A STUDY OF THE REPRODUCTIVE ORGANS OF THE COMMON MARINE SHRIMP, PENAEUS SETIFERUS (LINNAEUS)

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Introduction

In connection with the investigations of the common commercial shrimp, *Penaeus setiferus* (Linnaeus), carried on by the U. S. Fish and Wildlife Service, studies have been made of the structure of the reproductive organs and accessory sex characters and the general nature of the reproductive process.

This report gives information on the anatomy and histology of the male and female sex organs, the maturation of the germ cells, and certain observations on the phenomena of impregnation and ovulation.

This study was undertaken to determine if there are structural characters within the gonads which might serve as an index to age and longevity and furnish information bearing on the frequency of spawning of an individual within a single breeding season. Such data are needed for estimating mortality rates and for an understanding of the reproductive potential of the organism.

Materials and Methods

The observations which follow are based upon the macroscopical and microscopical examination of the gonads and accessory organs of several hundred shrimp taken at irregular intervals over a period of several years. Because of various circumstances, it was necessary to obtain much of the material from the commercial catch. These shrimp had been iced on the fishing grounds immediately upon capture and after 8 to 10 hours were still in a satisfactory state of preservation for general histological study. Much of this material, of course, was not suitable for detailed cytological work. When opportunity permitted trips were made to the fishing grounds and fresh material obtained.

At the beginning of the study the entire gonads of several specimens of each sex were serially sectioned and examined to determine if the various parts of the organ were homogeneous in structure and stage of development of the germ cells. As in general they were found to be so, samples, thereafter, were taken of only a portion of the gonads. In the female, this was usually the abdominal extension of the ovary lying in segments XVII and XVIII. In the male two or three lateral lobes of the testis were preserved from each specimen, together with one entire vas deferens and terminal ampoule.

Two generally different microscopical techniques were employed: in the first, tissues were prepared for general histological study; in the second, ovarian material was treated so as to preserve its true chemical nature for cytological study. In the first method, the tissues were fixed in either Bouin's or Kahle's fluid, imbedded in

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paraffin and stained with Delafield's Hematoxylin (Harris modification) and Eosin (1 per cent in dioxane) or Mallory's triple connective tissue stain. In this method dioxane was used in the imbedding and staining operations.

In the second method, the tissues were fixed in 20 per cent formalin, sectioned with a freezing microtome and stained with one of the following fat-specific stains: Sudan IV, Calco Oil Red, Calco Oil Blue or Oil Yellow OB. Sections obtained by this method were also treated with ninhydrin, a protein-specific microchemical reagent.

The sexes of *P. setiferus* are easily distinguishable. In the male the endopodites of the first pair of pleopods are modified to form a copulatory organ, the *petasma* (Plate C, 2 and 3). The corresponding abdominal appendages of the female do not show this modification but are similar to the other pairs of pleopods. Additional but less obvious differences between the sexes include the locations of the openings of the genital ducts, the possession by the female of a ventral thoracic structure, the *thelycum* (Plate A, 3), the slight modification of the second pair of pleopods in the male (Plate C, 4), and significant differences in total length attained. As an example of the latter, total length measurements made on April 15, 1942, of a random sample of 200 adult shrimp of the offshore commercial catch gave an arithmetic mean of 165 mm. for 110 males and 171 mm. for 90 females. The males ranged in length from 147 to 178 mm. and the females from 151 to 188 mm., with the corresponding modes at 165 mm. and 176 mm.

In the Penaeid shrimps, as contrasted with the Pandalidae (Berkeley, 1929), no cases of sex reversal have been noted. The spawned eggs are released free in the water and are not carried on the pleopods of the female as in most other Decapods.

The Female Reproductive System

Gross Anatomy

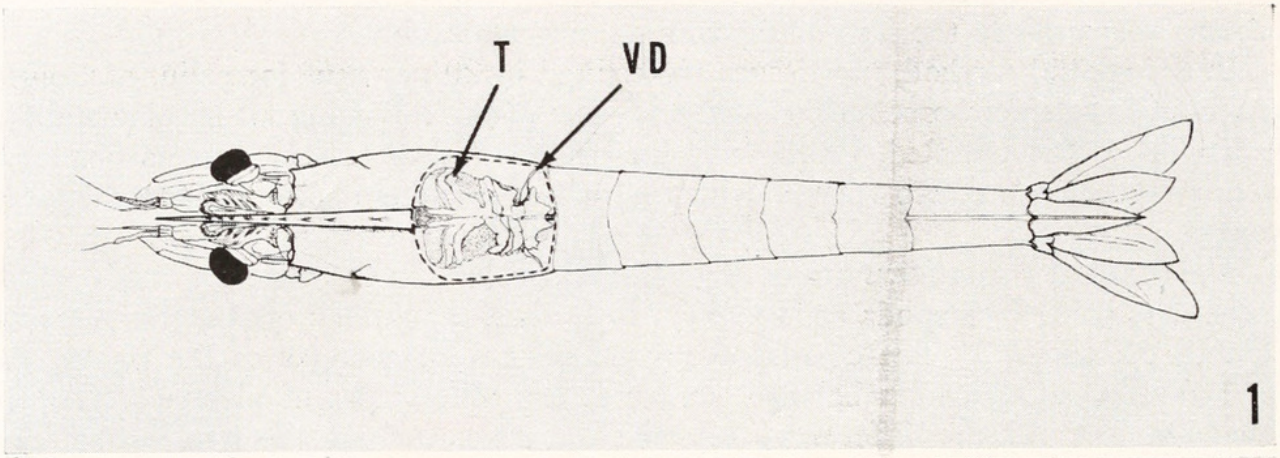
The female reproductive system (Plate B, 2 and Plate A, 2) consists of paired ovaries and oviducts and a single thelycum. The ovaries are partly fused, bilaterally symetrical bodies extending in the mature animal for almost its entire length, actually from the cardiac region of the stomach to the telson. In the cephalothoracic region each organ bears a slender anterior lobe and in most cases seven finger-like lateral projections. A pair of lobes, one from each ovary, extend the length of the abdomen.

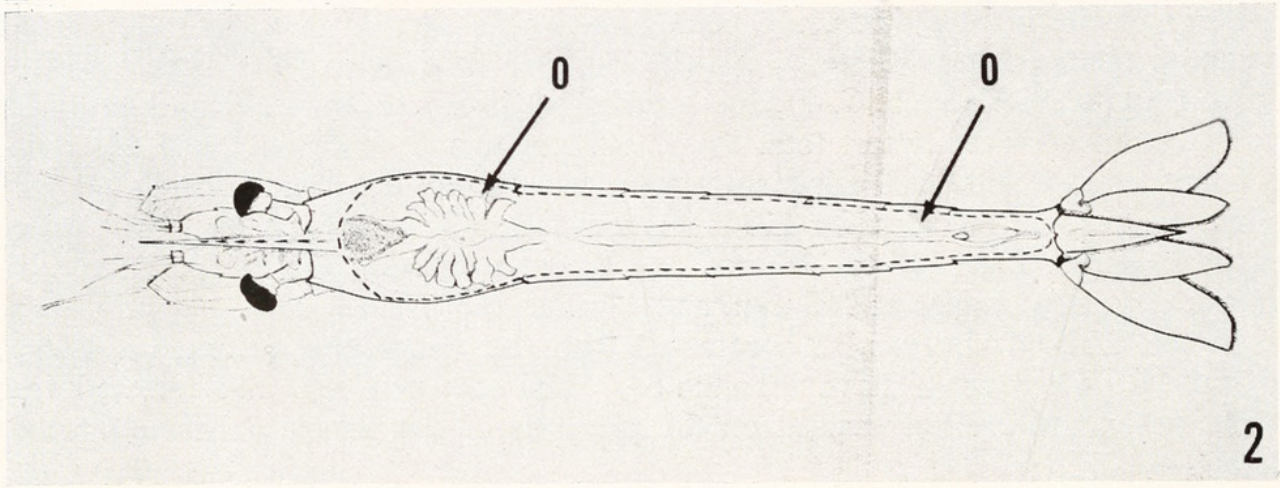
The anterior lobes lie closely applied to the esophagus and cardiac region of the stomach. The lateral lobes are located dorsally to the large mass of hepatopancreas and ventrally to the pericardial chamber. The heart rides like a saddle over this portion of the gonad. The abdominal extensions lie dorso-lateral to the intestine and ventro-lateral to the dorsal abdominal artery.

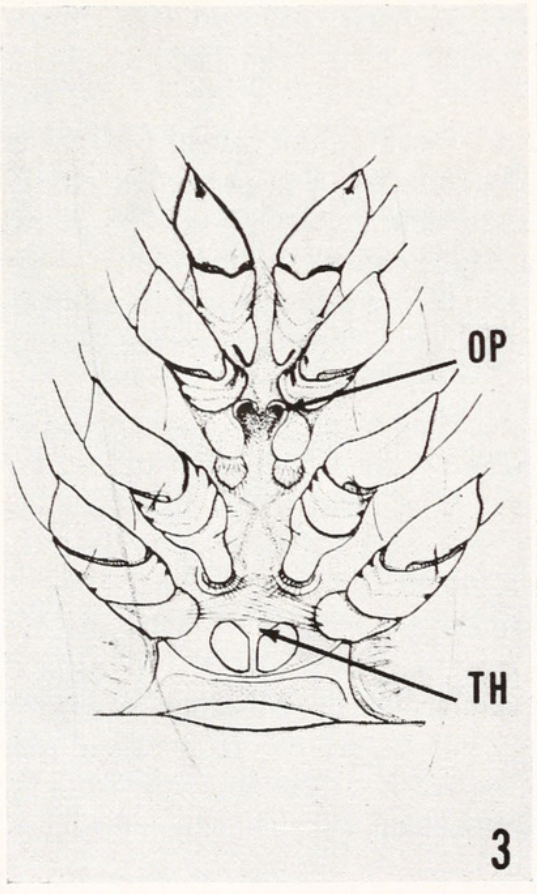
Fortunately for the observer in the field, maturation is accompanied by distinctive color changes in the ovary as well as changes in its size, which make it possible for one to identify the stage of development with fair accuracy without microscopic examination. The ovaries of the young shrimp (Plate D, 5) are so small in size and transparent in nature that their dissection in the fresh specimen is particularly difficult. Such a shrimp is recorded as *U* for undeveloped.[2] As the shrimp grows,

