian tubules and concentrations appear to be independent of the number of mature or maturing ova. These are eosinophilic, anucleate elliposoids of an amorphous material which furnish nutrient material to developing embryos. Occasional vitelline bodies are distributed randomly throughout most of the oviduct. Vitelline bodies apparently develop from specialized cells embedded in ovarian tubule walls. These cells have a very granular cytoplasm and large nucleus. The granules are probably small maturing vitelline bodies because some have all the morphological and staining characteristics of "mature" vitelline bodies. Other smaller granules staining deep blue with Harris Hematoxylin appear in the cytoplasm. Large numbers of granular macrophages appear both in the lumen of tubules and interstitial spaces of the ovary. George and Ferguson (1950) described the blood components of Busycon canaliculatum, B. carica, and Fasciolaria tulipa and the granular macrophages described for these species appear to be similar to those found in U. cinerea and E. caudata.

The distal secondary ovarian tubules coalesce forming primary tubules of larger diameter which open into a common ovarian chamber by means of five or six main branches at points along the entire length of the chamber.

The oviduct is a thin-walled structure lying just under the integument on the right ventrolateral side and exiting from the ovary at its base. As in U. cinerea, the oviduct of E. caudata is unciliated. It is lined with simple columnar epithelium which rests on a thin basement membrane. Nuclei of the columnar cells are oval and located in the base of the cell. The oviduct in gross aspect is easily confused with the large blood vessel which runs parallel to it and is also on the surface of the digestive gland. In places the wall of the blood vessel and oviduct are extremely thin. At short intervals the blood vessel gives off median branches to the viscera. About midway between the ovary and albumen gland the epithelial lining of the oviduct changes to a transitional type. In this region large multinucleate cells are embedded in the wall of the oviduct and are usually seen only on the median walls. At a point just posterior to the albumen gland the oviduct turns abruptly dorsad to enter the right posterior edge of the albumen gland. The circular muscle surrounding the oviduct is probably a sphincter which prevents the accumulation of excess ova in the albumen gland.

The walls of the albumen gland are folded due to the difference in the thickness of subepithelial glandular tissue. Here albuminous fluid secreted into the lumen is mixed with the mass of ova. Fertilization probably also occurs here. In hermaphroditic animals such as *Omalogyra atomus* fertilization occurs in a fertilization chamber which is situated at the junction of the ducts from the seminal receptacle, albumen gland, ovary, and capsule gland. The arrangement of the genital ducts in *O. atomus* is similar to that found in the female *Skeneopsis planorbis* (Fretter, 1948).

The cells lining the albumen gland are all of the same type. Lightly staining spherules are scattered throughout the cytoplasm. Presumably these spherules represent early albuminous fluid.

A sphincter is present between the albumen gland and capsule gland. The two sphincters, one anterior and the other posterior to the albumen gland may serve to regulate to a certain extent the number of ova passing at any time from one region to another.

MacKenzie (1958) stated that an average of 18 to 19 embryos (range 1 to 47) are deposited in each egg case of York River E. caudata. His data included samples from caged animals and those from natural bottoms.

The sperm ingesting gland which is four or five times as large as the albumen gland lies anteriorly and dorsal to the smaller albumen gland. A few intact, unoriented sperm are scattered through the large lumen along with lightly staining spherules. The same lightly staining spherules are also within the cytoplasm of cells lining the sperm ingesting gland. Presumably these are breakdown products of ingested sperm. Vacuoles are also present in the cytoplasm and contain darkly staining spherules. Fretter (1941) suggests that the females may derive some nutritional value from the ingested sperm as well as ridding themselves of an overabundance of sperm.

MacKenzie (1958) has demonstrated that viable sperm are retained by the female for periods as long as six months. This is probably a protective mechanism which serves to insure production of viable embryos the following year even though a mature male is not available for copulation. Its survival value seems obvious. Viable sperm may be retained in the ingesting gland from year to year. Unlike U. cinerea, E. caudata lacks a bursa copulatrix. Cells lining the sperm ingesting gland are tall, almost goblet-shaped unciliated columnar epithelium resting on a basement membrane (Figure 5C). The nuclei of these cells are round and basal. The basement membrane is underlain by rather loose connective tissue. The duct leading from the sperm ingesting gland to the capsule gland is lined with simple ciliated columnar epithelium.

The oviduct proceeds ventrally as a short ciliated duct lined with simple columnar epithelium to enter the right posterior corner of the capsule gland close to the ventral channel. Cilia of the epithelial lining of this duct are approximately twice the cell height. Longitudinal muscle fibers surround the entire length of the duct with an outer layer of circular muscle fibers forming a sphincter in the duct.

The thick-walled capsule gland lies anterior to the sperm ingesting gland and lateral to the large red hypobranchial gland. Here the first layers of the egg capsule are secreted and the egg capsule is given its initial shape which closely corresponds to the contour of the lumen itself. The capsule gland is somewhat rectangular from the dorsal aspect. The walls of the lumen are highly secretory and lined with simple ciliated columnar epithelium with a dorsoventral slit dividing the two thickened lateral walls. The dorsal and ventral walls are thin, corresponding to the sutures of the egg capsules. In the ventral wall a fold of ciliated epithelium forms a functional channel. It is probable that sperm are transferred from the vagina to the albumen and sperm ingesting glands via this ciliated channel. The ventral channel is present almost the entire length of the capsule gland terminating near the points of entry of both the albumen and sperm ingesting glands.

Three separate secretory areas are present in the capsule gland, a darkly staining area dorsally, and eosinophilic granular area medially, and another basophilic area ventrally. The basophilic areas perform some unknown function while the medial eosinophilic area presumably secretes the protein material of the egg case. Protein secreting cells are arranged in clusters with small ducts passing through the ciliated epithelium lining the lumen (Figure 5B). Fretter (1941) describes a similar structure in Nucella lapillus.

The terminal portion of the oviduct is a circular thick-walled ciliated tube 275 u in diameter which is parallel to the rectum and terminating just posterior to the anus.

Eupleura caudata has an anal gland which is composed of a large mass of black glandular tissue dorsal to the rectum. It is a branching system of blind tubules which opens by way of a short duct into the rectum immediately behind the anus. Fretter (1946a) has described a similar structure in Nucella lapillus, Ocenebra erinacea, and Urosalpinx cinerea. In these three animals the anal gland probably functions as an accessory kidney and presumably has the same function in Eupleura caudata.

As mentioned above Carriker (1943) and Fretter (1946b) describe a pedal sucker for U. cinerea. Carriker named this structure the accessory probosis. The same structure is present in E. caudata toward the anterior end of the foot located on the median line. The function of this organ in Eupleura caudata is not known, but in U. cinerea where special studies have been made, the function is still somewhat obscure although Carriker (1943) indicates that it secretes a substance which dissolves the prey's shell. It is probably analogous as well as homologous in both species.

Immediately posterior to the pedal sucker and separated from it by a thin wall is the pedal gland. The opening to this gland is seen as a lateral slit on the ventral surface of the foot. This gland hardens the walls and cements the egg cases to the substratum and probably gives egg cases their definitive shape.

At the anterior edge of the foot and opening between the propodia is the pedal mucus gland. It is lined with ciliated epithelium and mucus glands. The gland is about 120 u wide at the blind end, tapering to 60 u at its orifice. The length of the lumen is about 658 u with darkly staining secretory cells, extending 240 u on either side. The secretory cells have a granular cytoplasm and stain an intense blue with Harris Hematoxylin. Although the function is obscure at the present,the pedal mucus gland may secrete a lubricating agent for the probosis during the drilling operation or substances to dissolve the prey's shell. Apparently this gland is described by Dakin (1912) as the pedal gland of _Buccinum_ _undatum_. Histochemical methods would probably reveal its true function.

Male

The testis of _E_. _caudata_ is located on the right side of the digestive gland and its conspicuous yellow color stands out against the black digestive gland. The primary tubules of the testis coalesce to form tubules of larger diameter and open at the proximal end into three testicular chambers. The vas deferens joins these chambers and then passes forward along the ventral body wall as a thin transparent tube.

Near the posterior edge of the mantle cavity the vas deferens opens into a thick-walled structure, the prostate gland, which is flattened dorsoventrally. The prostate gland lies on the right lateral side ventral to both the anal and hypobranchial glands.

The vas deferens passes anteriorly from the prostate gland and lies immediately under the integument. At the level of the anus, the vas deferens makes an abrupt S-shaped turn dorsad and is seen as a hump beneath the integument. Traveling horizontally for a short distance, the vas deferens again turns dorsad to enter the base of the penis.

The penis is a C-shaped distensible organ on the right side of the cephalic hump behind the base of the tentacle. In the penis the straight vas deferens becomes highly coiled until near the distal end where it again straightens to open near the apex of the penis.

Histologically the highly diverticulated testis is lined with thin (2.7 u) unciliated epithelium. The tubules are embedded in the digestive gland with only a thin layer of connective tissue separating them from that organ. Sperm are located in dense pockets near the base of the testis where the vas deferens enters. Spermatocytes are abundant on the periphery lying three or four deep in the distal portions of the tubule. These are rounded cells measuring 4-5 u in diameter.

In the proximal end of the testis the vas deferens enters as a triply branched thin-walled tube and proceeds anteriorly as a single tube lying on the ventral side of the body just under the integument. It is circular in cross section with a lumen 78 u in diameter. Pseudostratified ciliated epithelium lines the vas deferens and there is a layer of circular muscle 4-14 u thick surrounding the entire structure. The cilia are moderately long (19 u) with the nuclei lying either in the center or base of each cell. The lumen becomes progressively more folded although the muscle layer still retains its circular shape. At this point the intestine is parallel to the vas deferens and roughly twice the diameter of the latter.

The prostate gland is thick-walled (150 u) and flattened dorsoventrally. The lumen is filled with a non-staining amorphous secretion. Its walls are lined with pseudostratified ciliated columnar epithelium. Nuclei are elongate and set deep within each cell. Cilia are short (4-5 u) and nuclei are 30-32 u from the cell walls which line the lumen of the prostate gland. At the widest point the prostate gland measures 190 u and is 720 u long. Below the layer of ciliated cells "cords" or rows of rounded nuclei extends to the outer periphery of the prostate gland. At the periphery of the gland lies a basement membrane beyond which is connective tissue.

The ventral wall of the prostate contains slit-like sinuses beneath the ciliated cells. Nuclei are more rounded and not arranged in as distinct rows as in the dorsal wall. Near the anterior end of the prostate gland a ventral channel forms and curves ventrally and laterally from the median wall. Here the prostate gland has lost the rows of nuclei in the subepithelial layer. The dorsal wall has a different appearance histologically from the ventral wall. Cilia are long and arise from the pseudostratified epithelium. Nuclei of these cells are elongate, reaching two-thirds of the total length of the cell. The cytoplasm contains spherules which stain lightly with hematoxylin. These may be breakdown products from sperm which would indicate a possible resorptive function of the anterior part of the prostate gland.

