T H E S I S

on

The Morphology of the Crustacean

*Callianassa californiensis* Dana

Submitted to the

O R E G O N A G R I C U L T U R A L C O L L E G E

In Partial Fulfillment of the Requirements

For the Degree of

MASTER OF SCIENCE

by

Nettie Lorene Murray

May 15, 1926

APPROVED:

[redacted]

Professor of Zoology and Physiology.

In Charge of Major

[redacted]

Chairman of Committee on Graduate Study.

# TABLE OF CONTENTS

INTRODUCTION

Callianassa is one of the six genera of shrimps belonging to the family Callianassidae of the burrowing tribe Thalassinidea. The Thalassinidea are usually classified as belonging to the order of Decapoda and sub-order Macrura. This tribe is composed of four families which, according to Borradaile's (1903) classification, contain 125 species. The Callianassidae are divided into two subfamilies; namely, the Upogebiinae and the Callianassinae, the latter of which is divided into three genera, of which Callianassa is one. The genus Callianassa contains fifty of the 125 species of the tribe. In his "Revision du Genre Callianassa", A. Milne-Edwards (1870) described seventeen living and three extinct species of Callianassa. Since his time the remaining species have been described.

Nearly all the members of the Thallassinidea burrow in the sand or mud in the littoral zone, but a few inhabit the deeper waters. Because of their isolated mode of life they perhaps seem less plentiful than is really the case. Such isolated forms are interesting because they retain many primitive characteristics, and they thus form valuable objects of study from the standpoint of their relationship to the more familiar types of crustacea.

Callianassa californiensis Dana is one of the five species of Callianassa found along our western coast. It was first described by Dana in 1854 and in 1857 it was again described by Stimpson under the name Callianassa occidentalis. Schmitt (1921) states that this species has been collected by Lockington as far north as Mutiny Bay, Alaska, and by Rathbun as far south as the mouth of the Tia Juana

River, San Diego County, California. Milne-Edwards (1870) has reported specimens from the Gulf of Mexico, and also states that inasmuch as their food consists largely of small crustacea and marine annelids, which are seized at the open ends of the burrows, it is safe to conclude that they rarely come out of their dwelling places. Eggs of Callianassa were found in the stomach of one of the specimens examined by the present writer. These may have been eggs that had become detached from the pleopods, or it may be that Callianassa is inclined to be cannibalistic like its kinsman, the lobster. Callianassa is in turn used for food by other crustacea and by fish.

Since the classification of the crustacea is based almost entirely upon the study of external characteristics, there is a wealth of literature on these topics; however, except for several excellent and detailed descriptions of the internal anatomy of a few type forms, there is a comparative dearth of literature on this phase of the crustacea. Among the various groups of the crustacea the Thalassinidea especially have been neglected, probably on account of their mode of life. The literature on the genus Callianassa has been confined almost entirely to descriptions of the species. Since, because of its general organization, this genus may be considered a type form, and also since it comprises nearly half the species of the entire tribe, it would be of interest to have a knowledge of the internal anatomy of one of its members. Accordingly, the writer has undertaken a study of the internal organs (exclusive of the muscles) and a more detailed account of the external anatomy of this one species. Several specimens have been examined in the hope of avoiding extended descriptions of mere individual variations. Drawings and photographs have been freely used, supplemented by descriptive material.

The writer is indebted to Dr. Nathan Fasten, and to Dr. Florence Hague, of this college, for suggestions and kindly criticism. She also wishes to express her appreciation to Dr. W. K. Fisher, Director of the Hopkins Marine Station of Stanford University, for suggesting the problem and for information concerning the habits of *Callianassa californiensis*.

## MATERIALS AND METHOD

The specimens used for dissection were preserved in a solution of formaldehyde or in Bouin's solution. They were obtained from a slough near Moss Landing, about twenty miles north of Pacific Grove, California, and were collected by Dr. W. K. Fisher, Director of the Hopkins Marine Station of Stanford University, and by the collectors of the Pacific Biological Laboratories of Pacific Grove, California. The writer wishes to express her appreciation to these individuals for their interest and cooperation.

All dissection, except that of the sense organs, was carried on under water with the aid of a Leitz dissecting binocular microscope. A high powered binocular microscope and an ordinary compound microscope were used for dissecting the sense organs.

The tissues used for sectioning were taken from specimens that were preserved in toto; and, consequently, some of the structures were not ~~always~~ very clear. Most of the sections were cut seven microns in thickness, and stained with Ehrlich's haematoxylin and counter-stained with erythrosin.

## EXTERNAL MORPHOLOGY

### General Characteristics

Callianassa californiensis is a soft bodied crustacean with a compressed carapace and a flattened abdomen. The cephalothorax is short, comprising only about one-fourth of the total body length. In addition to the transverse cervical groove, the carapace is further marked on each side by a longitudinal groove, the characteristic "linea thalassinica" (Fig. 4). These grooves mark the division between the median and lateral portions of the carapace. The rostrum is very small. The posterior margin of the carapace is setose. The bases of the first four pairs of thoracic legs are so crowded together that the sternum is practically obliterated (Fig. 1). Although these appendages have the customary seven segments, the basipodite is very short and is immovably articulated with the ischiopodite so that there are virtually only six segments. The last thoracic somite is movable and is only partially covered by the carapace. Because of its relative freedom from the other thoracic segments it becomes in effect a part of the abdomen. Connected with this peculiarity is the habit of carrying the fifth pair of thoracic legs somewhat above and apart from the others. The coxopodites of these legs are not so closely approximated as the others. These appendages further differ from the others in having only six segments, the dactylopodite being missing.

Of the abdominal segments the first is the smallest. At its junction with the cephalothorx it is very slender, and this facilitates turning within the burrow. The remaining abdominal somites are much broader than the first. The second segment is the longest; the sixth next in length; then the third and fifth, which are nearly equal; and lastly the fourth, which is somewhat shorter than the first. Abdominal pleura are lacking in the first segment, and are very small in the others.

Very little of the integument is calcified, the most highly calcified portions being in the chelipeds. Likewise, the internal skeleton or endophragmal system is uncalcified. However, the parts of this system are complete, so that the endosternites bridge over the sternal canal, but the last thoracic somite is not included.

## Appendages

The cephalic appendages, the maxillipeds, and the abdominal appendages are shown in plate I, the thoracic legs in plate II.

The eye-stalks (Fig. 5) are trihedral, the upper face being flattened or slightly concave; the inner, flat; and the lower, convex. The extremeties are sharp and divergent. A small, oval, darkly pigmented cornea (co) is placed obliquely in the middle of the upper surface.

Each eye-stalk rests upon the proximal segment of the first antenna (Fig. 6), the convex lower surface of the former fitting into the concave upper surface of the latter and completely covering the aperture of the statocyst (sta). The basal segment of the first antenna also presents a trihedral shape, the upper surface being concave; the inner flat; and the outer, convex. The longest segment of the peduncle is the third, and from this arise two annulated flagella, the upper or outer one (f) of which is thicker and somewhat shorter than the lower or inner one (f'). The annular segments of the former are shorter than those of the latter. The eight terminal segments (with the exception of the last) of the upper flagellum each bears a row of blunt finger-like setae (Fig. 53, os) on the inner anterior margin. The next to the last segment has two of these setae; the third from the last, five; and in the eighth the number has increased to eight. These probably function as chemical perceptors and may be referred to as olfactory setae. The other segments of the upper flagellum each bear one or two small spine-like setae on the anterior border. A tuft of plumose hairs is also found on each of the olfactory segments, and on the following or terminal segment. Except for four or five terminal annulations, the lower flagellum bears long non-plumose setae on the lower edge; whereas the second and third segments of the peduncle are provided with feathered setae principally.

The second antenna (Fig. 7) is about two-thirds as long as the body of the animal. The basal segment bears on its lateral face a small papilla (p) through which the antennary gland opens. The second segment bears a vestigial scale (sc). This segment and the two following are equipped with long plumose hairs on the outer border. The long flagellum is provided with a few simple setae of varying lengths on each segment, and on the upper side a few short bush-like setae occur at irregular intervals.

The mandible (Fig. 8) is a foliaceous organ with a long palp and a thin, scale-like body or coxopodite (c) the inner surface of which is concave. The biting edge of the mandible is unevenly serrated, one or two small teeth being placed between the larger ones. The mandibular palp (mp) is large compared with the body of the appendage, and its terminal segment is relatively long.

The first maxilla (Fig. 9) is a very much flattened organ. The inner margins of the basipodite (b) and the first podomere (en.1) of the endopodite are equipped with short setae which assist in mastication. The second podomere (en.2) of the endopodite is long and slender, and bears a tuft of plumose setae on its distal end.

The second maxilla (Fig. 10), like the first, is thin and foliaceous, and is provided with masticatory bristles on the cleft inner borders of the coxopodite and basipodite (c,b). The small endopodite (en) has two terminal tufts of plumose hairs. The exopodite or scaphognathite (ex) is broad and the upper edge is turned down to form a groove. The hairs which border this organ are jointed at the base, and, as in all of the longer setae, consist of a long basal portion followed by many shorter annulations (Fig. 55). Between the bases of these setae are goblet-shaped depressions (g) which, in the preserved specimens, seem to contain a granulated gelatinous mass that extends on to the basal portions of the setae.

The first maxilliped (Fig. 11) is characterized by a long, slightly fleshy basipodite (b). The endopodite is rudimentary; but the flattened exopodite is long and broad, and extremely long plumose hairs are found on the distal portion of its inner edge. A long epipodite (ep), which is without gills, extends parallel with the scaphognathite, with which it is associated in respiration.

The second maxilliped (Fig. 12) is slender and curves outward. Long plumose setae arising from the inner margin of the endopodite completely bridge the space between the two maxillipeds. A sword-like exopodite with serrated margins, upon which are borne jointed setae, lies behind the endopodite when at rest. A vestigial epipodite is also present.

The third maxilliped (Fig. 13) is a highly specialized operculiform organ, and, because of its size, shape, and unusual thickness, it stands out in marked contrast to the other appendages. A short and slender stem (c,b) supports an endopodite of remarkable proportions and structure. The two thick and broad basal segments (en.1 and en.2) of the endopodite are immovably articulated, and it is to the size and structure of these two segments that the organ owes its peculiarity. Each of these two basal segments (ischiopodite and meropodite) is marked by a longitudinal suture on its inner face. In the ischiopodite this suture is serrated. The outer faces (Fig. 14) of these segments are decidedly convex and are without sutures. The remaining three segments of the endopodite form a palp-like strucutre (Fig. 13) which folds over the inner surface of the first two. Together the two maxillipeds serve as a receptacle for carrying mud from the burrow.

The rifht and left chelipeds are always unequal in size, the larger or crushing claw being indifferently on the right or left. This asymmetry is much more marked in the male than in the female (compare Figs. 2 and 3). The basepodite is short and broad at the base. In the larger cheliped (Fig. 4) the ischiopodite presents a dentate inferior margin; while the meropodite is characterized by a basal spine on its inferior border.

The proportions of the carpodite form a classificatory distinction in that the length is only slightly greater than the breadth, but is longer than the propodite. The superior border of the carpodite curves inward. The propodite is deeply hollowed out between the dactyls and a small spine with denticulated inferior border projects between the bases of the latter. The terminus of the movable finger is curved like a hook, and the opposing edges of both dactyls are denticulated. Even when the dactyls are closed there is a considerable hiatus between their bases.

The smaller cheliped possesses no spine on the meropodite, and the caropdite is much longer than it is wide. Ther is no dentate process between the claws. In the female the chelipeds are much smaller in proportion to the size of the body, and the asymmetry is much less pronounced. In other respects, however, they are very similar to those of the male.

