tem with the superficial ventral thoracic and the superficial ventral thoracoabdominal muscles considered above in the section on the gnathothorax.

Like their thoracic counterparts, the superficial ventral abdominal muscles are very thin. Two of them are found on each side of the ventral nerve cord between the first and second and between the second and third abdominal segments. Only one is found on each side thereafter. Except for the ventral muscle that passes between the fifth and sixth abdominal segments, and which is ventrad of the nerve cord, all of them arise anterolaterally and run mesad. In this respect, the situation in *Pandalus* is much more like that of *Penaeus* than is *Astacus*. The superficial ventral muscles presumably function to hold the articular cuticle between the abdominal segments in place.

The superficial ventral muscles of *Pandalus*, *Astacus*, and *Callinectes* are probably homologous with the same muscles in *Penaeus*. Some differences exist. All of the superficial ventral muscles of the former crustaceans are single on a side, except for the last two abdominal segments of *Astacus* in which the muscles are double.

SUPERFICIAL LATERAL ABDOMINAL MUSCLES

Although these muscles are not illustrated here, their centers are indicated by small triangles on figure 60. The triangles represent apodemal depressions. Each superficial lateral abdominal muscle is attached to broad, tough apodemal material arising at the triangles. The muscles are very thin, fan-shaped structures, and apparently function to retain the position of the cuticle during movements of the white shrimp.

SUPERFICIAL DORSAL ABDOMINAL MUSCLES

FIGURE 62

Lateral to the midline on the dorsal surface of the abdomen lie the thin superficial dorsal abdominal muscles. The muscles arise in superficial connective tissue in the abdominal segments and pass to apodemal material at the anterior margins of the succeeding segments. Those inserting on the fourth, fifth, and sixth abdominal segments are square, flat muscles, situated laterad of the main dorsal abdominal muscles. The superficial dorsal abdominal muscle attached to the second abdominal somite is a long, thin muscle lying dorsad of the main dorsal muscles. Inserting on the third abdominal segment are two superficial dorsal abdominal muscles. The medial one is long and slender, while the lateral muscle is rectangular and has a lateral anterior projection. The superficial dorsal muscles probably hold the articular cuticle in position.

The superficial dorsal abdominal muscles have counterparts in *Pandalus* and *Astacus*. Those of *Pandalus*, however, are all single muscles on each side of the midline. In addition Berkeley illustrates a sixth superficial dorsal muscle in *Pandalus* inserting on the telson. In *Astacus*, 6 pairs of strong superficial dorsal muscles are found lateral to the midline and a single seventh muscle attached to the telson.

MAIN DORSAL ABDOMINAL MUSCLES

FIGURES 60, 61, 62

The main dorsal abdominal muscles function as abdominal extensor muscles in opposition to the action of the huge ventral abdominal muscle mass. The dorsal abdominal muscles make apodemal connection with the dorsal thoracoabdominal muscles (fig. 61) and as such represent a functional abdominal continuation of the latter. The dorsal abdominal muscles may be divided into two groups, the dorsolateral abdominal muscles, and the dorsomedial abdominal muscles. Both groups are easily distinguished from the underlying ventral muscles. Their removal exposes the midgut and various dorsal circulatory and nervous elements. The arrangement of the dorsolateral and dorsomedial muscles of *Astacus* appears to be similar to that of *Penaeus*, in that the two groups of muscles are distinct. In *Pandalus*, on the other hand, these muscle groups are so intertwined that Berkeley refers to the lateral and medial parts as slips of the same muscle.

In *Penaeus* the dorsolateral and dorsomedial abdominal muscles are markedly segmental and readily separable from one another, except for the dorsal abdominal muscle of the second segment (occupying the dorsum of the first abdominal segment (fig. 62)). Here, the muscles are fused. The medial portion is connected with the dorsal thoracoabdominal muscle and a lateral slip of fibers is attached to superficial connective tissue. The whole structure passes caudad to insert on the dorsal apodemal yoke dividing the first and second somites. The dorsolateral muscles occupying the second, third, fourth, fifth, and sixth abdominal segments all arise from the cuticular yokes

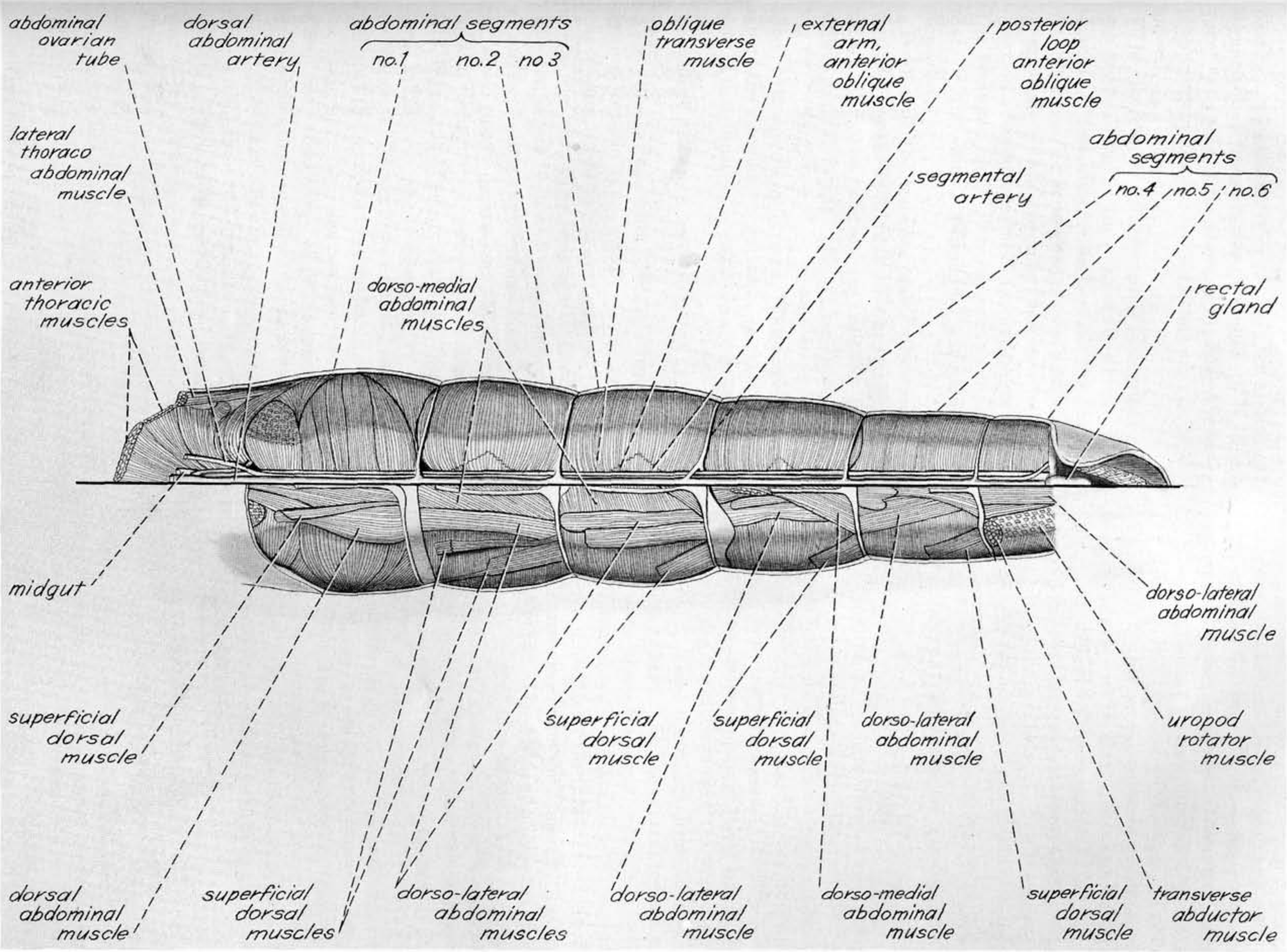

FIGURE 62.—Dorsal views of abdominal muscles. Lower section, intact musculature. Upper section, dorsal abdominal muscles removed.

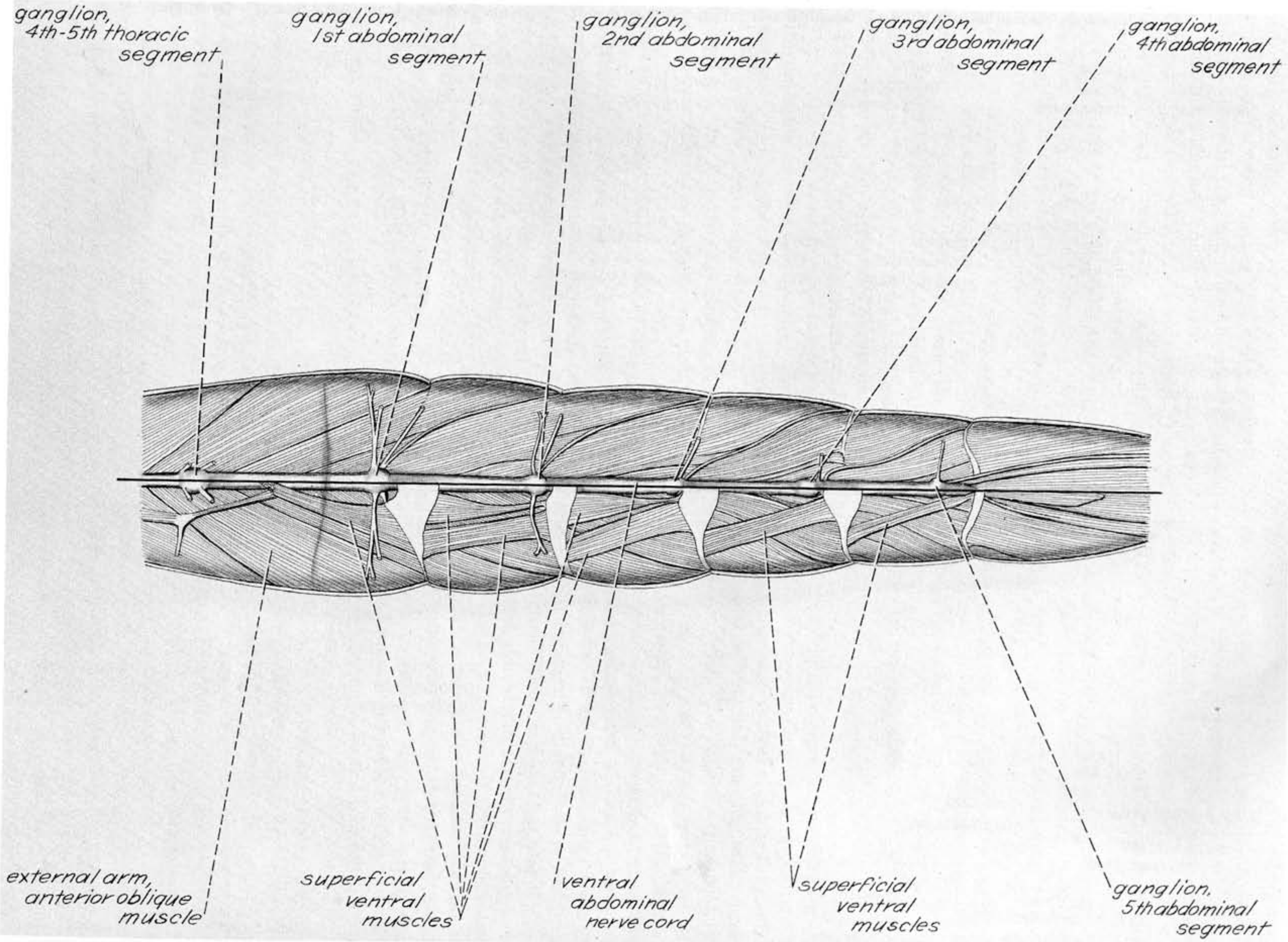

FIGURE 63.—Ventral views of abdominal muscles. Lower section, intact musculature. Upper section, superficial ventral muscles removed.

passing across the anterior part of each abdominal segment and from them run caudad to the next yoke. The axis of the fibers of the lateral muscles is approximately parallel with the long axis of the animal.