A vent lined with ciliated epithelium and mucus cells opens into the mantle cavity. This is probably another mechanism of ridding the male of excess sperm. A double row of nuclei giving the appearance of a suture runs from the lumen to periphery of the prostate gland. This condition is the same as in *Nucella lapillus* and indicates that the prostate may have evolved from an open type as represented by the prostate of the three species of *Littorina* described by Linke (1933), to the closed, vented tube as in *Eupleura*. Fretter (1941) describes a short duct closed by a sphincter connecting the lumen of the prostate gland with the mantle cavity in *Buccinum undatum*.

A very thin layer of circular muscle is present in the anterior end of the prostate, but the thickness of this layer appears to be insufficient to cause any forcible ejection of sperm and prostatic secretions into the vas deferens. This muscle layer increases in thickness to form a sphincter between the true vas deferens and prostate gland.

In the anterior end of the prostate sperm are oriented with their heads embedded in the ciliated epithelium which indicates that this region also may function as a seminal vesicle. Cilia of the cells lining this region are long (17 u), approximately the length of the cell (23 u). These cells rest on a basement membrane which is underlain by a layer of circular muscle.

Anterior to the prostate gland the vas deferens lies immediately under the integument. In contrast to the prostate it has lost all secretory cells. Cells lining the lumen are ciliated and have basal nuclei and a basement membrane surrounded by a moderately thick layer of circular muscle. Continuing anteriorly as a dorsoventrally flattened duct lying between the body wall and the eosinophilic, cresentic hypobranchial gland, the vas deferens is about four times as large as the adjacent esophagus. At the base of the penis the cilia lining the vas deferens are short (6 u) and the lumen is 64 u in diameter with a circular muscle layer extending 154 u on either side. The epithelial covering of the penis is ciliated (8-9 u) and cuboidal. Near the base of the penis two large branching blood sinuses develop. The medial sinus is about 140 u in diameter and the large lateral sinus 270 u in diameter. The vas deferens is 54 u in diameter and surrounded by a circular muscle layer 20-25 u thick. A large nerve runs most of the length of the penis giving off branches at intervals. The vas deferens is a straight tube near the base of the penis but becomes highly coiled until near the distal end, where it again straightens to open on the side of the penis 160 u from the end. As the vas deferens continues on the lateral side of the penis, there is a gradual decrease in diameter accompanied by a corresponding decrease in the circular muscle layer.

There is no pedal gland in the male although a pedal sucker is present. It is the same morphologically and histologically as the same structure in the female. The pedal mucus gland opening between the propodia described in the female is also present.

DISCUSSION

The following is a discussion and comparison of the evolution of the reproductive systems of the Prosobranchia. An evolutionary trend from simple reproductive organs and external fertilization to more complex genital systems and internal fertilization and how *U. cinerea* and *E. caudata* fit into this scheme is discussed. An abbreviated classification of the Class Gastropoda (Abbott, 1954) is presented below to indicate the phylogenetic position of *U. cinerea* and *E. caudata* within this class as it is now generally conceived. The species names listed are those which are considered in the comparative study below.

- Class Gastropoda
  - Subclass Prosobranchia
    - Order Archaeogastropoda
      - Superfamily Trochacea
        - Family Trochidae
          - *Calliostoma zizyphinum*
        - Family Neritidae
          - *Theodoxsus fluviatilus* (L.)
    - Order Mesogastropoda
      - Superfamily Littorinacea
        - Family Littorinidae
          - *Littorina littorea* L.
          - *Littorina obtusata* L.
          - *Littorina rudis*

Superfamily Rissoacea

Family Rissoidae

Rissoella diaphana

Skeneopsis planorbis

Omalogyra atomus

Superfamily Cypraecea

Family Lamellariidae

Lamellaria perspicua (L.)

Family Eratoidae

Trivia monarcha (da Costa)

Trivia arctica (Montagu)

Order Neogastropoda

Superfamily Muricacea

Family Muricidae

Urosalpinx cinerea (Say)

Eupleura caudata (Say)

Ocenebra erinacea

Nucella lapillus

Superfamily Buccinacea

Family Buccinidae

Buccinum undatum L.

Family Nassaridae

Nassarius reticulatus (L.)

Subclass Opisthobranchia
    Order Tectibranchia
        Family Acteonidae
            Acteon tornatilis
Subclass Pulmonata

Archaeogastropoda

The earliest known ancestral molluscs had no separate genital ducts (Morton, 1958). Sperm and ova were shed directly into the sea from paired or single gonads which opened into the pericardium. Coelomoducts or renal organs opened to the exterior and fertilization was external. In some of the Aplacophora, as in the monoplacophoran *Neopilina*, such an archaic state persists today. In the Archaeogastropoda and Scaphopoda gametes pass through one renal organ and with few exceptions fertilization is still external.

The otherwise primitive chitons have acquired separate ducts from the gonad which lead to distinct genital pores which is a somewhat advanced characteristic. In primitive gastropods, as in the earliest gastropods, the eggs have very little yolk and no thick protective capsule since they are fertilized externally. The fertilized eggs develop quickly into free swimming trochophores which is followed after a few hours by the veliger stage. Such molluscs are usually restricted in range to shallow inshore areas of the seas. Since fertilization is external this factor alone probably presents the largest barrier to new habitats, thus the Archaeogastropoda and chitons are for the most part marine and coastal.

All known gastropods have only a single gonad which may or may not open directly into the renal organ. In the archaeogastropods both the right and left kidneys are well developed and each opens into the posterior mantle cavity by way of a short ureter. A reno-pericardial duct connects the pericardial cavity with the renal organ and opens into the ureter near the base of the kidney. The single gonad discharges its products by way of a gonadal duct into the right kidney, so that the gonadal products pass through the kidney before being discharged into the mantle cavity by way of the renal aperture. From the mantle cavity the sperm and ova are expelled through the exhalant siphon and fertilization is accomplished externally.

Callistoma zizyphinum exhibits marked sexual dimorphism. In the male the left and right renal apertures lie at the same level in the posterior end of the mantle cavity, but in the female the right aperture is considerably farther forward, since a glandular section is added. This section is assumed to be derived from a closed off portion of the mantle (Fretter, 1946a). Eggs passing through this glandular section receive a fluid of gelatinous consistency which binds them into an egg ribbon. Fretter (1946a) states that in Calliostoma the oviduct is made up, proceeding anteriorly, of (a) the ovarian duct, (b) part of the right kidney and its duct, and (c) a glandular duct derived from the mantle, and this triple origin of the genital duct is the general plan on which both male and female of higher gastropods are built. The aberrant freshwater archaeogastropod Theodoxus fluviatilis (L.)

which approaches the condition of the secondary sexual system of the mesogastropods not only in the loss of the right kidney, possesses genital ducts which are as complex as any prosobranch. The opening of the genital duct is along side the anus at the anterior end of the mantle cavity. Bourne (1908), cited in Fretter (1946a), suggested that the loss of the ctenidium in the Neritidae is correlated with the development of these accessory genital organs which occupy all the space on the right side of the mantle cavity. In the Neritacea, which resemble the Mesogastropoda although grouped among the archaeogastropods, have lost the right kidney and produce egg capsules which enclose the young until they emerge as miniature adults.

The glandular section of the ovarian duct in the archaeogastropod *Calliostoma zizyphinum* is probably formed, as Thiele (1935) suggests, by an ectodermal intucking of the mantle and is referred to as the *pallial oviduct* by Fretter (1946a). It lies anterior to the original opening of the right renal organ. Bourne (1908) states that the *pallial oviduct* must be derived from the ectoderm of the mantle. Following the terminology of Fretter (1946a), the short duct which is probably derived from the renal area and which links the *pallial oviduct* with the ovarian duct is termed the *renal oviduct*. In the Mesogastropoda and Neogastropoda the male genital system has homologous segments. The testicular duct is connected to the posterior end of the mantle cavity by a *renal vas deferens*, which is in turn continued by the anteriorly situated *pallial vas deferens*.

The aberrant freshwater archaeogastropod Theodoxus fluviatilis is similar to the mesogastropods in possessing a continuation of the testis duct which is homologous with the renal vas deferens. The vas deferens adjacent to the testis is dilated and coiled and acts as a seminal vesicle, a condition seen in many of the Mesogastropoda and Neogastropoda. The lumen of the prostate is U-shaped in cross-section due to a downgrowth of the dorsal wall and ciliated throughout its length. The genital aperture lies anterior to the anal opening and opens into the penial groove, which is a deep groove lined with cuticular epithelium.

In the female T. fluviatilis the vagina is entirely separate from the oviduct and runs parallel to the rectum and oviduct. The oviduct leads to a bursa copulatrix and seminal receptacle. Except for the complete separation of vagina and oviduct, the female system agrees with the general mesogastropod plan--a proximal ovarian duct, with an epithelium resembling the ovary--which, in turn leads into a wide glandular pallial oviduct, and into the inner end of this opens a seminal receptacle. As in the mesogastropods, the glandular section, which is the same length as the mantle cavity, comprises an albumen gland followed by a bilobed capsule gland.

The most unusual feature in the reproductive system of female Neritidae is the crystal sac which lies at the anterior end of the oviduct with the blind posterior end resting against the capsule gland. Andrews (1935), cited in Fretter (1946a), first described the function of the crystal sac in the Neritidae. From the anus the crystal sac opens into the dorsal wall of the rectum from which it collects fecal scraps. In Theodoxus these consist of diatom scraps, sand grains and sponge spicules. Andrews (1935) states that the crystal sac in Nerita collects spherules which have come from the liver. The contents of the crystal sac are passed into the oviduct where they are used to reinforce the wall of the egg capsule.

Mesogastropoda

The general organization of the Mesogastropoda has already been stated in connection with the Archaeogastropoda. Internal fertilization, and conveyance of sperm and ova require special genital ducts. These two factors plus the provision of better nutritive and protective layers for the embryos are prerequisites for shortening the larval life or for retaining or brooding the embryos. Further evolution in gastropods in these directions therefore demanded specialized or special genital ducts. Shedding ova singly to be fertilized is biologically uneconomical although some of the archaeogastropods, such as Patella, Helcion, and Gibbula, seem to have compensated for this handicap to some extent by not proceeding with spawning until an individual of the opposite sex is present (Morton, 1958).

Specialization in reproduction requires either additional or modified segments of the genital ducts. In the Mesogastropoda a new terminal portion of the intestine which is probably derived from a folding of the mantle wall, brings the anus farther forward in the mantle cavity. Parallel to the rectum and extending to the anus is an additional segment of the oviduct which Fretter (1946a) states is comparable to the terminal part of the intestine and is also derived from the mantle. This segment is termed the pallial oviduct, to distinguish it from the renal oviduct which precedes it. This segment of the oviduct probably evolved as an open groove from the mantle but is not seen in this simple form in any of the living gastropods. From the genital aperture the egg mass, sperm, or capsule may be directed to an ovipositor as in *Littorina littorea* (Linke, 1933) or be given a definite shape and cemented to the substratum by a part of the foot as in the case of *Trivia* (Fretter, 1946a) and the Neogastropoda (Fretter, 1941).