The remaining four pairs of pereiopods present no sexual differences. The second pair is also chelate, but exhibits no special characteristics. However, the sub-chelate third pair of pereiopods has become peculiarly modified into a shovel-like appendage for use in burrowing. This modification is in the palm, which has become flattened and oval, and is much broader than it is long. A small dactyl is found on the anterior end. The fourth pair of pereiopods which terminate in a simple dactyl, exhibit no characteristics of special interest. The last pair are very similar to the fourth pair, but are without a dactyl.

In the male the pleopods of the first abdominal somite are vestigial styliform structures (Fig. 18) that are too degenerate to be functional; and on the second segment they are entirely lacking. In the female the first pair of pleopods (Fig. 15) are uniramous, three jointed organs bearing long plumose filaments for carrying eggs. The second pair of pleopods (Fig. 16) are larger and they bear a flagelliform exopodite. Both endopodite and exopodite are fringed with long setae, but in the specimens examined only those of the endopodite were bearing eggs.

The remaining pleopods are the same in both sexes. The third, fourth, and fifth pairs (Fig. 17) are broad, foliaceous structures which extend across the entire width of the abdomen, the inner margins of the endopodites of each pair meeting in the mid-line of the body. Although present in many of the Thalassinidea, an "appendix interna" is lacking in Callianassa californiensis. The exopodites curve medially and overlap each other; and the curve of the inner margin of the protopodite conforms to the convexity of the ventral surface of the abdomen. They thus form a broad paddle for swimming, or for aerating the burrow.

The tail-fan (Fig. 4) is broad and powerful. The short unsegmented protopodite of the uropods supports broad lamellar rami, the larger of which is the outer or exopodite. Neither the telson nor the exopodite of the uropods is divided by a transverse joint. This is in marked contrast to one family (the Laomediidae) of the Thalassinidea, in which both rami of the uropods are divided by a transverse suture. Large bundles of muscle fibers are visible through the integument of the uropods and telson.

## INTERNAL MORPHOLOGY

### Digestive System

With the exception of the labrum and metastoma, the mouth parts have been described above. The labrum is a fleshy shield-shaped structure which fits into the upper part of the mouth. The latter is a narrow slit with an expanded upper portion and it is into this V-shaped part that the labrum fits. The middle portion of the upper face of the labrum is elevated into a firm beak-like papilla (Fig. 21, b). On each side of this papilla is a concavity in which lies the distal segment of the mandibular palp (mp), The masticatory blade (c) of the mandible also lies over this concavity and the tip of the palp, so that the cutting edges meet in the mid-line. On the under surface of the labrum is a soft rounded papilla (p) which closes the upper part of the mouth. Elongated rounded swellings of the esophageal wall form the sides of the mouth, and from these the hatchet-shaped metastoma (m) project. Each of these blades fits closely over the convex surface of the body of the mandible.

A short muscular esophagus (Fig. 22, o) leads upward from the mouth to the stomach. Its dorsal wall is thrown into a broad ridge which extends the entire length and terminates in a papilla (Fig. 26, op) at the entrance to the anterior division of the stomach. This ridge, which is continuous with the ventral papilla of the labrum, projects into the esophagus sufficiently to make its lumen somewhat Y-shaped. Two lateral folds also project into the stomach from the posterior end of the esophagus. The walls of the esophagus consist of the inner chitinous lining (Fig. 33, ch), an epithelial layer (t), and a broad connective tissue layer (ct) containing striated muscle tissue. The columnar cells of the epithelium vary greatly in length, those lining the central portion of the Y-shaped lumen being fully twice as long as those along the dorsal or ventral portions of the lumen. The nuclei are located near the basal borders of the cells. The connective tissue layer contains in its central portion a few striated muscle fibers (m") which run obliquely, and near its outer border a layer of longitudinal bundles of voluntary muscle fibers (m).

The anterior or cardiac division of the stomach is somewhat larger than the posterior or pyloric division, from which it is separated by the gastric mill and cardio-pyloric valves. The anterior portion serves for sorting and storing food, the posterior portion for filtering out all except minute particles of food. The entrance to the cardiac division is guarded by thin chitinous folds (Figs. 24, 25, 26, ev) which arise one from each lateral wall and project mediad. Long setae border the inner or free margin of each fold and extend across the aperture of the esophagus. On each side, posterior and ventral to these valvular folds, are two others (a) which are continued backward and then upward to the region of the lateral teeth (lt). Their edges are also setose, and they serve to direct food into the gastric mill, or permit the fine particles to pass to the side of the latter into the pyloric division. Just below the lateral teeth the anterior of these folds thickens and elaborates into a setose "pusher" (f) for keeping the food within the range of the teeth. Also subserving this same function is a large bilobed tongue-like elevation (f') from the ventral floor. Both of these structures are provided with short stiff bristles which no doubt aid in mastication. The ventral elevation arises between the cardiac and pyloric divisions, and, together with a thin, setose-margined fold from each side, constitutes a cardio-pyloric valve.

Two lateral plates of teeth and a median dorsal tooth, together with associated ossicles, constitute the gastric mill (Fig. 28). The principal muscles which operate this grinding mechanism are shown in Fig. 22. In the following description of the ossicles, the terminology used by Huxley (1880) for those of the crayfish will be followed in so far as it suffices. On the dorsal wall of the stomach is a large flat ossicle (Fig. 28, ca) which somewhat resembles the form of a spread eagle design. This ossicle begins at the anterior boundary of the cardiac division. The wings of this cardiac ossicle spread laterally and connect with the outer surface of a small pterocardiac ossicle (pt). The latter is a heavy V-shaped structure, the medial bar of which is attached along its entire edge to the lateral process of the base of the cardiac ossicle and also to a process of the urocardiac ossicle (u); whereas the lateral bar is attached only at the tip by a long elastic ligament (l) to the zygocardiac ossicle (z). Its structure and arrangement are such that it serves as a hinge between the medial ossicles and the lateral tooth.

Posteriorly the cardiac ossicle is joined to a heavy structure corresponding to the urocardiac process of the cardiac ossicle in the crayfish. In Callianassa, however, this is a separate structure, and will be referred to as the urocardiac ossicle (u). Anteriorly it sends out heavy transverse bars, while the main body continues backwards. The middle and posterior portions of the body become greatly thickened, and from its posterior end a large brownish median tooth (mt) projects downward. This tooth is inclined anteriorly, and its action, combined with that of the ventral "pusher" would keep returning the larger particles of food to the lateral grinders. A slender bar or prepyloric ossicle (pp)is connected to the posterior end of the urocardiac ossicle. The posterior end of the bar is in turn attached to a median crescent-shaped pyloric ossicle (p). If the prepyloric ossicle is stretched out (as in the diagram) by muscular contraction the median tooth is raised. The elastic joints at each end of the bar provide for recoil of the tooth. The lateral zygocardiac ossicle is a large body with a concave inner surface and a heavy medial border. This thickened medial portion gives rise to the lateral plate of teeth (lt). The latter is a yellowish-brown triangular plate, the surface of which is divided by transverse furrows into about twenty ridges whose free ends project inward. The middle ridges are the longest; those on the anterior end of the plate are heavy, but they gradually decrease in size posteriorly. In the crayfish the large pyloric ossicle extends laterally to unite with the zygocardiac ossicle. The pyloric ossicle of Callianassa, however, is small; and a separate structure, which the writer will refer to as the "zygopyloric" ossicle (Fig. 28, zy), serves to connect the pyloric and zygocardiac ossicles. The anterior portion of the zygopyloric ossicle is inserted into a notch in the posterior border of the zygocardiac ossicle; while its posterior end conforms to the curve of the crescent of the pyloric ossicle.

The posterior division of the stomach is almost filled with setose pads and ridges. On each side on the dorso-lateral wall just posterior to the lateral teeth is a large oval pad (Figs. 24, 25, 26, b), the entire surface of which is beset with short hairs. These pads lie diagonally so that their posterior ends converge toward the mid-dorsal line. Posterior to this point is a deep recess or dorsal pouch (dp).

Paired ventro-lateral pouches (Fig. 26, lp) each contain a small pad (Figs. 25 and 26, b') which arises from the lateral wall and over which a conforming surface of the ventral floor fits like a cover. These covers (Fig. 26, r) are united in the mid-ventral line into a ridge (Figs. 25 and 26, vv), the free end of which projects posteriorly into the mid-gut. The pads are densely covered with short hairs. Each of the ventral folds or covers is an aggregate of closely-set longitudinal parallel ridges, the inner edge of each of which is fringed with a row of fine hairs which overlap those of the following ridge.

The wall of the stomach is composed of the chitinous lining with its elaborate thickenings, an epithelial layer, and a broad layer of connective tissue containing near its outer margin bundles of striated muscle fibers running in various directions. The cells of the epithelial layer resemble those of the esophageal wall, and their nuclei are likewise located at the outer borders of the cells.

The chitinous lining of the stomach terminates in six processes (a dorsal, a ventral, and four lateral ones) which project into the lumen of the mid-gut and form a valve between the stomach and intestine. The longest valvular process (Figs. 25 and 26, dv) is a median triangular structure from the dorsal wall. The ventral process (vv) is the continuation of the ridge between the surfaces which cover the small pads. Each of the outer lateral valves (lv) is a triangular process, the base of which is continuous on each side with a fold of chitin arising from the posterior end of the large oval pad, and on the other with a fold arising from the smaller ventro-lateral pad. The inner lateral valves (cv) are curious complicated structures that fill the lumen of the intestine. They consist of five small hollow chitinous caeca on each side. Each group of five caeca originates from a hollow enlargement of the lateral fold of the posterior division of the stomach. This enlargement is attached to the base of the outer lateral valve. The distal ends of the ten caeca converge, and they thus form a sort of conical porous plug through which the food may pass. Each caecum (Fig. 27) is beset with patches of microscopic hairs (s) that project backward.

The mid-gut (Figs. 19 and 22, i) is the longest portion of the alimentary tract, extending from the region of the third pereiopod to the anterior suture of the sixth abdominal segment. Smith (1909) states that Mr. E. H. Schuster noted the proportionate lengths of mid- and hind-guts in several crustacea, among them *Callianassa subterranea*, but that his drawings were never published. With respect to length of mid-gut, Callianassa resembles the lobster, but is in marked contrast to the crayfish. The walls of the mid-gut are delicate, consisting of only two layers, an inner one of epithelium (Fig. 30, e) which is thrown into longitudinal folds, and an outer one of connective tissue (ct).

On each side of the anterior end of the mid-gut a short, flattened evagination of the latter projects anteriorly as a flap along the lateral walls of the stomach for only a few millimeters. These are the remnants of anterior intestinal caeca. The epithelial lining of these caeca is prominently convoluted. At its beginning the mid-gut receives, on the ventral surface, the openings (Figs. 22, 24, 26, do) of the ducts of the digestive glands (Figs. 19, 20, 22, dg) or hepato-pancreas. Each of these glands, which extend on either side of the mid-gut as far as the fourth or fifth abdominal somite, consists of innumerable slender, hollow caeca which open into a common duct. This duct traverses the entire length of the gland, and the caeca empty into it separately or in pairs (Fig. 23) on all sides throughout its entire length. The caeca of each gland are so arranged that they form a sort of concavity on the medial surface. The concavities fit around the mid-gut, and each also incloses an hepatic artery (ha), which thus lies near the hepatic duct. The right and left digestive glands are never equal in length, one always exceeding the other by four or five millimeters. The longer one is arbitrarily on the right or left side.

The entire gland is surrounded by a very thin transparent membrane. The distal ends of the caeca are lighter in color (Fig. 23) than the remaining portion. Each caecum consists of a single layer of columnar cells (Fig. 32, e) surrounding a large lumen, and an extremely delicate investing serous membrane (sm). The cytoplasm of these cells is highly vacuolated, the vacuolation becoming more prominent toward the distal end of the caecum. Part of the fluid produced by the cells of the caeca consists of globules of yellow oil.

