branch is the subgastric artery (fig. 79) and it runs around the posterior end of the gastric mill to a curious glandlike organ lying beneath the gastric mill. The subgastric artery is similar to the internal ramus of the lateral anterior artery described by Baumann (1919) in *Astacus*. Rostrad of the subgastric branch, the lateral anterior artery puts out the dorsal gastric artery (figs. 79, 80) which serves the dorsal regions of the gastric mill. The gastric artery, too, divides into at least three major divisions (fig. 80), one running some distance rostrally, another caudad into a glandlike structure of unknown function (see fig. 79, dorsal gland, and a third passing around the gastric mill ventrally.

The lateral anterior artery now turns to the midline to join its counterpart from the opposite side. The optic artery continues anteriorly to the eyestalk from this turn, giving off a branch, the cerebral artery, to the supraesophageal ganglion. At the midline, the two lateral anterior arteries form a median longitudinal vessel. The anterior portion extends into the rostrum while the posterior part, the recurrent artery, runs caudad to the dorsal surface of the gastric mill. At the junction of the optic artery with the oculomotor, a small branch is given off which runs beneath the optic tract and thence to the midline to meet its opposite number from the other side (fig. 80) slightly rostrad of the dorsal brain. No evidence of the frontal heart so prominent in this region in other decapods (Baumann 1917) has been found in *Penaeus*.

The next major branch of the lateral anterior artery anterior to the gastric branch is the mandibular artery. Upon leaving the lateral anterior artery this branch passes between the lateral mandibular condyle and the origin of the lateral anterior thoracic muscle 1 (fig. 80) into the substance of the mandibular muscles where the vessel undergoes further subdivision.

Rostrad of the mandibular artery, the lateral anterior artery gives off the large antennal artery whose subdivisions include a branch to the antennule. The major portion of the antennal artery leads to the muscles and other organs of the antenna.

HEPATIC ARTERY

Running from the heart is another pair of arteries, the hepatic arteries (fig. 79). These project from the anteroventral surface of the heart and run into the hepatopancreas. They are difficult to follow within the gland in preserved material because of postmortem effects.

DORSAL ABDOMINAL ARTERY

The largest artery passing from the broad, posterior end of the heart is the unpaired dorsal abdominal artery (figs. 61, 62, 79, 80). This vessel runs the length of the abdomen between the dorsal abdominal muscles and the gut. As it proceeds caudad, the dorsal abdominal artery gives off pairs of segmental arteries at each segmental junction (fig. 62). In addition, numerous small vessels from the dorsal abdominal artery irrigate the gut throughout its length. Posteriorly, the dorsal abdominal artery bifurcates around the hindgut gland (fig. 82) and runs alongside the rectum as a paired vessel. In the neighborhood of the rectum the paired vessels turn ventrad, after giving several branches to various structures of the region, including the telson, and anastomose beneath the posterior part of the rectum. Having fused, the vessel passes caudad of the ganglion of the sixth abdominal segment and then turns anteriorly as the posterior subneural artery (figs. 81, 82). So far as can be determined, the posterior subneural artery extends no further rostrad than the anteroventral part of the sixth abdominal segment.

On the dorsal surface, the segmental arteries give off branches adjacent to the dorsal abdominal artery (fig. 62). These branches enter the large ventral abdominal muscles. The remainder of the segmental arteries now pass ventrally along the lateral surface of the abdomen at the intersegmental lines. A substantial branch splits off internally and runs across the external arm of the anterior oblique muscle in each segment (fig. 60). The segmental artery (see lateral artery, fig. 81) continues ventrad between the abdominal muscles and the promoter-remotor muscle mass of the pleopod and sends a branch, the pleopod artery, into the pleopod (fig. 81). A second branch proceeds into the substance of the abdominal ganglion. This branch also divides again to form the postganglionic loop (fig. 81) which provides a vascular connection between the segmental arteries of both sides.

STERNAL ARTERY

In general, the ventral vascular supply is less distinctly laid out than are the dorsal circulatory

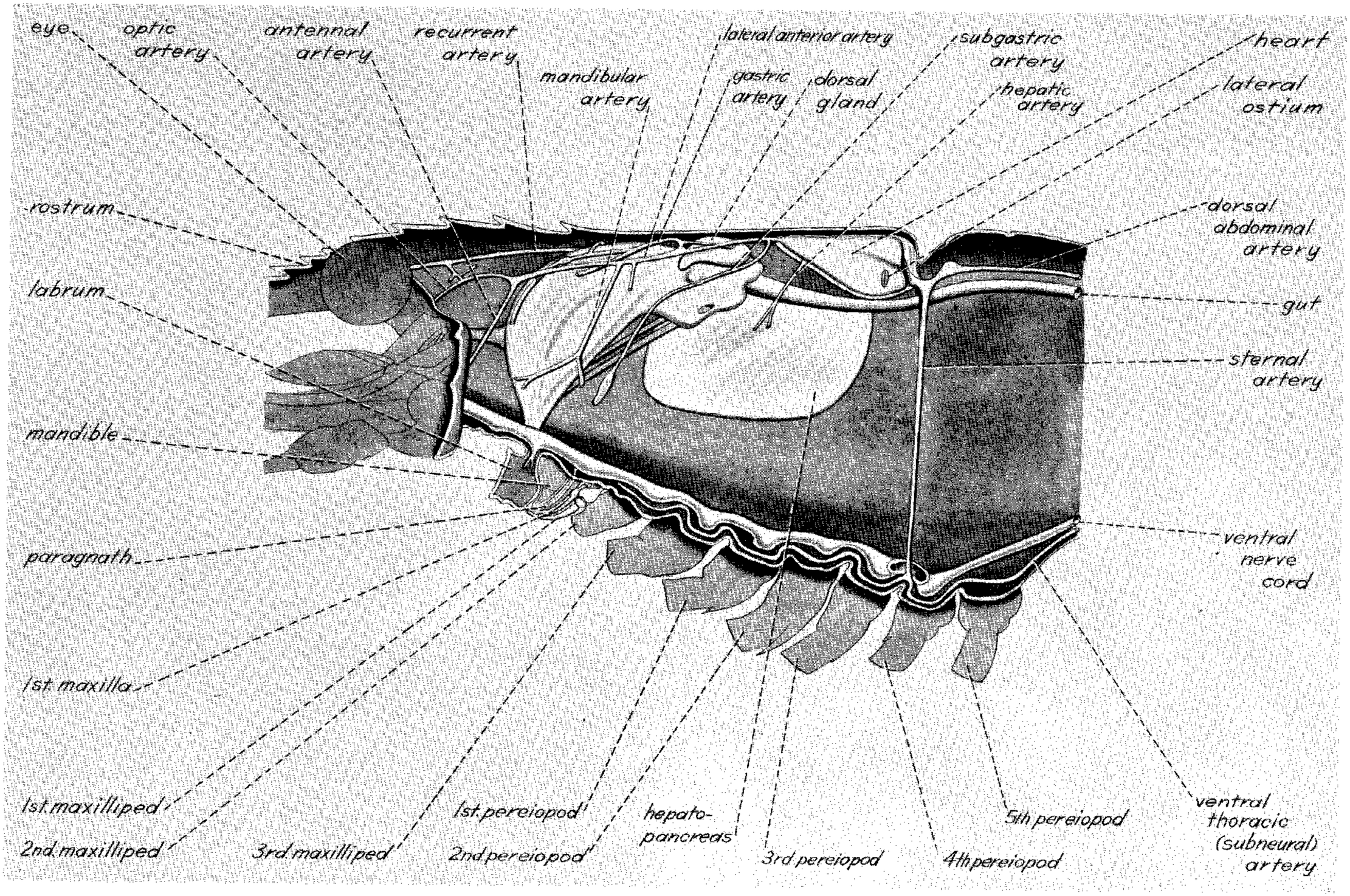

FIGURE 79.—Lateral view of gnathothorax showing circulatory elements.