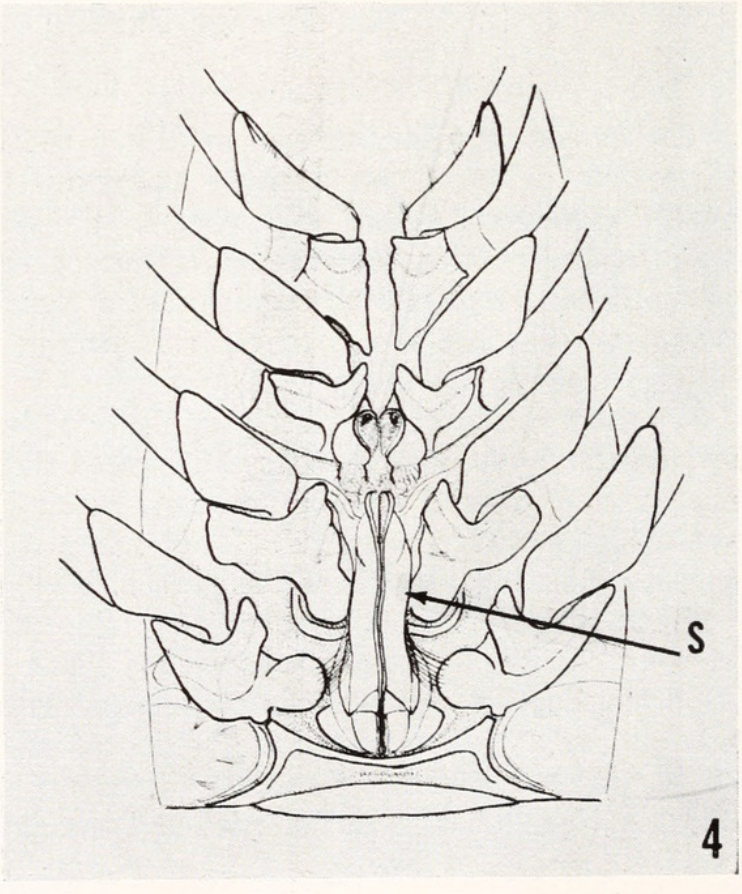
[2] Early in the history of the Investigations it was decided that the symbols *U, D, Y, R* and *Sp* were to be used by field workers in designating the obvious stages of ovarian development.

PLATE A









the glands increase in size, scattered melanophores appear over the surface, and in general appearance, the ovaries become somewhat opaque. This stage is classed as *D*, or developing (Plate D, 3 and 4). As maturation continues, the ovary takes on a yellowish cast which deepens to a yellowish-orange, and is designated as the *Y*, or yellow stage (Plate D, 2). This is followed by the drab olive-brown color of the ripe, or *R* ovary (Plate D, 1). The ovaries, at this point, are so distended that they now fill all available space and appear to crowd considerably the other organs of the body cavity. During the yellow and olive-brown color phases, the ovary can be seen quite clearly through the abdominal tergites and membraneous connectives between the first abdominal somite and the carapace. The recently spawned ovary, designated as spent (*Sp.*), has collapsed from its distended condition and is not as deeply colored as in the ripe phase. As regression continues, the green color disappears but the structure remains opaque. A shrimp in this stage is difficult to distinguish from the large shrimp of the O-year class with developing ovaries. Microscopical examination, however, reveals the difference in most cases.

The oviducts (Plate B, 2) are short, narrow tubes leaving the ovaries at the tips of the 6th pair of lateral lobes and opening through the genital pores at the bases (coxae) of the 3d pair of pereiopods (Plate A, 3). Each opening is concealed in a bristle-filled, ear-shaped protuberance.

From a survey of the literature (Andrews, 1911; Burkenroad, 1934; Heldt, 1938; Filbo, 1943) it appears there are several ideas as to exactly what constitutes the thelycum (Plate A, 3). In *P. setiferus* it might be described as modifications of the sternal surfaces of somites XII, XIII, and XIV, which provide for the attachment of the spermatophore received from the male during copulation. In this species there are principally three things responsible for the retention of the spermatophore:

1. When discharged by the male, the spermatophore is accompanied by a mass of glutinous material (Plate B, 4 and 5) which is an important factor in its adherance to the female.

2. On the coxae of pereiopods four and five of the female there are protuberances bearing clumps of stiff bristles (Plate A, 3 and 4) which are directed medially and overlap flanges of the spermatophore, thus helping to hold it in place.

3. The "wings" of the spermatophore are securely anchored in a groove in the sternal surface between the 3d and 4th pereiopods (Plate A, 4). The horn-like structure on the posterior margin of each wing appears to be inserted between the bristle-bearing protuberance of the coxae of the 4th pereiopod and a raised shelf-like portion of sternite XIII.

PLATE A

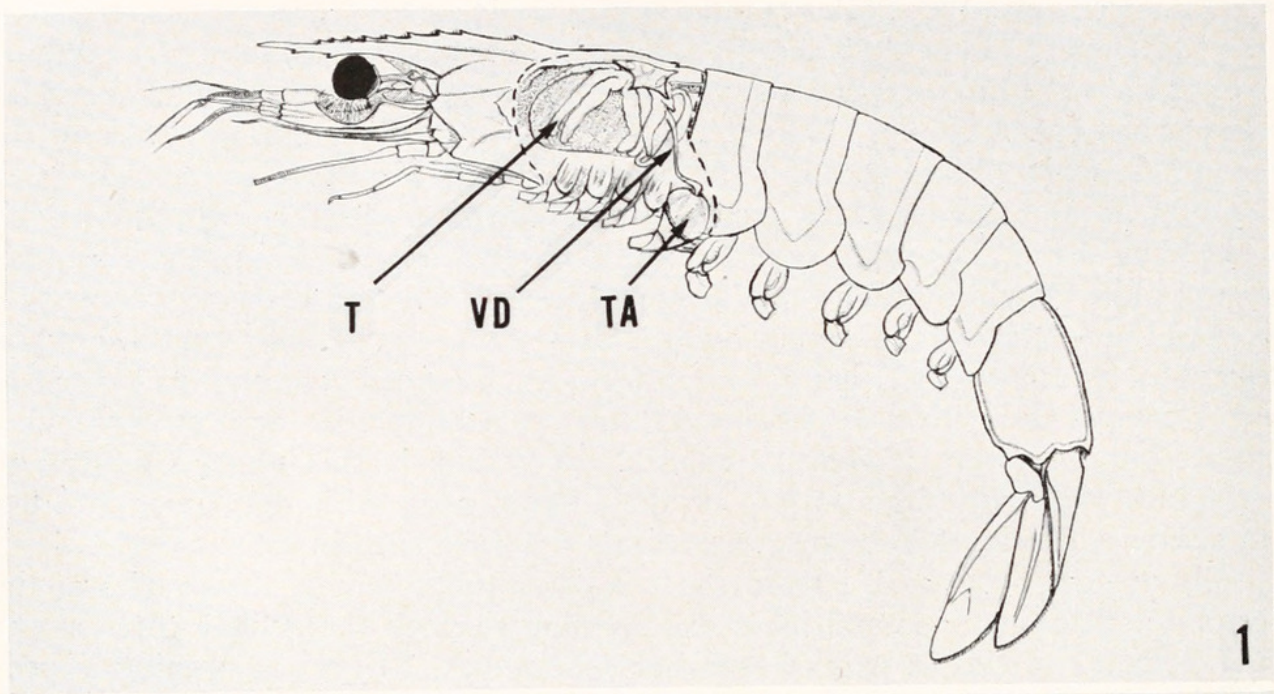
1. Diagram of male, dorsal view, dissected to show testes and portions of the vasa deferentia. T—testis; VD—vas deferens. × 0.5.

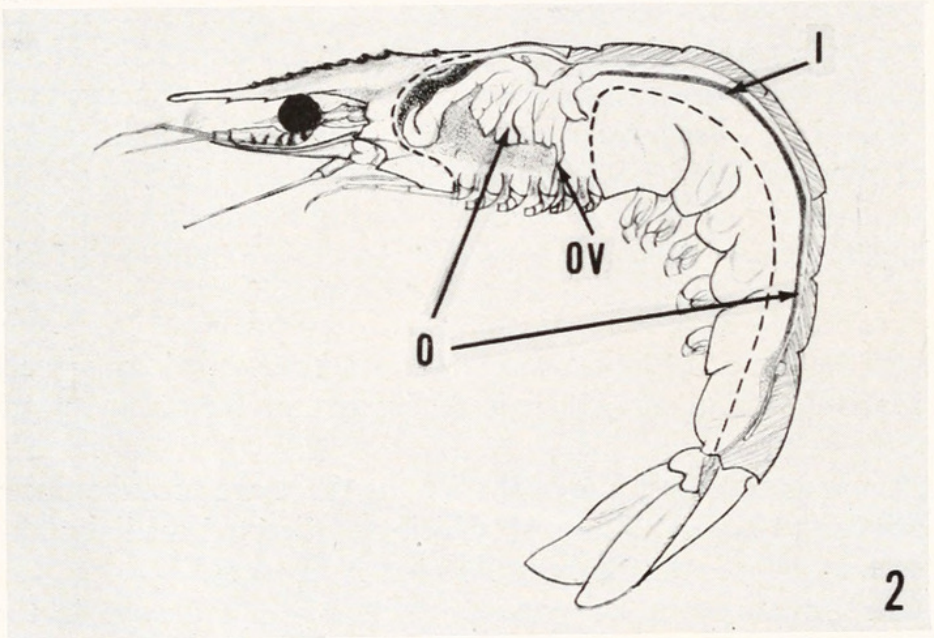
2. Diagram of female, dorsal view, dissected to show ovaries. O—ovary. × 0.5.