The fibers of the dorsomedial abdominal muscles are oblique to the long axis of the white shrimp. These muscles lie beneath the dorsolateral muscles. Each originates on a median sagittal apodeme within a segment and runs laterad to insert on an intersegmental apodeme, posteriorly. The arrangement in *Penaeus* is far simpler than that of the dorsal abdominal musculature of *Pandalus.*

Dorsad of the muscles under discussion, and very close to the middorsal line, are paired structures passing rostrad from the cuticular tissue dividing the abdominal segments (see lower half of fig. 62). The structures appear to be flattened tubes, soft and easily broken. They resemble vessels of the circulatory system more than anything else. Their function is unknown.

MAIN VENTRAL ABDOMINAL MUSCLES

The illustrations show that relatively few abdominal muscle types exist. However, the few that do are serially repeated and so extensively interwoven that their isolation is extremely difficult. Consequently no one should be surprised that an understanding of abdominal muscle function is of fairly recent derivation. Much of what we know is based upon the work of Daniel (1928, 1929, 1931a, 1931b, 1931c, 1931d, 1933) who first set forth the details of the comparative anatomy of abdominal muscles in higher Crustacea.

One of the most interesting features of abdominal anatomy is the contrast between the lightly sclerotized abdominal skeleton and the very heavy abdominal musculature. One would almost expect the light cuticle to be damaged by the powerful flexions of the abdomen. That such does not occur is explained by the unusual arrangement of the abdominal muscles. Some of them are attached to prevent extreme distortions that might otherwise take place. Some muscles, in a sense then, substitute for the skeleton. In addition, certain muscles act in the functional sense as great apodemes of other muscles, thereby freeing the abdominal skeleton of the requirement to produce all but the simplest apodemal material. These apodemal muscles, furthermore, act as fulcra to improve the mechanical advantage of long muscles, such as the anterior obliques, connected between two widely separated abdominal segments.

The terminology of the abdominal musculature of *Penaeus* has been adopted from the work of Daniel. For this reason, substantial differences in nomenclature will be found between the present study and the older morphological research. Daniel (1931c, 1932) has renamed some abdominal muscles and subdivided others. For the most part, however, he makes use of the classical abdominal muscle names.

CENTRAL MUSCLES OF ABDOMEN

FIGURE 61

The longitudinal central muscles are among the main fulcral muscles of the abdomen. They lie deep within the abdominal muscle mass. Six pairs of central muscles are found in the abdomen of *Penaeus*, joined together end to end in a wavy chain. Each central muscle takes origin on an apodeme of a dorsal branch of the preceding central muscle. These dorsal apodemes lie above the transverse muscles. As the central muscle passes caudad into the succeeding segment, it is first joined from above by the fibers of the oblique transverse muscle and then, in the neighborhood of the succeeding transverse muscle, the central muscle divides. The dorsal slip joins the apodeme of the next central muscle and the larger ventral part turns mesad along the anterior face of the transverse muscle. The central muscle apodemes dorsad of the transverse muscles also give rise to the posterior oblique muscles.

The counterparts of the central muscles of *Penaeus* in *Astacus* are not easy to determine. The only muscles in the European crawfish corresponding to the central muscles are the musculi ventrales profundi of Schmidt. The central muscles function to support the oblique muscles during the contractions of the latter.

TRANSVERSE ABDOMINAL MUSCLES

FIGURES 60, 61, 64

The large transverse abdominal muscles attach dorsolaterally on the abdominal tergum (fig. 60) and run across the abdomen in association with strong fasciae (the fasciae arise at points indicated by small triangles in fig. 60). The abdomen of *Penaeus* contains six transverse muscles. A midsagittal view of the abdomen (fig. 61) shows the

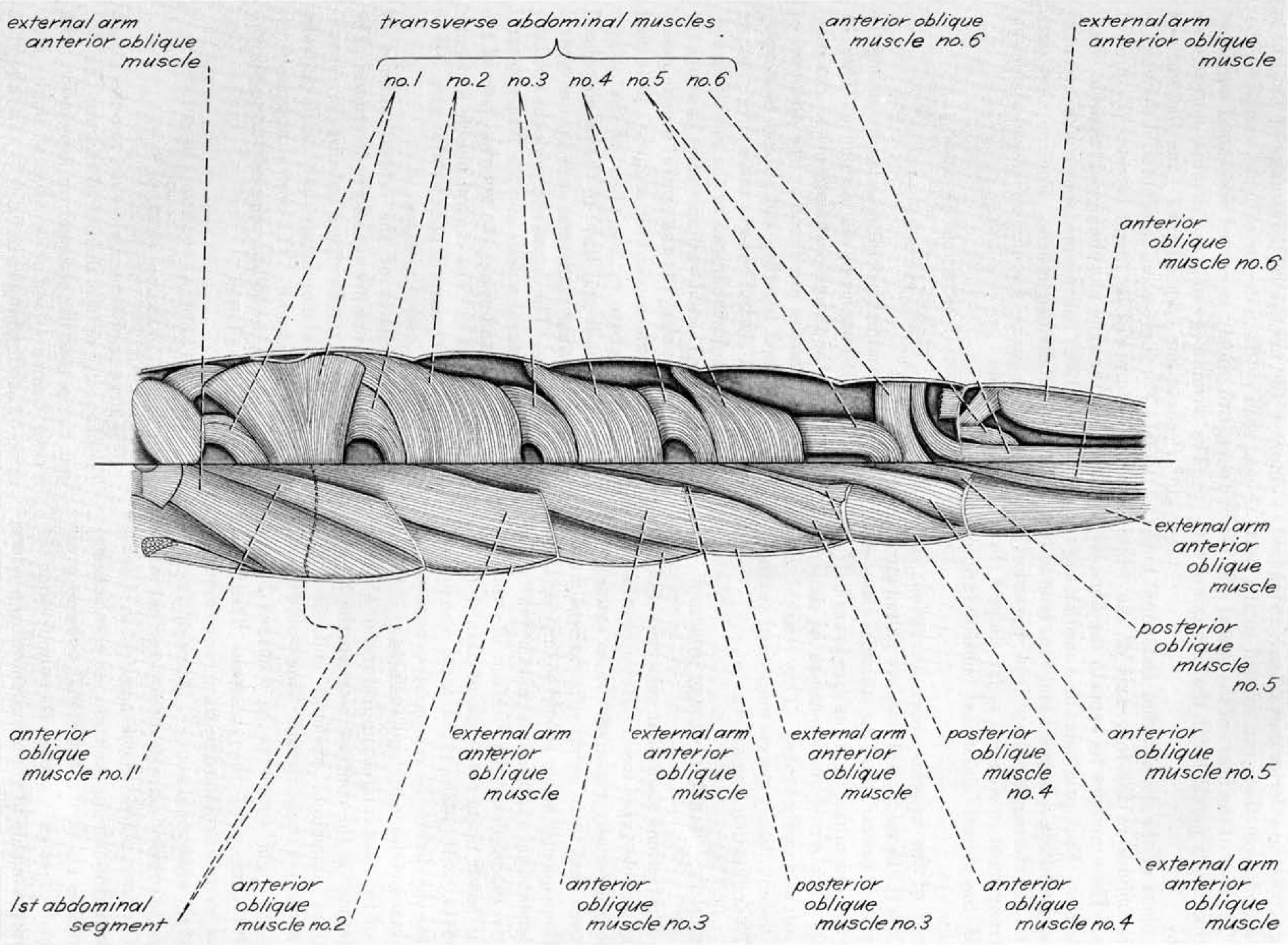

FIGURE 64.—Ventral view of abdominal muscles. The lower section shows the arrangement of the oblique muscles. The upper section shows the transverse abdominal muscles dorsad of the oblique muscles.

transverse muscles crossing the midline. Their great size at the midline is partly due to the addition of fibers of the posterior loop of the anterior oblique muscle, as well as those of the ventral slip of the central muscle, mentioned above. The muscles function in the fulcral support of the central muscles, together with lateral compression of the abdomen. The transverse abdominal muscles of *Penaeus* are fully homologous with those of *Pandalus* and *Astacus*. Both of the latter forms have six of these muscles.

ANTERIOR OBLIQUE MUSCLES OF ABDOMEN

FIGURES 60 TO 64

The anterior oblique muscles are directly responsible for the strong abdominal flexions of which the white shrimp is capable, and as such are on functional grounds the most important longitudinal muscles of the abdomen. Each anterior oblique muscle is made up of several parts. The thickest part runs mesad of the central muscle and is closely applied to its opposite number at the median sagittal line (fig. 61). From the midline, the main part of the anterior oblique turns ventrally and curves caudad to an insertion area two segments to the rear. The area of its insertion is on the posteroventral margin of the abdominal segment concerned. *Penaeus* has 6 anterior oblique muscles, compared with 7 each for *Pandalus* and *Astacus*.

FIRST ANTERIOR OBLIQUE MUSCLE OF ABDOMEN

The first anterior oblique muscle arises in connective tissue in the fifth or last thoracic segment, mesad of the lateral thoracoabdominal muscle (fig. 61) and runs ventrocaudally through part of the last thoracic and all of the abdominal segment to an area of insertion on the posterior edge of the first abdominal segment (fig. 64). The muscle functions to pull the ventral surface of the first abdominal segment forwards about its hinges with the fifth thoracic segment. The muscle appears in the abdomen of *Pandalus* and *Astacus*.

SECOND ANTERIOR OBLIQUE MUSCLE OF ABDOMEN

This muscle (fig. 61) traverses the first and second abdominal segments, inserting on the posteroventral portion of the second segment (fig. 64). By the contractions of the second anterior oblique muscle the ventral part of the second abdominal segment is brought rostrad. Homologs of this muscle have been described in *Astacus* and *Pandalus*.

THIRD ANTERIOR OBLIQUE MUSCLE OF ABDOMEN

Beginning in the second abdominal segment (fig. 61), the third anterior oblique muscle sweeps posteroventrad and inserts on the posteroventral rim of the third abdominal segment. It pulls the ventral part of the third segment forward. The same muscle is found in the abdomen of *Pandalus* and *Astacus*.

FOURTH ANTERIOR OBLIQUE MUSCLE OF ABDOMEN

From its origin in the third abdominal segment, the fourth anterior oblique runs directly ventrad, then turns sharply caudad and passes along the ventral surface of the abdomen to its insertion on the fourth segment (fig. 61). The muscle in *Penaeus* is represented in *Astacus* and *Pandalus*.

FIFTH ANTERIOR OBLIQUE MUSCLE OF ABDOMEN

This muscle runs in a gentle curve from its dorsal origin in the fourth abdominal segment to its insertion in the rear of the fifth segment (fig. 61). The medial manifestation of the fifth anterior oblique is much slenderer than is that of the preceding anterior oblique muscles. Contractions of the muscle flex the fifth segment ventrad with respect to the fourth segment. Schmidt and Berkeley describe the muscle in *Astacus* and *Pandalus*.

SIXTH ANTERIOR OBLIQUE MUSCLE OF ABDOMEN

Like the fifth anterior oblique, the sixth curves gently from the dorsal part of the fifth abdominal segment to its special insertions at the caudal end of the long sixth segment (fig. 61). The ventral part of the sixth anterior oblique muscle lying in the sixth segment may be seen to be very thick. Actually, its cross-sectional area is no greater than the caudal portions of the other anterior oblique muscles, but by virtue of its concentration along the midline, a median sagittal view reveals a large portion of the muscle. The muscle is functionally similar to the preceding anterior oblique muscles. However, its insertions upon the sixth segment and the parts of the tail fan are substantially modified from the typical plan of the preceding anterior oblique muscles.