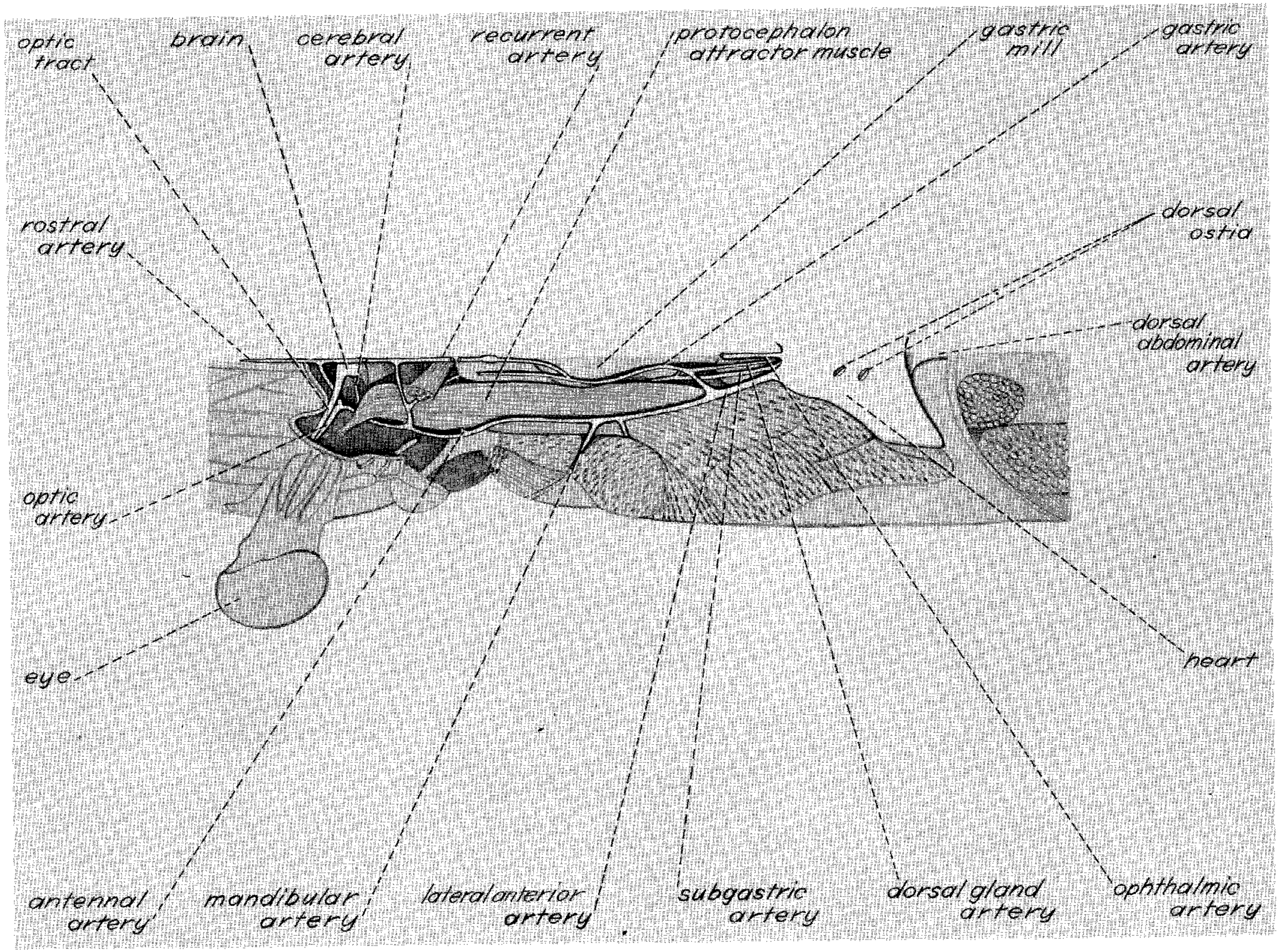

FIGURE 80.—Dorsal view of gnathothorax showing circulatory elements.

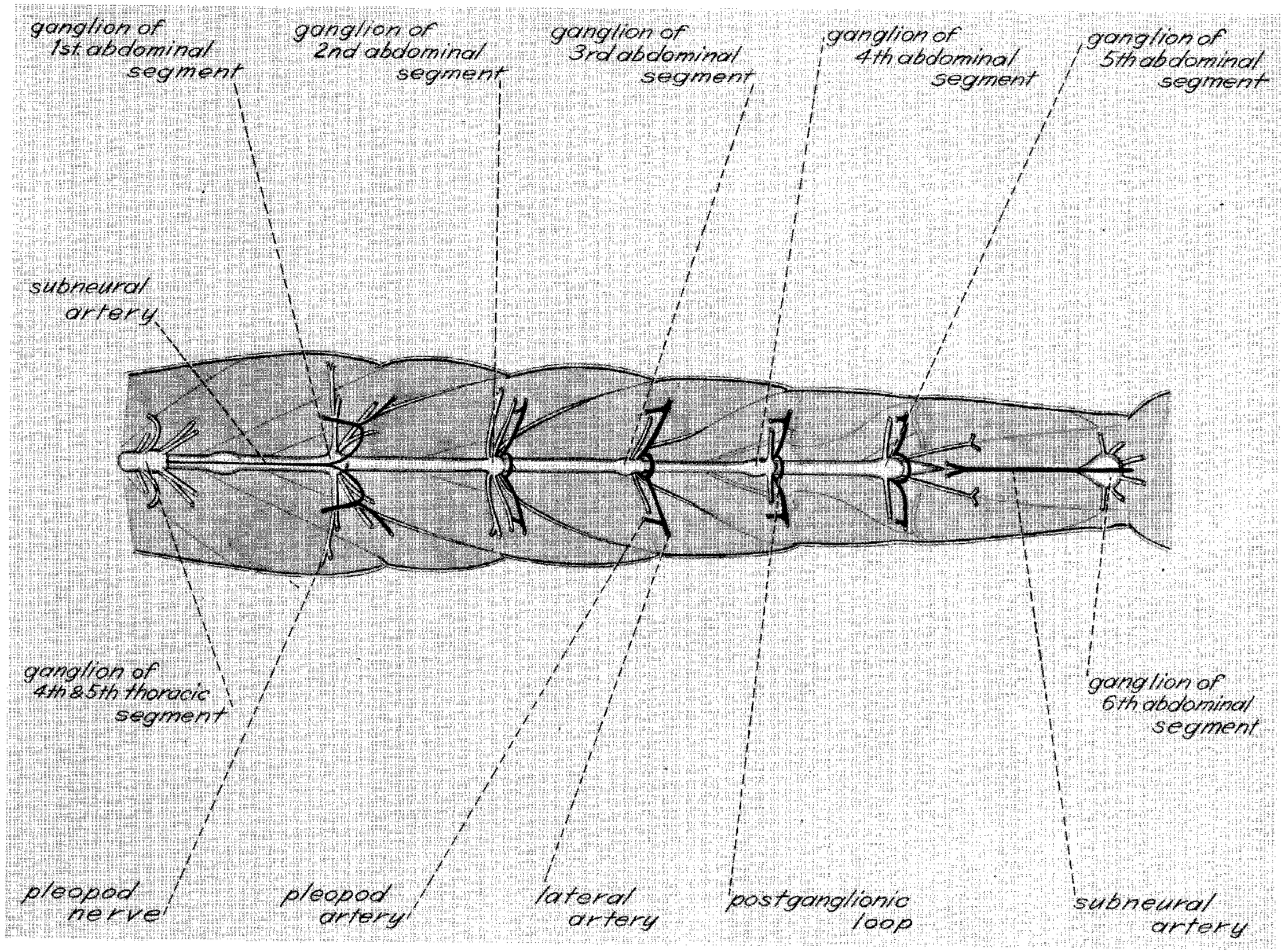

FIGURE 81.—Ventral view of abdomen showing neural and circulatory elements.