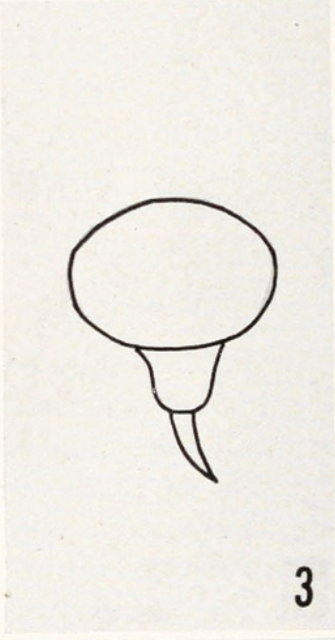
3. Diagram of ventral surface of cephalotharax of female. OP—opening of oviduct; TH—thelycum. × 2.5.

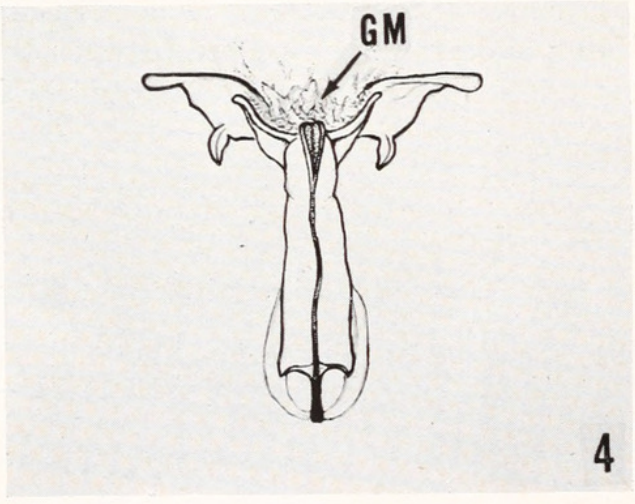
4. Diagram of ventral surface of cephalotharax of female with spermatophore attached. S—spermatophore. × 2.5.

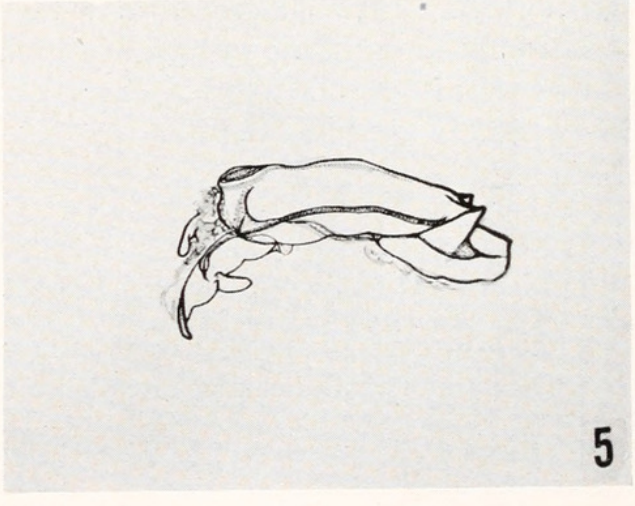
PLATE B











On somite XIV are a pair of light-colored, pad-like structures which in *P. setiferus* play no active role in the impregnation process. In most other Decapods, however, these structures are open at their anterior margins, thus forming pockets that function as seminal receptacles.

Despite these holdfast devices, the spermatophore is rather easily dislodged, which may, to a certain extent, explain why spermatophore-bearing females are not commonly taken (Weymouth, Lindner and Anderson, 1933).

Histology and Development

The ovary

The wall of the ovary is composed of three layers: a thin outer layer of pavement epithelium, a relatively thick layer of connective tissue, and an inner layer of germinal epithelium. No layers of muscle fibers could be detected with the Mallory's triple staining technique. Extending longitudinally throughout the ovary are septa, also of connective tissue. Small blood sinuses can be seen in most cross-sections.

Germinal epithelium, functioning as such and giving rise to oogonia, is not distributed uniformly over the inner wall of the ovary but is confined to a certain well-defined area which has been termed the "zone of proliferation" (Gutsell, 1936). In the abdominal extension of the ovary there is a streak of such germinal epithelium along the medial-ventral wall of each lobe (Plate D, 1, 2, and 3; Plate E, 2, 3, and 4). In the lateral lobes this tissue occurs in a more strictly ventral position.

As the oogonia pass through the developmental stages of primary oocyte and secondary oocyte, they move in a column from the "zone of proliferation" toward the center of the ovarian lobe. Because of the rapid multiplication of cells, from this point the oocytes are forced to the peripheral regions of the lobe. As development proceeds, the peripheral and more mature oocytes are surrounded with "nurse" or follicle cells (Plate E, 3) which appear to arise from the germinal epithelium. Follicle formation continues until, in the ripe ovary, all the mature ova are enclosed by these nutritive cells.

The cytoplasm of the young ova, of *U* and *D* ovaries, appears finely granular with the staining methods used. As the egg matures these fine particles become enlarged and globule-like. In the *R* ovum we find very prominent rod-like bodies (Plate D, 6) imbedded in the cytoplasm in the peripheral regions of the cell and arranged radially about the nucleus.

With the Hematoxylin-Eosin staining technique, the cytoplasm of the *U* and *D* ova takes on a blue color indicating a basophilic reaction. As the egg matures into

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PLATE B

1. Diagram of male, lateral view, dissected to show reproductive organs. T—testis; VD—vas deferens; TA—terminal ampoule. × 0.5.

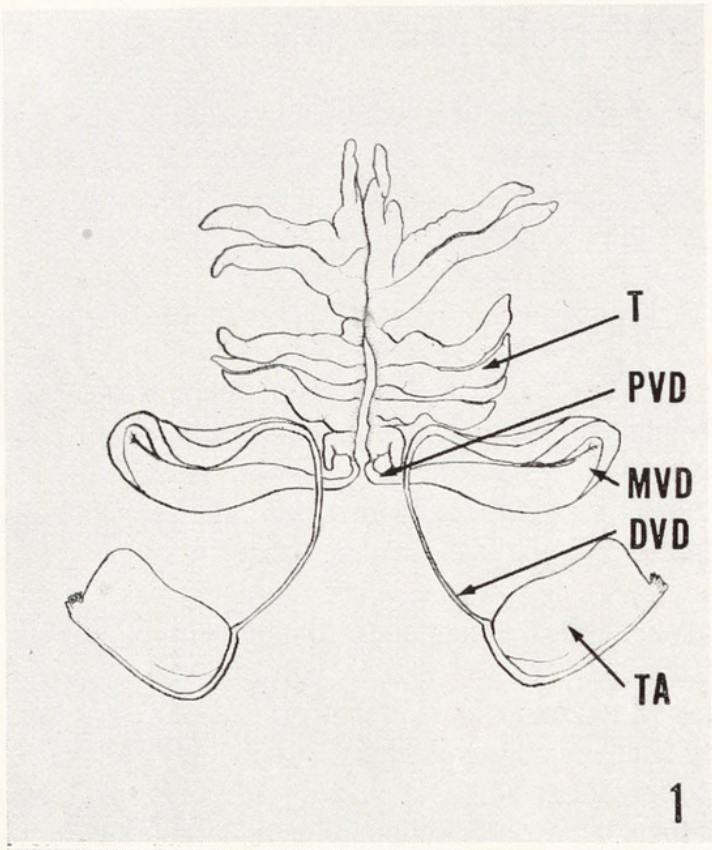
2. Diagram of female, lateral view, dissected to show relationship of ovary and oviduct. O—ovary; OV—oviduct; I—intestine. × 0.5.

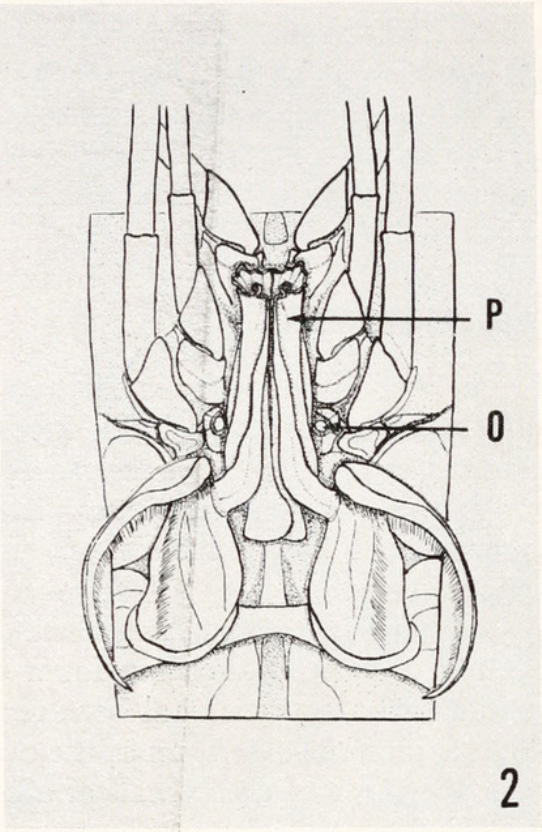
3. Diagram of shrimp spermatozoan. × 9000 (approx.).

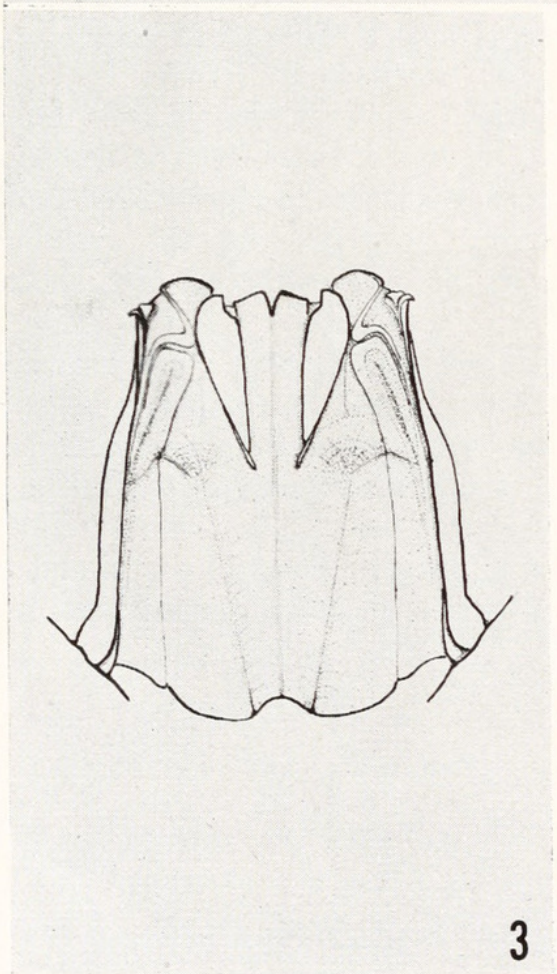
4. Diagram of ventral view of spermatophore (as in attached position). GM—gelatinous material. × 2.75.