At the posterior end of the last segment, the sixth anterior oblique muscle has three areas of insertion. Moving caudad from the anterior end of the sixth segment, certain fibers of the sixth anterior oblique muscle insert in tough connective tissue over a large area on the ventral surface of the sixth somite (figs. 71, 72). These fibers are obviously associated with the flexion of the sixth abdominal segment on the fifth. The major portion of the ventral fibers of the sixth anterior oblique continue caudad beyond the sternal insertion area to insert on a strong tendon, or apodeme of anterior oblique muscle (figs. 71, 72). This apodeme is firmly connected to the uropod protopodite, the base element from which the uropods arise. Thus the sixth anterior oblique flexes the uropods as well as the sixth segment.

The third area of sixth anterior oblique insertion is slightly dorsad of the ventral anterior oblique apodeme. It, too, is apodemal, and, while lighter than the ventral apodeme, is a strong tendon. This dorsal anterior oblique apodeme is best seen in median sagittal aspect (figs. 61; 74, *B*). In contrast to the ventral anterior oblique apodeme, the dorsal tendon bifurcates anteriorly into two parts. Two large and distinct portions of the sixth anterior oblique muscle insert on the tendinous bifurcations. The two parts of the dorsal apodeme fuse and run caudad to a point on the ventrolateral surface of the telson. The sixth anterior oblique muscle clearly flexes the telson in addition to its previously mentioned activities.

The sixth anterior oblique muscle of *Penaeus* is undoubtedly homologous with that of *Pandalus* and *Astacus*. Berkeley and Schmidt indicate the presence in the latter forms of the ventral apodeme of the anterior oblique muscle. They do not mention the dorsal apodeme of this muscle.

POSTERIOR LOOP OF ANTERIOR OBLIQUE MUSCLE OF ABDOMEN

Figures 60, 61

Arising from the posterior portion of the dorsomedial area of the anterior oblique muscle, where the bilateral pairs of the latter are fused at the midline, is the posterior loop of the anterior oblique muscle. The muscle runs ventrocaudally, laterad of the central muscle, and then passes mesad to join the transverse muscle. At the midline, the fibers of the posterior loop connect with those of its partner on the other side of the segment. Each anterior oblique muscle of *Penaeus* appears to have a posterior loop.

EXTERNAL ARM OF ANTERIOR OBLIQUE MUSCLE OF ABDOMEN

Figures 60, 63, 64

The external arm of anterior oblique muscle is much larger and more important than the posterior loop. The external arm connects with the broad dorsal end of the anterior oblique muscle at the midline (fig. 61). The muscle sweeps over the central muscle dorsally and then runs anteroventrad along the outside of the abdominal muscles to a ventrolateral point just inside the next anterior abdominal somite (fig. 60). Daniel (1931c) considers this point the origin of the external arm, and he notes that the area is the common insertion of the anterior and posterior obliques of an anterior segment. To summarize, each external arm originates on the posteroventral edge of an abdominal segment and traverses very nearly the whole of a segment to its insertion on the main body of the anterior oblique muscle. Taking the anterior oblique muscle as a whole, including its external arm, the muscle functionally traverses three segments from the ventral surface of one, over the central muscle of the second, dorsally, and hence to the ventral surface of the third segment.

As one would expect, the abdomen of *Penaeus* contains 6 external arms accompanying 6 anterior oblique muscles (fig. 60). Its counterparts in the abdomen of *Pandalus* and *Astacus* are not clear.

POSTERIOR OBLIQUE MUSCLES OF ABDOMEN

Figures 61, 64

The abdomen of *Penaeus* has five posterior oblique muscles, beginning with the first abdominal segment. The posterior obliques are associated with the anterior obliques and function with the latter in the flexion of the abdomen. Except for the first posterior oblique, the muscles arise dorsal to the transverse muscles in close association with the head or anterior end of the central muscles. The posterior oblique then runs ventrocaudally through two segments to insert ventrad in common with its accompanying anterior oblique muscle (fig. 61). The first posterior oblique originates in tendinous tissue dorsal to the anterior thoracic muscles. No posterior oblique muscle has been identified in the highly modified sixth abdominal segment of *Penaeus*. The posterior oblique muscles of *Penaeus* are represented in the abdomen of *Astacus* and *Pandalus*. The latter forms also have five posterior obliques.

OBLIQUE TRANSVERSE MUSCLES OF ABDOMEN

FIGURE 61

The oblique transverse muscle splits off the anterior oblique muscle dorsomedially at the junction of the main anterior oblique muscle and the external arm. The fibers turn ventrad between the anterior oblique and the central muscle and there join the central muscle. The affinities of the oblique transverse muscles of *Penaeus* in *Astacus* and *Pandalus* are not known.

1. Pleopods

The pleopods or swimming legs in many natant Crustacea are well-developed swimming appendages that enable the animals to propel themselves forward rapidly for great distances. In *Penaeus setiferus* the pleopod is not only heavily muscled but so constructed that the muscles move the pleopod, and in particular the propellers, the exopodite and endopodite, through a long power stroke. Each pair of pleopods beats in unison. The beat of the pleopods is synchronized by volleys of nerve impulses passing along the ventral abdominal nerve cord so that a beat wave reminiscent of ciliary action passes down the abdomen from anterior to posterior. *P. setiferus* has five pairs of pleopods, typical of the Crustacea Natantia. The third set has been chosen for study here because of their unspecialized structure.

When feeding, the white shrimp creeps along the bottom on its long, slender walking legs, testing the substrate for food particles. The cephalic region of the shrimp is held high while the tail fan and telson rest on the bottom. As the animal moves about, the pleopods beat gently from time to time. The resulting flow of water aids in the animal's progress by slightly lifting the tail fan from the bottom. Close examination of the white shrimp on the bottom reveals that the main propulsive elements, the exopodites, beat in a lateral position, not brushing the substrate. The present writer assumed that when the shrimp, encountering an obstruction, rises free of the substrate, the pleopod exopodites would beat in a vertical plane, in a straight line with the proximal elements of the pleopods. Such is not the case, however. In *P. setiferus* the pleopod exopodites always beat in a horizontal plane at right angles to the proximal pleopod elements during the power stroke, no matter whether the animal is creeping along the bottom or swimming freely in the water above. Dr. Edward Peebles, Tulane Medical School, has suggested that the lateral position of the pleopod exopodites places these organs outside of the stream of turbulence created by the walking legs.

The return or recovery stroke, during which the pleopod exopodite must be feathered, is made in the vertical plane, or nearly so. This action might be thought to cause the long exopodite to drag on the bottom, but during the return stroke the organ is relaxed and bends before the pressure of the water passing over it. The distal tip of the exopodite describes an oval. The power stroke draws the tip in a flat arc lateral to the ventral plane of the abdomen. At the end of the power stroke, water pressure from the anterior causes the exopodite to bend caudally and, together with the contraction of rotator and flexor muscles, to rotate one-quarter of a turn about its longitudinal axis. Upon rotation of the exopodite, the inertial drift of the animal through the water helps extensor muscles bring the exopodite from the lateral position of the power stroke to a ventral position. Rotation of the exopodite also enables the organ to present to the flow of water its cross section of least resistance as it is brought forward in recovery.

SKELETAL ELEMENTS

The skeletal and muscular elements of the third pleopod of *Penaeus setiferus* are arranged to perform the functions described above. The skeletal parts are roughly similar to those of the third pleopod of the European crawfish *Astacus astacus*, to those of the first pleopod (the pleopod of the second abdominal segment) in the female of *Callinectes sapidus*, to those of the third pleopod of *Cambarus longulus longulus*, and to the parts of the third pleopod of *Pandalus danae*.

Where the third pleopod of *Penaeus setiferus* is attached to the abdominal venter, the region of articulation of the ventral skeleton is reinforced by two **V**-shaped structures comprised of sclerotized bars (fig. 59). The lateral **V** (fig. 65, ventral skeletal support), traditionally said to be a contribution of the pleuron, has its apex directed

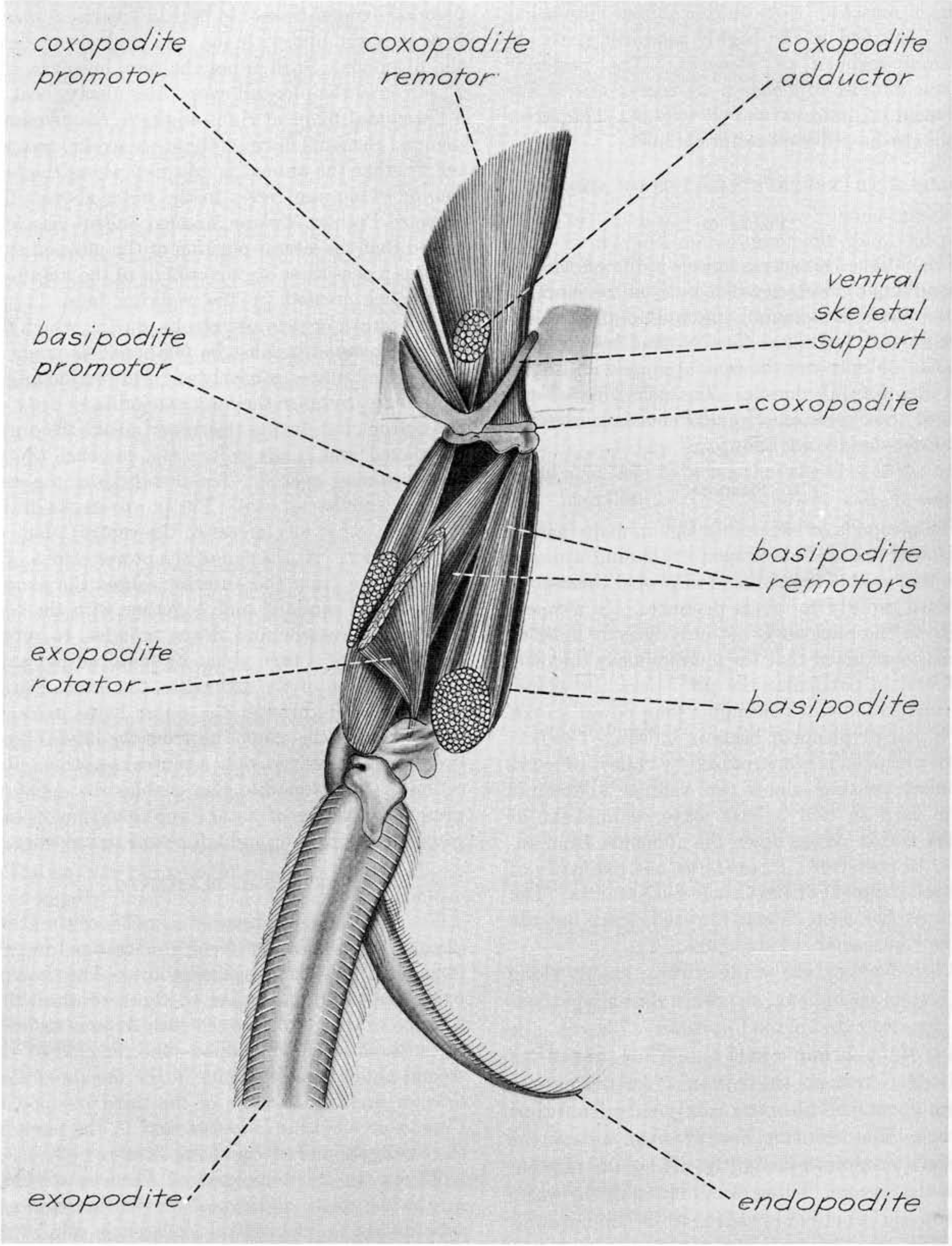

FIGURE 65.—Lateral view of left third pleopod showing basipodite and coxopodite musculature.

ventrad. At this point the structure articulates with the pleopod coxopodite. The mesial **V**, which also points ventrad, constitutes the support for the inner articulation of the pleopod coxopodite. The mesial **V** is a sternal element. The dorsal or free ends of the lateral and mesial arms of the **V**'s are joined. The resulting ventral skeletal structure represents a set of combined triangles, if the coxopodite is included as a structural member, which can be described as a kind of Warren truss. The structural triangles provide support for the articular foramen to which the pleopod is attached. The ventral skeletal structure pertaining to the support of the pleopod is lighter in construction in *Penaeus* than in *Astacus* or *Cambarus*, although the pleopods of *Penaeus* are comparatively much larger and more powerful.