The functional right renal organ is lost in the mesogastropods except for a vestige which forms part of the genital tract linking the gonoduct with the mantle cavity.

The epithelial lining of the gonadal duct sometimes resembles that of the gonad (Linke, 1933), and the musculature of the gonadal duct is feebly developed compared with that of the renal gonadal duct. In the male the lower part functions as a seminal vesicle with the epithelial lining capable of absorbing effete sperm (Linke, 1933). The seminal vesicle of *Lamellaria perspicua* (L.) also serves a similar function. Leading forward immediately beneath the body wall, the vas deferens is delimited from the prostate gland by a sphincter which surrounds the short renal vas deferens. The prostate gland traverses the mantle cavity to open into the base of the penis. A short duct connects the lumen of the prostate with the mantle cavity near its posterior origin. A corresponding structure is described by Fretter (1941) for *Buccinum undatum*. This duct is normally closed by a sphincter. As in *Buccinum* the duct probably permits the escape of excess sperm and prostatic secretions. *Trivia monacha* and *T. arctica*, two more advanced mesogastropods, have a dorsoventral slit in the wall of the prostate gland. Cilia direct sperm through the gland but beat away from the slit. The lateral lips are normally closed and thus prevent leakage of gonadal products from the prostate. Linke (1933) describes the resorptive capacity of the prostate gland in *Littorina littorea*, *L. obtusata*, and *L. rudis*. In *Littorina* the vas deferens and prostate are really open but the walls are folded together to form a functionally closed tube. The seminal vesicle of *Littorina* resorbs sperm during the whole period of sexual activity. Linke (1933) also observed that the epithelial cells lining the seminal vesicle frequently contain sperm in various stages of digestion. The penis of *Lamellaria* and *Trivia* is rather large and is, in both cases, equivalent to the length of the pallial oviduct of the female. Fretter (1946a) implies that the penis deposits sperm directly in the spermatheca through a filamentous flagellum located at the distal tip of the penis.

The female genital ducts of *Lamellaria* and *Trivia* both follow the same general plan. The ovarian duct is lined with an epithelium characteristic of the ovary. The egg capsule is formed in the pallial oviduct, which includes the albumen gland, a capsule gland, and a capsule duct terminating in the genital aperture. The capsule gland has a dorsoventral slit with thickened lateral walls characteristic of the Neogastropoda. The seminal receptacle of *Lamellaria* is in the form of a diverticulated sac lying between the capsule gland and albumen gland. In *Trivia arctica* the seminal receptacle takes the form of long finger-like diverticula from the renal oviduct, but in *T. monarcha* it is a simple sac connected to the thin albumen gland.

Lamellaria lacks a ventral pedal gland whereas all three species of *Trivia* described by Fretter (1946a) have a ventral pedal gland present in the females. She notes that the egg case of *Lamellaria* does not have a prominent rim projecting around the plug. The snail rasps a hole in the test of a compound ascidian. A thickening of the test around the plug of the egg case probably represents an attempt on the part of the ascidian to close the hole.

In small intertidal mesogastropods such as *Omalogyra atomus* and *Rissoella diaphana* simultaneous hermaphoditism occurs. Ripe sperm and ova appear simultaneously. Fretter (1948) describes this phenomenon as fairly common among the prosobranchs and is often found in such unrelated forms as *Valvata*, *Velutina* and *Cerithiopsis*. The Pyramidellidae, which have been placed in the Opisthobranchia by Fretter and Graham (1949), are also simultaneous hermaphrodites. Little is known to what extent self-fertilization is practiced, but it seems likely in *Omalogyra atomus*, and there is no morphological barrier to it in *Rissoella diaphana* and *R. opalina*. In *O. atomus*, the summer stock lacks the copulatory organ. Despite this reproduction takes place rapidly and the answer may be self-fertilization (Fretter, 1948).

Hermaphroditism in the Mesogastropoda appears to be the exception rather than the rule and occurs in unrelated forms throughout this order.

Neogastropoda

Most of the neogastropods are dioecious and are built along the general nesogastropod plan with further functional and morphological specializations. The anal opening is well forward in the mantle cavity. Parallel to it is the pallial oviduct. The Neogastropoda have specialized structures in the foot for manipulating the egg case. The functional right renal gland of the Archaeogastropoda is lost except for a vestige which forms part of the genital tract linking the oviduct or vas deferens with the pericardial cavity. In the male the lower part of the gonadal duct is coiled and sometimes functions as a seminal vesicle with the epithelium absorbing effete sperm (Fretter, 1941). The renal oviduct and vas deferens serve to conduct the sex products to the next organ or outside. This is indicated by a ciliated epithelium surrounded by a muscular coat. A gonopericardial duct may also be present in the female. If present, it arises between the ovarian duct and renal oviduct, resembling the latter histologically. Although never described for the male, the gonopericardial duct may be present as dense strands of connective tissue passing from the origin of the vas deferens to the pericardium (Fretter, 1941).

The Male System

Since the ova leave the female aperture embedded in at least a thick gelatinous covering or in a multi-layered capsule, fertilization must be internal. For the function of insemination a well-developed penis has developed behind the right tentacle. In the Neogastropoda described by Fretter (1941) and in *Urosalpinx cinerea* (Figure 7A) and *Eupleura caudata* the terminal segment of the vas deferens is coiled and embedded within the body of the penis. The coiled condition allows for the increase in length of the vas deferens when the penis is extended for copulation. This suggests an advanced condition from such Mesogastropoda as *Littorina littorea* where the opening of the vas deferens is still at the posterior end of the mantle cavity. In the three species of *Littorina* described by Linke (1933) a sperm conducting groove, which functions as a closed tube, directs sperm forward across the floor of the mantle cavity and up the right side of the head of the snail to its penis. The vas deferens lies in a lateral position in *U. cinerea* and *E. caudata* whereas in *Buccinum undatum* and *Nassarius reticulatus* it is in a central position. In *Nucella lapillus* and *Ocenebra erinacea* the vas deferens is located laterally in the penis.

The prostate glands of *U. cinerea* and *E. caudata* differ only slightly from each other. The vent opening into the mantle cavity of *U. cinerea* appears to be slightly larger than in *E. caudata*.

The lumen of the prostate gland of Nassarius reticulatus and Buccinum undatum is connected with the mantle cavity by a short duct which is closed by a sphincter. The opening of O. erinacea is comparable in size to U. cinerea while Nucella lapillus has a very small vent opening into the mantle cavity. A double row of nuclei traversing the full length of the prostate probably represents the line of closure. This condition is seen in U. cinerea, E. caudata, N. lapillus, and O. erinacea, while no suture has been observed by Fretter (1941) in B. undatum and Nassarius reticulatus. The lack of a suture in the prostate and the presence of a duct instead of a slit opening into the mantle cavity suggests a more advanced condition in B. undatum and N. reticulatus than in the other gastropods described. The more primitive condition is demonstrated by Littorina littorea in which Linke (1933) described an open prostate which functions as a closed tube.

In E. caudata the anterior end of the prostate is different from the posterior end. Lightly staining spherules which are possibly breakdown products of sperm suggest that the anterior segment of the prostate resorbs sperm. The prostate gland of U. cinerea is not divisible into distinct areas as in the case of E. caudata. In the prosobranchs described by Fretter (1941) sperm are not resorbed by the prostate gland and the prostate is not divisible into separate histological areas.

Fretter (1941) suggests that sperm resorption occurs in the coiled segment of the vas deferens near the testis, and that this segment also functions as a seminal vesicle. The vas deferens in

U. cinerea and E. caudata is relatively straight and apparently does not function as a seminal vesicle nor does it appear to have resorptive capacities, but functions only as a tube for conduction of spermatozoa. High concentrations of sperm in the base of the testis suggests that sperm may be stored there. The prostate gland of E. caudata probably functions in part as a seminal vesicle, and the prostate gland of U. cinerea may have an homologous function although sperm have never been observed there in this study.

It has been suggested that the vas deferens of the prosobranchs described by Fretter (1941) resorb only senile sperm or that resorption is a mechanism by which blockage of the vas deferens is prevented. Both types of sperm are ingested which indicates no selectivity in this segment of the vas deferens.

In both U. cinerea and E. caudata there is no trace of a gonopericardial duct. Fretter (1941) did not find any trace of such a duct in B. undatum or in Nucella lapillus. Only traces of the gonopericardial duct were found in males of Nassarius reticulatus and O. erinacea. These two instances may represent homologs of the female.

The testes of U. cinerea, E. caudata and the prosobranchs described by Fretter (1941) are quite similar so that further discussion of these organs is not warranted.

The Female System

The most striking difference between the females of Urosalpinx cinerea (Figure 9A) and Eupleura caudata (Figure 9B) is that the latter lacks a bursa copulatrix while the former has a large well-developed bursa copulatrix. *O. erinacea*, *Nucella lapillus* (Figure 8B) *Nassarius reticulatus*, and *B. undatum* each have a well-developed bursa copulatrix. The lack of this organ in *E. caudata* suggests that another part of the reproductive system has assumed the function of the bursa. The exact function of the organ being called the bursa copulatrix still is somewhat obscure. Hargis (personal communication) has found sperm in the bursa throughout the year in drills taken from York River, Virginia. In *U. cinerea* it may be a seminal receptacle or spermatheca rather than an actual bursa copulatrix. Roth (1960) states that in *Oncomelania formosana*, sperm enter the bursa copulatrix by way of the vagina and then are transferred to the seminal receptacle. In the case of *O. formosana* migration of sperm to the seminal receptacle continues well beyond twenty-four hours, where the sperm are stored on a long term basis. Sperm apparently remain viable in the seminal receptacle from one season to the next. Roth considers that the bursa copulatrix functions as little more than a temporary storage place for sperm. He suggests this organ may have a nutritive function for the sperm, or sperm motility may be stimulated by a secretion from the bursa. The fact that sperm are regularly concentrated and oriented in the seminal receptacle of *O. formosana* is an indication of their motility in that organ. In *Buccinum undatum* the bursa copulatrix is lined with unciliated columnar epithelium which contains a yellow pigment. Amoebocytes are plentiful in this region and also appear between the epithelial cells and in the lumen. They appear to act as scavengers and carry away prostatic secretions after copulation

(Fretter, 1941). The stratified squamous epithelium lining the bursa copulatrix of *Urosalpinx cinerea* probably allows great flexibility and distention of the walls of this structure. There are no mucus cells as in the case of *Nassarius reticulatus*.