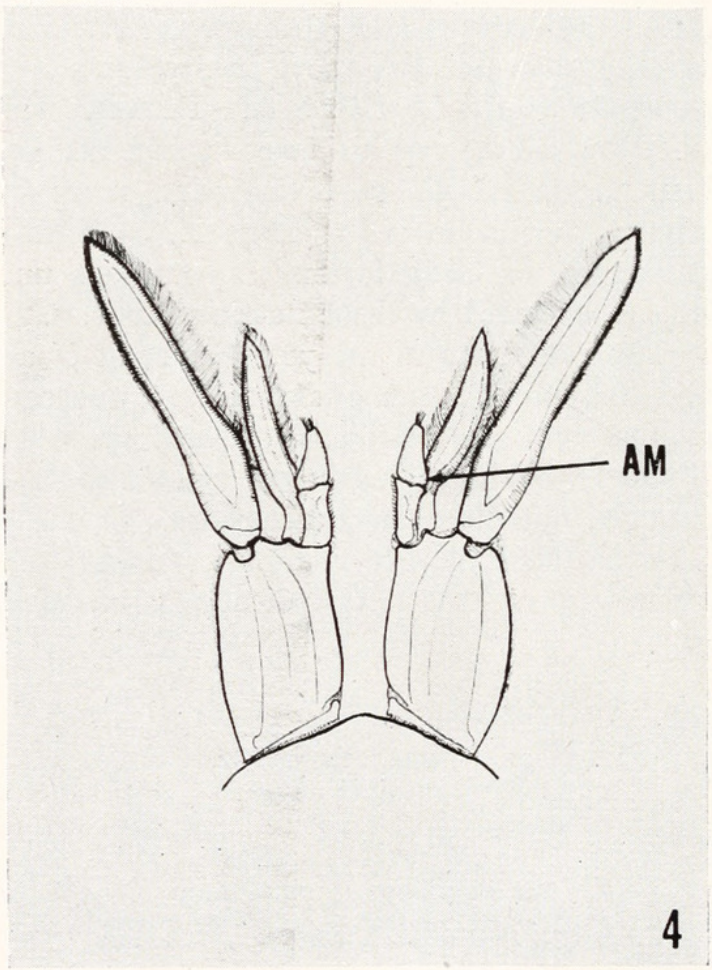
5. Diagram of lateral view of spermatophore. × 2.75.

PLATE C









the *Y* and *R* stages, the cytoplasm becomes acidophilic, staining red with Eosin. The rodlike peripheral bodies just described also stain red with Eosin.

Through the use of fat-specific dyes, such as Sudan IV, Calco Oil Red, Calco Oil Blue and Oil Yellow OB, it was found that no fat was present in the *U* ovaries, a very little in the more advanced *D* ovaries, and a great amount in the *Y* and *R* stages. The presence of fatty yolk in significant quantities coincides, therefore, with the appearance of the yellow color in the ovary.

In the ripe ovum the yolk globules reacted strongly with all of the fat soluble dyes used. The peripheral bodies, however, did not take on the dye, but appeared as distinct clear areas in the cytoplasm. It was concluded, therefore, that they are not of fatty nature.

Sections of ripe ova were treated also with ninhydrin, a protein-specific reagent, to determine if the rod-like bodies might be albuminous yolk. No reaction was obtained. Bhatia and Nath (1931) have observed very similar cell characters in the ova of *Palaemon lamarrei,* another species of shrimp. They believed the bodies to be albuminous yolk derived from mitochondria.

The recently spawned ovary is easily distinguishable from the ripe stage. It is flaccid rather than turgid, of a muddy green color, and microscopical examination reveals numerous ripe eggs undergoing resorption. As the degenerative process continues the gland becomes greatly reduced in size and assumes an opaque milky color. At this time it is very difficult to distinguish from an ovary in a late *D* stage. By taking into consideration such factors as total length, weight, and time of year, it is usually possible to segregate these groups in the field. When examined microscopically it is found that the two ovaries have a distinct differentiating character. The spent ovary is fairly swarming with left-over follicle cells (Plate D, 8). In the late *D* stage (Plate E, 3) follicle formation is just beginning and these cells are present only in small quantities.

A careful study of the spent ovary has been made to determine if it might be used as an index to the shrimp's age and number of times spawned. Although space in the ripe ovary is almost entirely given over to the crop of mature eggs, the "zone of proliferation" is still evident and a few young oocytes are continually being formed. Spent ovaries, three to four months after spawning, have undergone considerable regrowth. Even as early as March spent ovaries have been examined which showed evidence of regrowth. On this basis it appears quite possible for a shrimp spawning in March to spawn again later in the season. In view of the long spawning season, which in Louisiana offshore waters is March through September (Anderson, Lindner and King, 1948a), sufficient time may remain for the second crop of eggs to mature. We have been unsuccessful, however, in finding

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PLATE C

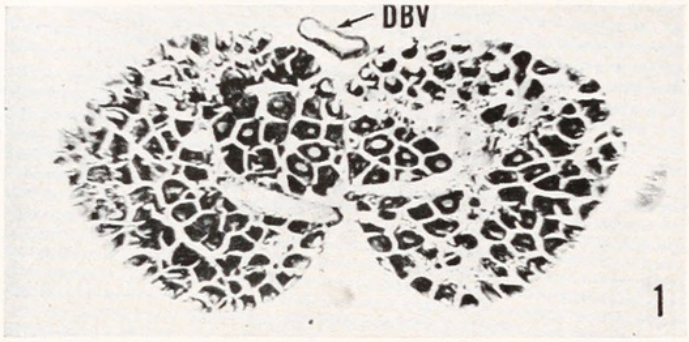
1. Diagram of male reproductive system. T—testis; PVD—proximal vas deferens; MVD—medial vas deferens; DVD—distal vas deferens; TA—terminal ampoule. × 1.75.

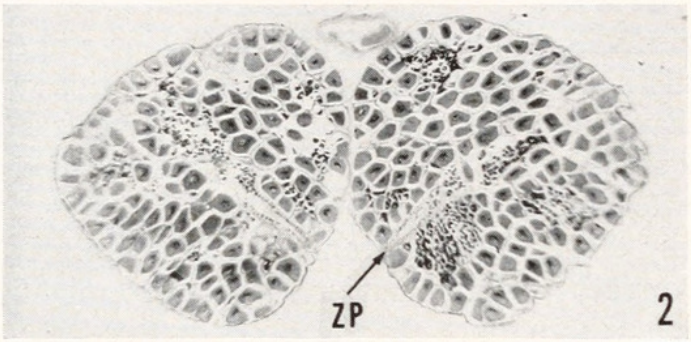
2. Diagram of ventral surface of mature male. P—petasma; O—opening of vas deferens. × 1.75.

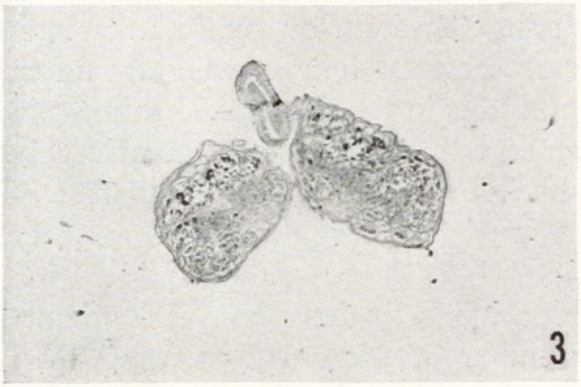
3. Diagram of petasma of mature male spread open to show interior arrangement of folds. × 2.9.

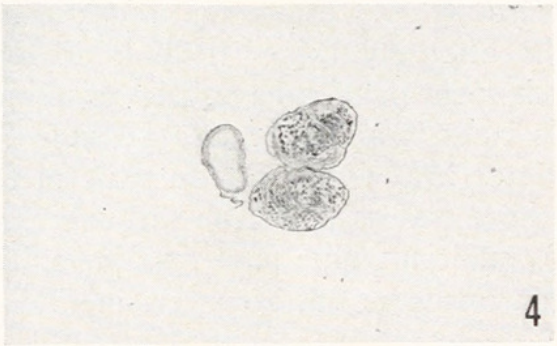
4. Diagram of second pair of pleopods of male. AM—appendix musculina. × 1.75.