A further structural difference of note between the ventral skeletal pleopod support in *Penaeus* and that of the Astacura and the Brachyura is the position of the appendage relative to the ventral abdomen. In the Astacura particularly, the articular foramen of the pleopod is fully ventral, the ventral sternum and the so-called ventrolateral pleural plates being flat and lying horizontally. In *Penaeus* by contrast the sternum is convex and the lateral plates heretofore considered pleural are nearly vertical, placing the pleopod in a ventrolateral position exposed to the water in which the organ functions. Although Berkeley does not consider the subject, her illustrations indicate that the situation in *Pandalus* is similar to that in *Penaeus.*

The coxopodite (fig. 65) of the pleopod is a narrow, incomplete band or ring which articulates with the ventral skeletal elements dorsally and the basipodite ventrally. To the coxopodite are inserted muscles having their origins on the tergal plates of the abdominal skeleton and in the basipodite. The basipodite (fig. 65) is a broad and elongate structure, shaped like an inverted heart. The form of its cross section through the broad, distal portion is streamlined to reduce its resistance to the water during the recovery stroke. The basipodite articulates with the coxopodite proximally and with the endopodite and exopodite distally. By virtue of the arrangement of points of articulation and of its extensive musculature, the basipodite substantially reinforces the length and power of the propulsive stroke of the pleopod.

Distal to the basipodite, and visible only on the mesial side of the pleopod, lies a small, heavily sclerotized structure (fig. 68), the exopodite articular element, which articulates with the basipodite and the exopodite. Until more information is available, this structure will be considered an exopodite component. In *Penaeus*, several muscles insert in the structure. No trace of this appendage segment appears in the modified pleopods of *Astacus*, *Cambarus*, or *Callinectes.* Berkeley makes no reference to the structure in *Pandalus.*

The endopodite (fig. 68) articulates with the basipodite by a somewhat constricted area on the mesial side of the pleopod. Functionally the endopodite is simple, accompanying the exopodite in its movements. The exopodite (figs. 65 to 69) is a large, broad, oar-shaped organ, convex anteriorly and concave posteriorly. Like the endopodite, it is comprised of a long series of lightly sclerotized rings alternating with bands of thin cuticle. The skeleton of the exopodite is arranged thereby to bend when a stream of water strikes it from the anterior and to remain straight when water strikes it from the posterior. The exopodite functions like a curved, steel carpenter's rule which may be rolled on a spool in one direction, but which presents resistance to bending in the opposite direction. The functional surface of the endopodite and exopodite oar blades is greatly increased by long, plumose setae embedded in the margins. The pleopod endopodite and exopodite have been called flagella in *Astacus* and other reptant decapods in which the organs are extremely reduced by comparison with those of *Penaeus* and *Pandalus.* The term will not be used here, since the endopodites and exopodites of *Penaeus setiferus* are not flagella.

MUSCLE ELEMENTS

The third pleopod of *Penaeus setiferus* is operated by 17 or more muscles. The number of discrete muscles intrinsic to the pleopod endopodite in *Penaeus* is not clear, although the organ may contain two or more muscles. Schmidt in his account of *Astacus* describes 9 muscles for the third pleopod, Cochran lists 6 for the first pleopod of *Callinectes*, Hart (1952) describes 9 for the third pleopod of *Cambarus longulus longulus*, and Berkeley finds 11 in *Pandalus.*

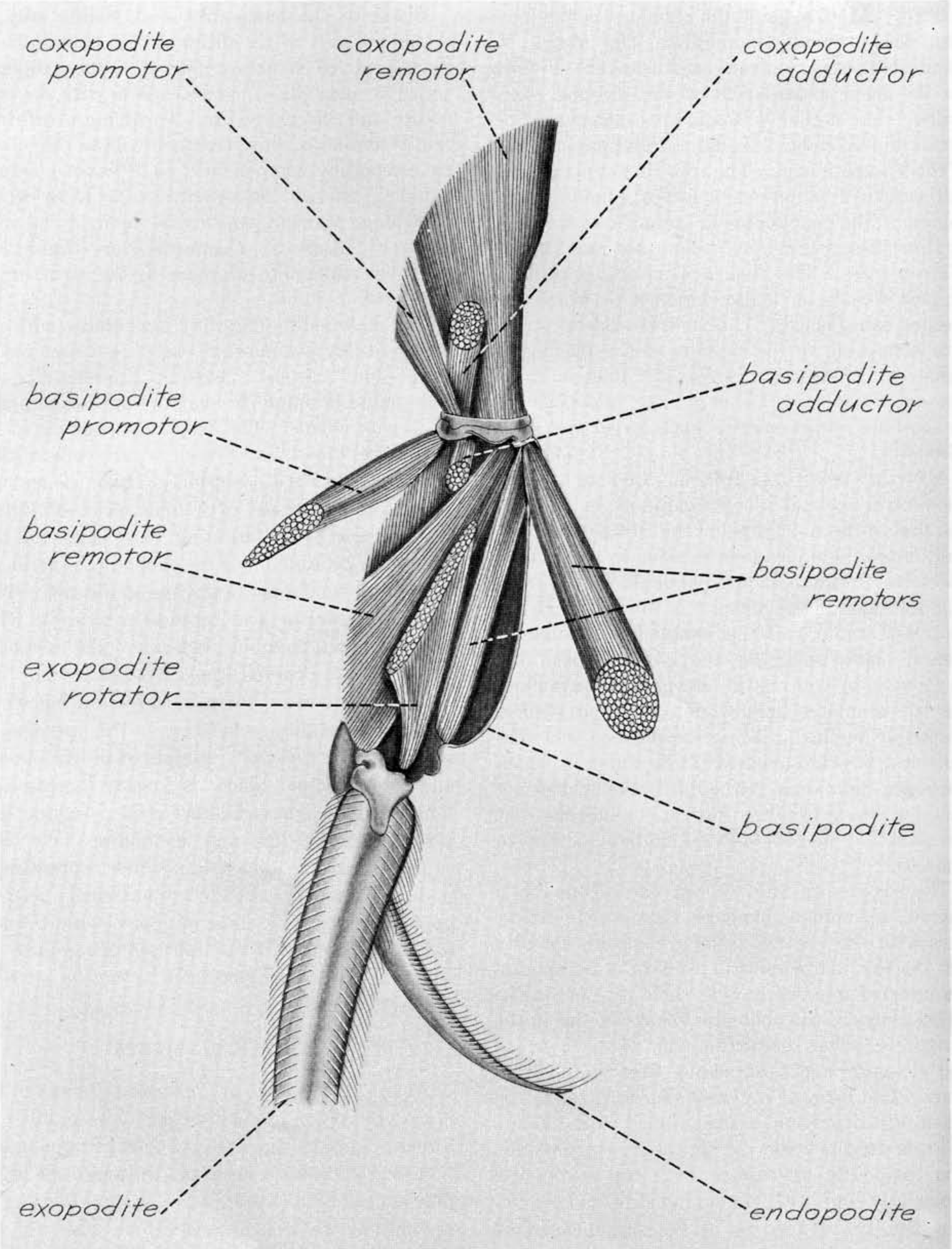

FIGURE 66.—Lateral view of left third pleopod showing basipodite and coxopodite musculature.

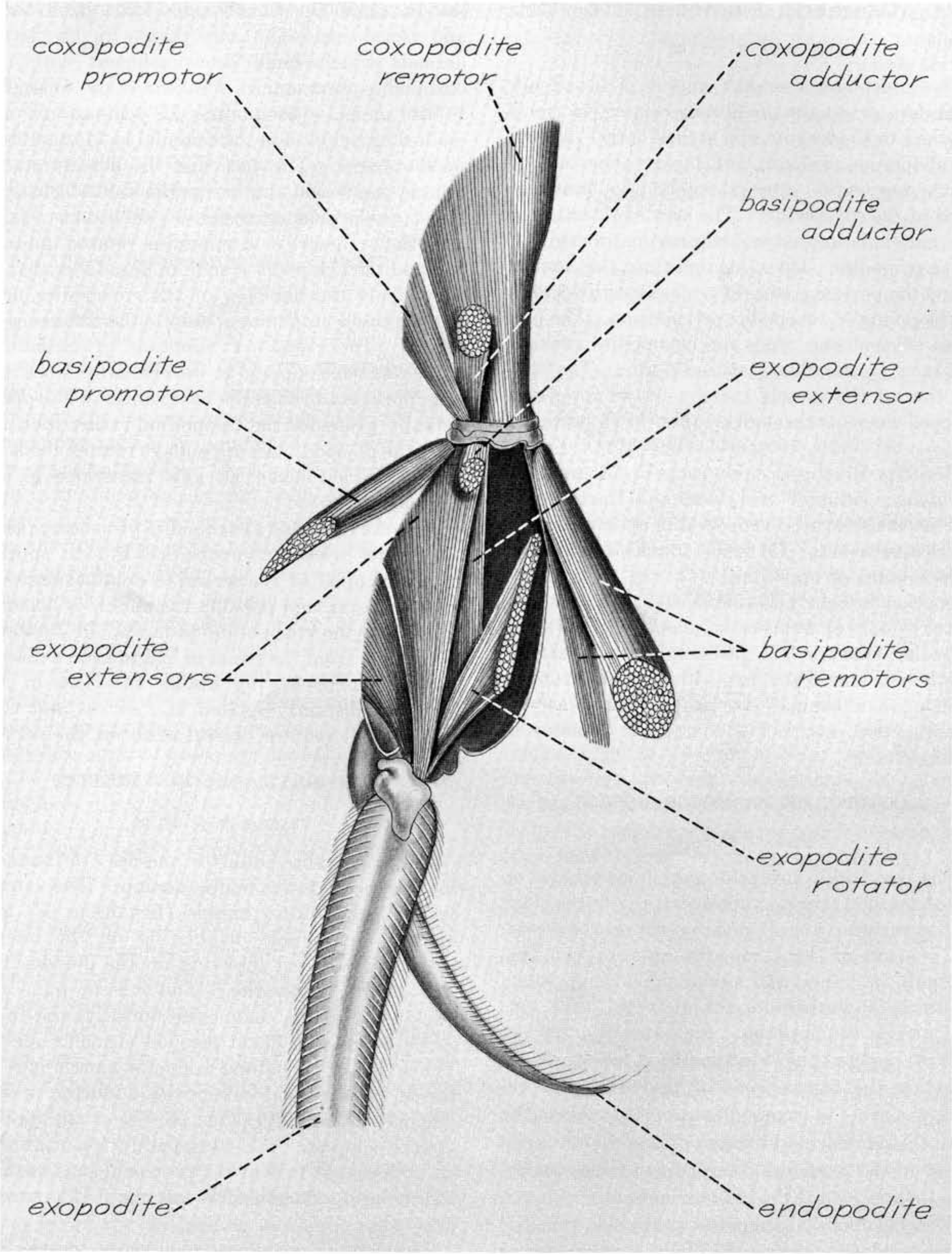

FIGURE 67.—Lateral view of left third pleopod showing basipodite and coxopodite musculature.

COXOPODITE REMOTOR MUSCLE

FIGURES 65 TO 69

The coxopodite remotor muscle, a broad upright fan, originates in fibrous connective tissue attached to the tergum, the arched dorsal plate of the abdominal skeleton, and inserts about an arc which represents approximately the posterior third of the coxopodite. The area of insertion of this muscle is located on the proximal margin of the coxopodite. Upon contraction the muscle draws the posterior edge of the coxopodite dorsad on the points of coxopodite articulation. The pull is an efficient one, since the coxopodite remotor contracts in an almost straight line. The contraction of the muscle thereby draws the distal pleopod elements through an anterior-to-posterior arc.