A short intestinal caecum (Fig. 22, c) arises at the junction of the mid-gut and hind-gut. It originates on the right dorso-lateral surface of the intestine, and, after proceeding a short distance anteriorly, curves upward and to the left, passing over the dorsal surface of the intestine and over and around the left gonad. In many cases the caecum passes directly under the ovary, or testis, without encircling it. From there the caecum proceeds posteriorly as far as the telson, following an irregular course ventral to the gonad. In one specimen the caecum went through the tissue of the ovary. This probably happened during the embryonic development, but since the ovary was mature it may have occurred during the ripening of the latter.

The walls of the caecum (Fig. 31) are made up of the same layers as those of the mid-gut, and, as in the mid-gut, the epithelial layer is thrown into longitudinal folds. Although an excretory function has commonly been ascribed to the intestinal caeca of decapods, this scarcely seems tenable. In view of the fact that it arises from the mid-gut, it is quite probable that its function is to increase absorptive surface. It is well supplied with arteries, both from the superior abdominal artery and from branches of the sixth lateral segmental artery.

The hind-gut (Fig. 22, hg) extends from the point of origin of the intestinal caecum to the anus, located in the mid-ventral surface of the telson. The walls of the hind-gut (Fig. 29) are very thick compared with those of the mid-gut. Next the chitinous lining (ch) is a layer of columnar epithelium (e) that is thrown into a few deep longitudinal folds. Surrounding the epithelial layer is a layer of connective tissue (ct). This stroma extends into the folds of the epithelium. Longitudinal bundles of striated muscle tissue (m) are found scattered in that part of the connective tissue layer that projects within these folds. Outside the connective tissue is a prominent layer of bundles of striated muscle fibers (m') arranged circularly. The outer layer, which is as wide as the muscular layer, consists of a stroma of connective tissue (ct') similar to the preceding one, but containing fewer fibers and more cells.

A mass of glandular tissue (Fig. 22, igl) surrounds the intestine at the junction of mid- and hind-guts. It is made up of small tubules (Fig. 29, tu) which are held together by connective tissue that is continuous with the outer layer of the intestine. Each tubule consists of a single layer of secretory cells surrounding a central lumen. The cytoplasm of these cells seems to be filled throughout with coarse granules that stain a deep violet in Ehrlich's haematoxylin. The lumen apparently is not lined with epithelium, but a colloidal matrix extends from the inner borders of the cells towards the central cavity. Both longitudinal and transverse sections were made of the intestine and gland, but in neither case was there an indication of any duct leading from the gland into the intestine or the caecum. Clots of blood (cb) occur in the connective tissue supporting the tubules. A very few scattered tubules of this type were found toward the posterior end of the rectum.

## Circulatory System

The heart is located in the pericardial sinus between the cervical groove and the posterior margin of the carapace. The dorsal surface of the heart (Fig. 34) is unequally hexagonal in outline. The depth of its posterior wall and the sharpness of its anterior part cause the organ to appear somewhat wedge-shaped. Supporting bands of fibers extend from the angles of the heart to the pericardial walls. There are two dorsal ostia, two dorso-lateral ones, and two that are ventro-lateral in position. Paired antennary arteries (Fig. 34, a) are given off from the middle of the anterior margin of the heart and pass along the lateral walls of the stomach where they lie above the bladder (Fig. 37, bl) of the antennary gland to which they adhere. They send branches to the stomach, to the end-sac of the antennary gland, and to the antennae. A smaller median ophthalmic artery (o) arises between the antennary arteries, and passes over the dorsal wall of the stomach to supply the eyes, the brain, and the portions of the green gland in this region.

From the anterior margin of the ventral wall of the heart, paired hepatic arteries (Fig. 36, ha) arise. These dip downward to the digestive glands, giving off branches to the ventral wall of the stomach, the anterior portion of the liver and the gonads, and then extend posteriorly, one on the median side of each gland. Toward the distal end of the liver the hepatic artery ramifies throughout the organ, and a few branches extend to the intestine.

The large superior abdominal artery (Fig. 35, saa) originates from the base of the posterior wall of the heart, and proceeds caudad between the gonads (Fig. 19). From this artery arise six pairs of lateral segmental arteries, the branches of which supply the muscles and gonads, the main trunk extending on around to supply the swimmerets. Considerable asymmetry occurs in connection with the intestinal caecum. An extra branch originates from the left one of the fifth pair of lateral arteries (Fig. 37) and this sends branches to the caecum, to the intestinal gland, and to the intestine. The lateral arteries of the sixth segment extend caudad throughout the length of the somite and into the telson, giving off several branches to the muscles and to the uropods. On the medial side of the left artery several branches pass to the caecum. The intestinal gland, however, receives one branch each from the right and the left artery. Throughout its course the superior abdominal artery gives rise to numerous ventral arteries which lead to the intestine and to the gonads. In the diagram (Fig. 37) the former are represented by the intersegmental branches on the right side, the latter by those on the left side.

The sternal artery (Fig. 35, sa) arises just below the superior abdominal artery, and, passing over one gonad but between the digestive glands, goes downward and forward on either the right or the left side of the intestine until it reaches the ventral nerve cord in the sternal sinus. At this point it passes through the nerve cord between the third and fourth thoracic ganglia (sixth and seventh thoracic somites) and immediately divides (Fig. 38) into an anterior thoracic branch (at) and a posterior branch or inferior abdominal artery (iaa), which lie just beneath the nerve cord. The anterior thoracic artery sends large branches to the three anterior pairs of walking legs and to the mouth parts. The inferior abdominal artery supplies the fourth pair of pereiopods and then extends backward to the fifth thoracic ganglion where it divides into two large arteries which supply the last pair of walking legs. These arteries follow the course of the nerves which supply these appendages. From one of these arteries (usually the left) a slender branch (iaa') is given off to supply the floor of the abdomen. The portion of the inferior abdominal artery which extends into the abdomen is therefore merely a branch from a segmental artery. It is so small that in a non-injected specimen it cannot be traced beyond the third abdominal somite.

Herrick (1909), in his Natural History of the American Lobster, calls attention to the common error of stating that the swimmerets receive their blood supply from the inferior abdominal artery instead of from the lateral segmental branches of the superior abdominal vessel. However, he states that the inferior abdominal artery "supplies a small part of the ventral surface of the abdomen, but none of the appendages." In Callianassa and the crayfish, at least, the inferior abdominal artery does supply the fourth and fifth pairs of walking legs; and, since the sternal artery divides between the third and fourth pairs of walking legs, it seems logical to suppose that this is also true in the lobster.

From the arterial branches the blood empties into sinuses, which in Callianassa are rather spacious, and it is then carried from the ventral sinus to the gills by means of afferent branchial veins. From the gills other veins conduct the aerated blood to the pericardial sinus.

## Respiratory System

The gills of Callianassa are reduced to ten pairs, all of which are arthrobranchiae. Two small ones are present on the arthroidial membrane of the third maxilliped, and two on each of the next four somites. The gills increase in size from before backwards (Fig. 39). In structure they are phyllobranchiae, and are attached near the ventral end of the main axis (Fig. 40). Calman (1909) calls attention to the interesting fact that among the Thalassinidea both phyllo- and trichobranchiae are found, and also gills of an intermediate character. However, in the majority of the Thalassinidea the gills are trichobranchiate. There are about one hundred pairs of laminae (Fig. 41, _l_) in one of the posterior gills of _Callianassa californiensis_. Blood is carried to the laminae by means of the afferent or external canal (_a_) of the stem of the gill, and is returned by the efferent or internal canal (_e_). The ten afferent branchial veins are supplied from five channels leading from the ventral sinus. The efferent canals of the two branchiae of each somite empty into a common channel, so that the blood is conveyed from the gills to the pericardial sinus by five branchio-pericardial channels. The scaphognathite for maintaining the branchial current of water has already been described in connection with the second maxilla.

A large epipodite (Fig. 11, ep) is present on the first maxilliped, and a vestigial one on the second (Fig. 12). The former extends backward under the branchiostegite parallel with the scaphognathite, and cooperates with the latter in maintaining the respiratory current.

Callianassa has several adaptations for carrying on respiration within a burrow. First, the large cheliped acts as an operculum to prevent objects from falling into the burrow. Second, the densely bristled thoracic appendages strain out the sand, and it may be that these are folded so as to form a sand-free reservoir of water beneath the body, such as Smith (1909) mentions in the case of Atelecyclus. The last and most important adaptation is that the three pairs of broad posterior swimmerets keep a current of water circulating.

## Excretory System

The antennal or green gland (Figs. 42 and 43) in Callianassa is a large complicated structure, opening to the exterior through a papilla (Fig. 7, p) on the lateral face of the basal segment of the second antenna. The end-sac (Fig. 43, es) occupies the space at the base of the antenna, extending into the basal segment of the latter, and a ventral porjection (es') even fills the basal portion of the mandible. A large bladder or vesicle (bl) lies along the lateral wall of the stomach just below the antennary artery, and extends caudad as far as the anterior pericardial wall where it meets the gonad, liver, and lateral intestinal caecum. About midway of the length of the vesicle is a medial porjection (Fig. 42) which passes beneath the stomach and joins a similar structure from the opposite side. There is, however, no connection between the cavities of the two vesicles at this point. On the lateral side, arborizations of the bladder (b) extend into the branchiostegite, entirely surrounding the branchiostegal muscle (Fig. 43, bm). In the anterior region the cavities of the two sides of the bladder are connected at two points,--one by a broad channel over the brain and another by a smaller extension which encircles the esophagus. In the region of the brain the vesicle ramifies extensively, filling all the spaces around the nerves and esophagus and projecting into the eye-stalks as far as the cornea. Minor portions ramify among the thoracic muscles. The duct (u) leading from the bladder to the papilla lies along the dorsal surface of the end-sac.

The walls of the bladder consist of columnar epithelium (Fig. 44, ebl) surrounded by a thin membrane of connective tissue (ct). The epithelium of the bladder invests the end-sac and forms the septa of the latter, resembling in this respect the green gland of Pandalus described by Weldon (1891). The connective tissue continues around the end-sac, extending inward to support the labyrinth. In the vesicle proper the bladder epithelium consists of narrow granular cells which stain deeply with haematoxylin. The nuclei are rounded and granular and are usually found near the bases of the cells. Near the point where the cavity of the end-sac opens into the bladder, numerous mucous cells (mu) appear in the epithelium of the latter. As the bladder epithelium (ebl') invests the epithelium of the end-sac the cells become shorter, the cytoplasm stains more deeply with haematoxylin, and the nuclei are placed more nearly in the center.

The cavity (c) of the end-sac is lined with a single layer of epithelial cells (ees) which project irregularly into it. These cells are pale and finely granular, with rounded granular nuclei very similar to those of the bladder epithelium. However, these nuclei may range from the bases to the free borders of the cells where they often seem to project beyond the margin of the cytoplasm. Occasional patches without epithelium may occur. Irregular clots of a homogeneous substance are found within the cavity of the end-sac.

## Reproductive System

a. Reproductive System of Male.-- The testes (Fig. 46) consist of paired slender rods of tissue which throughout most of their course lie dorsal to the liver, one on each side of the superior abdominal artery. These organs arise in the sixth abdominal segment, at the same level as the intestinal caecum, and extend anteriorally beneath the digestive gland to the region just posterior to the third pleopod. At this point they curve around the liver until the dorsal surface is reached, and then continue anteriorally, one on each side of the superior abdominal artery. The testes are associated with the artery to the point where the latter leaves the heart. Then, still lying on the dorsal surface of the liver, they continue forward beneath the heart to the anterior margin of the latter, where they unite. They thus resemble a loop of thread with the free ends pointing posteriorly. Near the anterior margin of the seventh thoracic somite each testis gives off a slender transparent vas deferens (vd) which passes postero-laterally for a short distance, then extends laterally and ventrally as an enlarged vesicula seminalis (vs), finally narrowing into a slender ductus ejaculatorius (d) which finds exit on the medial surface of the distal end of the fifth pereiopod. One vas deferens arises somewhat anterior to the other.