The opening of the bursa in *Nucella lapillus* is directed anteriorly into the short vagina, so it is possible for the male to deposit sperm directly therein. The bursa copulatrix of *U. cinerea* is connected with the anterior segment of the oviduct by a rather long curved duct which is directed posteriorly toward the capsule gland. With such an arrangement it seems that it might be very difficult for the male to deposit sperm directly in the bursa copulatrix. In order to accomplish such a feat the penis of the male would not only have to penetrate the long terminal segment of the oviduct, but bend in an obtuse angle into the duct of the bursa copulatrix. Rather the transfer of sperm from the male to the bursa of the female is probably accomplished by ciliary and muscular actions and the sperm flow directed by a system of sphincters. The large sphincter at the anterior end of the capsule gland probably prevents the passage of unfinished egg cases forward and the passage spermatozoa posteriorly during copulation. With this sphincter restricting the flow of sperm into the capsule gland and the sphincter in the duct of bursa copulatrix relaxed, sperm would be shunted into the bursa copulatrix during or shortly after copulation. While a true sphincter has not been observed in the terminal segment of the oviduct, this whole segment may act as a sphincter since it is well supplied with longitudinal muscles and probably some circular muscle fibers throughout its length, although these circular muscle fibers have not been observed in our preparations. To transfer sperm from the bursa copulatrix to the sperm ingesting gland this anterior valvular system would operate in reverse. The sphincters at the anterior end of the capsule gland and in the duct of the bursa copulatrix would relax while the terminal segment of the oviduct would remain closed. In such a situation sperm would be transferred by the bursa to the ventral channel of the capsule gland probably by a combination of peristalsis and ciliary action and carried through the capsule gland by the ciliated epithelium of the ventral channel.

Since _E_. _caudata_ lacks a bursa copulatrix sperm are probably transferred directly to the sperm ingesting gland by way of the ventral channel of the capsule gland. The absence of a bursa copulatrix may be correlated with the length of copulation. Hargis and MacKenzie (in press) found that _E_. _caudata_ of York River, Virginia copulate over a relatively long period of time. The minimum duration of continuous copulation of these drills in an aquarium ranged from fifty-five minutes to four hours and thirty-nine minutes. Apparently it is quite common for copulating pairs to cease activity, remain in position, and then resume copulation, so a single pairing may last eleven hours or more. In contrast to _E_. _caudata_, _U_. _cinerea_ copulates only a short period of time. These same authors observed that copulation of _U_. _cinerea_ lasted four to eleven minutes, seldom more than four or five minutes. They also found that the male usually moves away from the female after copulation whereas in _E_. _caudata_ the male may remain attached to the shell of the female. Fretter (1941) does not mention copulatory activity in her description of Nucella lapillus and Ocenebra erinacea, both muricids which have a bursa copulatrix. Presumably copulation in these species is similar to U. cinerea. Buccinum undatum and Nassarius reticulatus may also react similarly.

In cross section the capsule glands of U. cinerea (Figure 4B) and E. caudata (Figure 4A) resembles most closely the capsule glands of Nucella lapillus and Ocenebra erinacea. Fretter (1941) describes the function of these organs and U. cinerea and E. caudata probably function similarly, although this has not been studied. As in Littorina littorea (Linke, 1933) and the four species of Muricaceae described by Fretter (1941), the ventral channels of the capsule glands of U. cinerea and E. caudata probably function as closed tubes to convey sperm to the posterior genital tract.

The sperm ingesting gland of E. caudata is several times larger than its counterpart in U. cinerea. This may be correlated with the absence of a bursa copulatrix and the increased frequency and duration of copulation in E. caudata. In the neogastropods described by Fretter (1941) the duct leading to the sperm ingesting gland may serve as a seminal vesicle for the storage of viable sperm, while the sperm ingesting gland probably has the function of ingesting sperm. The sperm ingesting glands of Ocenebra erinacea and Buccinum undatum seen not only to ingest sperm but also to resorb vitelline bodies. This may also be true for U. cinerea since vitelline bodies have been observed in this organ. However, it is possible that these are artifacts of fixation since vitelline bodies have not been seen within the cytoplasm of the ingesting cells. Sperm oriented in the duct leading from the sperm ingesting gland to the capsule gland were not observed in our preparations of either species of drill. Therefore, it is doubtful that the lumen of these ducts actually function as a seminal vesicle. Sperm are probably stored on a long term basis in the sperm ingesting gland itself and only effete sperm actually ingested. Motile sperm have been found in the sperm ingesting gland of both *U. cinerea* and *E. caudata* throughout the year (Hargis, personal communication). The sperm ingesting gland of *E. caudata* therefore appears to be analogous with the seminal receptacle of *Littorina littorea*.

The albumen gland of *E. caudata* is reduced in size with a corresponding increase in size of the sperm ingesting gland. The converse is true of *U. cinerea*. The lateral walls of the albumen gland are compressed in *Nassarius reticulatus* with its dorsal wall deeply convex and the ventral wall concave. In gross appearance the albumen gland of *E. caudata* is similar to *N. reticulatus*. *Buccinum undatum* possesses an albumen gland which is comparable in size to *N. reticulatus* and is smaller than either *Nucella lapillus* or *Ocenebra erinacea*. Sphincters both anterior and posterior to the albumen gland evidently control the flow of ova and albuminous secretions to the more anterior parts of the reproductive system.

In contrast to the other four species of neogastropods described by Fretter (1941) neither *U. cinerea* nor *E. caudata* have a gonopericardial duct. The gonopericardial duct of *O. erinacea* is large enough to permit a mature ovum to enter. Even though Fretter considers *B. undatum* and *Nassarius reticulatus* to be more advanced than either *O. erinacea* or *N. lapillus*, a gonopericardial duct persists in the female of all four species. In the males of *Nucella lapillus* and *B. undatum* the gonopericardial duct is completely lost while only a vestige of this duct is present in *Nassarius reticulatus* and *O. erinacea*. The persistence of the gonopericardial duct in the female indicates that such a duct does not interfere with the functioning of the genital system. However, the presence of an open duct in the male would probably allow sperm to escape into the pericardial cavity. Fretter (1946a) suggests the gonopericardial duct may be functional in protanderous hermaphrodites such as *Calyptraea chinensis* and *Crepidula unguiformis*. In these two species the gonopericardial duct appears only in the female stage and degenerates during the male phase.

Another minor difference between *U. cinerea* and *E. caudata* worthy of mention is the manner in which the ducts of the albumen and sperm ingesting glands enter the posterior end of the capsule gland. In *U. cinerea* the oviduct from the anterior side of the albumen gland is joined by the duct from the sperm ingesting gland shortly before entering the capsule gland near the ventral channel. The duct of the albumen gland of *E. caudata* enters the capsule gland in a similar manner, but the duct of the sperm ingesting gland opens by a separate orifice slightly to the right and on the ventral side of the capsule gland. In *Nucella lapillus* and *O. erinacea* the ducts of the albumen and sperm ingesting glands are arranged similarly to *U. cinerea*. The arrangement of these two ducts in *E. caudata* suggests that the evolutionary trend is toward developing separate ducts each with its own aperture as is the case of the hermaphroditic opisthobranch *Acteon tornatilis* (Guiart, 1901) (Figure 8).

So far as the remaining groups of Neogastropoda are concerned few comparisons can be made. It remains that the Neogastropoda are a very specialized order within the Prosobranchia. The high degree of specialization is not only demonstrated in the highly modified reproductive system, but in the embryonic mode of life as well as the elongation of the probosis and complexity of the esophagus.

Function of the Female Ducts and Ventral Pedal Gland

Fretter (1941) describes the function of the female genital system, and the genital system of *Urosalpinx cinerea* probably approaches *Nucella lapillus* closely in function. *Eupleura caudata* may differ only in a few points.

In *U. cinerea*, sperm pass into the bursa copulatrix after copulation. They may remain there in viable condition for six to nine months and, in fact, in *U. cinerea* the bursa copulatrix is the primary storage place for sperm, (Hargis, personal communication). Sperm may remain here before passing up the ventral channel of the capsule gland. However, in *E. caudata* sperm are apparently transferred directly to the sperm ingesting gland. There is no bursa copulatrix.

The duct of the sperm ingesting gland apparently functions as a seminal receptacle, but this is probably not true in either *U. cinerea* or *E. caudata* since sperm have been observed in the lumen of the sperm ingesting gland but not in its duct.

It is not known how soon after copulation egg capsule formation begins. In *N. lapillus* and *O. erinacea* Fretter (1941) suggests the two events closely follow each other. Copulation may, in the case of *E. caudata* and the species described by Fretter, stimulate egg capsule formation since copulation is frequent and relatively long in duration. However, it is known that copulation in the fall may not be followed by egg case deposition until the following spring, by much as 4-6 months (MacKenzie, 1958).

The exact site of fertilization is not known for either *U. cinerea* or *E. caudata*. It is possible that sperm from the sperm ingesting gland and ventral channel pass into the albumen gland upon relaxation of the sphincter anterior to the albumen gland; thus, the albumen gland may be the site of fertilization. Otherwise fertilization may occur as the ova enter the capsule gland. This situation could be comparable to the one described for *Nucella lapillus* and *Ocenebra erinacea* (Fretter, 1941). Since the ducts of the albumen and sperm ingesting glands are not joined before entering the capsule gland in *E. caudata*, but enter as completely separate ducts, fertilization probably occurs as the ova enter the capsule gland.

Apparently the egg capsule occupies the full length of the capsule gland with the aperture lying at the upper end near the posterior mucus tips of the capsule gland. These mucus tips apparently secrete the operculum which seals the egg capsule after the embryos and albumen have been injected. When the duct of the albumen and capsule glands opens, eggs and albumen are forcibly passed into the central portion of the secretions from the capsule gland. The ciliated lumen of the capsule gland undoubtedly plays an important part in the formation of the egg case. The ciliary currents of the walls of the capsule gland in _U_. _cinerea_ and _E_. _caudata_ were not determined in this study but are probably similar to those of _Nucella lapillus_ and _Ocenebra erinacea_ described by Fretter (1941). Hancock (1956) has shown that the mucus plug of the egg case is dissolved by the protoconchs when they are ready to hatch.

A deep temporary groove is formed in the right side of the head and foot. The thin-walled flexible egg capsule passes from the capsule gland through the oviduct. This movement is probably a combination of ciliary action and peristalsis of the muscular oviduct walls assisted by mucus secretions. When the egg capsules leave the vagina, their walls are slightly wrinkled, pliable, and may be transparent as in _E_. _caudata_. The egg capsule of _U_. _cinerea_ is also slightly wrinkled and pliable but translucent in appearance. The embryos of the _U_. _cinerea_ egg capsule which was taken from the pedal gland, fixed, and sectioned for this study were in the first division. Very small chromosomes were seen at either spindle with spindle fibers still connecting both asters. The egg capsule is then passed into the ventral pedal gland where it is given a definitive shape, cemented to the substratum and its walls hardened.

Prior to the passage of the egg capsule to the ventral pedal gland the substratum is cleaned with the probosis. *U. cinerea* may clean a relatively large area prior to the deposition of each egg capsule. In contrast, *E. caudata* does not clean the substratum, but merely cements the egg capsule to it. In the pedal gland the walls of the egg capsule are hardened. When this process is completed the female backs away and the whole process of capsule formation and deposition is repeated.