Berkeley illustrates the muscle in her work on *Pandalus*. Schmidt in *Astacus* and Hart (1952) in *Cambarus* describe a coxopodite remotor muscle (musculus remotor III pedis spurii) for each of these species of crawfishes. On the basis of information presently available, the coxopodite remotor muscle of *Penaeus* is homologous with the musculus remotor III pedis spurii of *Astacus*, *Cambarus*, and *Pandalus*, although proof must wait upon a comparative study of the nerves. Cochran does not find a coxopodite remotor in *Callinectes*.

COXOPODITE PROMOTOR MUSCLE

FIGURES 65 TO 69

The coxopodite promotor muscle originates on the abdominal tergum anteroventrally to the coxopodite remotor muscle and inserts on the proximal margin of the coxopodite anterior to a line through the lateral and mesial articulation points at which the coxopodite articulates with the ventral abdominal skeleton. Mechanically, the action of the coxopodite promotor is much weaker than are the contractions of the coxopodite remotor, since the coxopodite promotor is smaller than the remotor and its area of insertion is much closer to the proximal fulcral line of the coxopodite than is that of the remotor muscle.

The coxopodite promotor pulls the preaxial margin of the coxopodite dorsad. The distal pleopod elements thus are drawn through an arc anteriorly, in opposition to the action of the coxopodite remotor. The coxopodite promotor muscle has no exact functional counterpart in *Astacus* and *Cambarus*. The only muscle in the latter animals which could be homologous with the coxopodite promotor in *Penaeus* is the musculus rotator dorsalis basipoditis II pedis spurii described by Schmidt in *Astacus* and by Hart (1952) in *Cambarus*. The fact that the dorsal rotator muscle inserts on the basipodite in *Astacus* and *Cambarus* argues against this conclusion.

Berkeley describes a musculus rotator dorsalis basipoditis III pedis spurii in *Pandalus* that is very likely the homolog of the coxopodite promotor muscle in *Penaeus*, despite the difference in origin. However, her adoption of Schmidt's name for this muscle is unfortunate, since the musculus rotator dorsalis basipoditis in *Pandalus* actually promotes the basipodite, rather than rotates the pleopod. An appendage rotates about its long axis, not about an axis transverse to the appendage.

Cochran describes a coxopodite promotor muscle (musculus promotor coxopoditis I pedis spurii) in the pleopod of the second abdominal segment of *Callinectes*, and possibly the muscle is homologous with the coxopodite promotor in *Penaeus*. To remove from the realm of speculation a discussion of muscles having similar functions in two forms as distantly related as *Penaeus* and *Callinectes* will require careful study of the nerves.

COXOPODITE ADDUCTOR MUSCLES

FIGURES 65 to 67, 69

Two coxopodite adductor muscles are found in the pleopod of the white shrimp. The lateral coxopodite adductor muscle (figs. 65 to 67) is a small, short muscle originating on the lateral tergal surface and inserting on the dorsomedial rim of the coxopodite. The muscle pulls the mesial side of the coxopodite dorsally, and in so doing brings the distal pleopod elements mesad. The action of the lateral adductor muscle is reinforced by a second coxopodite adductor muscle (fig. 69) located on the mesial side of the ventral skeletal support. The mesial adductor originates on a phragmal fold of the postcoxal sternum and inserts on the dorsomedial margin of the coxopodite.

The lateral coxopodite adductor muscle has been lost in the Astacura to which reference has been made, but appears in *Callinectes* as the largest muscle in the blue crab pleopod. The mesial coxopodite adductor muscle, which has disappeared in *Callinectes*, possibly exists in *Astacus*, *Cambarus*, and *Pandalus* as the ventral basipodite rotator muscle (musculus rotator ventralis basipoditis III pedis spurii). From Berkeley's account of the origin, insertion, and action of the muscle in *Pandalus*, the musculus rotator ventralis basipoditis is really an adductor muscle. Again, a study of the nerves is called for.

BASIPODITE ABDUCTOR MUSCLE

FIGURE 68

Opposing the action of the coxopodite adductor muscles which tend to draw the basipodite and other distal parts of the pleopod towards the abdomen is the basipodite abductor muscle. This fan-shaped muscle originates on the mesial surface of the basipodite. The area of origin is elongate in the long axis of the basipodite (fig. 68). The muscle becomes narrow as it courses dorsolaterally to insert on the ventrolateral margin of the coxopodite. When the basipodite abductor muscle contracts, the basipodite and the distal pleopod elements are drawn away from the abdomen. The muscle has been lost in *Callinectes* and in the Astacura referred to above. The basipodite abductor muscle of *Penaeus* may have a homolog in *Pandalus* as the musculus adductor basipodite II pedis spurii, a muscle that, according to the description of Berkeley, is evidently an abductor.

BASIPODITE PROMOTOR MUSCLE

FIGURES 65, 66, 67, 69

The basipodite promotor muscle originates on an area of the anterior margin of the basipodite about one-third of the distance from the distal end of the basipodite. The muscle inserts on the anteroventral margin of the coxopodite. Muscle contractions draw the basipodite, and the distal parts of the pleopod, cephalad with respect to the coxopodite. Together with the coxopodite promotor, the basipodite promotor muscle moves the pleopod in its recovery stroke. The basipodite promotor extends the length of the stroke. No homolog of the basipodite promotor muscle in *Penaeus* is evident in the pleopod of *Astacus*, *Cambarus*, or *Callinectes*.

The third pleopod of *Pandalus*, however, has a muscle, the musculus productor basipoditis III pedis spurii, that is similar in function and arrangement to the basipodite promotor muscle of *Penaeus*. The muscles in the two animals are almost certainly homologous, although proof must wait upon a study of nerve-muscle connections. Berkeley's use of the term "productor" for this muscle is questionable. She says, in part, that the musculus productor basipoditis ". . . moves the basipodite forward. . . ." In the opinion of the present writer, the action described by Berkeley for the muscle is not production, but promotion. Production, in the present context, is synonymous with the extension in length of a limb, and the musculus productor basipoditis of the third pleopod of *Pandalus* does not appear to be an extensor muscle.

BASIPODITE REMOTOR MUSCLES

FIGURES 65 to 69

The pleopod of the white shrimp contains 3 basipodite remotor muscles. Their contractions serve to increase greatly the length and power of the propulsive stroke initiated by the coxopodite remotor muscle. The anterior basipodite remotor muscle originates over a broad area in the anteroventral lobe of the basipodite (figs. 65, 66). From its origin the muscle runs diagonally across the interior of the basipodite to insert on the ventral edge of the coxopodite, posterior to a line through the points of articulation between the basipodite and the coxopodite. The posterior basipodite remotor muscles, of which there are two (figs. 65, 68), originate in the posteroventral lobe of the basipodite and extend dorsad to insert on the ventral margin of the coxopodite postaxially.

On the basis of arrangement and size, the anterior basipodite remotor muscle of *Penaeus* is evidently a homolog of the musculus reductor basipoditis III pedis spurii of *Pandalus*. The muscles are also functionally similar. Here again a question is raised over the use of terms. Berkeley describes the action of the musculus productor basipoditis as antagonistic to that of the musculus reductor basipoditis. If, as has been established above, the name "productor" for muscle function is synonymous with the term "extensor," then it follows that a reductor muscle is the same as a flexor muscle. Unfortunately, reduction has not in the anatomical sense the opposite meaning of production, but implies additional functions. For this reason the name "reductor" for muscle

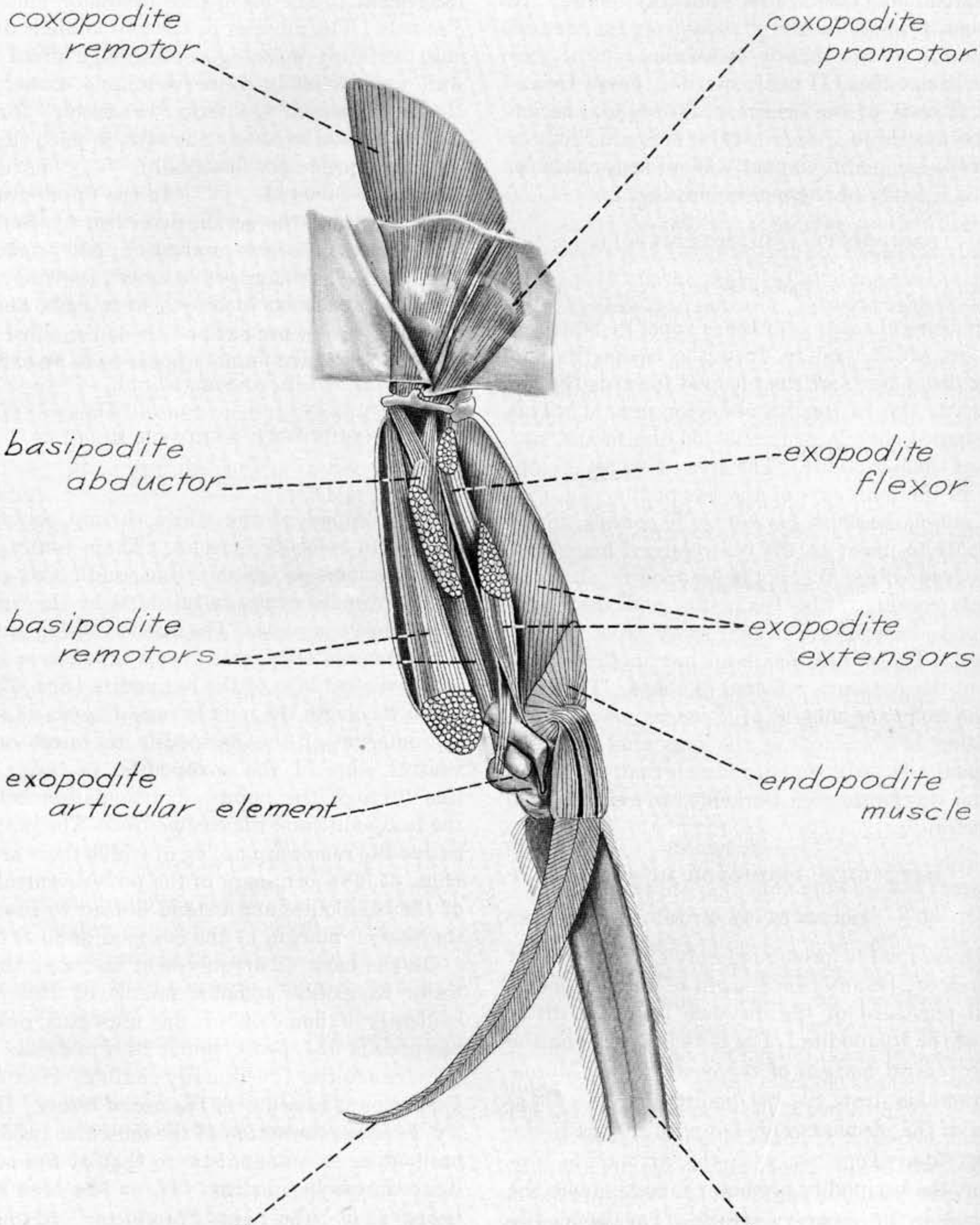

Figure 68.—Mesial view of left third pleopod showing coxopodite, basipodite, and endopodite musculature.