The germinal epithelium of the testicular walls (Fig. 48) could not be identified, a thin capsule of connective tissue (ct) being the only layer that was recognizable. This connective tissue appears to follow the walls of the compartments in which the spermatozoa are differentiating and developing. The younger cells appear in compact groups (sp'), but separate as the spermatozoa (sp) mature and push out into the lumen of the testis. The mature spermatozoa (Fig. 51) are spheroidal bodies with a light cap-like structure at one end.

In the vas deferens the spermatozoa are agglutinated into spherical spermatophores (Fig. 50) which have a thick case (sph). They are about 0.2 mm. in diameter. The wall of the vas deferens (Fig. 49) consists of an outer layer of fibrous connective tissue (ct), a circular band of involuntary muscle cells (m), and an inner layer of columnar epithelium (ep). The cells of the latter are elongated, being scarcely wider than the nuclei, which are located near the bases. The distal borders of these cells present ragged edges as though cilia were cemented together into tufts. Without doubt definite cilia could be distinguished if fresh tissues were properly fixed and preserved for sectioning. Fasten (1917) has found cilia bordering the epithelial cells of the vasa deferentia of four species of crustacea, among them types belonging to the Macrura and Anomura.

b. Reproductive System of Female.-- The ovaries (Fig. 45) also consist of two long tubular bodies which extend anteriorally from the sixth abdominal segment along each side of the superior abdominal artery. They lie dorsal to the liver throughout their entire course. In the region of the first abdominal segment the ovaries diverge slightly to form a loop, uniting just beneath the anterior portion of the heart.

The oviducts (od) arise opposite the third pereiopods and immediately expand into a glandular portion. They pass in a more nearly direct course to the exterior than do the vasa deferentia. Each oviduct opens on the medial side of the base of the third pereiopod, but because of the narrowness of the thoracic sternum, the two openings are almost contiguous. The intestinal caecum usually loops around the left ovary and extends posteriorad beneath it, or else passes under it directly. In one specimen the caecum passed through the tissue of the ovary instead of around or under it. In only one instance was the caecum looped around the right ovary.

As in the wall of the testis, the germinal epithelium of the ovarian wall could not be distinguished. The connective tissue coat (Fig. 47, _ct_) is like that of the testis. From a fold of tissue (_gr_) on one side of the ovary, cells differentiate and develop into ova. As the ova mature they become surrounded by a capsule or follicle and migrate outward from the germinal region. The ova have pale granular nuclei with a single nucleolus. Deutoplasmic granules are evenly distributed throughout the cytoplasm.

## Nervous System

The central nervous system (Fig. 52) is composed of a brain or supra-esophageal ganglion (_sg_) and a ventral nerve cord consisting of a sub-esophageal ganglion (_sg'_), five thoracic ganglia (IV-VIII), and six abdominal ganglia (1-6), united by double commissures. The brain is formed by the fusion of the three anterior pairs of cephalic ganglia, and each half is seen to consist of a dorsal anterior lobe, a median ventral portion, and a postero-lateral lobe. The anterior lobes supply nerves (_e_) to the eyes, and the postero-lateral lobes each give off a nerve (_a_) to the antenna. The nerves which supply the antennules arise from the median ventral surface. A single median nerve (_s_), which arises from the posterior margin of the brain, extends upward over the dorsal wall of the stomach and branches to supply the gastric muscles and the lateral walls of the stomach. Several small nerves from the dorso-lateral margin of the brain supply the green gland. The brain is connected with the sub-esophageal ganglion by esophageal commissures, and the latter are connected by a transverse commissure below the esophagus. The sub-esophageal ganglion is formed by the fusion of the last three pairs of cephalic ganglia, and the first three pairs of thoracic ganglia. Numerous nerves lead from the esophageal connectives and the sub-esophageal ganglion to the mouth parts, esophagus, and stomach.

The two halves of the nerve cord are united in the thoracic region except between the third and fourth thoracic ganglia (sixth and seventh thoracic somites) where they are separated by the sternal artery. Each thoracic ganglion sends a large nerve trunk downward to the corresponding walking legs. These nerves in turn give rise to branches to the gills, thoracic muscles, and integument.

The fifth thoracic ganglion is somewhat anterior to the last pair of pereiopods so that the nerves supplying these appendages must proceed backward a short distance before leading downward into the latter.

Both the first and second abdominal ganglia (the former of which is quite small) are located in the second abdominal somite. This is probably due to the shortening of the first abdominal segment, and apparently the nervous system has not been modified in accordance with the other structures. Each abdominal ganglion, except the first, gives off paired nerves to the corresponding appendages, and the sixth also supplies the telson. The lateral nerves (ms) arising from the sixth abdominal ganglion supply the muscles and skin. Arising posterior to these are two nerves (u) which supply the uropods, and medial to the latter are two others (th) which supply the telson and hing-gut. A single median nerve (i) arises from the dorsal surface of this ganglion to supply the intestine and gland. The commissures between the third and fourth and fourth and fifth abdominal ganglia are quite widely separated; and those between the fifth and sixth, although not separated, are very distinct.

In each segment, except the first, two pairs of nerves are given off from the connectives between the ganglia in the abdomen. In general, the more anterior pair supplies the ventral muscles and integument, and the posterior one supplies the lateral and dorsal regions particularly.

## Sense Organs

a. Statocysts.-- These are of the type usually found in the Macrura. They open to the exterior by a wide aperture which is roughly triangular in shape, and which is closely covered by plumose setae that originate from the postero-lateral lips and then project diagonally across it (Fig. 6). The laterally compressed sac contains numerous loosely agglutinated grains of sand. Two rows of plumose sensory setae project from the lower wall of the sac. In structure these "auditory" setae resemble those of the crayfish described by Huxley (1880).

b. Eyes.-- The eyes are placed in the middle of the upper surface of short sub-triangular eye-stalks (Fig. 5), so that the stalk projects beyond the cornea. The latter is deeply pigmented, and the facets, which are all of the hexagonal type, number less than one hundred.

c. Olfactory Organs.-- As suggested under "appendages," the nearly cylindrical, modified setae (Fig. 53, os) on the distal extremity of the outer flagellum of the first antennae probably are capable of receiving stimuli of a chemical nature. These, like the plumose setae, consist of a basal portion followed by several annulations. They do not, however, possess filaments; but are smooth and blunt, with a large hollow center, giving a somewhat swollen or caecal appearance. The size of the central cavity and the extremely delicate cuticle of these organs render them somewhat pendent. In all, there are about thirty-five of these organs on each of the first antennae.

d. Auditory Organs.-- Whether or not crustacea are capable of detecting sound vibrations has been a much disputed question. As a result of numerous experiments performed by various investigators, the general concensus of opinion seems to be that crustacea are not capable of hearing in the strict sense of the term. However, it is quite possible that the filaments of certain plumose setae can perceive vibrations in the water to the extent of notifying the animal of the approach of an enemy. The rapidity with which certain forms burrow when approached would seem to indicate that this is the case. The setae (Fig. 54, as) referred to above as occurring irregularly on the upper surface of the flagellum of the antennae of Callianassa may be of this nature. They do not occur on the distal segments; but on the basal two-thirds of the flagellum they average one to every two or three segments. In structure they are comparatively short and heavy and are non-annulated. The filaments, which arise on all sides of the main axis, seem to be more thickly set than those of the plumose setae on other parts of the body.

e. Tactile Organs.-- By far the majority of the sense organs of crustacea are tactile, and these take the form of both simple (Fig. 54, ts) and feathered setae (Fig. 55). They occur in places on all parts of the body of Callianassa, more particularly on the appendages. This animal is unusually well supplied with setae, especially with those of the plumose type. The majority of those on the flagella of the antennules and antennae are simple, but the feathered type prevails on the other appendages. They serve not only for tactile organs but also for straining out the sand, and the latter no doubt accounts for the plentiful supply of setae on Callianassa.

## DISCUSSION

Externally, Callianassa bears several points of resemblance to the lobster, crayfish, and hermit crab. Borradaile (1903) lists the following characteristics that suggest the latter: reduced gills, soft abdomen, small pleura, non-chelate third legs, freedom of last thoracic sternite, and manner of carrying fifth legs. They differ from the Paguridea in having a symmetrical abdomen, a broad tail fan, and chelate second legs, and in the likeness of the fifth legs to the others. In the broad tail-fan and the structure of the first and second legs Callianassa resembles the Nephropsidea, but differs from them in the points in which it resembles the Paguridea.

Internally, Callianassa californiensis differs in several respects from the type forms of crustacea heretofore described. In other forms the green gland opens through a papilla on the ventral surface of the base of the second antenna instead of on the lateral face as in Callianassa. The freedom of the last thoracic somite and its virtual addition to the abdomen, together with the smallness of the first abdominal somite, is associated with corresponding changes in the nervous and circulatory systems. For example, the last thoracic ganglion does not lie within the last thoracic somite, but sends nerves backwards to supply the structures of this somite. The ganglion of the first abdominal somite is very small and is located at the anterior end of the second, the former being supplied chiefly from the commissural branches. The inferior abdominal artery terminates as a branch from the artery which supplies the left fifth pereiopod.

To the writer's knowledge no gland, such as that described in Callianassa californiensis at the junction of mid- and hind-guts has been reported in any other crustacean. The processes of the pyloric valve are unusually complicated, due to the presence of the two groups of five chitinous caeca.

Very few decapods are entirely without gills on the last thoracic somite. Callianassa has none of any type on this segment.

In the length of the mid-gut and unpaired caecum Callianassa resembles the lobster. There are two rows of sensory hairs in the statocyst, as in the lobster and crayfish. Like the latter, Callianassa possesses the maximum number of ganglia found in any of the decapods, but the fusion of the two halves of the nerve cord is not nearly so complete.

Callianassa resembles the Paguridae in that the liver lies chiefly in the abdominal region, and further in the complexity of the vesicle of the excretory system. The Caridea also have an extensive bladder. Calman (1909) makes the following statement regarding the development of the Thalassinidea: "The earliest larva is a Zoea, which in some cases (Callianassa and Calocaris) resembles that of Caridea in having the three maxillipeds biramous and natatory; but in others (Upogebia and Jaxea) only the first and second are present on hatching, ......." The testes are tubular as in the Caridea. The greater part of the testes and ovaries lie within the abdomen, while in the Paguridea they lie wholly within the abdomen.

In most Macrura the spermatozoa are in rod-like masses; but in Callianassa the spermatophores are separate, resembling the Brachyura in this respect.

SUMMARY

1. Callianassa is a primitive soft bodied burrowing shrimp with a compressed carapace and a flattened abdomen. The last thoracic somite is movable.

2. The mandibles, maxillae, and first and second maxillipeds are thin, foliaceous structures. The third maxillipeds are huge, fleshy organs adapted for carrying mud from the burrow. The chelipeds are extremely unequal, especially in the male. The first pair of walking legs are equal and chelate; the second, subchelate with a flattened

oval propodite adapted to shoveling sand; the third terminates in a simple dactyl, and the fourth is without a dactyl. Pleopods are lacking in the first abdominal somite and vestigial in the second. In the female these appendages are functional egg-bearing organs. The broad posterior pleopods are used for aerating the burrow. The tail fan is broad, and both uropods and telson are without a transverse joint.

3. The mid-gut is the longest portion of the alimentary canal. Paired vestigial caeca, which are nothing more than folds of the intestine overlapping the stomach, mark the beginning of the mid-gut, and a short slender caecum marks its junction with the hind-gut. At this point a large mass of glandular tissue, of unknown function, and apparently without a duct, surrounds the intestine. The liver is a long unbranched organ with slender caeca which empty directly into a main duct. The filtering and sorting mechanism of the stomach is extremely complicated, the most unusual structure being two groups of five chitinous caeca each, which form a part of the pyloric valvular processes.