Some controversy still exists as to the function of the pedal sucker of *U. cinerea*. In Fretter's (1946b) opinion, this organ which is immediately anterior to the pedal gland, increases the stability of the foot during the boring activity. Carriker (1943) suggests that the pedal sucker, which he calls the accessory probosis, has the function of softening the shell of the prey. He observed that the drills alternately rasped with the radula and moved the foot over the drilled hole in the general vicinity of the pedal sucker. Since his original description, Carriker (personal communication) has observed the pedal sucker of *U. cinerea* extended into the drilled hole of its prey. Although no information is available on the function of the pedal sucker of *E. caudata*, it is assumed that this organ has a similar function since *E. caudata* is a carnivorous gastropod with feeding habits similar to *U. cinerea*.

CONCLUSIONS

Fretter (1941) concludes that *Nucella lapillus* and *Ocenebra erinacea* belong to a more primative group than *Buccinum undatum* and *Nassarius reticulatus*. Although her conclusions are based primarily on a study of the reproductive system in these gastropods, the same conclusions have been drawn from studies of other systems. This is indicated clearly by the persistence of an open prostate gland in *N. lapillus* and *O. erinacea*, and the presence of a gonopericardial duct in the male.

It appears that both *U. cinerea* and *E. caudata* are more advanced than either *N. lapillus* and *O. erinacea*, even though all four species belong to the same family. The lack of even a vestige of the gonopericardial duct is particularly clear in both male and female of *U. cinerea* and *E. caudata*. Based solely on the study of the genital system, it appears that *U. cinerea* belongs to a more primitive group than *B. undatum* or *N. reticulatus*. This conclusion agrees with Fretter's (1941) statement on the relative position of the four species she studied.

Eupleura caudata represents a more advanced member of the Muricidae than *U. cinerea* and may be more advanced than either *B. undatum* or *N. reticulatus*. A number of factors warrant making this statement. First, the separate ducts from the albumen and sperm ingesting glands to the capsule gland suggest a more advanced condition. The opening of the prostate gland of the male is smaller in *E. caudata* than in *U. cinerea*. This indicates an evolutionary trend toward complete closure. The albumen gland is reduced in size as in the case of B. undatum and N. reticulatus, while the sperm ingesting gland is greatly increased in size in E. caudata. The reverse is true of U. cinerea, N. lapillus, and O. erinacea. The sperm ingesting gland in E. caudata probably functions as a seminal receptacle and is apparently of greater importance than the corresponding structure in U. cinerea where a bursa copulatrix is present. The bursa copulatrix apparently functions as a spermatheca or seminal vesicle since sperm are found in this structure throughout the year. Though more primitive gastropods lack a bursa copulatrix, in E. caudata this condition may be due to a higher degree of specialization of other parts of the reproductive system or degeneration and eventual loss of the bursa copulatrix.

There is no indication that the duct of the sperm ingesting gland of U. cinerea and E. caudata functions as a seminal receptacle as in N. lapillus and O. erinacea. Since vitelline bodies have been observed in the sperm ingesting gland of U. cinerea, yolk resorption probably also occurs here.

In other respects the two species described in this study have apparently attained a high degree of similarity, such as the pedal gland and loss of a free-swimming veliger as found in Littorina neritoides, L. littorea (Lebour, 1935), and N. reticulatus (Fretter, 1941) in the embryonic stage.

It appears that both of these species have sacrificed wider distribution by natural means conferred by a free-swimming larva for the greater certainty of the embryos developing to the protoconch stage and reaching a suitable habitat by the provision of food material in the egg capsule.

It is impossible to make further comparisons concerning other groups of Neogastropoda due to the lack of information.

SUMMARY

The morphology and histology of the genital ducts of Urosalpinx cinerea (Say) and Eupleura caudata (Say) has been described. The account includes observations on the function of the genital ducts and pedal glands.

Both U. cinerea and E. caudata conform to the same basic plan and the genital ducts may be divided, in both male and female, into a narrow thin-walled posterior segment which leads into a thick-walled glandular region anteriorly. A gonopericardial duct described by Fretter (1941) for Nucella lapillus, Ocenebra erinacea, Buccinum undatum, and Nassarius reticulatus is absent in both sexes of U. cinerea and E. caudata.

In males the thin-walled vas deferens is a straight tube connecting the prostate gland with the gonad. A slit is present in the wall of the prostate gland and probably allows excess sperm to escape into the mantle cavity. This slit is reduced in size in E. caudata compared with U. cinerea. From the prostate gland the vas deferens leads to the penis wherein it is highly coiled. The anterior end of the prostate of E. caudata apparently ingests sperm while U. cinerea does not.

In the female the thin-walled transparent oviduct conveys ova and vitelline bodies from the ovary to the glandular section anteriorly. This glandular region may be sub-divided into (a) the albumen gland (b) sperm ingesting gland, (c) capsule gland, (d) bursa copulatrix, present only in U. cinerea, and, (e) the vagina (Figures 9A and 9B). The albumen gland produces secretions which surrounds ova, and fertilization probably occurs in this region. The capsule gland secretes the egg capsule around the mass of eggs and albumen, with the mucoid operculum of the egg capsule being produced by specialized regions within the posterior end of the capsule gland.

The sperm ingesting gland probably functions as a seminal receptacle in *E. caudata* with the additional capacity of sperm ingestion. The albumen gland of *E. caudata* is greatly reduced in size compared with the sperm ingesting gland. The converse is true of *U. cinerea* which approaches most closely the description of *Nucella lapillus*. Since *E. caudata* lacks a bursa copulatrix, the sperm ingesting gland evidently stores sperm on a long term basis.

In *U. cinerea* the bursa copulatrix stores sperm after copulation and may stimulate motility or furnish nutrients to the sperm. A valvular system of sphincters in both species described in this study controls the flow of ova anteriorly and sperm posteriorly.

The soft pliable egg capsule is passed from the capsule gland down the temporary transverse groove to the pedal gland where the walls of the egg capsule are hardened to a definitive shape and cemented to the substratum. The transverse groove may be analogous with the ovipositor of mesogastropods. In both sexes of *U. cinerea* and *E. caudata* a second glandular structure, the pedal sucker or accessory probosis is present. Although the function of this structure is still obscure, it apparently is associated with the carnivorous feeding habit of both these gastropods.

The relationships of U. cinerea and E. caudata as well as relationships to other Neogastropoda and lower Prosobranchia are discussed.

LITERATURE CITED

ABBOTT, R. T. 1954. American seashells. D. Van Nostrand Co., Inc. N. Y. 541 pp.

ANDREWS, E. A. 1935. The egg capsules of certain Neritidae. Jour. Morph. 55: 31-59.

BAKER, B. B. 1951. Interesting shells from the Delmarva Peninsula. Nautilus 64(3): 73-77.

BOURNE, C. G. 1908. Contributions to the morphology of the group Neritacea of Aspidobranch gastropods. Part I. The Neritidae Proc. Zool. Soc. London. 810-887.

CARRIKER, MELBOURNE R. 1943. On the structure and function of the probosis in the common oyster drill, Urosalpinx cinerea (Say). J. Morph. 73: 441-506.

CARRIKER, MELBOURNE R. 1955. Critical review of biology and control of oyster drills. U. S. Fish and Wildlife Serv., Spec. Rept. Fisheries, 148: i-vi, 1-150.

CARRIKER, MELBOURNE R. AND JOHN W. BLAKE. 1959. A method of full relaxation of muricids. Nautilus. 73: 16-21.

CARSLEY, ROBERT A. 1938. An investigation of technical methods for a microscopical study of the Virginia oyster, Ostrea virginica Lister. Unpubl. M.S. thesis. University of Richmond. 52 pages.

COLE, H. A. 1941. Sex-ratio in Urosalpinx cinerea. Nature. 147: 116-118.

DAKIN, W. J. 1912. *Buccinum* (The Welk). L.M.B.C. Memoirs. No. 20. London, Williams and Norgate.

FEDERIGHI, HENRY. 1931. Studies on the oyster drill (*Urosalpinx cinerea* Say) Bull. U. S. Bur. Fish. 47: 83-115.

FRETTER, VERA. 1941. The genital ducts of some British stenoglossan prosobranchs. Jour. Mar. Biol. Assoc. U. K. 25: 173-211.

FRETTER, VERA. 1946a. The genital ducts of *Theodoxus*, *Lamellaria* and *Trivia*, and a discussion on their evolution in the prosobranchs. Jour. Mar. Biol. Assoc. U. K. 26: 312-351.

FRETTER, VERA. 1946b. The pedal sucker and anal gland of some British Stenoglossa. Proc. Mal. Soc. London. 27(3): 126-130.

FRETTER, VERA. 1948. The structure and life history of some minute prosobranchs of rock pools: *Skeneopsis planorbis* (Fabricius), *Omalogyra atomus* (Philippi) *Rissoella diaphana* (Alder), and *Rissoella opalina* (Jeffreys). Jour. Mar. Biol. Assoc. U. K. 27: 597-632.

FRETTER, VERA AND A. GRAHAM. 1949. The structure and mode of life of the Pyramidellidae, parasitic opisthobranchs. Jour. Mar. Biol. Assoc. U. K. 28: 493-532.

GEORGE, W. C. AND JOHN H. FERGUSON. 1950. The blood of gastropod molluscs. J. Morph. 86(2): 315-328.

GUIART, J. 1901. Contribution a l'etude des Gasteropodes Opisthobranchs et en particulier des C'ephalaspides. Mem. Soc. Zool. Franc. 14: 5-219.

HANCOCK, D. A. 1956. The structure of the capsule and the hatching process in *Urosalpinx cinerea* (Say). Proc. Zool. Soc. London. 127(4): 565-571.

HARGIS, WILLIAM J. JR. 1957. A rapid live-sexing technique for *Urosalpinx cinerea* and *Eupleura caudata*, with notes on previous methods. Limnol. and Oceanogr. 2(1): 41-42.

HARGIS, W. J. JR. AND CLYDE L. MACKENZIE JR. (In press) Sexual behavior of the oyster drills *Eupleura caudata* (Say) *Urosalpinx cinerea* (Say).

LEBOUR, M. V. 1935. The breeding of *Littorina neritoides*. Jour. Mar. Biol. Assoc. U. K. 20: 373-378.

LINKE, O. 1933. Morphologie und Physiologie des Genitalapprates der Nordseelittorinen. Wiss. Meeres. Komm. Unt. Deutsch. Meere, N. F., Abt. Helgoland, Bd. XIX, 5, 60 pages.

MACKENZIE, CLYDE L. JR. 1958. Growth and Reproduction of *Eupleura caudata* in the York River, Virginia. Unpubl. M.A. thesis. College of William and Mary. 84 pages.

MORTON, J. E. 1958. Sex and reproduction *In* Molluscs. pp. 121-143. Hutchinson University Library, London.

ROTH, ARIEL A. 1960. Aspects of the function of the bursa copulatrix and seminal receptacle in the prosobranch snail *Oncomelania formosana* Pilsbry and Hirase. Trans. Amer. Micr. Soc. 79: 412-419.