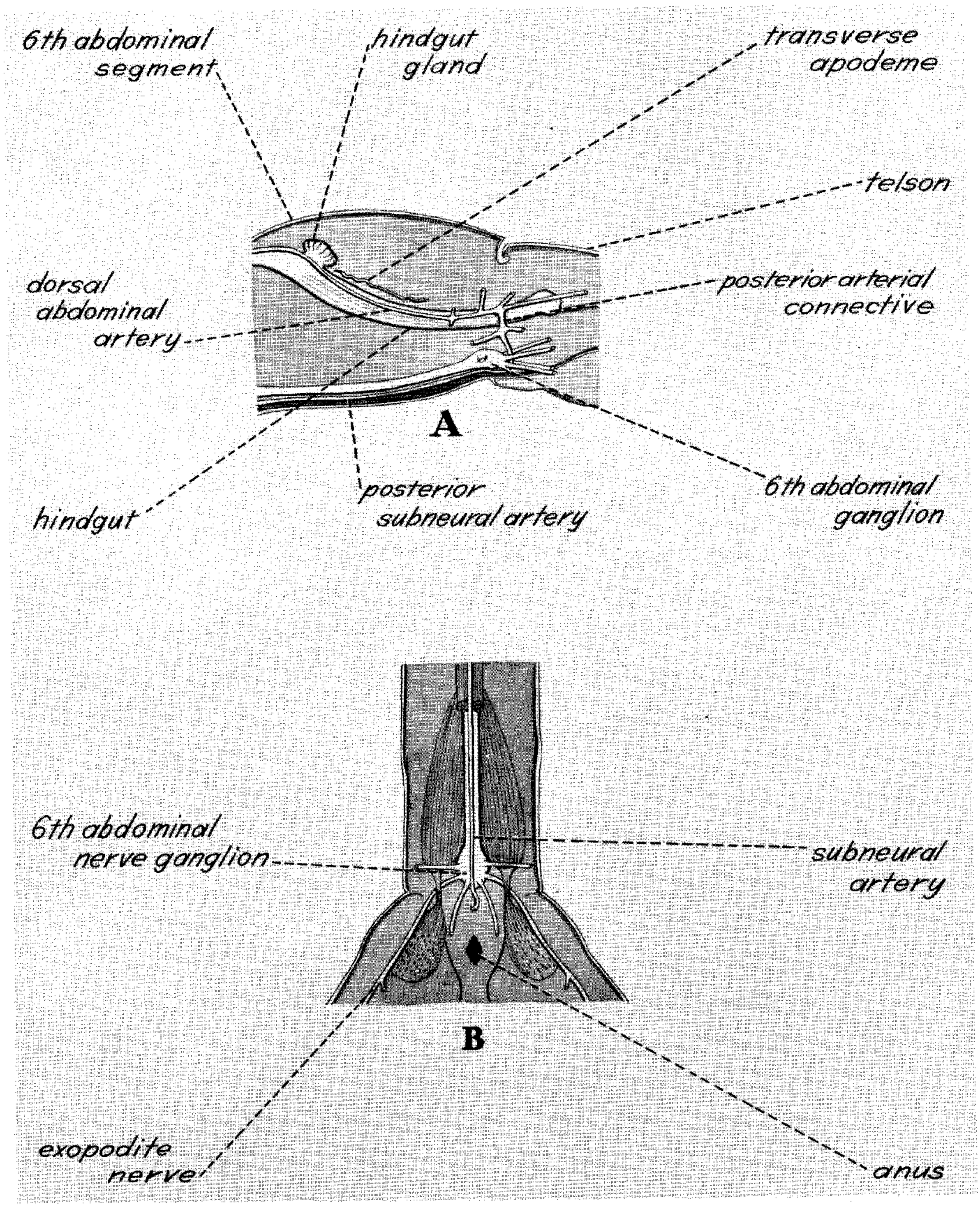

FIGURE 82.—Neural, circulatory, and digestive structures in posterior abdominal segments. *A*. Lateral view of sixth abdominal segment and part of telson. *B*. Ventral view of sixth abdominal segment, and parts of uropods and telson.

elements. The principal vessel supplying blood to the ventral regions is the sternal artery (fig. 79) which in some Malacostraca arises from the posteroventral surface of the heart, but in *Penaeus* is a branch of the very rostral portion of the dorsal abdominal artery. The sternal artery descends directly ventrad past the gut and through the ventral nerve cord between the ganglia of the third and fourth ambulatory legs (figs. 76, 79). Here, the artery divides into an anterior portion running forward beneath the nerve cord in the gnathothorax and a posterior piece which eventually enters the abdomen (figs. 36, 79, 81).

VENTRAL THORACIC ARTERY

The ventral thoracic (subneural) artery (figs. 36, 79) supplies blood to the gnathothoracic appendages (fig. 36) as it passes anteriorly. Slightly rostrad of the nerve to the second maxilla, the ventral thoracic artery bifurcates. The two branches turn sharply laterad, sending branches into the nerve cord in the region of the mandibular nerve and also into the anterior structures of the ventral thorax. No connection between the anterior branches of the ventral thoracic artery and the lateral anterior artery has been found in *Penaeus*.

The portion of the ventral thoracic artery posterior to the sternal junction gives off large branches to the fourth and fifth walking legs and the anterior ends of the anterior oblique muscles (fig. 36). A small branch continues subneurally to join other vessels beneath the first abdominal ganglion.

B. Appendicular Blood Vessels

EYESTALK VASCULAR SUPPLY

FIGURES 7 TO 10

Blood is pumped to the eyestalk through the optic branch of the lateral anterior artery. Once in the eyestalk the vessel, now known as the oculomotor artery, runs medially along the optic tract and divides into several branches at the distal end of the eyestalk. The most proximal branch bifurcates on the dorsal surface of the optic tract (figs. 7, 8), sending a short vessel to and apparently through a small gland on the optic tract here designated as the X-Organ of Hanström (1948) and about which something has been said in the section on the nervous system. A small part of the arterial branch to the gland continues proximally along the dorsal surface of the optic tract and has not been traced beyond the connective tissue of the basal segment of the eyestalk. The larger part of the proximal oculomotor branch runs distally into the distal optic ganglionic mass (figs. 7, 8).

Distally, the oculomotor artery divides into two large branches, one of which (figs. 8, 9) carries blood into a highly branched, dendritic structure embedded deeply among the optic ganglion cells (fig. 9). The organ has been named the capillary arbor (Young 1956), since it appears to distribute blood to ganglionic cells. Nothing similar has been found in the literature of the arthropod eye. However, Professor Mayrat reminds me that he has described (Mayrat 1956) a similar structure in *Praunus flexuosus* (O. F. Müller).

The other, and most-distal oculomotor branch, repeatedly divides to form a vascular plexus on the medial surface of the eyestalk, just beneath a pore to the exterior (figs. 9, 10). The pore is designated as the anterior eyestalk pore. This structure was first described by Hanström (1948) as the eye papilla or sensory papilla and is shown by him as having some kind of structural and spatial relationships with the X-Organ in several crustaceans. Mayrat (1956) also finds the X-Organ near the eyestalk pore in *Praunus*. The function of the anterior eyestalk pore is unknown.

ANTENNULAR BLOOD SUPPLY

FIGURE 14

The blood vascular supply to the antennule is comprised of a large branch of the antennal artery, which is in turn a branch of the lateral anterior artery. The antennal branch enters the antennule in the mesial region near the point of entry of the antennular nerves. The antennular artery courses anteriorly along the mesial side of the antennule giving off small branches to muscles and other structures and finally dividing to supply the two flagella. The arterial branches are seen to subdivide to form capillary beds about the antennule.

ANTENNAL BLOOD SUPPLY

FIGURES 21, 79, 80

The antenna receives its blood from the antennal branch of the lateral anterior artery. The vessel gives off branches in the region of the large

antennal muscles and enters the antenna proper with the antennal nerves. Here it divides to supply the antennal scale and endopodite segments.

VENTRAL APPENDAGE BLOOD SUPPLY

The ventrally located appendages of the head and gnathothorax all appear to receive blood from branches of the ventral thoracic artery. Those of the abdomen, as has already been mentioned, receive fluid from the segmental branches of the dorsal abdominal artery.

D. Venous System

Arterial circulation consists of a closed afferent system subdivided into capillary beds in muscles and other organs. Venous return to the heart appears to be carried out in an open system, through sinuses in the appendages which empty into larger sinuses in the hemocoel. In general, the appendicular sinusoids are found on either one margin or the other of the appendage, rather than in the middle. The sinuses of the body which drain the venous blood from the appendages are located in particular places in the body. The sinus into which the eyestalks empty occupies the anterodorsal regions of the protocephalon. This sinus runs into a larger one anterior to the gastric mill into which blood from the other protocephalon appendages drain. The largest thoracic sinus lies along the sternum. It receives blood from the dorsal sinuses and the gnathothoracic appendages and supplies blood to the respiratory organs. From the sternal sinus the venous blood passes dorsolaterally to the pericardium.

In the abdomen, the sinus system is relatively simple. The dorsal regions are drained by a sinus or set of sinuses between the dorsal and ventral abdominal arteries. These appear to run directly rostrad into the heart. On the ventral surface segmentally arranged, conjoint sinuses pass venous blood rostrally to the sternal sinus of the thorax and thence to the heart. The sternal sinuses of the abdomen extend some distance dorsolaterally in conjunction with the sinuses of the pleonic appendages.