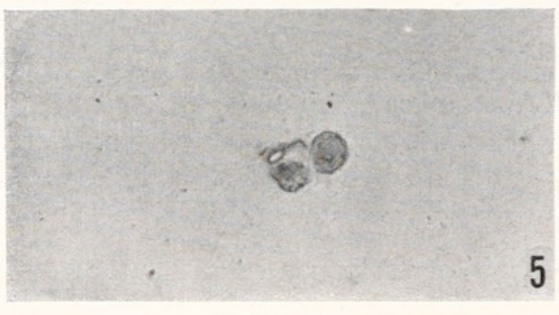
PLATE D

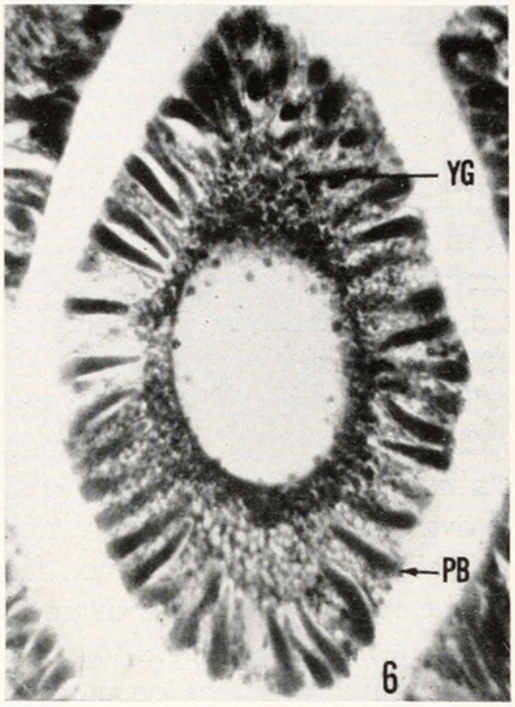


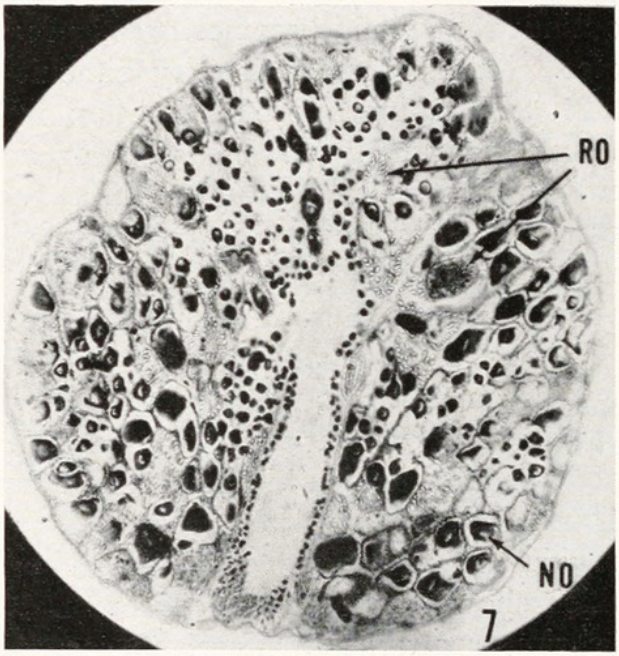


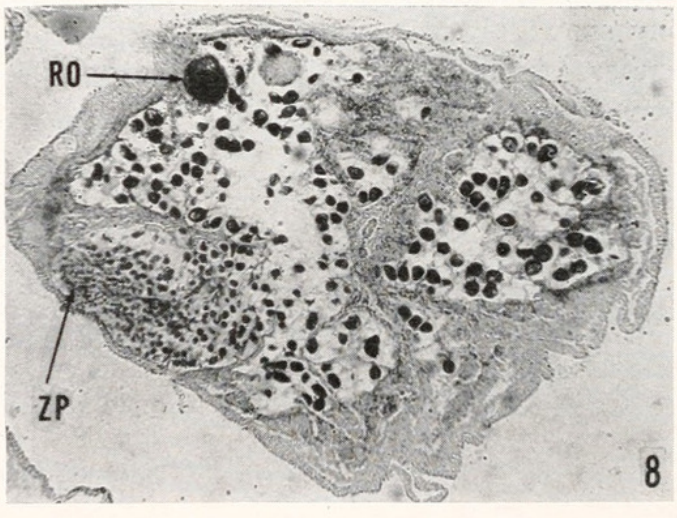












any ovarian characters such as are present in the higher animals which would enable us to distinguish between the once-spawned and the twice-spawned ovary.

It was hoped that the structure of the ovary would supply clues as to the approximate age and length-of-life of the shrimp. This possibility was removed by the likelihood of multiple spawning and the absence of any permanent "scars" or walled-off spent areas within the ovary resulting from each spawning. For our knowledge of the longevity of the shrimp, therefore, we have had to rely upon information obtained through length frequency studies (Anderson, Lindner and King, 1948b, 1948c). These data have shown that young-of-the-year shrimp are dominant in the commercial catch after August of each year. By October and November, old of the previous year are very scarce and form a small percentage of the commercial catch. It is possible to follow through a trace of this old group until about the middle of January, after which they either die out or become merged with the following year class so that, with our present information, they cannot be distinguished (Lindner, Anderson and King, 1948). By the middle of January these old shrimp are approximately 1½ years of age. If shrimp live beyond this point, they are at least not found in the commercial catch much beyond December and not at all beyond the middle of January.

The oviduct

The wall of the oviduct (Plate E, 6) appears to be made up of three layers. Bordering on the lumen is a somewhat folded columnar epithelium which, it is assumed, secretes a lubricating fluid to facilitate the passage of eggs down the tube. The main supporting structure of the duct is a thick layer of connective tissue. Although not apparent in cross-section, the outer layer would consist of a thin epithelial membrane. No muscle tissue was shown to be present by the Mallory's triple staining technique.

Ovulation

It does not appear that nature has made the proper provision for the egress of the half million or so eggs which the average female will produce. As mentioned

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PLATE D

1. Ripe (R) ovary from 195 mm. shrimp taken March 7, 1944, cross-section of abdominal lobes. DBV—dorsal blood vessel. × 14.

2. Yellow (Y) ovary from 200 mm. shrimp taken March 7, 1944, cross-section of abdominal lobes. ZP—zone of proliferation. × 14.

3. Developing (D) ovary from 191 mm. shrimp taken December 15, 1944, cross-section of abdominal lobes. × 14.

4. Early developing (D) ovary from 180 mm. shrimp taken December 15, 1944, cross-section of abdominal lobes. × 14.

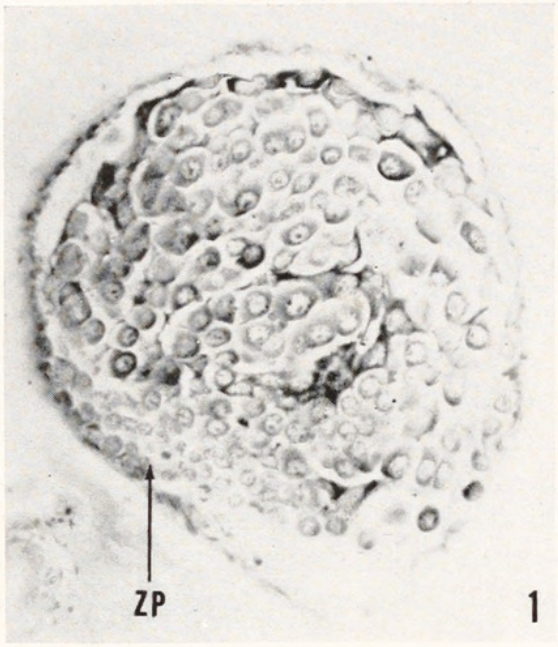
5. Undeveloped (U) ovary from 112 mm. shrimp taken November 15, 1944, cross-section of abdominal lobes. × 14.

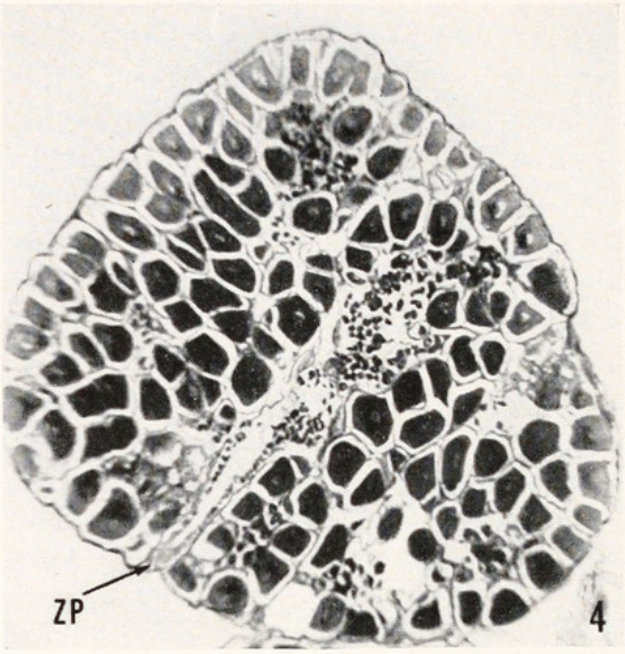
6. Ripe ovum, showing nucleus, yolk globules and rod-shaped peripheral bodies. YG—yolk globule; PB—peripheral body. × 279.

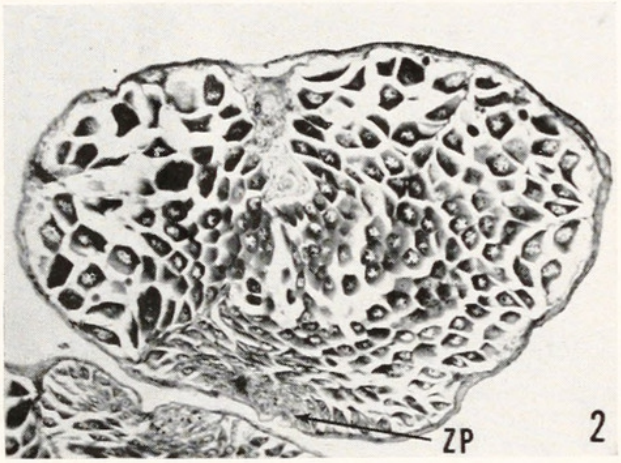
7. Spent (Sp.) ovary, cross-section of abdominal lobe of recently spawned shrimp. New crop of ova being produced. NO—new ovum; RO—resorptive ovum. × 35.

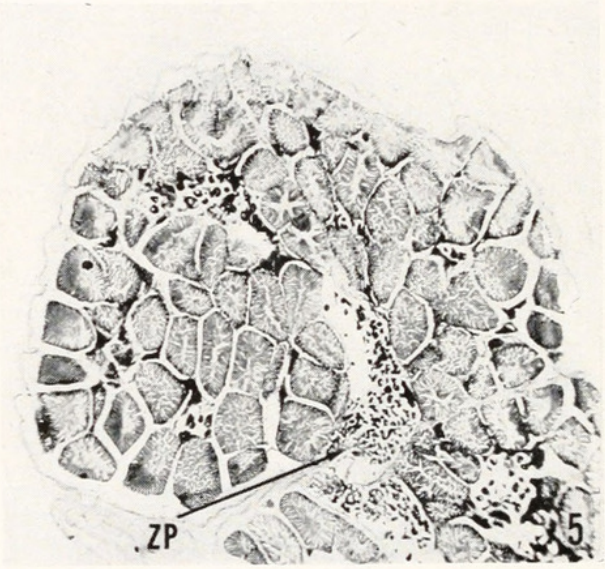
8. Spent (Sp.) ovary, cross-section of abdominal lobe showing almost complete recovery. Ovary is largely filled with dense masses of follicle cells and new oocytes. RO—resorptive ovum; ZP—zone of proliferation. × 52.