4. The circulatory system closely resembles that of the crayfish. The superior abdominal artery supplies the pleopods; the anterior thoracic artery supplies the first three pereiopods and the mouth parts; and the inferior abdominal artery supplies the fourth and fifth pairs of pereiopods. A slender branch from the artery to the left fifth pereiopod supplies the floor of the abdomen.

5. The gills are reduced to ten pairs of arthrobranchiae of the phyllobranchiate type. They are present on the third to the seventh thoracic somites inclusively. The first maxilliped possesses a large epipodite, the second a vestigial one.

6. The excretory system consists of an end-sac and a large vesicle which extends backward as far as the pericardium, sending a diverticulum under the stomach to meet the one from the opposite side. The vesicle ramifies extensively in the branchiostegite, and around the esophagus and brain. The epithelium of the bladder invests the epithelium of the end-sac.

7. The ovaries and testes are long tubular unbranched organs, extending from the sixth abdominal segment to the region of the third pereiopods where the right and left organs unite. The oviduct opens on the base of the third pereiopod, the vas deferens on the distal end of the coxopodite of the fifth pereiopod. The spermatozoa are spheroidal and are grouped into separate spherical spermatophores about 0.2 mm. in diameter.

8. In general the nervous system resembles that of the crayfish, but the sub-esophageal ganglion is small and the two halves of the nerve cord are not fused in the posterior somites. The last thoracic ganglion and the first abdominal ganglion (which is insignificant) do not lie within their respective somites.

9. The statocysts have a double row of sensory hairs and the aperture is wide. The eyes are small and pigmented and are placed in the middle of the upper surface of a short eye-stalk. Olfactory setae are confined to the last few segments of the outer flagellum of the

first antenna. They are long and number about 35 on each antennule. A few short bushy setae occur irregularly on the flagellum of the second antenna.

10. In addition to the general external appearance, Callianassa californiensis exhibits several internal features of a primitive nature. These may be briefly enumerated as follows:

a. The relative length of the mid-gut.

b. The lack of fusion of the two halves of the nerve cord in the posterior somites.

c. The unbranched, tubular form of the ovaries and testes, and the slight differentiation between these organs.

d. The non-lobulated form of the liver.

e. The wide aperture of the statocysts.

## PROBLEMS SUGGESTED

There are several interesting problems that might be undertaken in connection with Callianassa, some of which apply to the crustacea in general.

1. The function of the gland at the junction of mid- and hind-guts.

2. The function of the intestinal caecum.

3. The complete life-history.

4. Oogenesis and spermatogenesis and the cyclical changes of the gonads and their ducts.

5. The method of fertilization in burrowing forms.

6. The relationship of the food habits of the individual species of crustacea to the difference in length of the various divisions of the alimentary tract.

7. The correlation, if any, between the number of sensory hairs in the auditory sac of decapods and the habits of life (burrowing or pelagic) of these animals.

8. The function of the plumose setae of the antennal flagellum.

9. The reason for the asymmetry of the chelipeds and some of the internal organs, and the correlation, if any, between these.

# LITERATURE CITED

Borradaile, L. A., 1903 On the classification of the Thalassinidea. Ann. Mag. Nat. Hist., vol. xii, series 7, pp. 534-551.

Calman, W. T., 1909 Crustacea. A treatise on zoology, edited by Sir Ray Lankester. Part vii, fascicle 3, London; A. & C. Black.

Dana, J. D., 1854 In Proc. Acad. Nat. Sci. Phila., vol. vii, 175 pp.

Fasten, Nathan, 1917 Male reproductive organs of decapoda, with special reference to Puget Sound forms. Puget Sound Marine Sta. Pub., vol. i, pp. 285-307, Pl. 68-72, Fig. 1-34.

Herrick, F. H., 1909 Natural history of the American lobster. Bull. U.S.B.F., vol. xxix, pp. 149-408, Pl. 33-47.

Huxley, T. H., 1880 The crayfish, an introduction to the study of zoology. xiv 371 p., 82 illus. London: C. Kegan Paul & Co.

Milne-Edwards, A., 1870 Révision du genre Callianassa. Nouvelles Archives du Museum d'Histoire Naturelle, pp. 75-102, 2 pl.

Schmitt, Waldo L., 1921 The marine decapod crustacea of California. U. of Cal. Pub. in Zool., vol. xxiii, pp. 1-470, Pl. 1-50, 165 fig.

Smith, G., and W. F. R. Weldon, 1909 Crustacea. The Cambridge natural history, vol. iv, pp. 1-217, 135 fig. London: Macmillan & Co.

Stimpson, W., 1857 On the crustacea and echinodermata of the Pacific shores of North America. Jour. Bos. Soc. Nat. Hist., vol. vi, pp. 444-532.

Weldon, W. F. R., 1891 The renal organs of certain decapod crustacea. Quar. Jour. Micros. Soc., vol. xxxii, pp. 279-291, 2 pl.

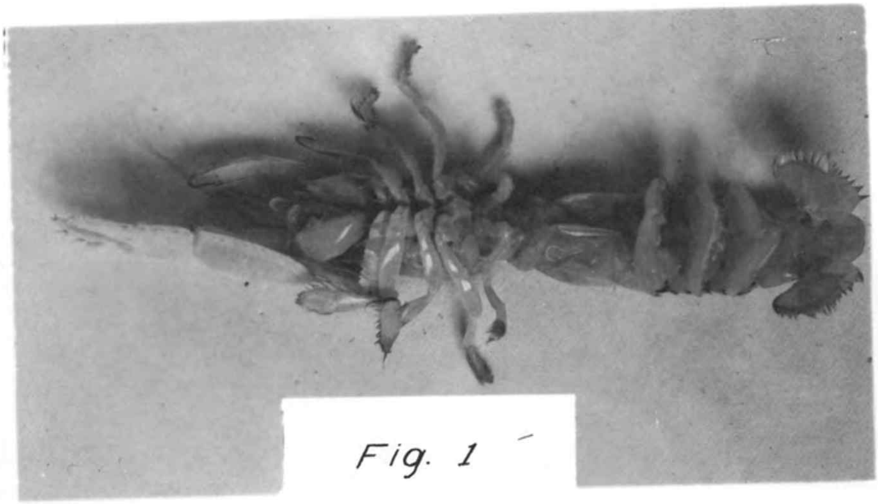

Fig. 1

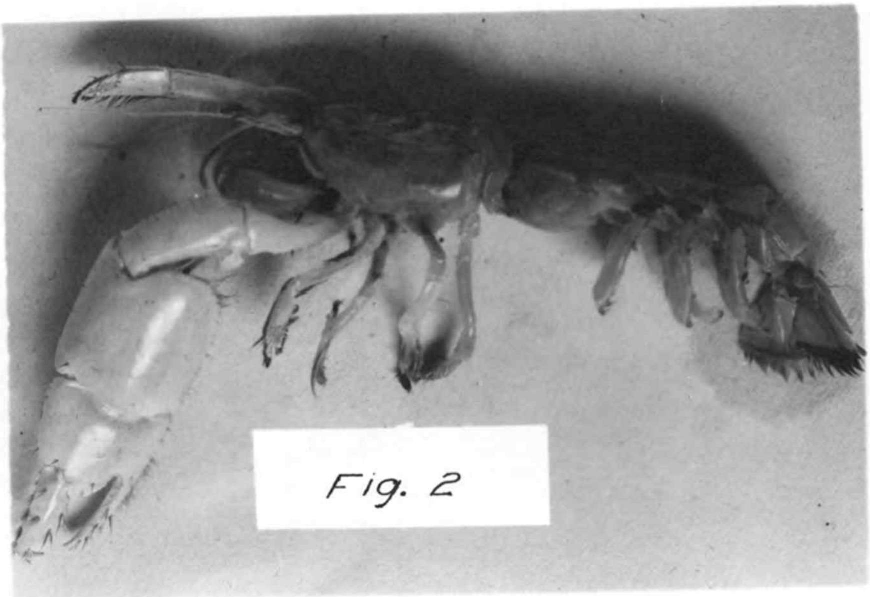

Fig. 2

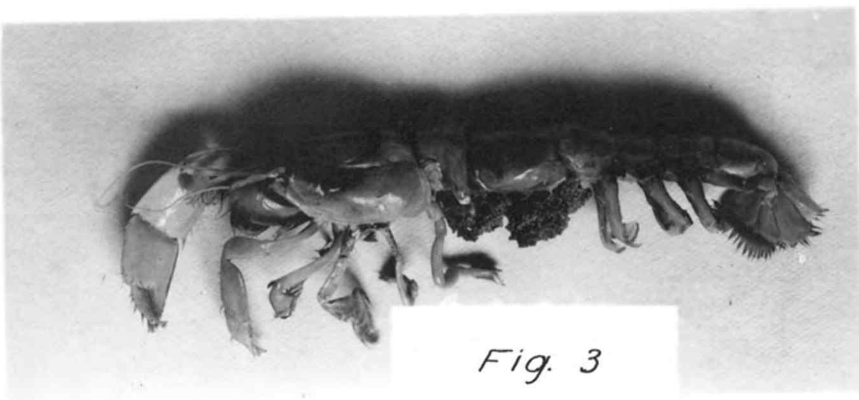

Fig. 3

Plate II

Explanation of Figure

Fig. 4. Outline drawing of dorsal view of male *Callianassa californiensis*. Natural size.

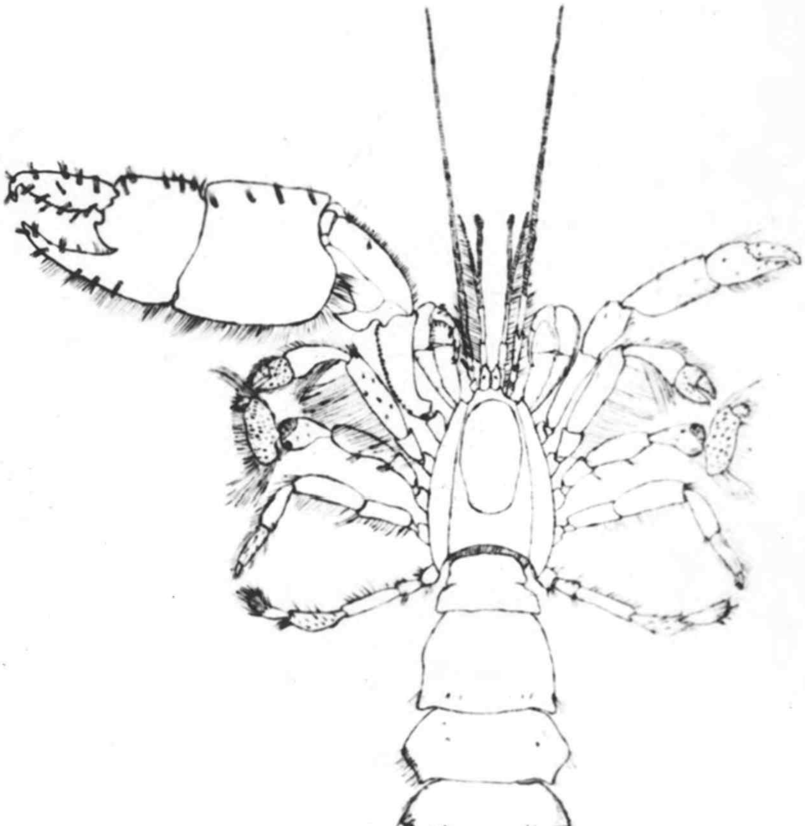

Fig. 4

Abbreviations

b, basipodite

c, coxopodite

co, cornea

en, endopodite

en.1, first podomere of endopodite

en.2, second podomere of endopodite

ep, epipodite

ex, exopodite

f, inner flagellum of first antenna

f', outer flagellum of first antenna

mp, mandibular palp

p, opening of green gland

sc, vestigial scale

sta, statocyst

Plate III

Explanation of Figures

Fig. 5. Dorsal view of left eyestalk. X 3.