E. Respiratory System

The subject of gill formulae and arrangement in *Penaeus* and other crustaceans has been discussed previously in the general section on the gnathothorax. The details of the respiratory system will be taken up at this point, since the organs concerned with gas exchange are intimately associated with the circulation of body fluids.

The gills of *Penaeus* are of the dendrobranchiate type (Calman 1909). This type of gill is comprised of a primary axis or rachis from which pairs of secondary structures bearing gill filaments arise at right angles. The secondary structures and gill filaments thus appear to be laminar units. Proceeding distally, each succeeding layer of secondary structures and filaments nests within the preceding layer.

For the details of gill circulation we are indebted to Prof. Jerome E. Stein, Texas Agriculture and Mechanical College, Galveston, Tex. He finds that blood enters the primary rachis of the gill by means of a primary afferent blood vessel (fig. 78, *A*, *B*) which is separated from the primary efferent blood vessel by a longitudinal septum. Primary afferent blood is directed into the secondary afferent blood vessels (fig. 78, *C*) by a secondary septum. Blood now passes out into the secondary structures to the gill filaments, into which it runs due to the arrangement of a tertiary septum dividing the tertiary afferent and efferent blood vessels in each filament. Blood thus flows around the tip of the filament and returns to the sternal sinus through the efferent vessels of the gill. The gill filament cuticle and epidermis appear to be very thin to allow for gas exchange.

An important accessory organ of respiration is the branchiostegite. The inner cuticle adjacent to the gills is thin and the underlying epidermal layers are heavily vascularized. Specimens preserved in Zenker's fluid display with great clarity the branchiostegal vessels (fig. 77) and fine nerves. The vessels appear to be of two types. One set represents the subdivisions of a large vessel seen at the dorsal margin of the branchiostegite a short distance caudad of the hepatic spine. The capillaries of the vessel approach the periphery of the branchiostegite at right angles to its margin. A second set of vessels run parallel to the margin of the branchiostegite (fig. 77), and are reminiscent of growth rings, since the larger shrimps in general have more rows of these vessels than do the younger animals. Whether the marginal vessels reflect the age of the white shrimp in terms of the number of molts is not known.

IV. DIGESTIVE SYSTEM

The digestive system is made up of those structures concerned with the enzymatic and mechanical reduction of food particles, the absorption of their products, and the evacuation of particulate wastes. The digestive systems of Crustacea Decapoda are all relatively uniform, being comprised of a stomodaeum, or foregut, which includes the esophagus and gastric mill, and probably the hepatopancreas; the midgut, or mesenteron, which in *Penaeus* appears to run from the gastric mill to the hindgut gland on the anterior end of the sixth abdominal segment; and the hindgut, or proctodaeum, which includes the rectal gland, rectum, and anal canal. The alimentary structures will be treated according to these three regions. The subdivisions of the gut are based upon the presence of a cuticular lining of the fore- and hindgut. That section not lined with cuticle is supposed to be the midgut. This criterion is here adopted for whatever it is worth.

A. Foregut

ESOPHAGUS

FIGURES 83 TO 85

The esophagus is a vertical tube which receives food particles thrust into the mouth by the labrum and postoral mouthparts. The tube is lined with cuticle, yet is so constructed that extensive contraction and expansion is possible. A cross-sectional view of the esophagus (fig. 85, *A*) indicates how these movements come about. The cuticular lining is folded inwards between the corners. Esophageal constrictor muscles (fig. 83), short fibers running transversely, draw the corners together and thereby close the lumen of the tube. Expansion of the lumen is accomplished by anterior and posterior esophageal dilatator muscles (fig. 83) which are inserted into the inward folds. Their contractions pull the folds outwards. The esophagus is constricted at its junction with the gastric mill preventing backflow of the food particles from the latter.

GASTRIC MILL

FIGURES 83 TO 85

The gastric mill is a bulbous, folded structure occupying the dorsomedial region of the thorax. As decapod gastric mill structure goes, that of *Penaeus* is relatively simple. Its surface is invested with thin sheets of constrictor muscles. Numerous dilatator muscles attach about the outside of the structure. The gastric mill, like the esophagus, is lined with cuticle, but here the latter substance is reflected into deep folds and toothlike structures (fig. 84) for the grinding of food. Transverse sections through the mill (fig. 85) indicate that the theoretical tubular form of the gastric mill is much modified. In general, the walls have been thrown into three pairs of folds. The uppermost fold (fig. 85, *B*), which disappears caudally (figs. 85, C_1, et seq.), serves no other purpose than the expansion and contraction of the gastric mill in response to feeding and digestion.

The middle fold, in contrast, constitutes a movable ridge or shoulder upon which a row of increasingly large teeth, the lateral denticles (fig. 84; 85, *B*, C_1, C_2) are borne. These apparently play an important role in the reduction in size of the gastric mill contents. The lower, or ventral, fold (fig. 85) is separated from the dorsal folds by an extensive lateral fold. The inner margin of the ventral fold is setose. The setae tend to set apart a ventral channel, or channels, running the length of the gastric mill. This ventral channel broadens posteriorly (fig. 85, *D*) and in the posterior end of the gastric mill the lateral ends of the channel bend ventrad (fig. 85, *E*). Here, the channel enters a filter (fig. 84) which is made up of the closely appressed, setose walls of the ventral channel. The setae are arranged in regular rows. According to Calman (1909), the filter is very constant in the penaeids. At its posterior end, the filter has a pair of ducts through which the digestive fluids of the hepatopancreas enter the gastric mill (fig. 85, *E*). Presumably the filter prevents the entry of particulate matter into the main collecting ducts of the hepatopancreas.

The principal device for chewing in the gastric mill is the median tooth, situated in the midline at the dorsalmost point of the mill (figs. 84; 85, C_2, *D*). The median tooth is a heavily sclerotized structure, a proliferation of the gastric mill wall. The tooth rests on articular rods which enable its operating muscles to move it some distance into and out of the lumen of the mill and with considerable force.

Posterior to the regions of the median tooth and beyond the filter the terminal lappets of the gastric mill project into the lumen of the midgut