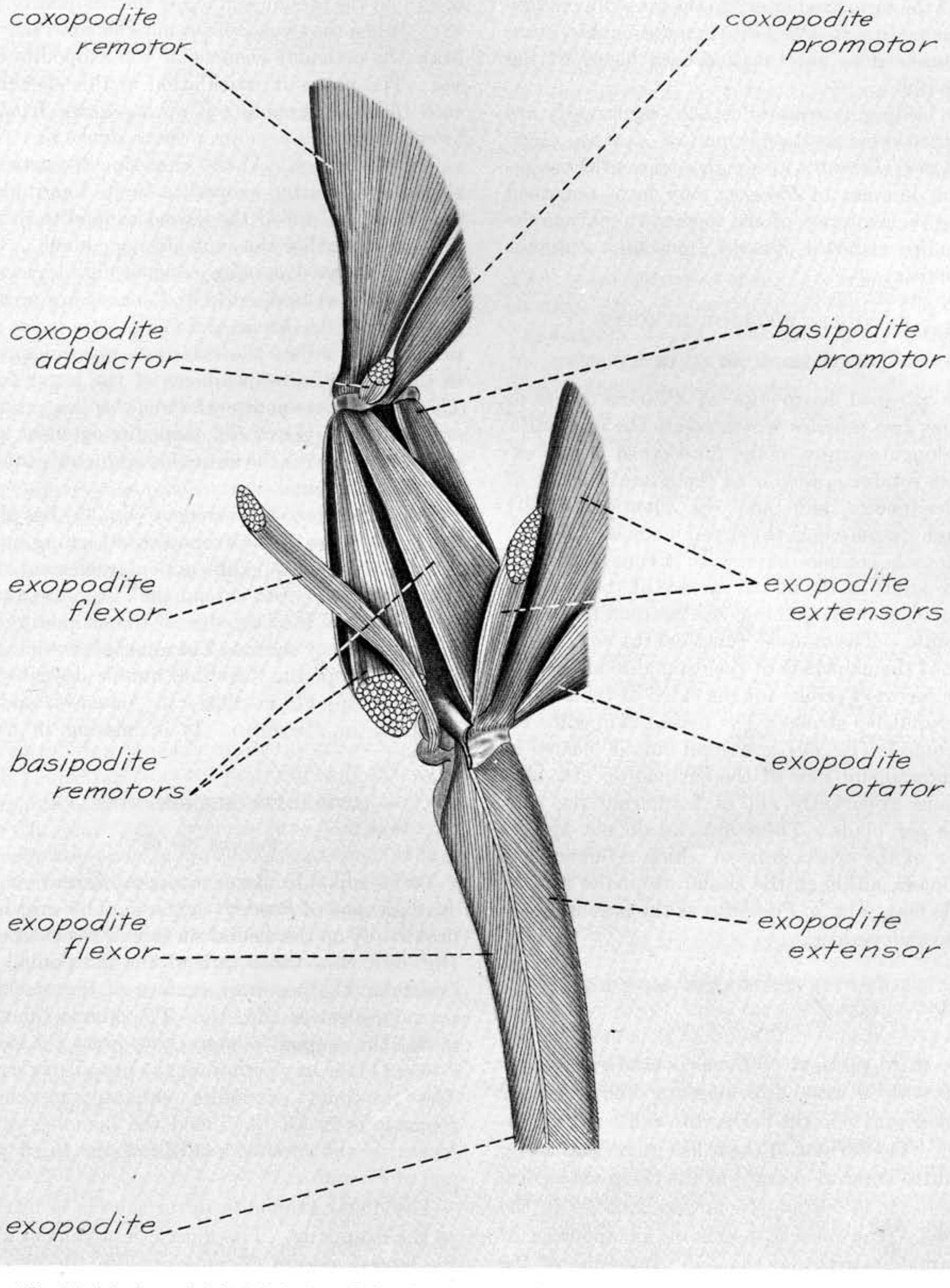

FIGURE 69.—Mesial view of left third pleopod showing muscles of coxopodite, basipodite, and exopodite. Endopodite removed.

action should be avoided. Moreover, the application of the term "reductor" to the musculus reductor basipoditis in *Pandalus* is questionable, since the muscle does not function as a flexor of the basipodite.

The basipodite remotor muscles apparently are not represented in the pleopod of *Astacus*, *Cambarus*, or *Callinectes*, although a trace of these important muscles in *Penaeus* may have remained during the evolution of the former animals as the basipodite reductor muscle (musculus reductor basipoditis).

EXPODITE ROTATOR MUSCLES

FIGURES 65, 66, 67, 69

The pleopod basipodite of *Penaeus setiferus* contains two muscles which rotate the exopodite. The elongate origin of the fan-shaped lateral exopodite rotator muscle is on the lateral surface of the basipodite and may be identified easily through the cuticle in preserved material (fig. 65). The muscle becomes narrow as it runs distomesially to insert on the mesial surface of the complex articular element joining the basipodite to the exopodite. The muscle functions to square the plane of the oar blade of the exopodite at the end of the recovery stroke for the catch of the following propulsive stroke. The mesial exopodite rotator muscle (fig. 69) is a small muscle located in the anterodistal lobe of the basipodite. Its contractions apparently aid in feathering the exopodite oar blade. These muscles do not appear in any of the crustaceans to which reference has been made, although the mesial exopodite rotator muscle may exist in *Pandalus* as the musculus adductor endopoditis.

EXOPODITE EXTENSOR MUSCLES

FIGURES 67 TO 69

The third pleopod of *Penaeus setiferus* is provided with 3 exopodite extensor muscles, 2 of which originate in the basipodite and 1 in the exopodite. The largest of these has its origins along the entire anterior margin of the basipodite (figs. 67, 68). It is one of the largest muscles in the pleopod. The muscle inserts on an apodeme of the exopodite articular element. Inserting on the same apodeme is a slender exopodite extensor muscle which is located just posterior to the anterior exopodite extensor muscle described above (figs. 68, 69). The posterior exopodite extensor has its origin on the mesial surface of the basipodite (fig. 68). When the two extensor muscles contract they draw the articular element of the exopodite dorsad. The plane of articulation of this element is such that the exopodite is swung down from its lateral position in the propulsive stroke to a fully extended position. At the same time the articular element rotates the exopodite on its longitudinal axis, with the aid of the mesial exopodite rotator muscle, to feather the exopodite oar blade.

That the two exopodite extensor muscles located in the pleopod basipodite of *Penaeus* are missing in *Astacus*, *Cambarus*, and *Callinectes* is not surprising in view of the extensive rearrangements in the swimming appendages of the latter form. The pleopod basipodite of *Pandalus* has retained at least the larger of the exopodite extensor muscles of *Penaeus*, as the musculus adductor exopoditis III pedis spurii.

The third exopodite extensor (fig. 69) lies along the mesial edge of the exopodite, attaching on the margin of the exopodite articular element. Its contractions serve to extend the exopodite and to straighten the leading edge of the exopodite during the recovery stroke. The muscle is homologous with the exopodite flagellum muscle described by Schmidt and Hart (1952) in Astacura, and by Berkeley in *Pandalus*. It is missing in *Callinectes*.

EXOPODITE FLEXOR MUSCLES

FIGURES 68, 69

Two exopodite flexor muscles appear in the third pleopod of *Penaeus setiferus*. One originates proximally on the medial surface of the basipodite (fig. 68), runs the length of the basipodite, and inserts on the posterior surface of the exopodite articular element (fig. 69). The muscle functions to flex the exopodite laterally to place the exopodite oar blade in position for the propulsive stroke. The proximal exopodite extensor muscle of *Penaeus* is in all likelihood the homolog of the musculus abductor exopoditis of the third pleopod of *Pandalus*.

The distal exopodite flexor muscle is intrinsic to the exopodite. The muscle is arranged along the lateral margin of the exopodite (fig. 69) and attaches to the posterior part of the exopodite articular element. The contractions of the muscle reinforce the flexing action of the proximal flexor muscle. Like the distal exopodite extensor muscle, the distal exopodite flexor muscle is a homolog of the exopodite flagellum muscle (musculus flagellaris exopoditis III pedii spurii) in *Astacus*, *Cambarus*, and *Pandalus*.

ENDOPODITE MUSCLE

FIGURE 68

The endopodite muscle, or muscles, appears to be a multipart structure in *Penaeus setiferus*. A portion of the muscle lies mesially in the anterodistal lobe of the basipodite (fig. 68). Fibers of the muscle run through the constricted article connecting the basipodite with the endopodite and continue distally into the endopodite. Additional fibers that arise in the proximal end of the endopodite suggest that the endopodite contains more than one muscle body. The function of the endopodite musculature consists of stiffening the endopodite during the power stroke and, by their relaxation in the recovery stroke, of enabling the endopodite to bend before the flow of water.

The endopodite flagellum muscle of *Astacus*, *Cambarus*, and *Pandalus* is very likely the homolog of the muscle in the pleopod endopodite of *Penaeus*. The muscle has been lost in the blue crab.

2. Tail Fan

The tail fan is made up of the telson and uropods projecting from the posterior end of the sixth abdominal segment and intimately associated with it. Classically, the uropods have been treated as serially homologous appendages having the typical limb parts, however modified. The telson, on the other hand, has usually been considered an unsegmented posterior element bearing the anus, on grounds of the embryological addition of abdominal segments before the telson (Calman 1909). The whole tail fan is well adapted for the purpose of drawing the white shrimp backwards through the water as the great ventral abdominal muscles flex the abdomen.

SKELETAL ELEMENTS

The telson (figs. 70 to 74) is an apparently unpaired structure. Its broad, anterior portion articulates with the caudal end of the posterodorsal part of the sixth abdominal somite. Lateral condyles allow free movements in the vertical plane, but limit horizontal motion. The telson becomes narrow posteriorly, tapering to a sharp point. In section, the telson is roughly triangular. The thin sternum varies in shape from flat to slightly concave and the heavily sclerotized laterotergal plates are convex. Instead of having a mid-dorsal carina or ridge, the telson has a pair of ridges produced by a shallow groove in the dorsal midline (fig. 70). The structure lies above parts of the uropods and affords them some protection dorsally.

The uropods (figs. 70 to 74) arise from the posteroventral area of the sixth abdominal somite. Each is comprised of a strongly sclerotized basal element, the protopodite, from which the broad, flat uropods project. The large lateral uropod is the exopodite while the inner is the endopodite. The protopodite is supposed to be made up of the coxopodite and basipodite, but no skeletal trace of these articles is evident. A faint relic of segmentation in the exopodite remains on the dorsal surface (fig. 70) in the form of a transversely oriented groove. A portion of this groove sets off the tip of the lateral exopodite adductor muscle.

Due to the hinging of the uropodal elements, the uropods are capable of free motion. The articulation between the protopodite and the sixth abdominal segment, while strong, is relatively loose. The protopodite can move in the vertical and horizontal planes and also may rotate about its long axis. The points of articulation between the protopodite and the uropods are, on the other hand, condylic, and limit the exopodite and endopodite to the horizontal movements of spreading the uropods. Certain marginal areas of the telson and uropods are fringed with natatory hairs, much like the pleopods.

MUSCLE ELEMENTS

The muscles of the tail fan are all disposed to the function of these organs in the rapid backward swimming of the white shrimp. In plan the muscles are widely different from that of the typical limb. The most notable difference is the presence inside the sixth abdominal segment of several muscle groups which operate parts of the tail fan. This does not occur in the preceding abdominal segments. In comparing the muscles of the area in *Penaeus* with the tail fan muscles of *Astacus* and *Pandalus*, two kinds of differences are encountered. The first has to do with the number of functional muscle types, *Penaeus* having 16 compared with 18 muscle types in the crawfish.