Figs. 6 and 7. Dorsal view of left first and second antenna. X 3.

Fig. 8. Posterior view of left mandible. X 3.

Figs. 9 and 10. Posterior views of first and second maxillae. X 3.

Figs. 11 and 12. Posterior views of first and second maxillipeds. X 3.

Figs. 13 and 14. Inner and outer views respectively of third maxilliped. X 3.

Figs. 15 and 16. Posterior views of first and second pleopods of female. X 3.

Fig. 17. One of the posterior pleopods. X 3.

Fig. 18. Vestigial first pleopod of male. X 3.


Fig. 6


Fig. 5


Fig. 7


Fig. 8

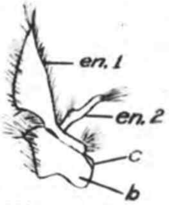


Fig. 9

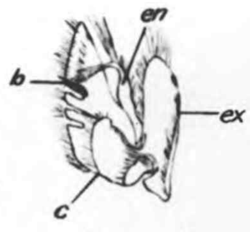


Fig. 10

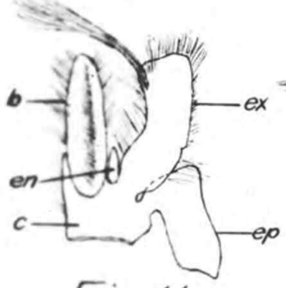


Fig. 11

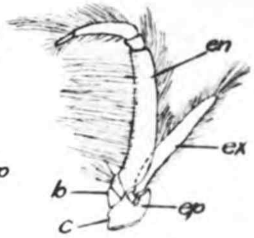


Fig 12

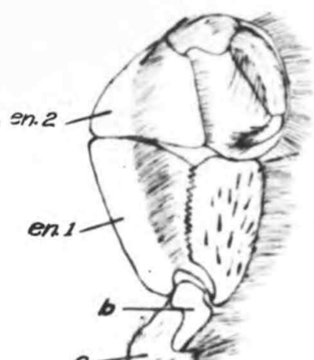


Fig. 13

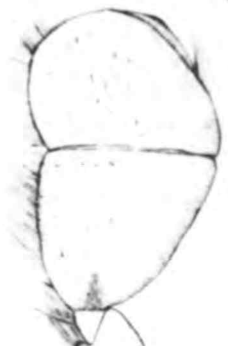

Fig. 14

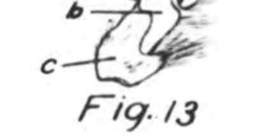

Fig. 15



Fig. 18


Fig. 16

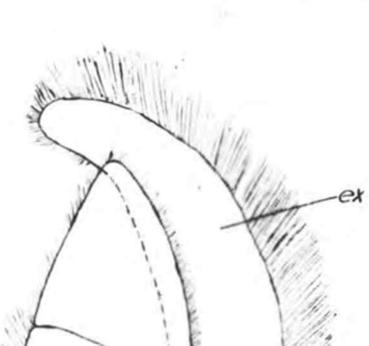


Fig. 17

Plate IV

Explanation of Figure

Fig. 19. Photograph of dorsal view of viscera after removing dorsal integument and muscles. (Specimen was photographed under water) agm, anterior gastric muscle; cae, intestinal caecum; dg, digestive gland or liver; ex, scaphognathite; i, intestine; ov, ovary; pgm, posterior gastric muscle; saa, superior abdominal artery. X 1.5.

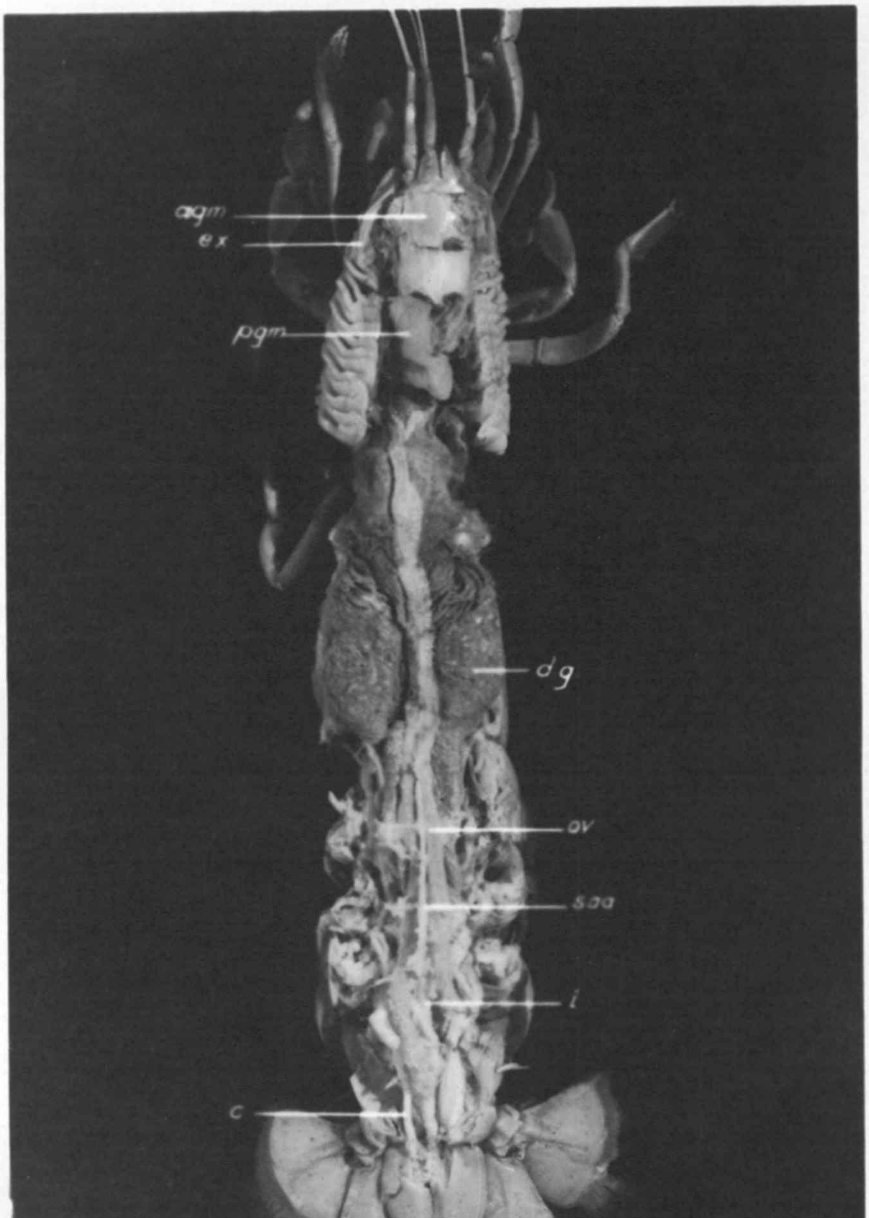


Fig. 19

Plate V

Explanation of Figure

Fig. 20. Photograph of viscera as seen from the side. aa, anterior thoracic artery; gg, green gland; h, heart; od, oviduct; ov, ov', ovary; sa sternal artery; saa, superior abdominal artery; st, stomach; vc, nerve cord. X 1.6.

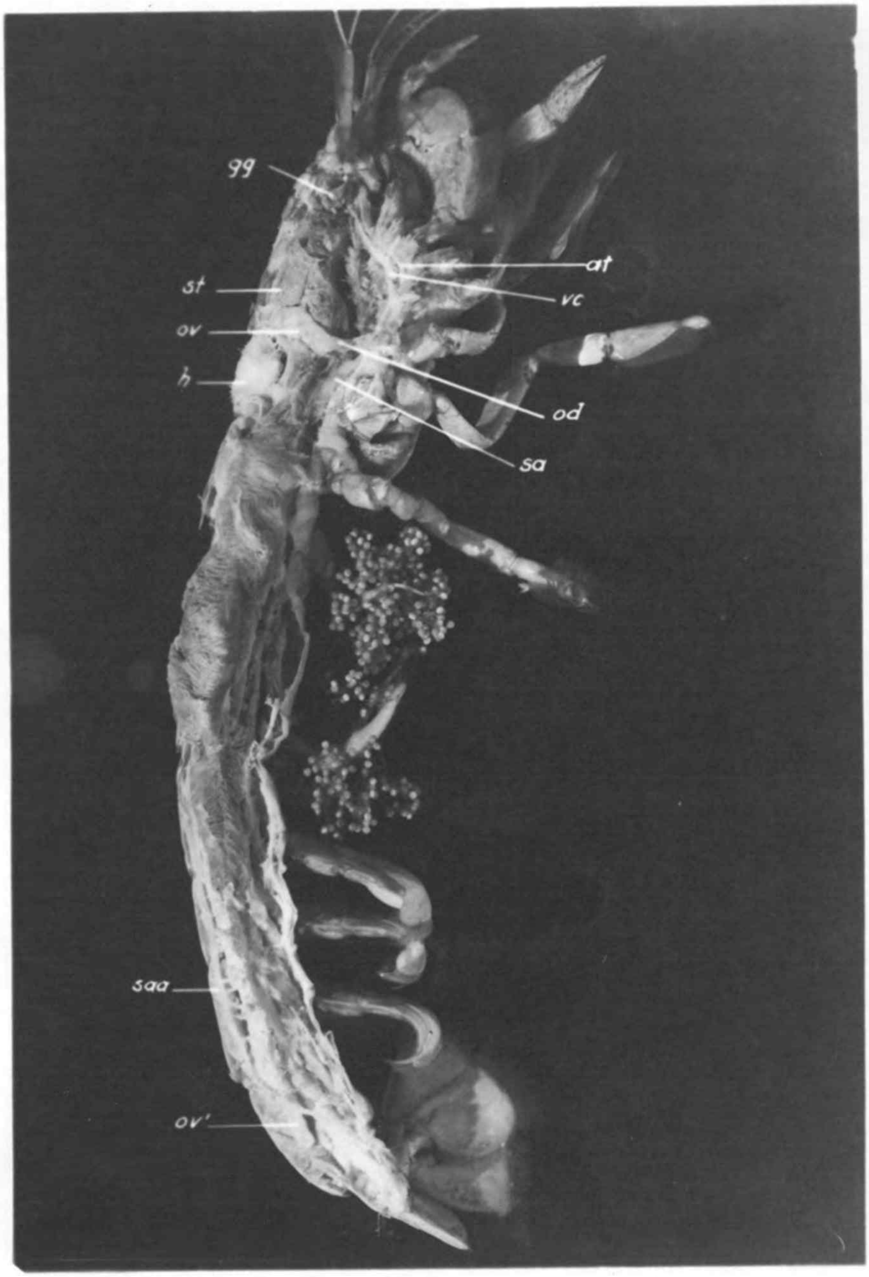


Fig. 20

Plate VI

Explanation of Figures

Fig. 21. Labrum and metastoma, with mandible in position on the right. b, beak-like papilla of labrum; c, body of mandible; m, metastoma; mp, mandibular palp; p, ventral papilla of labrum. X 3.

Fig. 22. Lateral view of digestive system. ag, anterior division of stomach; agm, anterior gastric muscle; c, caecum; dg, digestive gland; do, point at which duct of digestive gland enters mid-gut; hg, hind-gut; i, mid-gut; igl, intestinal gland; o, esophagus; pg, posterior division of stomach; pgm, posterior gastric muscle; sa, sternal artery. X 2.

Fig. 23. Cross section of digestive gland showing arrangement of caeca around duct. c, caecum; d, hepatic duct; ha, hepatic artery. X 3.