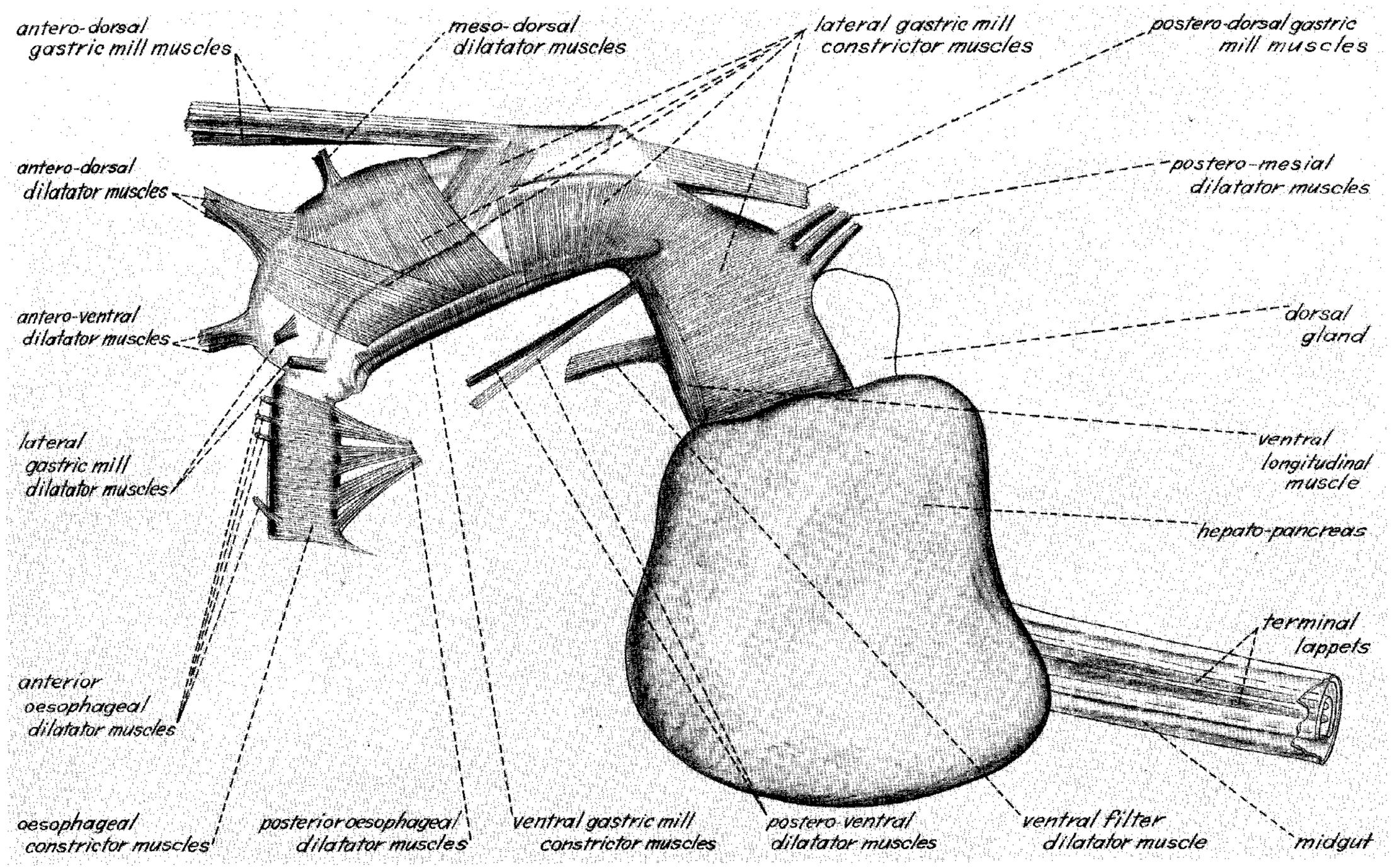

FIGURE 83.—Lateral view of left side of gastric mill and hepatopancreas.

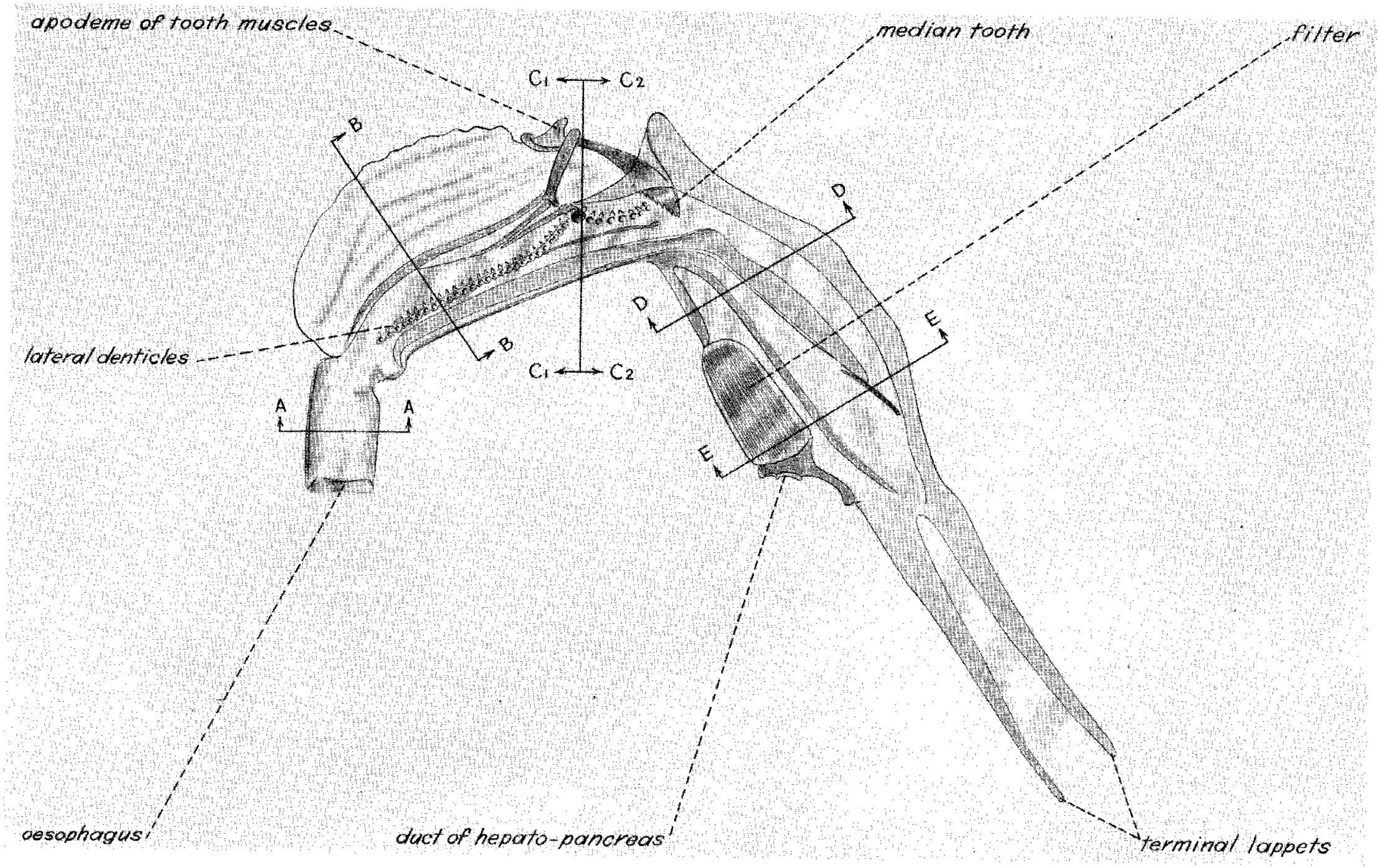

FIGURE 84.—Lateral view of cleared gastric mill showing sclerotized structures. The solid, lettered cross lines refer to the sections in figure 85. The arrows at the ends of the solid cross lines indicate the direction in which the viewer sees the sections in figure 85.