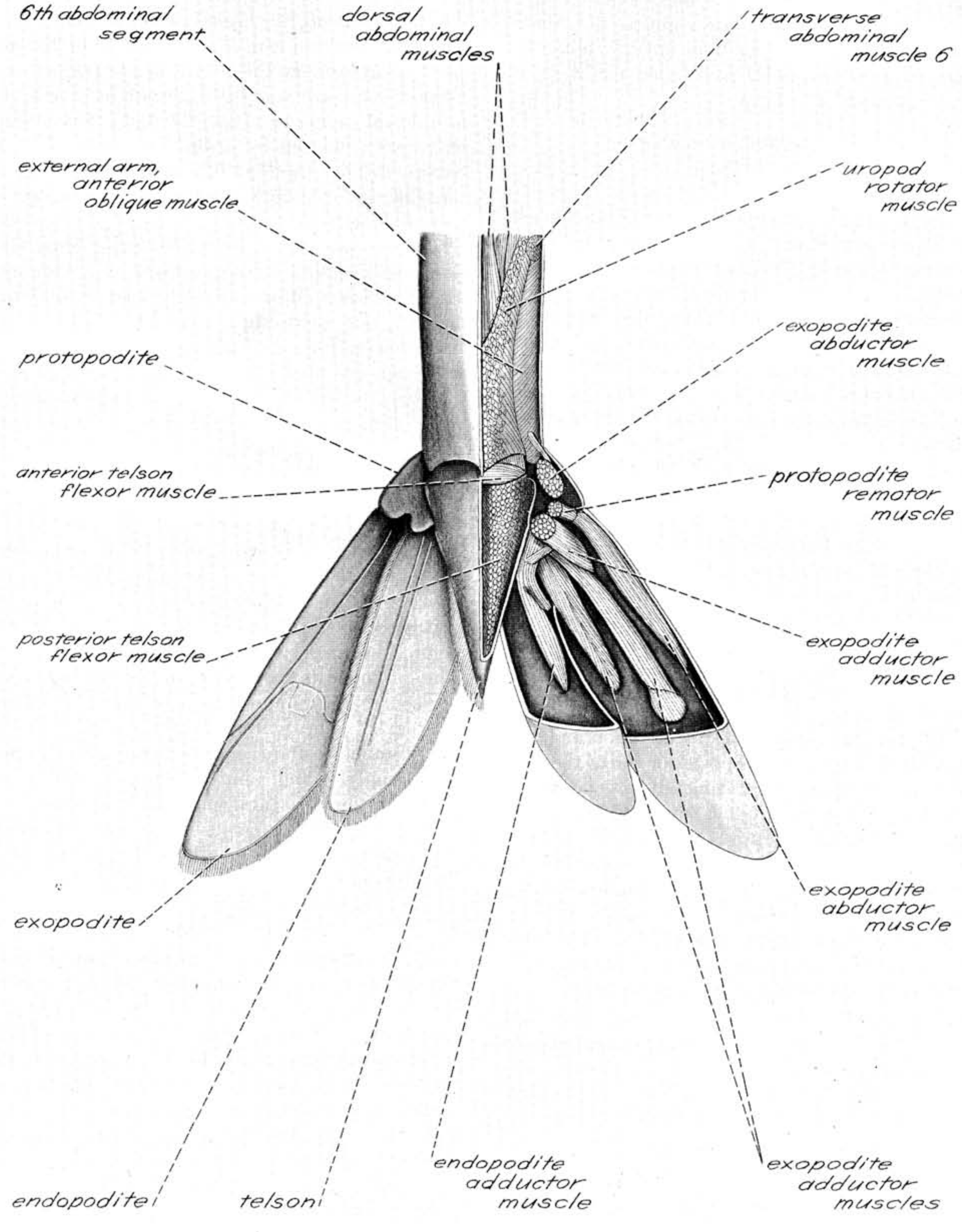

FIGURE 70.—Dorsal view of telson, uropods, and part of sixth abdominal segment. Left side intact. Dorsal cuticle of right side cut away to show muscles.

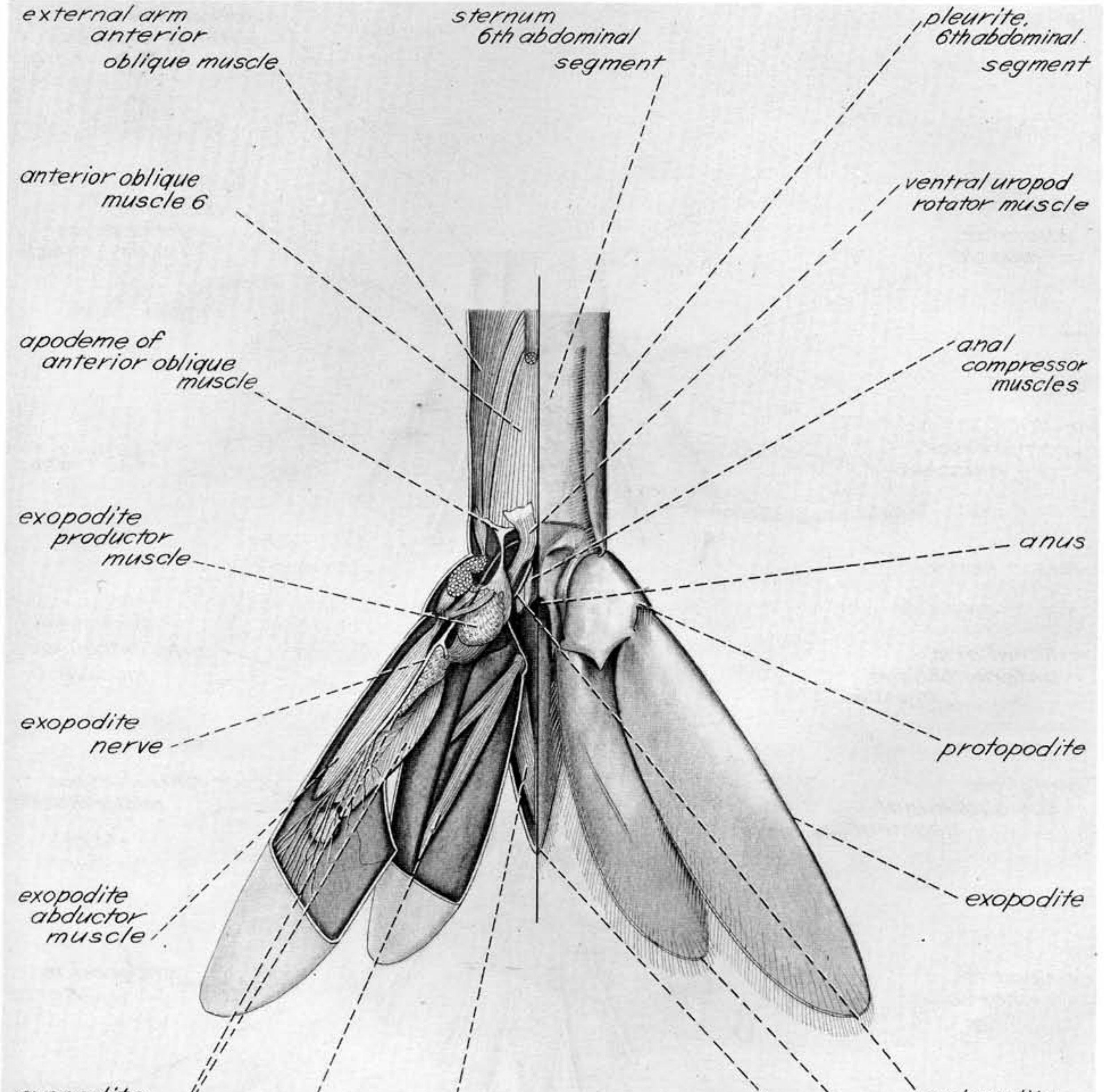

FIGURE 71.—Ventral view of telson, uropods, and part of sixth abdominal segment. Right side intact. Ventral cuticle of left side cut away to show muscles.

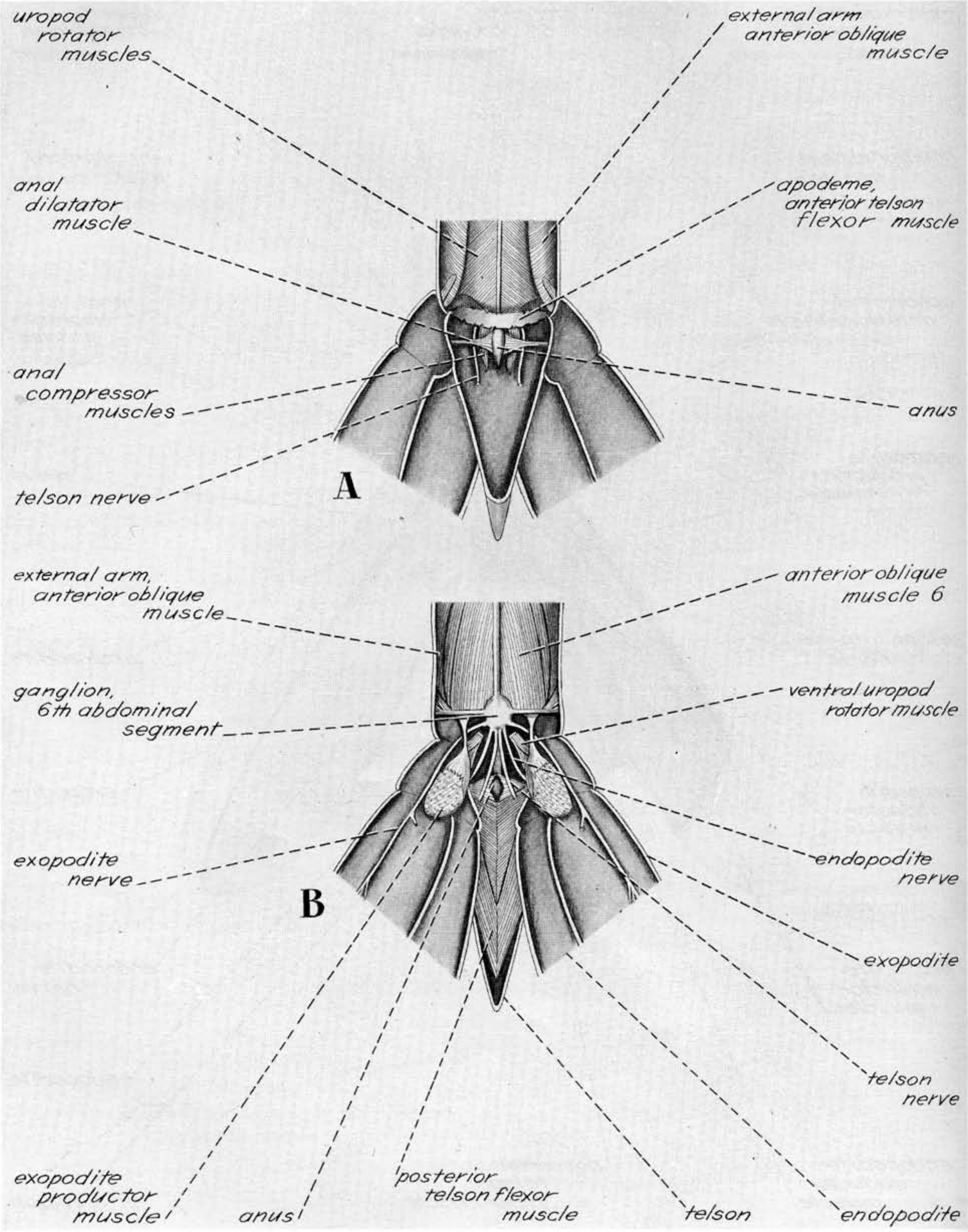

FIGURE 72.—Views of dissections of telson and uropods. *A.* Dorsal view. Muscles removed to show anus and posterior muscles of sixth abdominal segment. *B.* Ventral view. Muscles removed to show nerves.