Fig. 21

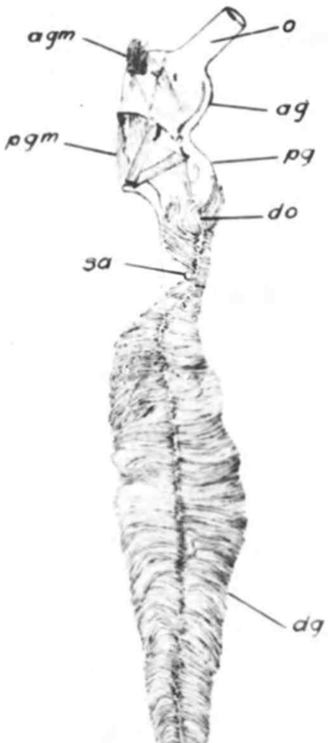


Fig. 22

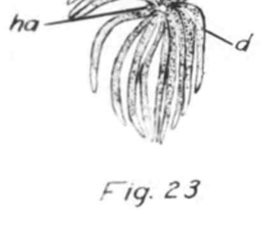


Fig. 23

Abbreviations

a, chitinous folds

b, oval setose pad

b', round setose pad

ca, cardiac ossicle

cv, caecal valve

do, opening of duct of liver

dp, dorsal pouch

dv, dorsal valve

ev, esophageal valve

f, anterior "pusher"

f', ventral "pusher"

i, mid-gut

l, ligament

lp, lateral pouch

lt, lateral tooth

lv, outer lateral valve

mt, median tooth

o, esophagus

op, papilla from ridge of esophagus

p, pyloric ossicle

pp, prepyloric ossicle

pt, pterocardiac ossicle

r, cover of round pad

r', same, opened outward

s, patches of setae

u, urocardiac ossicle

vv, ventral valve

z, zygocardiac ossicle

zy, "zygopyloric" ossicle

Plate VII

Explanation of Figures

Fig. 24. Longitudinal section of stomach. X 3.

Fig. 25. Showing floor of stomach after making longitudinal incision in roof and spreading out sides (median tooth not shown). X 3.

Fig. 26. Roof of stomach. X 3.

Fig. 27. Individual caecum of pyloric valve. X 20.

Fig. 28. Ossicles of gastric mill. Lateral ossicles are shown spread out on right side of diagram. X 3.

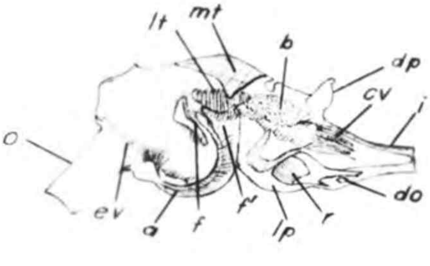


Fig. 24

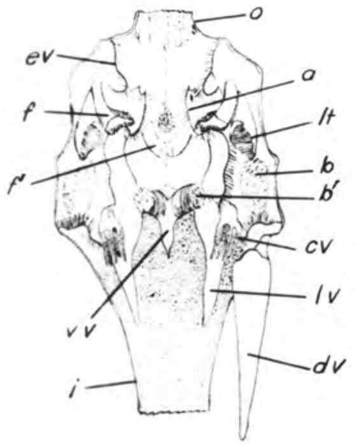


Fig. 25

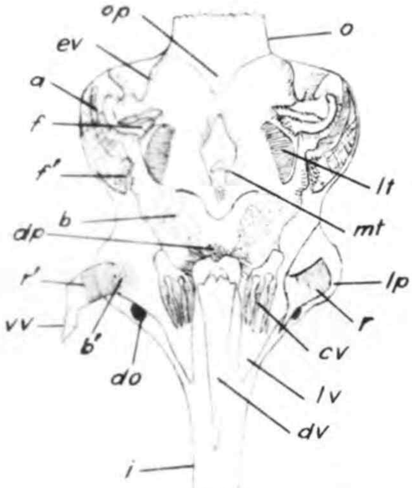


Fig. 26


Fig. 27

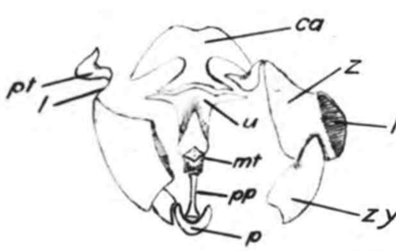


Fig. 28

## Abbreviations

cb, blood clot

ch, chitin

ct, connective tissue

ct', outer layer of connective tissue of hind-gut

e, epithelium

m, longitudinal muscle

m', circular layer of muscle

m", oblique muscles

sm, serous membrane

t, epithelium of esophagus

tu, tubule of intestinal gland

## Plate VIII

### Explanation of Figures

Fig. 29. Portion of transverse section of wall of hind-gut in region of intestinal gland. X 170.

Fig. 30. Portion of transverse section of wall of mid-gut. X 170.

Fig. 31. Portion of transverse section of wall of intestinal caecum. X 170.

Fig. 32. Transverse section of hepatic caeca. X 170.

Fig. 33. Portion of transverse section of wall of esophagus. X 170.

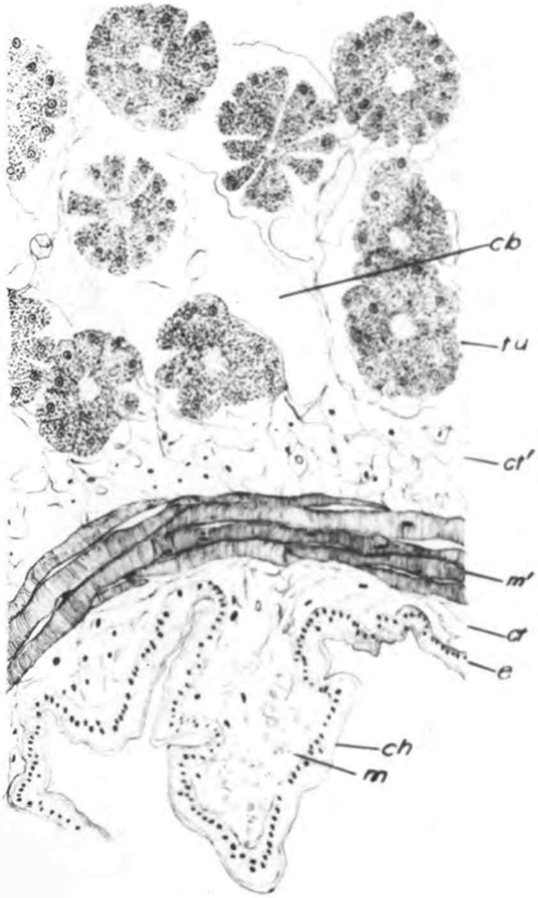


Fig. 29

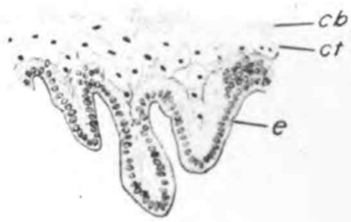


Fig. 30

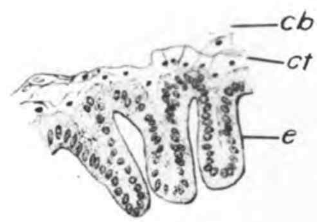


Fig. 31


Fig. 32

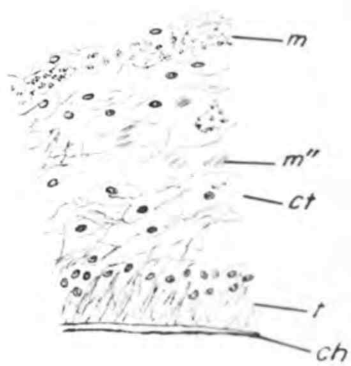


Fig. 33

## Abbreviations

| | |
|---|---|
| a, antennary artery | lo, dorso-lateral ostium |
| at, anterior thoracic artery | m, arteries to muscles |
| bl, bladder of green gland | o, ophthalmic artery |
| c, arteries to caecum | r, artery to gonad |
| do, dorsal ostium | sa, sternal artery |
| g, artery to intestinal gland | saa, superior abdominal artery |
| ha, hepatic artery | t, artery to telson |
| i, artery to intestine | u, artery to uropod |
| iaa, inferior abdominal artery | vo, ventral ostium |
| iaa', asymmetrical continuation of inferior abdominal artery | 1-5, arteries to corresponding pereiopods |

## Plate IX

### Explanation of Figures

Fig. 34. Dorsal view of heart. X 4.

Fig. 35. Lateral view of heart. X 4.

Fig. 36. Ventral view of heart. X 4.

Fig. 37. Dorsal view of circulatory system. The main portions of the bladder and end-sac of the antennary gland are shown along the antennary artery on the right side. X 2.

Fig. 38. Sternal artery and its principal branches. X 2.

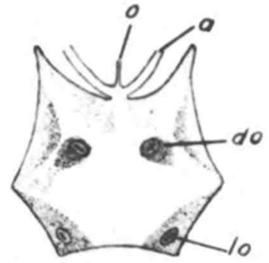


Fig. 34

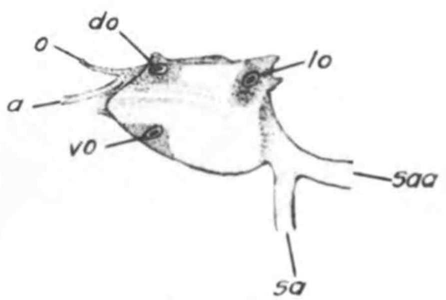


Fig. 35

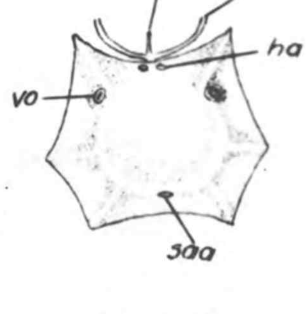


Fig. 36

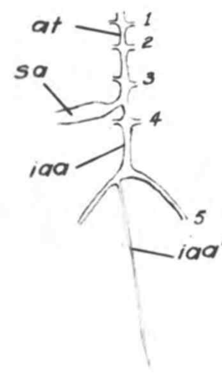


Fig. 38

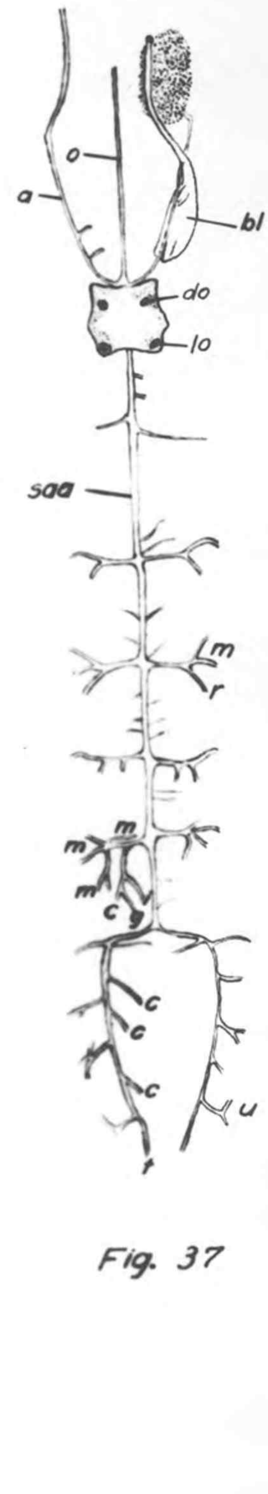


Fig. 37

## Plate X

### Explanation of Figures

Fig. 39. Photograph of gills. X 2.5.

Fig. 40. Posterior view of one of the posterior right gills. X 3.

Fig. 41. Cross section of gill. a, afferent canal of stem; e, efferent canal; l, lamina. X 3.