SAY, T. 1822. An account of some marine shells of the U. S. Jour. Acad. Nat. Sci. Phila. 2: 221-248.

STIMPSON, W. 1865. On certain genera and families of zoophagous gastropods. Amer. Jour. Conchol. 1865: 55-64.

THIELE, J. 1935. Handleuch der Systematischen Weichtierkunde. 4. Teil. Jena, Fischer.

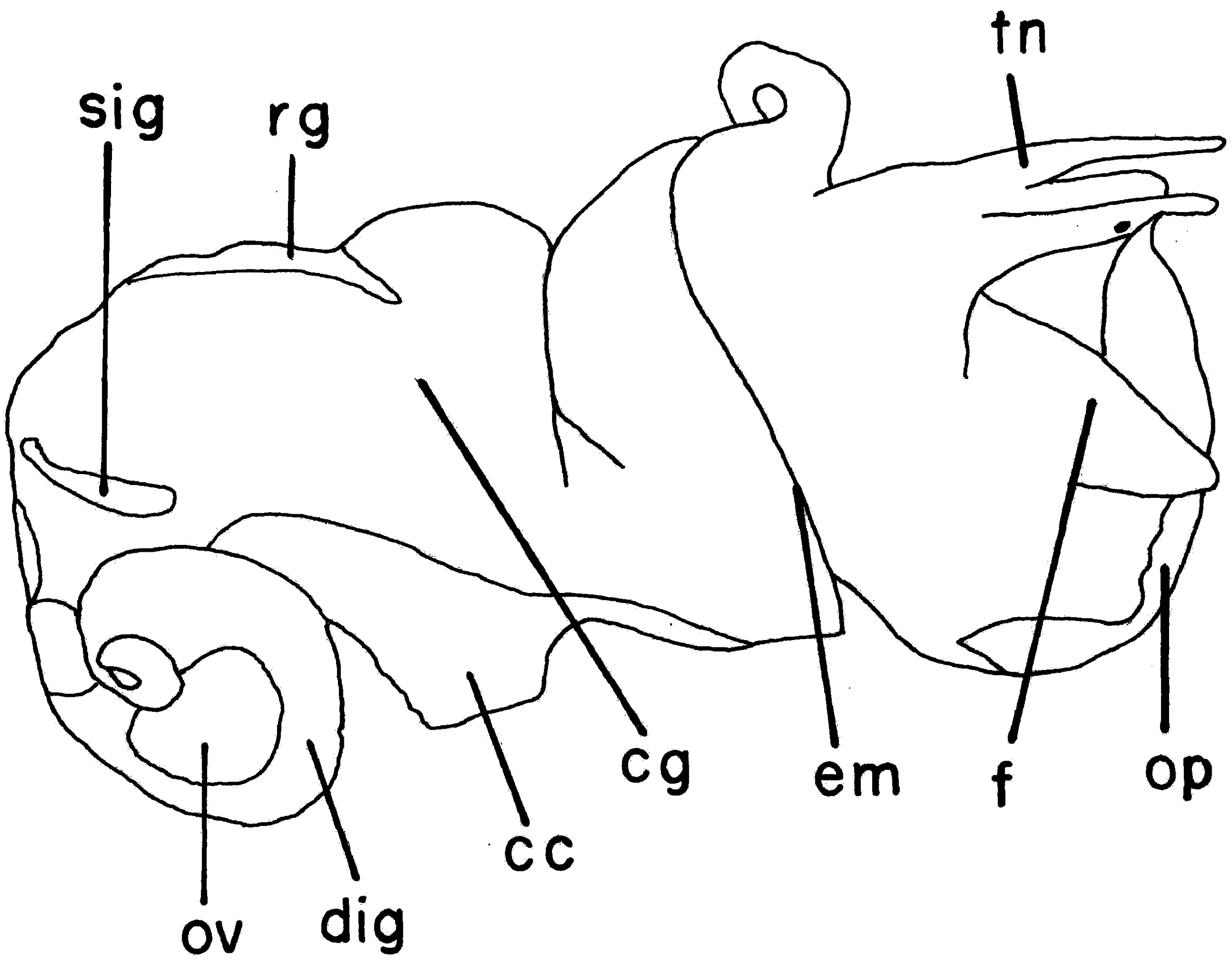

Figure 1. Female <u>Urosalpinx cinerea</u>. cc, columellar muscle; cg, capsule gland; dig, digestive gland; em, edge of mantle; f, foot; op, operculum; ov, ovary; rg, rectal gland; sig, sperm ingesting gland; tn, tentacle.

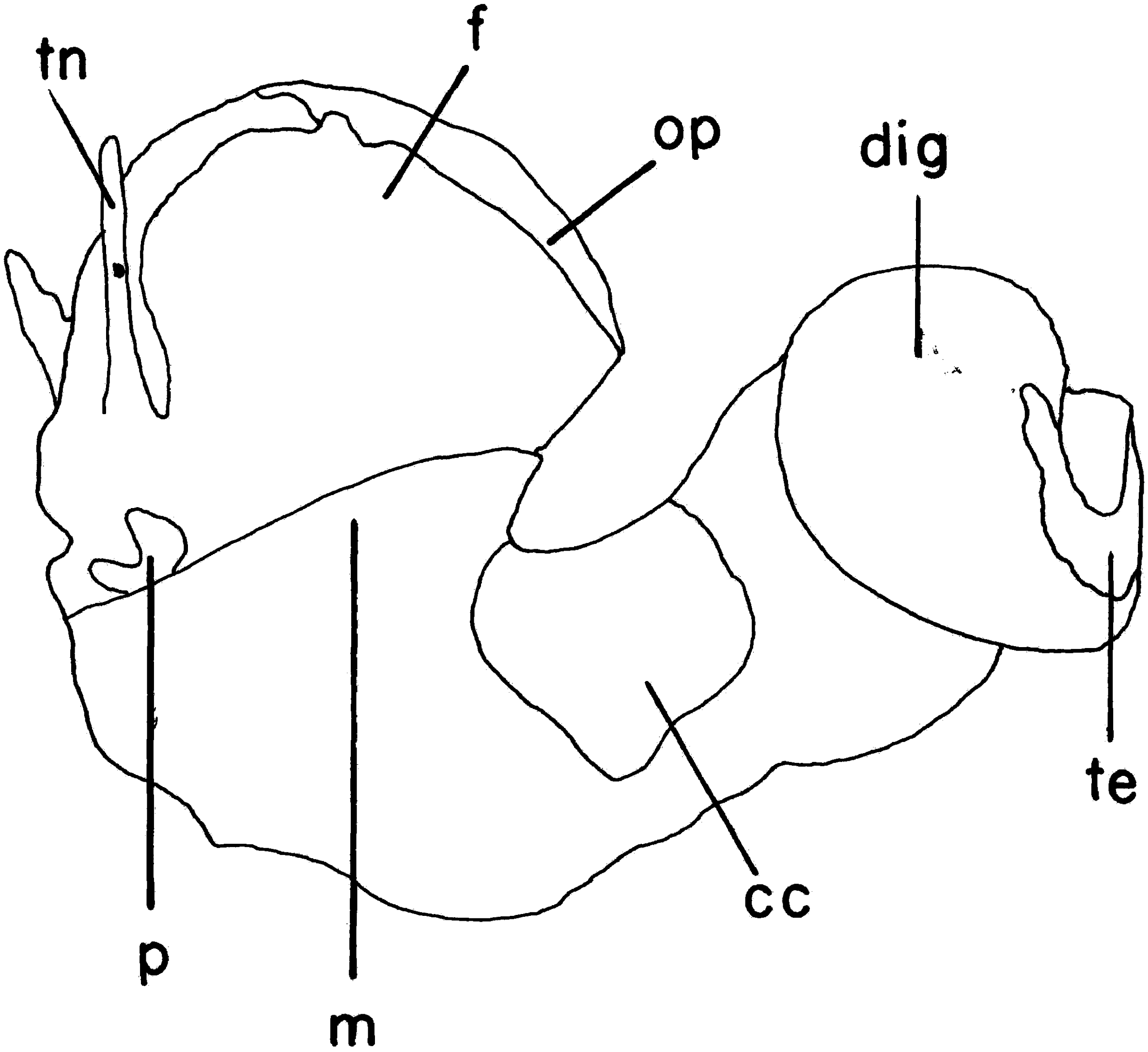

Figure 2. Male *Urosalpinx cinerea*. cc, columellar muscle; dig, digestive gland; f, foot; m, mantle; p, penis; te, testis; tn, tentacle.

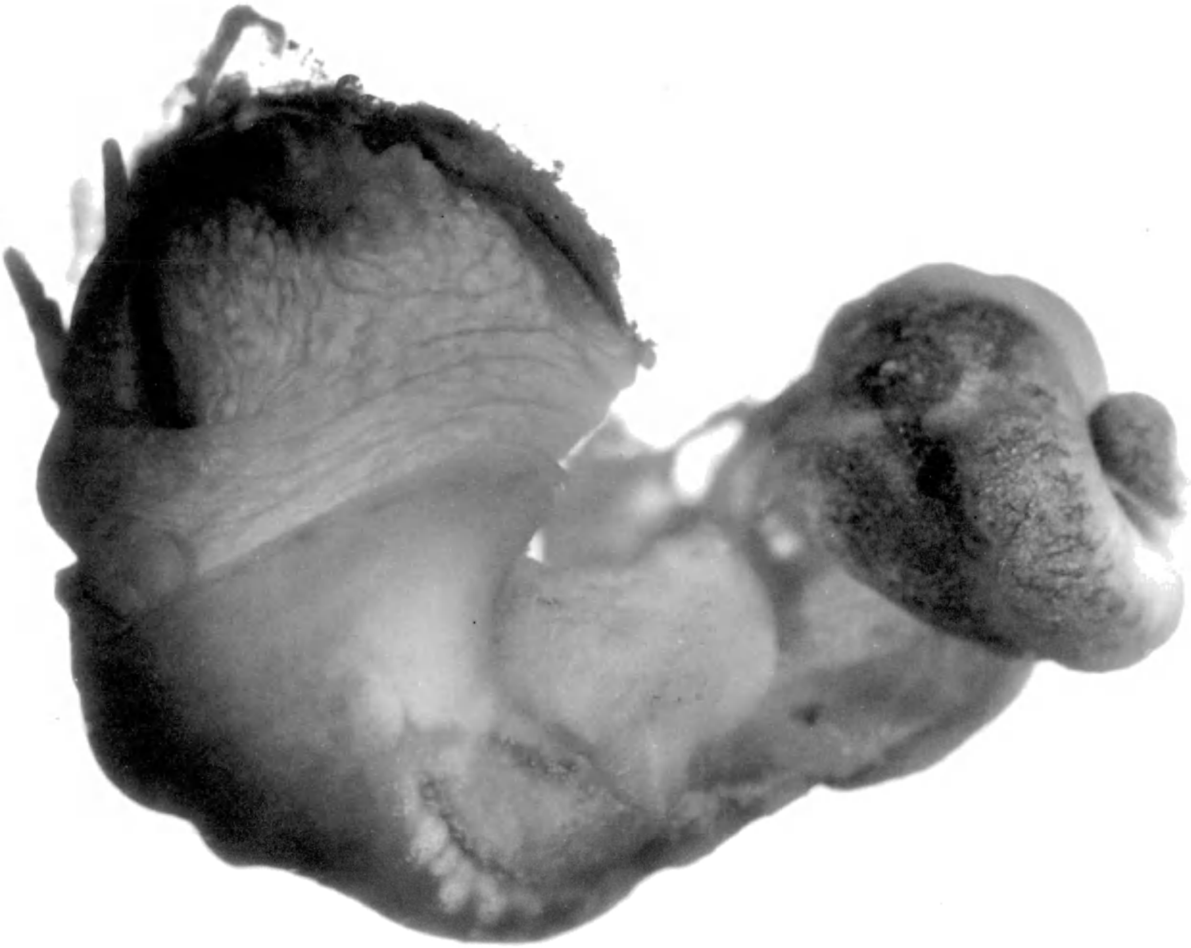

Figure 3. Saggital section through foot of <u>Urosalpinx cinerea</u>. From left to right; pedal gland; pedal sucker or accessory probosis; pedal mucus gland.