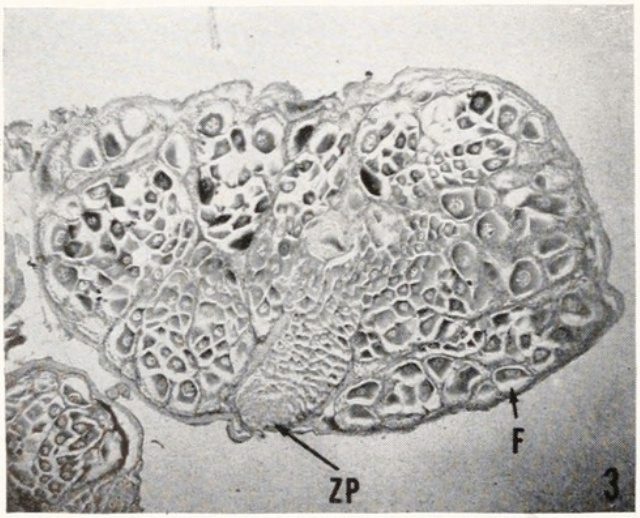
PLATE E











above, the oviduct is a slender though doubtless distensible tube connected with the ovary at the tip of one of the lateral lobes. No evidence was found of any branches of the oviduct extending beyond its junction with the ovary. In the ripe stage the ovary is very compactly filled with apparently no passageway through which the eggs might be directed to the mouth of the oviduct.

As the ovarian wall itself contains no muscle tissue, spawning is most likely brought about through the coordinated contracture of the cephalothoracic and abdominal muscles surrounding the ovary. It is probable that pressure is applied in such a way as to cause the eggs to move generally in the direction of the opening of the oviduct. Heldt (1938) observed the spawning of *P. trisulcatus* in an aquarium. She states that the female while resting on the bottom of the container emitted the eggs in great abundance. The process was completed in a few minutes.

As previously mentioned, a study of the "spent" ovary of *P. setiferus* reveals a large number of unspawned eggs in various stages of resorption (Plate D, 7 and 8), thus indicating that the ovary is not emptied in the spawning process and that a certain percentage of eggs never reach the exterior to be fertilized. Contrary to this, Heldt (1931) reports that in the spawning of *Penaeus caramote* Risso the ovary empties completely in one or two minutes.

The Male Reproductive System

Gross Anatomy

The male reproductive system (Plate A, 1 and Plate B, 1) includes paired testes, paired vasa deferentia and a petasma. The testes are unpigmented, translucent organs occupying a position in the body cavity very similar to that of the ovaries in the female, with the exception, however, that the testes lack the greatly extended abdominal lobes possessed by the ovaries. Each testis has projecting from its main axis an anterior lobe, apparently six lateral lobes, and a single short posterior lobe. The main trunks are more or less united for their entire lengths. In the young shrimp the testes are extremely delicate, transparent structures which can be located and removed only with great difficulty. As the animal matures, the testes change little in appearance, except to grow in size and become somewhat opaque.

The vasa deferentia arise from the posterior margins of the main axes of the testes and open to the exterior through genital pores located medially on the coxae

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Plate E

1. Undeveloped (U) ovary, cross-section of abdominal lobe. ZP—zone of proliferation. × 170.

2. Early developing (D) ovary, cross-section of abdominal lobe. ZP—zone of proliferation. × 82.

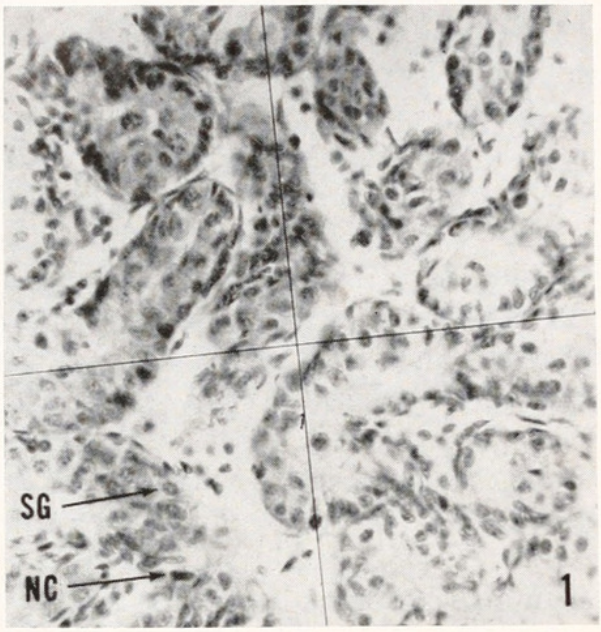
3. Advanced developing (D) ovary, cross-section of abdominal lobe. ZP—zone of proliferation; F—follicle cell. × 46.

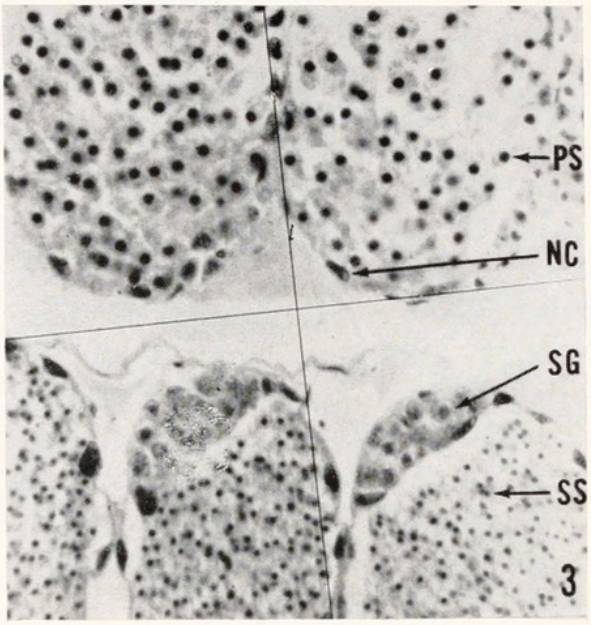
4. Yellow (Y) ovary, cross-section of abdominal lobe; cytoplasm of ova is filled with yolk globules which take on a deep eosin stain. ZP—zone of proliferation. × 24.

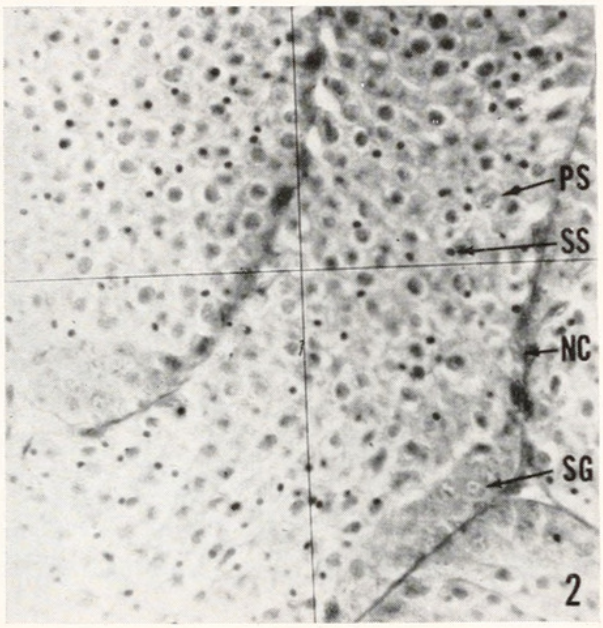
5. Ripe (R) ovary, cross-section of abdominal lobe; peripheral bodies present in ova; young oocytes still being produced. ZP—zone of proliferation. × 27.

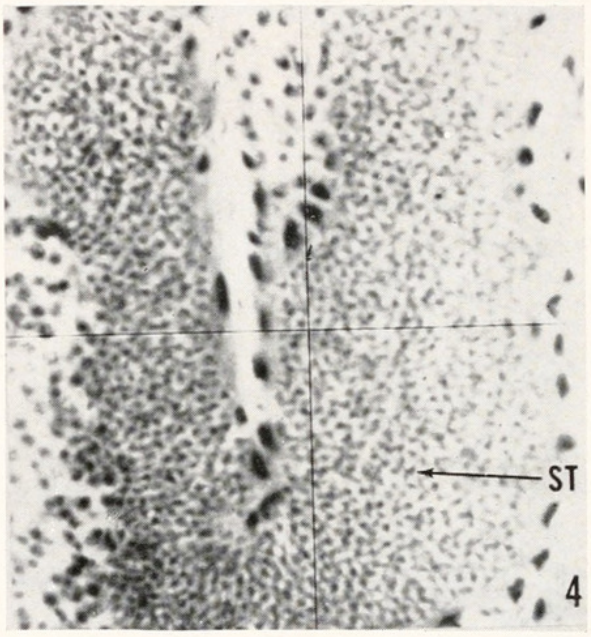
6. Oviduct, cross-section, showing thick outer wall and inner lining of tall columnar epithelium. × 102.