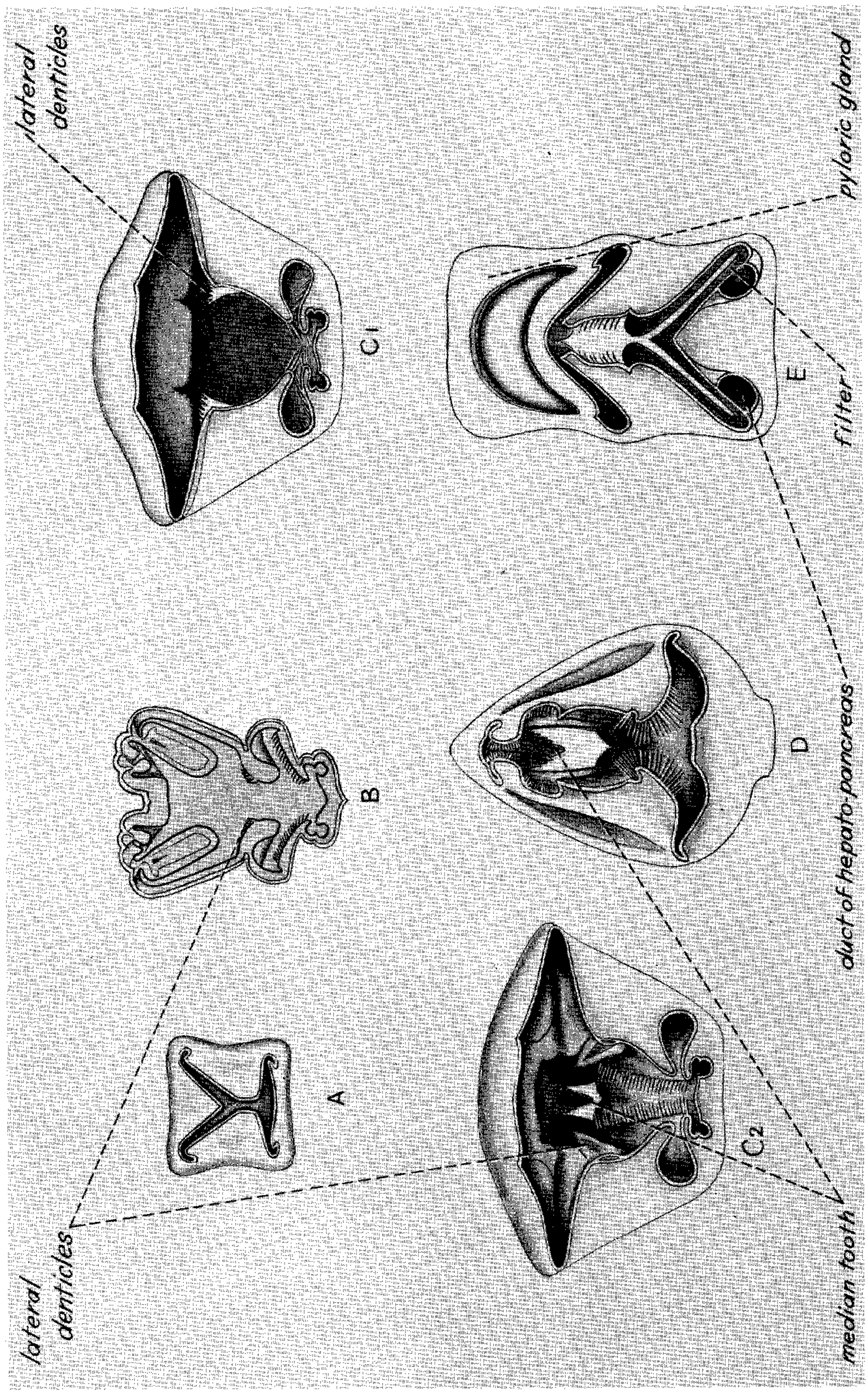

FIGURE 85.—Cross sections through the esophagus and gastric mill. The letters below the figures refer to the corresponding letters at the ends of the solid lines on figure 84.

(figs. 83, 84). In the posterior section of the gastric mill, dorsal to the filter, is a structure here designated as the dorsal (pyloric) gland (figs. 83; 85, *E*). The gland is mounted on the dorsal surface of the gastric mill. Its function is unknown.

The constrictor muscles of the gastric mill are arranged rather like those of the esophagus, in that the fibers are transverse to the long axis of the gut and are attached to lateral folds. The principal members of this group are the lateral gastric mill constrictor muscles (fig. 83). These attach between the long dorsolateral fold and the deep lateral fold dividing the inward ventral fold of the ventral channel. Contractions of the lateral constrictors reduce the diameter of the gut lumen and apply the lateral denticles to the gastric mill contents. Ventral gastric mill constrictor muscles (fig. 83) bring the setose margins of the ventral channel together. A third sheet of fibers, the ventral longitudinal muscle (fig. 83) runs between the lesser curvature of the gastric mill and the anterior end of the filter. Their function is not clear.

In general, the constrictor muscle systems is opposed by some 10 pairs of dilatator muscles. Just dorsad of the esophagus are two small lateral gastric mill dilatator muscles. Anterior to these is an anteroventral dilatator muscle, inserted hard by its mate on the other side. Next above is inserted the anterodorsal dilatator muscle, also close to its counterpart at the midline of the mill. On the anterodorsal surface of the gastric mill, caudad of the anterodorsal dilatators, is the mesodorsal dilatator muscle, inserting on the midline. Posteriorly, behind the curvature of the gastric mill, is inserted a group of perhaps three posteromedial dilatator muscles. Ventral to the gastric mill is found the long, thin posteroventral dilatator muscle which inserts with its counterpart into the ventral midline at the ventral curvature of the gastric mill. And lastly, a ventral filter dilatator muscle inserts into the ventral midline in the region of the filter.

Gross movements of the gastric mill, as well as operation of the median tooth, are accomplished by the large anterodorsal gastric mill muscle and the posterodorsal gastric mill muscle, both of which insert into the dorsal part of the mill, in the region of the median tooth. They are paired muscles. Some of the actions of these muscles may be observed in the living animal during feeding.

HEPATOPANCREAS

FIGURE 83

The main digestive gland of *Penaeus* appears to be the hepatopancreas. This large gland is situated in the posterior region of the thorax, anteroventrad of the heart. It surrounds the junction of the gastric mill with the midgut. In consistency, the hepatopancreas is a mass of closely packed secretory tubules whose products apparently are poured into the ducts of the hepatopancreas at the posterior end of the gastric mill filter.

B. Midgut

The extent of the midgut, or mesenteron, in Crustacea is evidently variable (Calman 1909). That part of the alimentary canal not sclerotized in *Penaeus* runs from some point near the posterior portion of the heptopancreas to the hindgut gland in, the reader will recall, the anterior end of the sixth abdominal segment. The midgut is a simple, straight tube throughout its length. Its association with the dorsal abdominal artery is intimate. Very many small vessels connect the two all the way from the heart to the hindgut gland. Transverse sections of the midgut at various points show that the gut lumen is lined with low columnar epithelium resting on a basement membrane. The outer layers appears to be connective tissue in which muscle fibers are distributed.

C. Hindgut

The proctodaeum, or hindgut, begins at the hindgut gland and includes the rectum and anus. Specimens cleared in strong alkali retain the cuticular lining of this region of the gut. The hindgut (rectal) gland (figs. 61, 62, 74) projects dorsad from the rectum. The gland is composed of tubules lined with large secretory cells. The tubules are blind dorsally and open into the dorsal surface of the rectum. The function of the gland is unknown. The rectum (figs. 61, 74, 83), too, is lined with secretory epithelium reflected into deep folds. The gland cells of the hindgut gland and rectum may play a part in osmotic balance. The anus (fig. 82) consists of a bulb of cuticle at the caudal end of the rectum and a large tube passing ventrad to the anal opening. As has been shown, the opening is controlled by muscles.

V. EXCRETORY SYSTEM

The details of the excretory system and antennal gland of *Penaeus* have not been worked out completely. Compared to the compact and easily visible green gland of the crawfishes, the excretory organs of the white shrimp are much more diffused. Attempts have been made to clarify the extent of the excretory glands of *Penaeus* by injecting dyes into the excretory pores, and such information as is here presented is based on these procedures.

The hemocoelic excretory gland of the white shrimp seems to be made up of two major portions. The smaller, dorsal portion lies above the supraesophageal ganglion (fig. 86). The gland is continuous with the larger, ventral part of the system by means of its lateral arms. The ventral gland lies beneath the dorsal brain on the midline (fig. 86) and extends into the body of the antennae. The dorsal and ventral glands are composed of soft, glandular walls and trabeculae enclosing myriads of sinusoids. The portion of the gland entering the antenna makes contact with a compact, nodular, antennal excretory gland (figs. 20, 21) in the basal segments of the antenna. If the surface of the antennal gland is removed, gland concretions or nodules are found embedded in the tissues. A short duct from the antennal gland leads to the exterior through the excretory pore (figs. 21, 23, 24). The median coxal location of the pore is a constant character of Decapoda.

VI. REPRODUCTIVE SYSTEM

The external sex organs of Crustacea Decapoda have been widely used as systematic characters in the groups and those of the Penaeidae are no exception. In the males the petasma (fig. 87), a modified endopodite of the first pleopod, and in the females the thelycum (fig. 89), the modified sternal plates of the fourth and fifth thoracic segments, have received attention. A system of descriptive nomenclature, largely meaningless, has grown up about the external sex characters, in particular the parts of the petasma. Of inferior taxonomic importance, but constant in the decapods, are the locations of the gonopores. Those of the male lie within folds of thin cuticle between the bases of the fifth walking legs (fig. 88), while the female gonoducts open to the exterior through labiate structures between the third walking legs (fig. 89). A modification of the second pleopods, the appendix masculina (fig. 3), varies in shape and size within the Tribe Penaeidae, that of some genera, as in *Penaeus*, being unspecialized compared to the complex appendix masculina in *Hymenopenaeus*.

The petasma of the male is a system of lightly sclerotized longitudinal rods connected to folds of thin cuticle which permit the petasma to inflate broadly. The structure is folded close to the basipodite of the first pleopod in young males. With the molt to sexual maturity, the medial margin of each half of the petasma becomes joined to its counterpart. Under the compound microscope one can see that the margins are invested with tiny, knobbed processes. Thrust together the knobs tend to form a lock, in the words of King (1948), "like a zipper." Although the copulatory act of penaeids has rarely been observed, apparently the spermatophore is extruded from the male gonopores and held on the posterior or ventral surface of the petasma and then thrust against the thelycum of the female where it is held in place by the setae and sculpturing of that region.

The thelycum of *Penaeus setiferus* (fig. 89) is made of a series of lobes and protuberances characteristic of the species (Burkenroad 1936). These presumably enable the animal to retain the spermatophore for a sufficient time to insure fertilization.