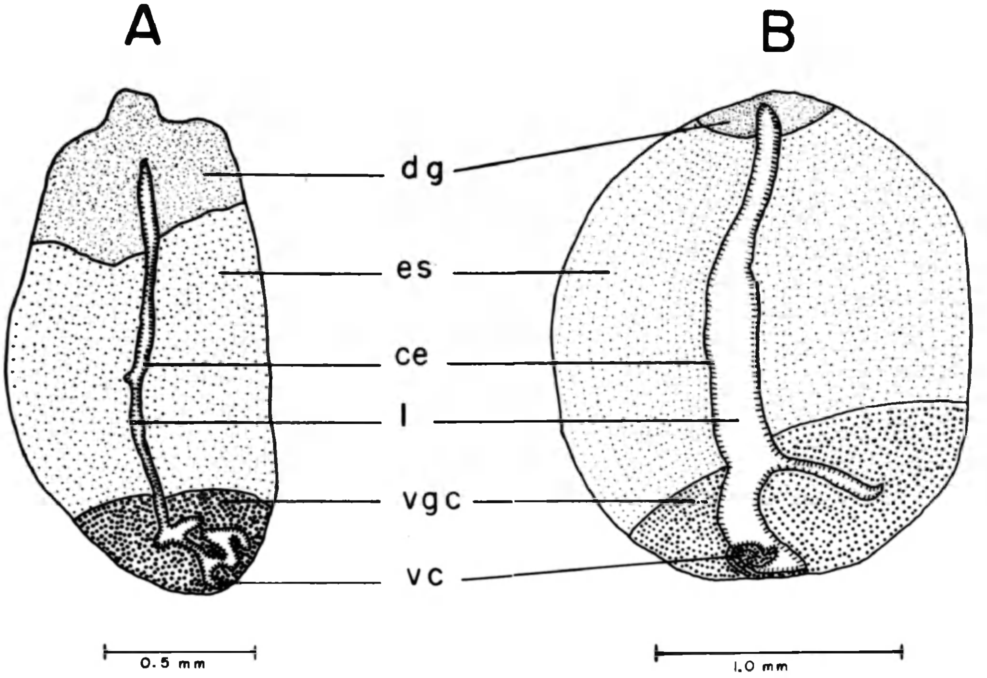

Figure 4. Diagramatic transverse sections through the mid-region of the capsule gland: A, Eupleura caudata; B, Urosalpinx cinerea. ce, ciliated epithelium; dg, gland cells of dorsal wall of capsule gland; es, medial eosinophilic segment; l, lumen; vc, ventral channel; vgc, gland cells of ventral wall of capsule gland.

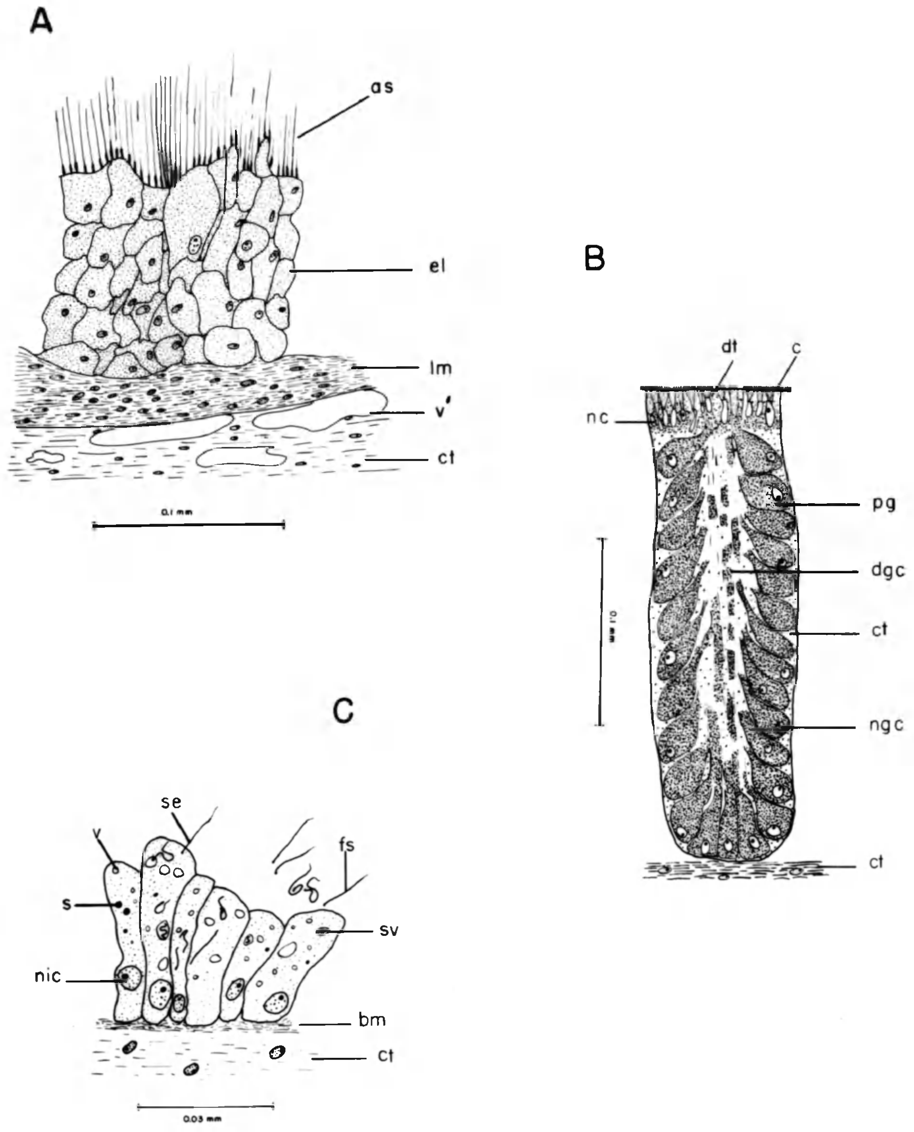

Figure 5. Camera lucida drawings of: A, wall of bursa copulatrix of *Urosalpinx cinerea*; B, cluster of secretory cells from capsule gland of *Eupleura caudata*; C, wall of sperm ingesting gland of *Eupleura caudata.* as, attached sperm; bm, basement membrane; c, ciliated epithelium; ct, connective tissue; dgc, duct of gland cells; dt, duct of gland cell opening into lumen capsule gland; el, epithelial lining of bursa copulatrix; fs, free sperm; lm, longitudinal muscle; nc, nucleus of ciliated epithelium; ngc, nucleus of secretory cell; nic, nucleus of ingesting cell; pg, protein granules in cytoplasm of secretory cell; s, spherule in cytoplasm of ingesting cell; se, entrapped sperm; sv, sperm in vacuole of ingesting cell; v, vacuole in cytoplasm of ingesting cell; v', blood sinus in connective tissue.

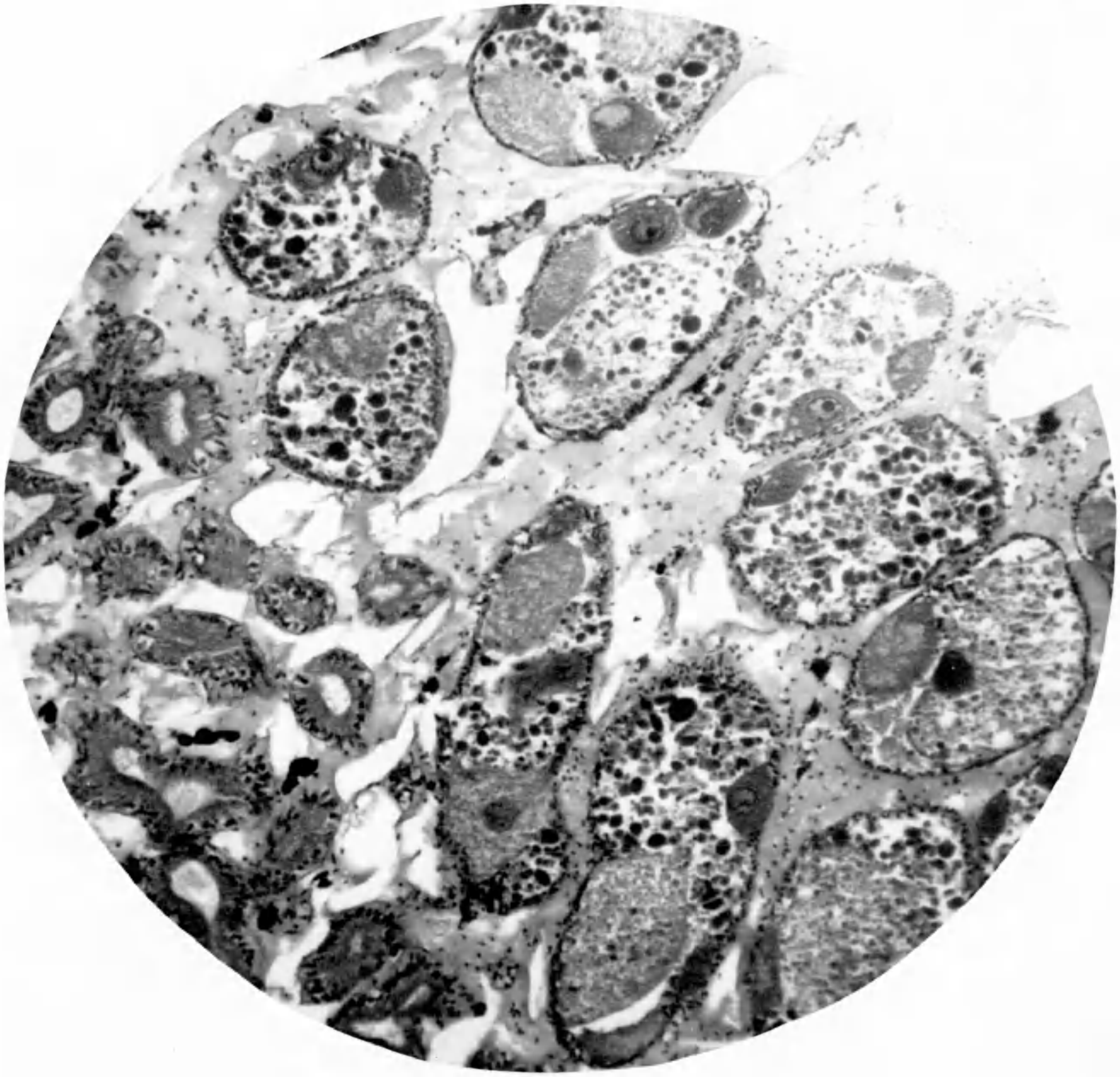

Figure 6. Saggital section through ovary of <u>Urosalpinx cinerea</u> showing ovarian tubules, ova, and vitelline bodies upper right; digestive gland tubules lower left.