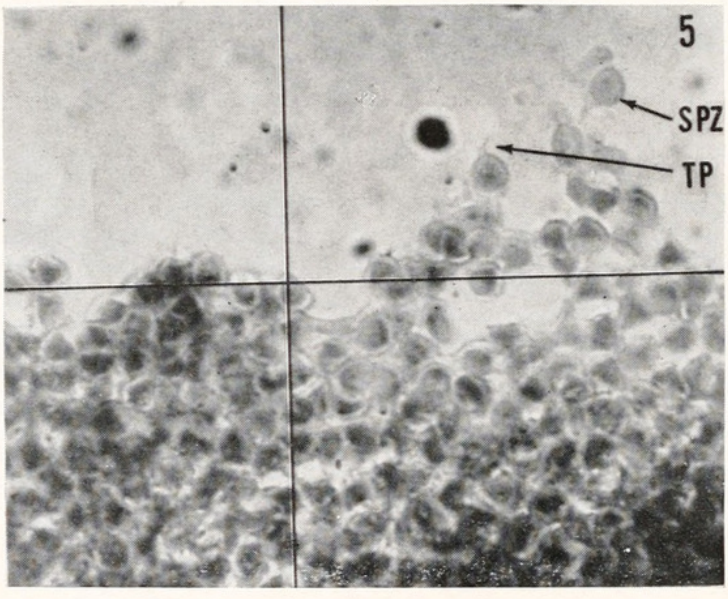
PLATE F











of the 5th pereiopods (Plate B, 1 and Plate C, 2). Each vas deferens consists of four distinct regions (Plate C, 1): (1) a short, narrow, proximal section passing abruptly into (2) a thickened medial portion having a double flexure which tapers to form (3) a relatively long narrow tube terminating in (4) a greatly dilated muscular region, the ductus ejaculatorius, or terminal ampoule. Here in this distal region is formed the spermatophore, the structure in which the sperm cells are conveyed from male to female.

The petasma (Plate C, 2 and 3) is a complicated membraneous structure of folds and troughs resulting from great modifications of the endopodites of the first pair of pleopods. The two symmetrical components are not fused but are held together in the mid-line by numerous, interlocking and very minute hooks, resembling a zipper in appearance and effect. The petasma supposedly functions in the transfer and attachment of the spermatophore to the ventral surface of the female.

In *P. setiferus* the endopodites of the second pair of pleopods are slightly modified to form the "appendix masculina," which may also assist to a small extent in the handling of the spermatophore.

The spermatophore is roughly pod-like in design (Plate B, 4 and 5), each terminal ampoule contributing a part, the halves being assembled outside the body immediately following their expulsion. The anterior end (as when in position on the female) of the spermatophore bears a pair of "wings" which are important in anchoring the structure in place. The posterior-dorsal region is extended to form a flange or shelf which also functions in attachment. It has been determined by dissection and by forcibly expelling the halves of the spermatophore with thumb and forefinger that each half is discharged from the terminal ampoule with the winged end foremost. And also that the right and left halves of the spermatophore, as in position on the female, are produced by the corresponding right and left terminal ampoules of the male, i.e., the right half originates in the right ampoule.

Never having observed the union of the sexes of the Penaeidae and being unable to find a description of the process in available literature, we can only attempt to imagine how this transfer must take place. It is assumed that the halves of the spermatophore are discharged almost simultaneously and with the aid of the walking legs are fitted together and placed in the clasping-like trough on the ventral surface of the petasma. In view of the origin and final orientation of the spermatophore, it appears necessary that the male and female should assume a head-to-tail position with their ventral surfaces in close proximity, in order to effect the transfer of the spermatophore. It is possible, however, that the petasma does not play as im-

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PLATE F

1. Section of immature testis containing spermatogonia and follicle cells. SG—spermatogonium; NC—nutritive cell. × 289.

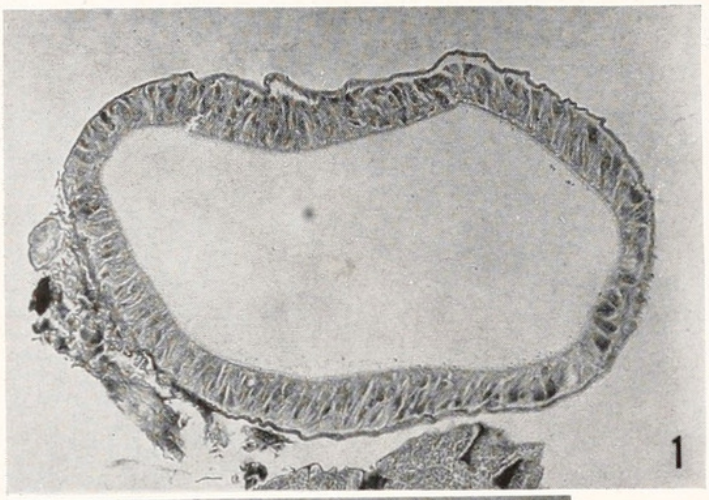
2. Section of mature testis, each tubule containing spermatogonia, primary spermatocytes and secondary spermatocytes. SG—spermatogonium; PS—primary spermatocyte; SS—secondary spermatocyte; NC—nutritive cell. × 289.

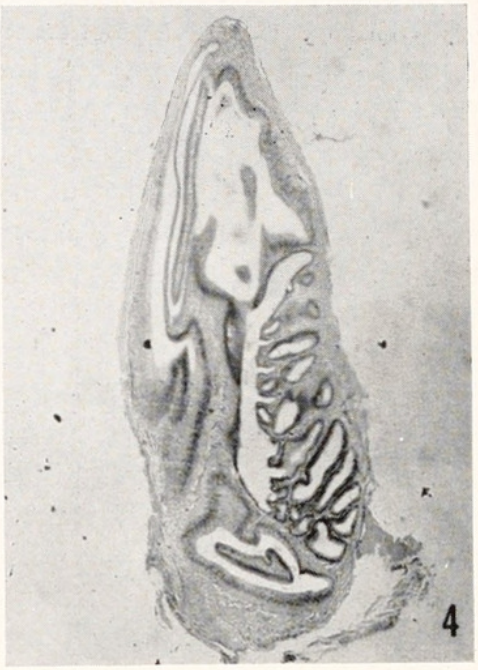
3. Section of mature testis, primary spermatocytes and secondary spermatocytes in separate but adjoining tubules. SG—spermatogonium; PS—primary spermatocyte; SS—secondary spermatocyte; F—follicle cell. × 289.

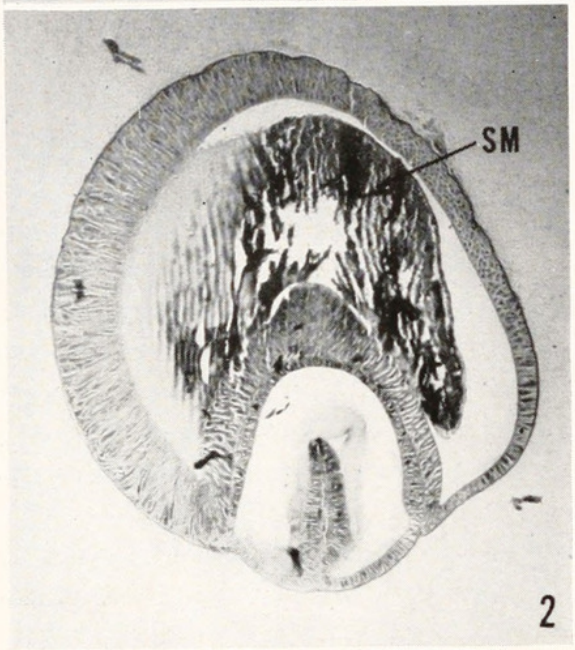
4. Section of mature testis, showing spermatids. ST—spermatid. × 289.

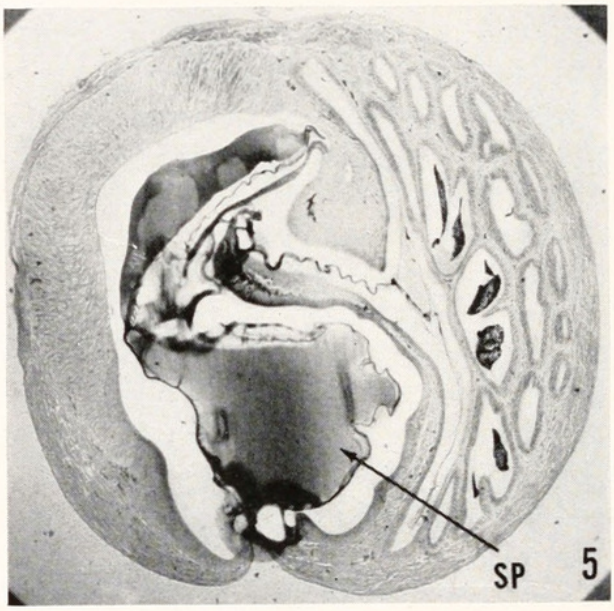
5. Spermatozoa from medial region of vas deferens. SPZ—spermatozoan; TP—tail piece. × 850.

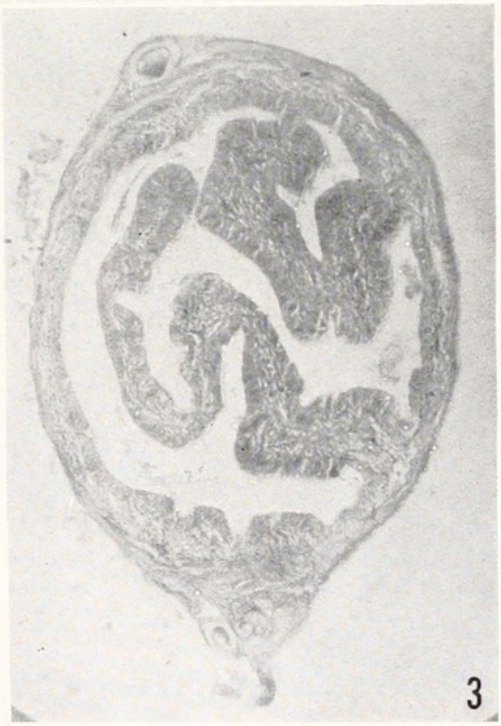
PLATE G

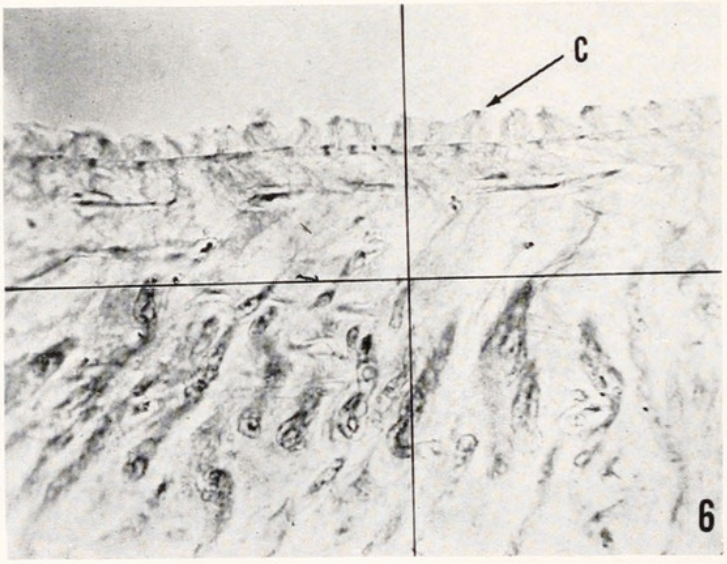












portant a role as is generally assumed and that the walking legs may possess sufficient dexterity to manipulate the spermatophore so as to effect its attachment with the male and female in a head-to-head position.