Enough research on the internal reproductive organs of *Penaeus setiferus* has been carried out in the present work to bear out the findings of King (1948), therefore no illustrations repeating his have been prepared on the subject.

The testes of the male are paired. They lie on the dorsal surface of the hepatopancreas ventral to the heart. Each testis is comprised of several lobes extending over the surface of the hepatopancreas. The vas deferens extends from the posterior end of the testis, makes a lateral loop and passes ventrad to the terminal ampoule, a vesicle situated above the male gonopore on the sternum. The ampoule is primarily a glandular structure that secretes the spermatophore.

The ovaries, like the testes, are paired. The ovary has a long, anterior projection which runs along the anterior portion of the esophagus and gastric mill and several lateral projections lying on the surface of the hepatopancreas. The heart is situated dorsal to the region with the lateral projections. Behind the heart a lobe of the ovary, the dorsal ovarian lobe (fig. 62), runs the length

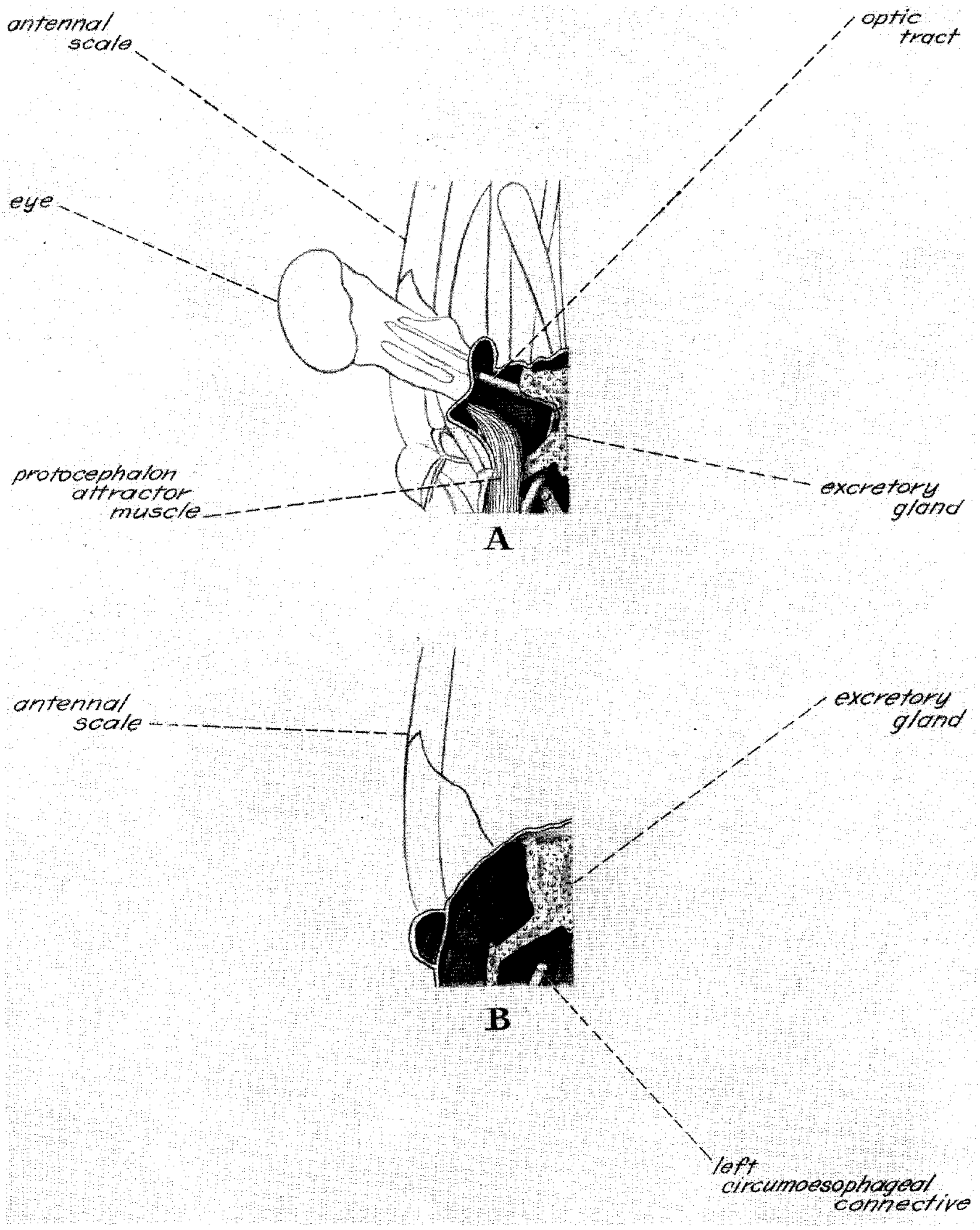

FIGURE 86.—Dorsal view of head region showing excretory gland. Carapace removed. *A*. Part of excretory gland dorsal to brain. *B*. Part of excretory gland ventral to brain.

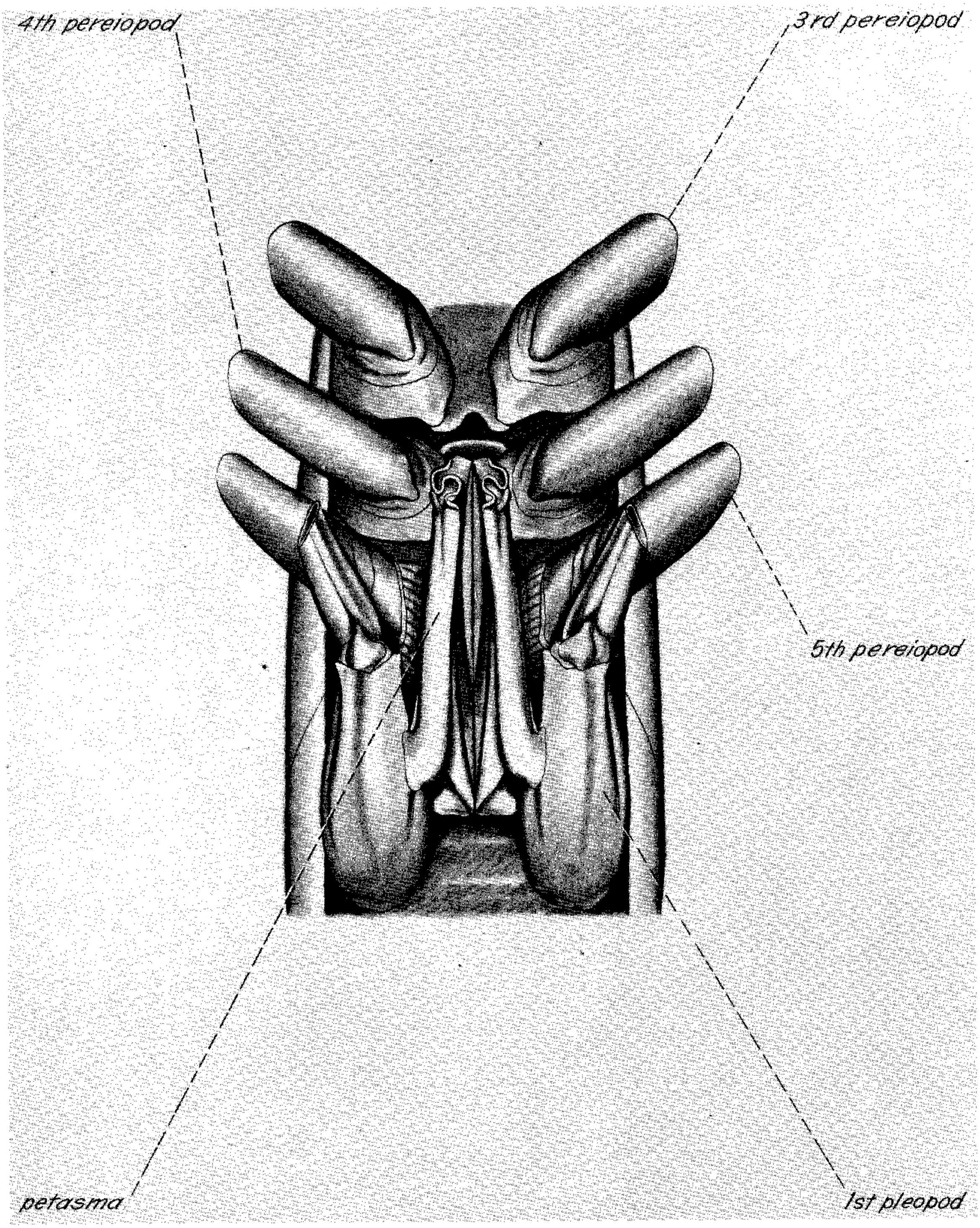

FIGURE 87.—Ventral view of parts of thorax and abdomen showing petasma of male.