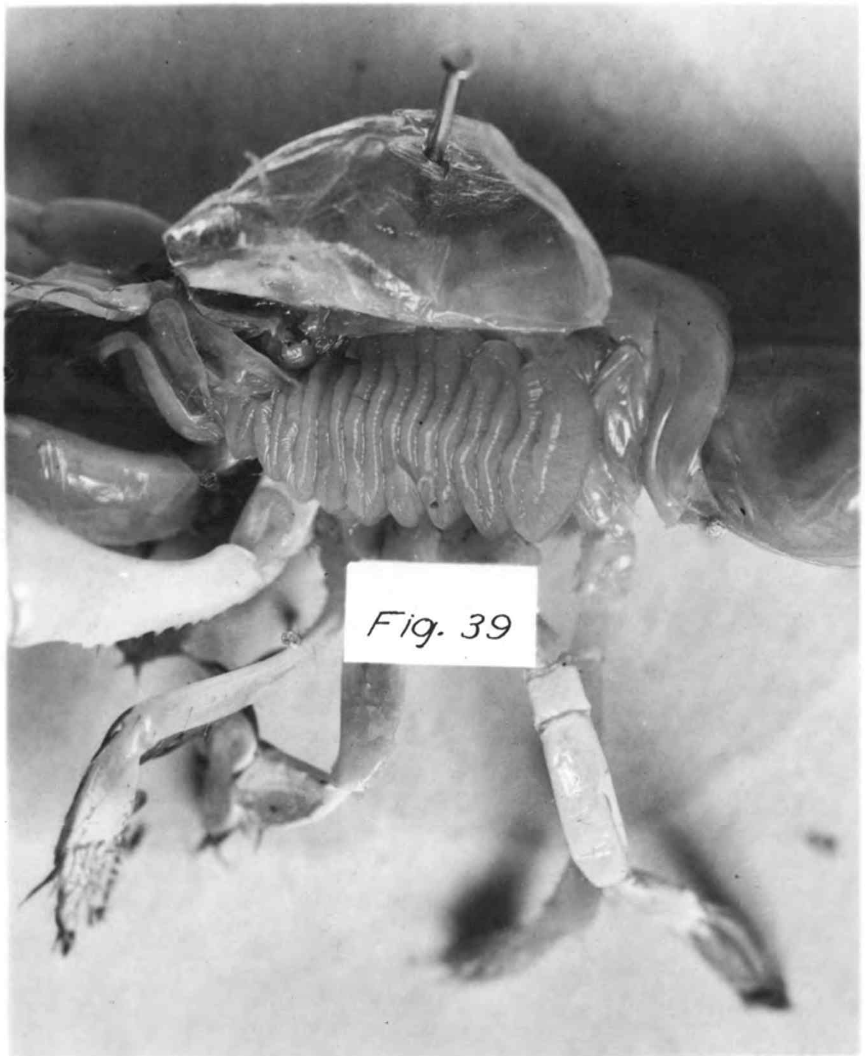

Fig. 39

Fig. 40


Fig. 41

Plate XI

Explanation of Figures

Figs. 42 and 43. Dorsal and lateral views respectively of antennal or green gland. b, ramifications of bladder in branchiostegite; bl, bladder; bm, branchiostegal muscle; es, end-sac; es', portion of end-sac extending into base of mandible; o, esophagus, u, ureter. X 4.

Fig. 44. Portion of transverse section of end-sac. bl, bladder; c, cavity of end-sac; ct, connective tissue; ebl, epithelium of bladder; ebl', bladder epithelium investing end-sac; ees, epithelium of end-sac; mu, mucous cells. X 90.

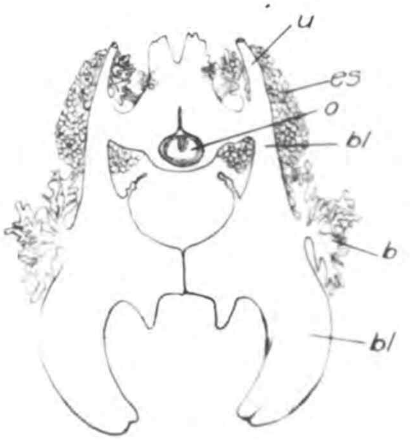


Fig. 42

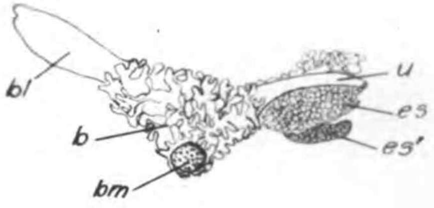


Fig. 43


Fig. 44

Plate XII

Explanation of Figures

Fig. 45. Female reproductive system. od, oviduct; ov, ovary. X 2.

Fig. 46. Male reproductive system. d, ductus ejaculatorius; t, testis; vd, vas deferens; vs, vesicula seminalis. X 2.

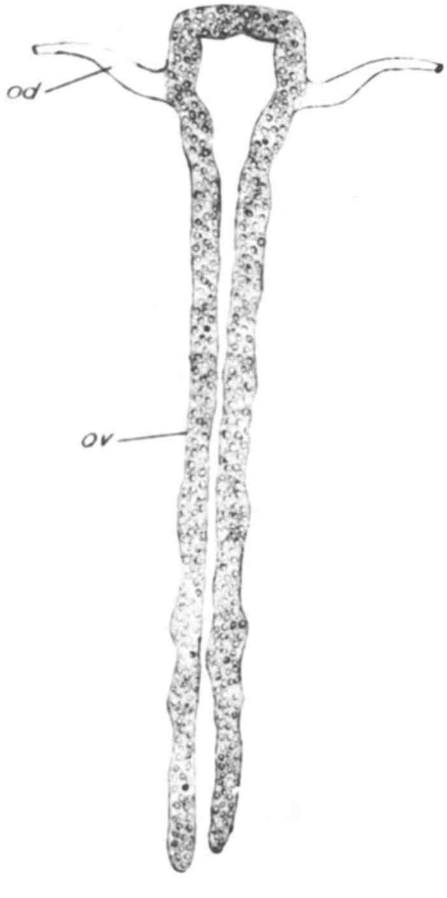


Fig. 45


Fig. 46

Plate XIII

Explanation of Figures

Fig. 47. Cross section of ovary. ct, connective tissue coat; gr, germinal region; o, mature ovum; o', immature ovum. X 80.

Fig. 48. Longitudinal section of testis. ct, connective tissue; sp, spermatozoa, sp', maturing spermatozoa. X 170.

Fig. 49. Portion of vas deferens wall (cross section). ct, connective tissue; ep, glandular epithelium; m, smooth muscle layer. X 170.

Fig. 50. Spermatophore (cross section). sp, spermtozoa; sph, spermatophore case. X 170.

Fig. 51. Spermatozoa. X 1500.


Fig. 48

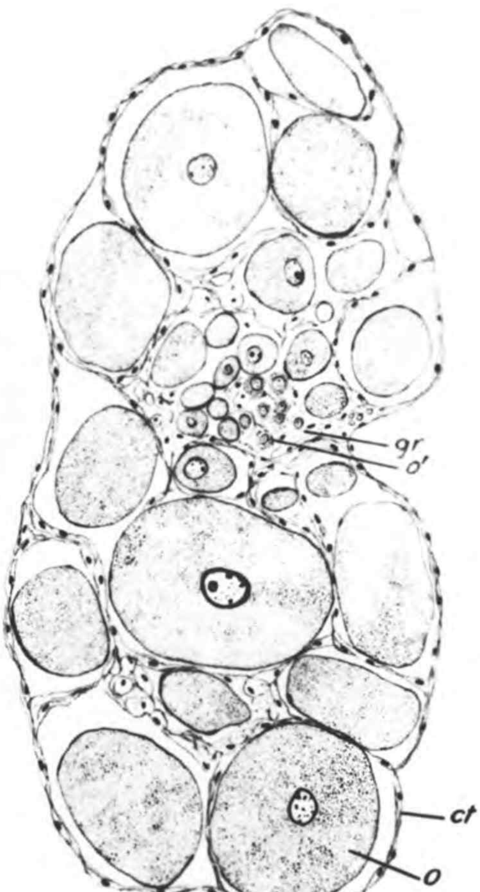


Fig. 47

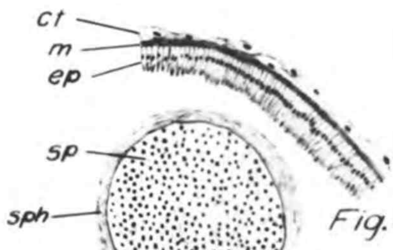


Fig. 49

Fig. 50

Fig. 51

Plate XIV

Explanation of Figures

Fig. 52. Dorsal view of nervous system. a, nerve to antenna; e, nerve to eye-stalk; i, to intestine and intestinal gland; ms, to muscles and integument; sg, brain; sg', sub-esophageal ganglion; t, nerve to telson; th, to telson and hind-gut; u, to uropods; IV-VIII, ganglia of corresponding thoracic somites; 1-6, ganglia of corresponding abdominal somites. X 2.

Fig. 53. Portion of outer flagellum of first antenna showing olfactory setae on the eighth from the last segment. os, olfactory setae. X 60.

Fig. 54. Portion of second antenna. as, auditory(?) setae; ts, tactile setae. X 60.

Fig. 55. Portion of border of scaphognathite showing bases of setae. g, goblet-shaped depression between setae; ps, plumose setae. X 170.

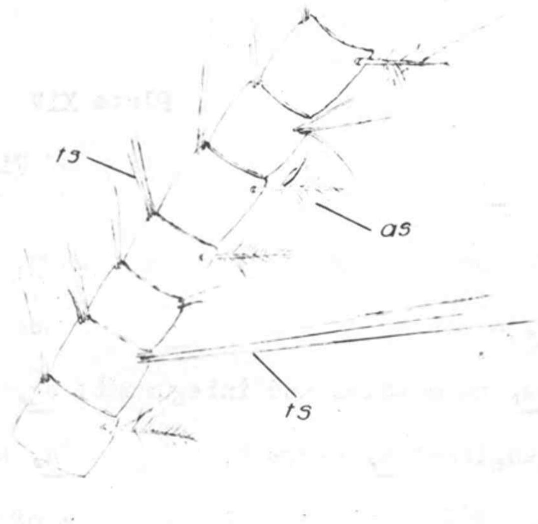


Fig. 54

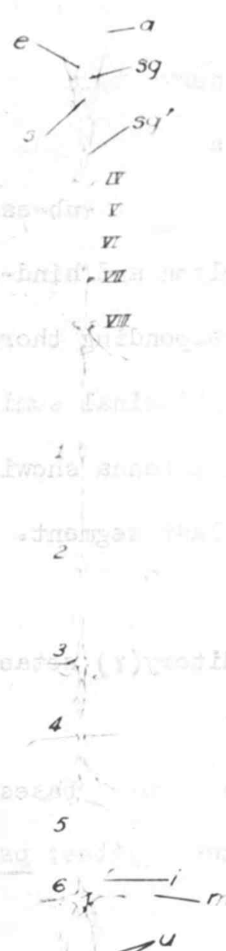


Fig. 52

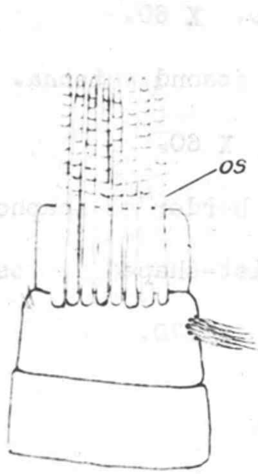


Fig 53

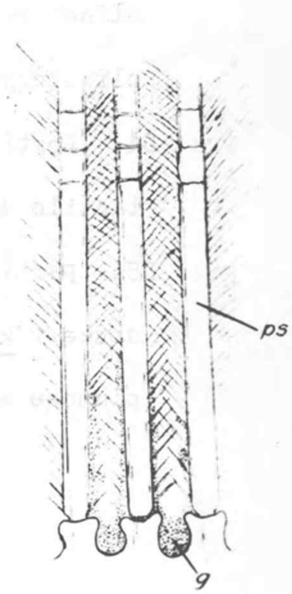


Fig. 55