When fixed in position on the female (Plate A, 4), the anterior end of the spermatophore is in close proximity to the openings of the genital pores. The factors coordinating the dehiscence of the spermatophore with the expulsion of the eggs are as yet unknown; however, it may be that the fluid accompanying the eggs has a chemical or physical effect causing the spermatophore to open and release the sperm at the appropriate moment.

Histology and Development

The testis

The thin wall or cortex surrounding the testis consists of two layers: an outer epithelium, and an inner layer of connective tissue. No muscle tissue is present. The body of the testis is composed of a mass of very minute, convoluted, seminiferous tubules in which the male reproductive cells are produced. It appears that the membrane-like wall of each tubule is also of two layers: the outer tunica or membrana propia, and the inner germinal epithelium.

The content of the tubules varies with the size of the shrimp and also with the season. For example, the testes of a young 130 mm. shrimp in February are much farther advanced than the testes of a 130 mm. shrimp in November. The tubules of small shrimp were found to contain spermatogonia and scattered nutritive or nurse cells (Plate F, 1). The spermatogonia have fairly definite cell walls and large round nuclei surrounded by a distinct mass of protoplasm. The nurse cells have irregularly-shaped nuclei imbedded in a syncitial mass of protoplasm with no visible cell boundaries.

As the season advances and the shrimp grows, the testes and the individual tubules increase greatly in size. Each spermatogonium passes through a period of quick growth to become a primary spermatocyte. A reduction division results in two secondary spermatocytes. These divide again to produce four spermatids which develop without further divisions into spermatozoa. The primary spermatocytes are larger than the secondary spermatocytes (Plate F, 2 and 3), which are in turn larger than the spermatids (Plate F, 4). In tubules containing these later stages, the nurse cells appear to be confined to the peripheral region of the tubule.

Once a shrimp reaches sexual maturity, the testes produce a continuous crop of sperm cells. At almost any time of the year an examination of the mature testis will reveal germ cells in all stages of development. Most of the tubules in cross-

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PLATE G

1. Vas deferens, cross-section, in proximal region. × 49.
2. Vas deferens, cross-section, in medial region, showing refractory sperm mass and extremely tall columnar epithelium lining cavities. SM—sperm mass. × 22.
3. Vas deferens, cross-section, in distal region. × 88.
4. Terminal ampoule, longitudinal-section, of immature shrimp. × 17.
5. Terminal ampoule, cross-section, of mature shrimp; spermatophore in process of formation. SP—spermatophore. × 14.
6. Cilia-bearing epithelium from terminal ampoule. C—cilia. × 367.

section show two typical stages but adjoining tubules may contain cells in different stages of development. The mature tubule (Plate F, 2) may normally contain along one margin a layer, several cells in thickness, of spermatogonia and primary spermatocytes. The main bulk of the tubule will be filled with secondary spermatocytes or spermatids or both.

The spermatozoa

Ripe spermatozoa were observed only in the vas deferens. The spermatozoan (Plate B, 3 and Plate F, 5) is composed of three typical parts: head, middle piece, and tail. The head is large and almost circular in outline, the middle piece is short and considerably more slender, while the tail is relatively thick and short. From its structure it is a logical assumption that the spermatozoan is capable of movement.

The vas deferens

The vas deferens leaves the testis as a simple tube (Plate G, 1) lined with cilia-bearing columnar epithelium and with some muscle and connective tissue in its outer wall. As the diameter of the tube increases, a longitudinal septum appears in its interior separating the tube into two channels of unequal diameter (Plate G, 2). The sperm cells move down the larger channel, their flow doubtlessly being facilitated by the beating of cilia and by secretions of the glandular epithelium. Within the smaller channel there develops from the margin a longitudinal fold which may be traced distally to the terminal ampoule. The epithelium lining the smaller channel produces a fluid which is probably involved in the formation of the spermatophore. This secretion and also the sperm mass become very hard and brittle when passed through the usual fixing and imbedding procedures, thereby making the sectioning process difficult.

After the second bend the vas deferens is reduced in diameter to form a narrow tube (Plate G, 3) which joins with the terminal ampoule. At the beginning of the narrow portion, the longitudinal septum becomes detached from the wall at one of its margins, forming a shelf or fold which continues to the terminal ampoule and parallels the other fold previously described. With the severing of this partition, the sperm-bearing fluid and the secretion of the other channel may come in partial contact for the first time. The arrangement of the folds, however, would tend to prevent any extensive intermingling of the two substances.

The greatly dilated distal region, or terminal ampoule (Plate G, 4 and 5), possesses a thick muscular wall lined with extremely tall columnar epithelial cells. From our observations the detailed composition of the wall is as follows: first a thin outer squamous epithelium underlain with connective tissue, several bands of circular muscles, then a wide zone which appears to be composed of interspersed longitudinal and circular muscle fibers, another layer of connective tissue, and finally the thick glandular epithelium. The latter contains enormous nuclei and bears cilia in certain areas. The numerous folds and partitions are formed by extensions of columnar epithelium supported by connective tissue.

In cross- or longitudinal sections the terminal ampoule of the mature shrimp presents a very complex picture. Examination of these organs from a number of individuals showed, however, that the general arrangement was quite uniform

for all. The most easily identifiable structures of the developing spermatophore are the sperm cells enclosed in a sheath and surrounded by a mass of chitinous material. In some sections the wings of the spermatophore may be seen in process of formation. Because of the refractory nature of the contents of the ampoule following fixation and imbedding, it is extremely difficult to obtain good sections for study.

Fasten (1917) has called attention to the fact that cilia have been considered universally absent from the Arthropoda. He found them, however, to occur in the vasa deferentia of Anomura and Brachyura. As reported here, striking examples of these processes are found also in the male tract of the Peneidea.

Summary

The general anatomy and histology of the reproductive organs of the shrimp, *Penaeus setiferus* (Linnaeus), have been studied and described.

Although the cytological phenomena of oogēnesis and spermatogenesis have not been completely worked out, gross developmental changes in size and coloration of the organs have been related to histological and cytological changes so that the field worker, without access to a microscopy laboratory, may more accurately determine and record the stage of development.

Observations have been included on the processes of impregnation and ovulation.

Unsuccessful efforts were made to find clues which would serve as an index to the age of a shrimp. Evidence was found, however, indicating that a female may spawn more than once in a single breeding season.

LITERATURE CITED

Anderson, William W., Milton J. Lindner, and Joseph E. King, 1948a. Observations on certain phases of the reproductive cycle in the common marine shrimp, Penaeus setiferus (Linn.). Manuscript submitted for publication.

Anderson, William W., Milton J. Lindner, and Joseph E. King, 1948b. Size distribution of the common shrimp, Penaeus setiferus (Linn.), occurring along the South Atlantic Coast and contributing factors. Manuscript submitted for publication.

Anderson, William W., Milton J. Lindner, and Joseph E. King, 1948c. Size distribution, and contributing factors, of the common marine shrimp, Penaeus setiferus (Linn.), occurring along sections of the Louisiana and Texas Coasts. Manuscript submitted for publication.

Andrews, E. A., 1911. Sperm transfer in certain Decapods. *Proc. U. S. Nat. Mus.*, **39**: 419–434.

Berkeley, Alfreda A., 1929. Sex reversal in Pandalus danae. *Amer. Nat.*, **63**: 571–573.

Bhatia, R. R., and V. Nath, 1931. Studies in the origin of yolk. VI. The crustacean oogenesis. *Quart. Jour. Micr. Sci., New Series*, **74**: 669–699.

Burkenroad, Martin D., 1934. The Penaeidae of Louisiana with a discussion of their world relationships. *Bull. Amer. Mus. Nat. Hist.*, **68**: 61–143.

Burkenroad, Martin D., 1939. Further observations on Penaeidae of the northern Gulf of Mexico. *Bull. Bingham Oceanographic Collection, Peabody Museum of Natural History*, **6**: 1–62.

Fasten, N., 1917. Male reproductive organs of Decapoda with special reference to Puget Sound forms. *Puget Sound Marine Station Publication*, **1**: 285–307.

Filbo, Elyamaun Magalhaes, 1943. Processo de determinacao de maturidade do camarao. Boletim do Ministeris da Agricultura, Septembio de 1943. Departamento Nacional da Producas Animal, Divisao de Caca e Pesca, Rio de Janeiro, Brasil.

GUTSELL, JAMES S., 1936. A study of the ovaries of the common shrimp Penaeus setiferus (Linn.) with reference to the life history. Unpublished manuscript in the files of the Gulf Investigations, U. S. Fish and Wildlife Service, New Orleans, Louisiana.

HELDT, JEANNE HENRI, 1931. Observations sur la ponte la fecondation et les premiers stades du development de l'oeuf chez Penaeus caramote Risso. *Comptes rendus des seances de l'Academie des Sciences,* **193**: 1039.

HELDT, JEANNE HENRI, 1938. La reproduction chez les Crustaces Decapodes de la famille des Peneides. *Annals de l'Institute Oceanographique,* **18**: 31–206.

LINDNER, MILTON J., WILLIAM W. ANDERSON, AND JOSEPH E. KING, 1948. The growth, life-span and weight-length relationship in the common marine shrimp, Penaeus setiferus (Linn.). Manuscript submitted for publication.

WEYMOUTH, F. W., MILTON J. LINDNER, AND W. W. ANDERSON, 1933. Preliminary report on the life history of the common shrimp Penaeus setiferus (Linn.). *Bull. of the U. S. Bureau of Fisheries,* **48**: 1–26.