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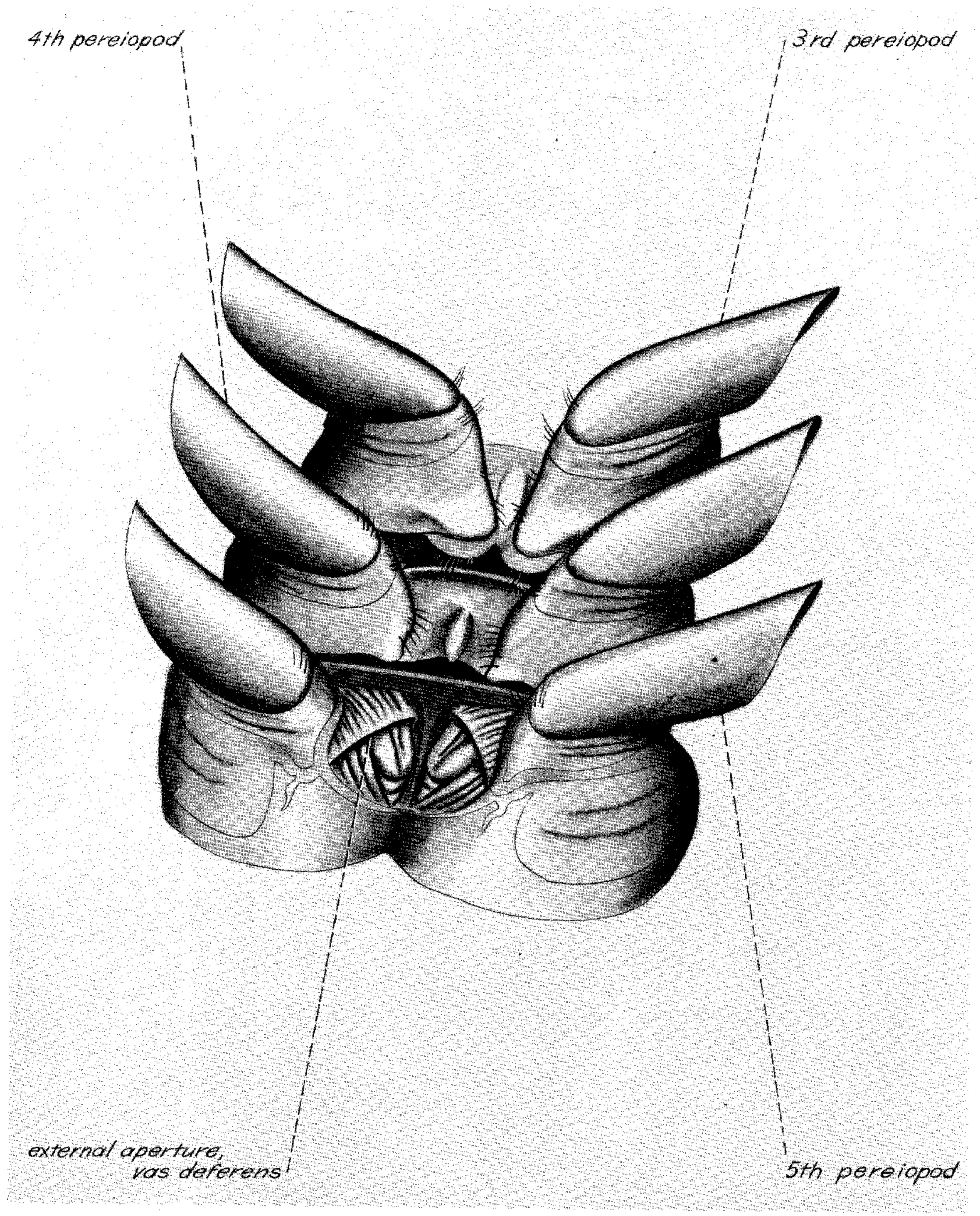

FIGURE 88.—Ventral view of parts of thorax in male. Petasma removed.

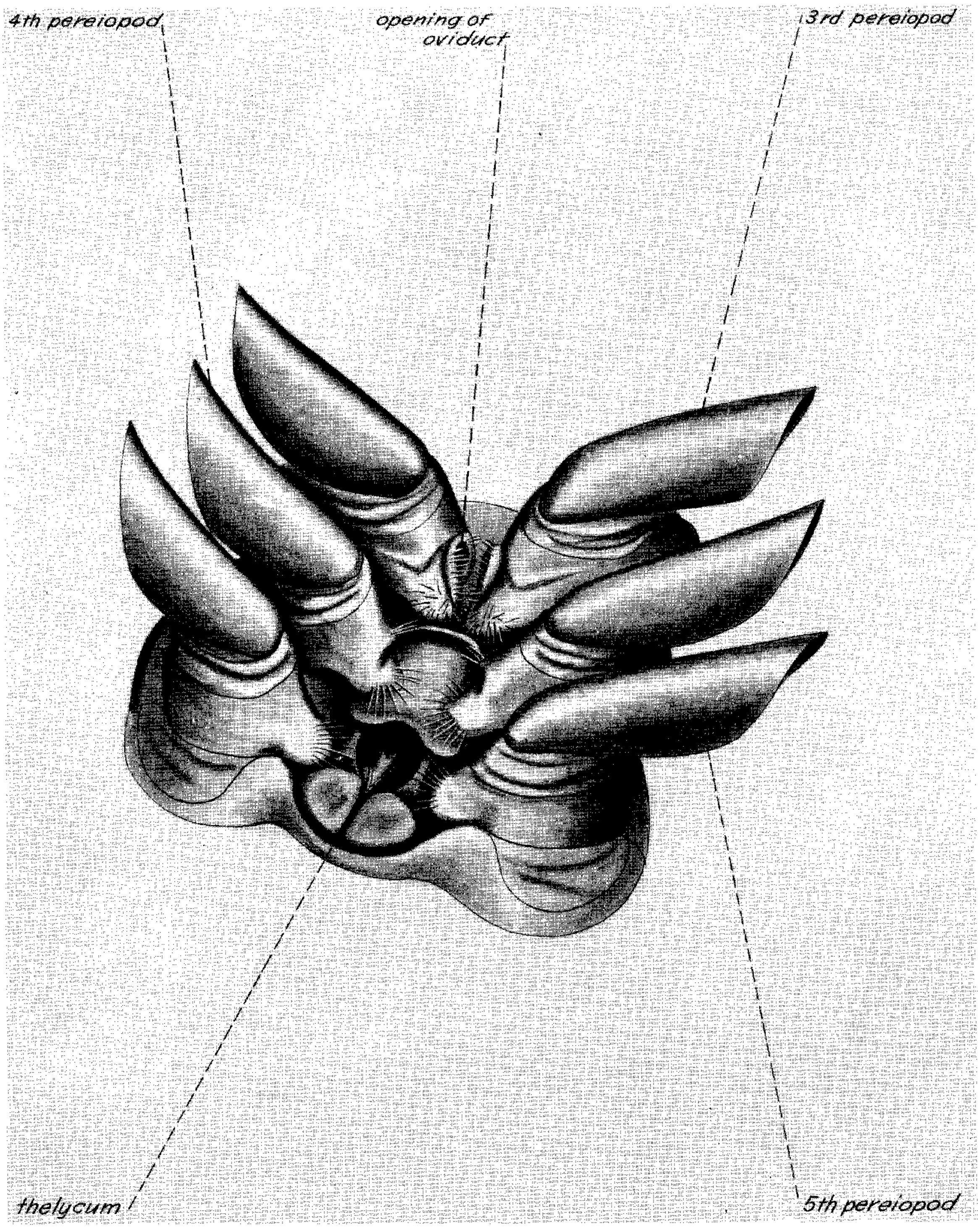

FIGURE 89.—Ventral view of parts of thorax in female.

of the abdomen dorsolateral to the midgut. The oviduct passes ventrad from the thoracic ovary to the female gonopore on the third thoracic leg.

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