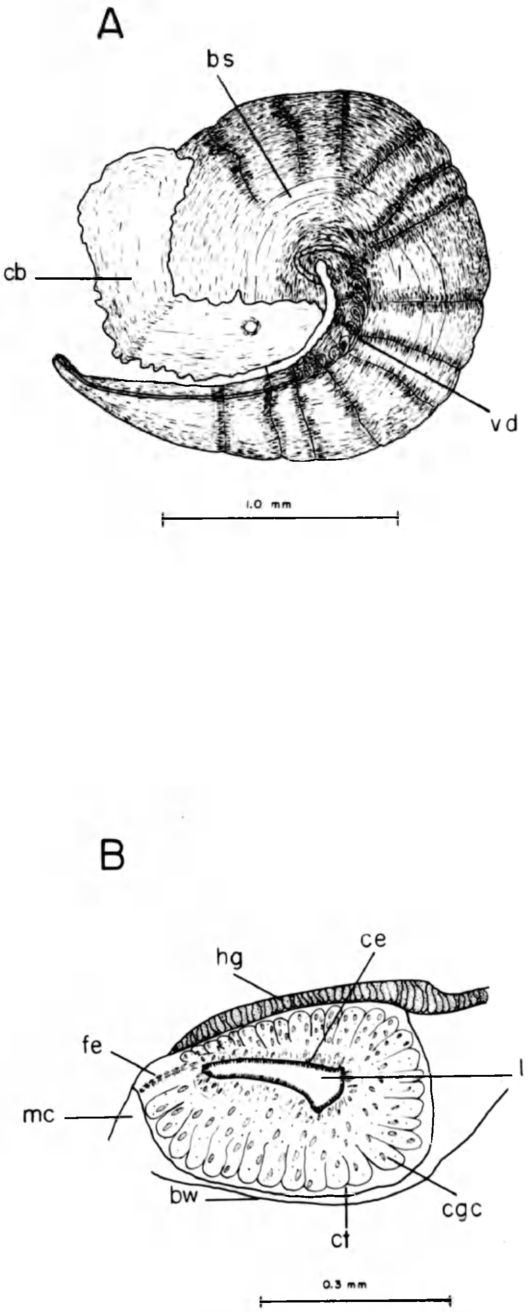

Figure 7. Camera lucida drawings of *Urosalpinx cinerea*: A, the penis in the relaxed state; B, cross-section through mid-region of the prostate gland. bs, blood sinus; bw, body wall; cb, cut base of penis; ce, ciliated epithelium; cgc, cluster of subepithelial gland cells; ct, connective tissue; fe, line of fusion of prostate gland; hg, hypobranchial gland; l, lumen of prostate; mc, mantle cavity; vd, vas deferens.

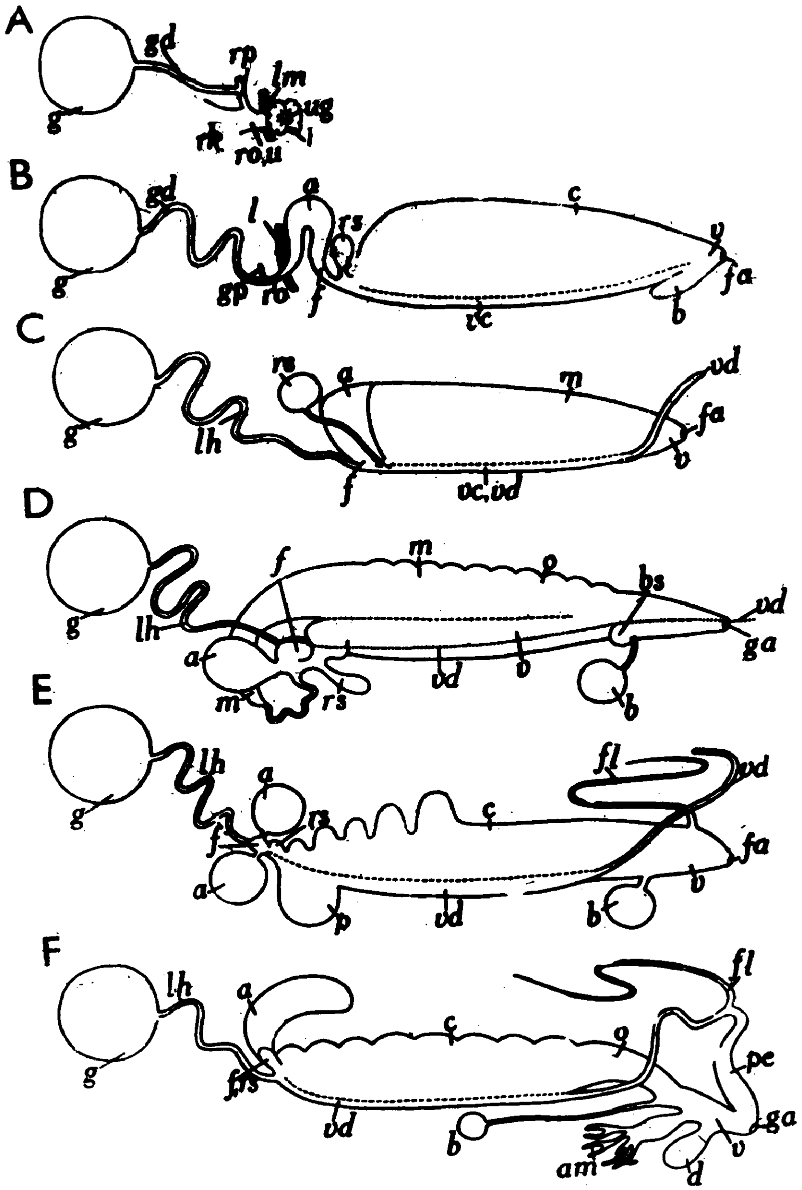

Figure 8. Comparative diagrams of the genital ducts of: A, the Trochidae ♀; B, *Nucella* ♀; C, *Actaeon* ♀♂; D, Aplysia ♀♂(after Eales); E, *Onchidella* ♀♂; F, *Helix* ♀♂. Broken lines represent incomplete separations between channels; the dotted line the vas deferens, an open groove throughout. a, albumen gland; am, additional mucous gland present in pulmonates; b, bursa copulatrix, commonly called spermotheca in D and F; bs, bursa seminalis; c, capsule gland, in F usually called female part of large hermaphrodite duct; d, dart sac; f, site of fertilization, in D, E and F a definite fertilization chamber; fa, female aperture; fl, flagellum; g, gonad; ga, common genital aperture; gd, gonadal duct; gp, gonopericardial duct; l, glandular lips; lh, little hermaphrodite duct of gonadal and renal origin; lm, inner limit of mantle cavity; m, mucous gland; o, oviduct; p, prostate; pe, penis; rk, right kidney; ro, renal oviduct; rp, renopericardial duct; rs, receptaculum seminis; u, ureter; ug, urino-genital aperture; v, vagina; vc, ventral sperm channel; vd, vas deferens. (from Fretter, 1946a).

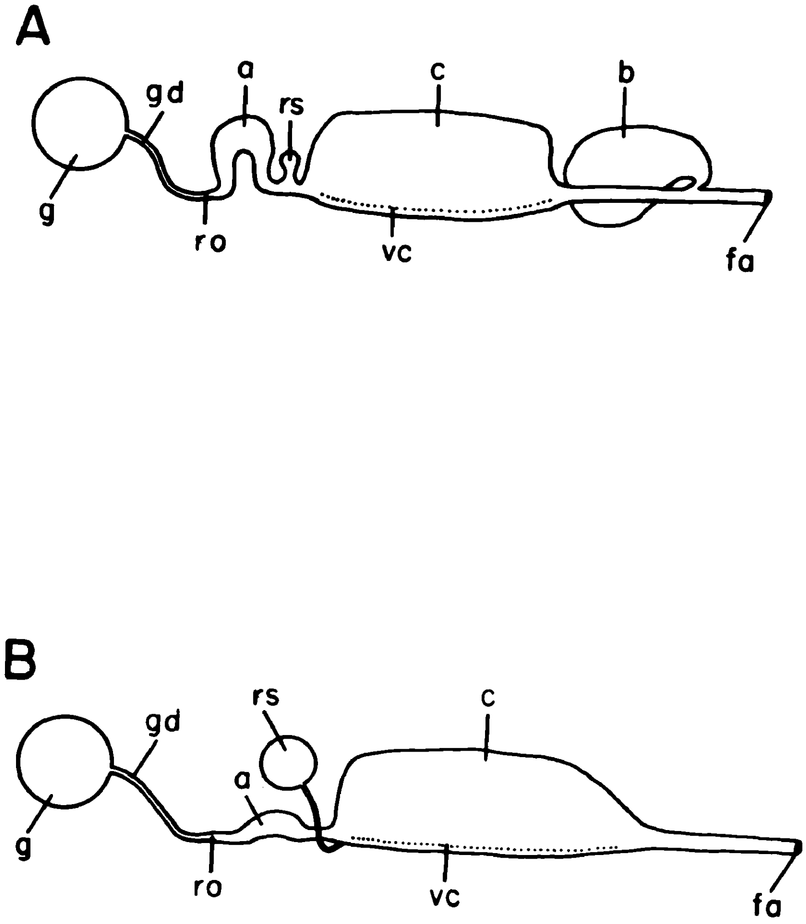

Figure 9. Comparative diagrams of the genital ducts of: A, *Urosalpinx cinerea*; B, *Eupleura caudata*. a, albumen gland; b, bursa copulatrix; c, capsule gland; fa, female aperture; g, gonad; gd, gonadal duct; ro, renal oviduct; rs, seminal receptacle or sperm ingesting gland; vc, ventral channel of capsule gland.