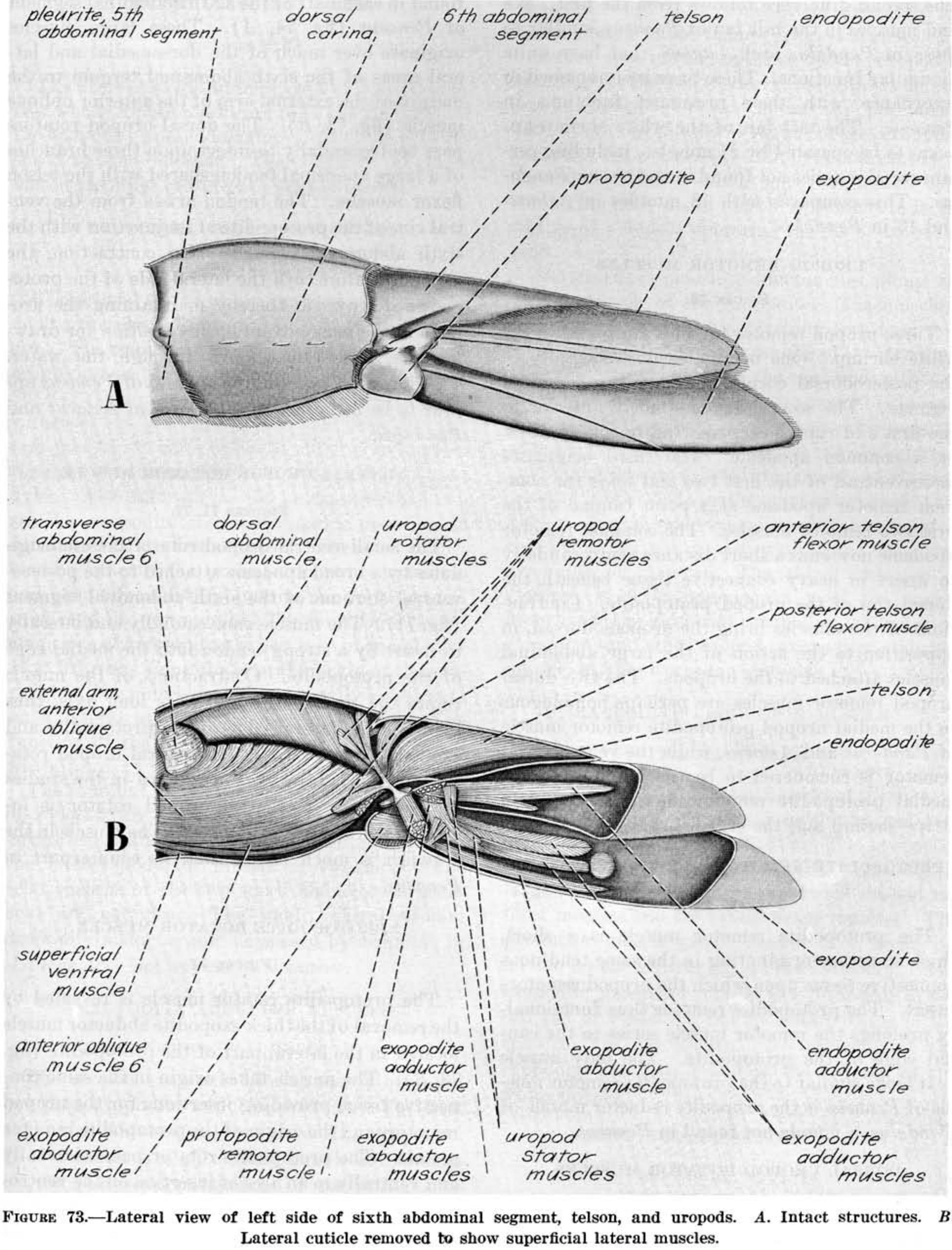

FIGURE 73.—Lateral view of left side of sixth abdominal segment, telson, and uropods. *A*. Intact structures. *B*. Lateral cuticle removed to show superficial lateral muscles.

The second difference follows from the first. We find muscles in the tail fan of *Penaeus*, similar to those in *Pandalus* and *Astacus*, that have quite dissimilar functions. These have been renamed in accordance with their presumed functions in *Penaeus*. The tail fan of the white shrimp appears to be operated by 27 muscles, including certain rectal muscles not found in *Astacus* or *Pandalus*. This compares with 18 muscles in *Astacus* and 13 in *Pandalus*.

UROPOD REMOTOR MUSCLES

FIGURE 73

Three uropod remotor muscles are found in the white shrimp. One originates dorsomedially in the posterodorsal corner of the sixth abdominal segment. The second arises slightly anterior to the first and runs posteroventrad to join the first on a common apodeme. The third originates lateroventrad of the first two and joins the common remotor apodeme at a point caudad of the first two remotor muscles. The common remotor apodeme now runs a short distance ventrocaudally to insert in heavy connective tissue beneath the dorsal rim of the uropod protopodite. Contractions of the muscles bring the uropods dorsad, in opposition to the action of the large abdominal muscles attached to the uropods. The two dorsal uropod remotor muscles are perhaps homologous to the medial uropod protopodite remotor muscle of *Pandalus* and *Astacus*, while the ventrolateral remotor is considered to be the homolog of the medial protopodite remotor muscle in the coon stripe shrimp and the crawfish.

PROTOPODITE REMOTOR MUSCLE OF UROPOD

FIGURES 70, 73

The protopodite remotor muscle is a short, thick structure originating in the same tendinous connective tissue upon which the uropod remotors insert. The protopodite remotor thus functionally prolongs the remotor muscle series to the caudal edge of the protopodite. The only muscle that looks similar to the protopodite remotor muscle of *Penaeus* is the exopodite reductor muscle of *Pandalus*, a muscle not found in *Penaeus*.

DORSAL UROPOD ROTATOR MUSCLES

FIGURES 70, 72, 73, 74

Due to the presence of transverse fasciae dividing them, three dorsal uropod rotator muscles are found in each half of the sixth abdominal segment of *Penaeus* (fig. 74, *A*). These large muscles originate over much of the dorsomedial and lateral areas of the sixth abdominal tergum to the margin of the external arm of the anterior oblique muscle (fig. 73, *B*). The dorsal uropod rotators pass ventrocaudally to insert upon three branches of a large apodemal tendon shared with the telson flexor muscles. The tendon arises from the ventral rim of the protopodite at its junction with the sixth abdominal segment. On contraction, the uropod rotators turn the lateral side of the protopodite downward, thereby maintaining the uropods in the most advantageous position for drawing the animal backwards through the water. The dorsal uropod rotator muscles of *Penaeus* appear to be homologous with those of *Astacus* and *Pandalus*.

VENTRAL UROPOD ROTATOR MUSCLE

FIGURES 71, 72

The small ventral uropod rotator muscle originates by a broad apodeme attached to the posteroventral sternum of the sixth abdominal segment (fig. 71). The muscle runs caudally and laterally to insert by a strong tendon into the medial edge of the protopodite. Contractions of the muscle rotate the protopodite about its long axis, thus bringing the lateral edge of the protopodite and exopodite downwards. The ventral uropod rotator muscle of *Penaeus* is not shown in the studies of *Pandalus*. A ventral uropod rotator is indicated by Schmidt in *Astacus*. The muscle in the crawfish is much larger than its counterpart in *Penaeus*.

PROTOPODITE ROTATOR MUSCLE

FIGURE 74

The protopodite rotator muscle is revealed by the removal of the thick exopodite abductor muscle located in the lateral part of the protopodite (fig. 73, *B*). The muscle takes origin in the same connective tissue providing insertions for the uropod remotors and the origin of the protopodite remotor muscle. The protopodite rotator passes laterally and ventrally to an area of insertion on the ventrolateral surface of the protopodite. The counterpart of the muscle in *Astacus* and *Pandalus* is not clear.

UROPOD STATOR MUSCLES

FIGURES 73, 74

The uropod stator muscles are 2 or 3 small muscles whose function appears to be the retention of the exopodite and endopodite in position with respect to one another. The affinities of these muscles in other crustaceans are not known.

EXOPODITE ABDUCTOR MUSCLES

FIGURES 70, 71, 73

The uropod of *Penaeus* contains 4 exopodite abductor muscles, all varying widely in shape and size. The anteriormost is a short, strong muscle occupying the lateral part of the protopodite (fig. 73, *B*). The muscle originates in the anterior curvature of the protopodite and inserts on the lateral margin of the exopodite. The muscle turns the exopodite laterally about its dorsoventral condyles. Also intrinsic to the protopodite are two smaller exopodite abductor muscles inserting in common with the first abductor. The small abductors lie beneath the protopodite remotor muscle and originate at two points on the ventromedial surface of the protopodite. The fourth and caudal exopodite abductor muscle, best seen in dorsal view (fig. 70), runs along the lateral margin of the exopodite. The muscle originates distally and inserts on a lateral apodeme of the protopodite. The function of the exopodite abductors is to spread the tail fan.

The first and fourth exopodite abductor muscles of *Penaeus* are homologous with the dorsal and lateral exopodite abductors of *Astacus* and with the lateral abductor muscle of *Pandalus*. The relationships of the two small abductors in *Penaeus* are not clear. The small ventral uropod exopodite abductor muscle shown by Schmidt in *Astacus* does not appear in *Penaeus*.

EXOPODITE ADDUCTOR MUSCLES

FIGURES 70, 71, 73, 74

The uropod exopodite of *Penaeus* is operated by three exopodite adductor muscles. The first exopodite adductor is rostral to the other two. It is a short, strong, twisted muscle originating on the posterodorsal surface of the protopodite (fig. 70). The first exopodite adductor passes ventrocaudally through other muscles to an area of insertion on the anteroventral surface of the exopodite (fig. 71). The second exopodite adductor muscle is the longest uropod muscle. The structure lies in the midline of the exopodite, inserting on the posterodorsal margin of the protopodite beneath the first adductor. The muscle takes origin in the distal region of the exopodite and on a little fascia dividing the main body of the muscle from a small, lenticular muscle (fig. 70). This little distal muscle is thought to be the vestige of a muscle operating the distal exopodite joint.

The third exopodite adductor lies along the medial margin of the exopodite. The muscle is made up of short fibers attaching to a long apodeme running through the middle of the structure. The apodeme arises from the posterodorsal margin of the protopodite. Contractions of the exopodite adductors turn the exopodite towards the midline of the animal, opposing the abductors.

The first exopodite adductor muscle of *Penaeus* appears in *Pandalus* as the anterior exopodite adductor. The second exopodite adductor found in the white shrimp is not represented in either *Pandalus* or *Astacus*. The third adductor of *Penaeus* is fully homologous with the muscle known as the posterior exopodite adductor in *Pandalus* and the uropod exopodite adductor muscle in the European crawfish.

EXOPODITE PRODUCTOR MUSCLE

FIGURES 71, 72, 74

The exopodite productor muscle of *Penaeus* is a broad, flat structure occupying the ventral part of the protopodite (figs. 71, 72). The productor originates in the heavy connective tissue of the large apodeme common to the dorsal uropod rotator muscles and the telson flexor muscles. The productor muscle passes caudad to a broad insertion on the ventral rim of the exopodite. The exopodite productor muscle is represented in the tail fan of *Pandalus*, but its relationships in the crawfish are not known. No reductor of the exopodite has been found in the tail fan of the white shrimp.

ENDOPODITE ADDUCTOR MUSCLE

FIGURES 70, 71, 73, 74

Originating in the distomedial part of the endopodite, the endopodite adductor muscle runs proximally in the endopodite to its point of insertion on the ventromedial edge of the protopodite. The muscle turns the endopodite toward the midline, with the result that the endopodites are closed. The endopodite adductor of *Penaeus* is probably homologous with the same muscle in the tail fan of *Pandalus* and *Astacus.*

ANTERIOR TELSON FLEXOR MUSCLE

FIGURES 70, 72, 73, 74

The anterior telson flexor muscle originates over most of the anterodorsal portion of the telson (fig. 70). The muscle passes directly ventrad to insert on the apodeme shared by the dorsal rotators and the telson flexors. The muscle has almost exact counterparts in the telson of *Pandalus* and *Astacus.* The anterior telson flexor muscle pulls the telson downward upon the uropods in the vertical plane.

POSTERIOR TELSON FLEXOR MUSCLE

FIGURES 70, 71, 72, 73, 74

The posterior telson flexor muscle is much larger than the anterior telson flexor. The posterior telson flexor originates over all of the dorsal and lateral tergum of the telson not taken up by the small anterior flexor. The muscle fibers run anteroventrally, narrowing to their insertion on the common apodemal material to which the dorsal rotators and anterior telson flexor are attached (fig. 74, *A*). The posterior flexor reinforces the action of the anterior telson flexor in bringing the telson ventrad. The posterior telson flexor muscle of *Penaeus* is represented in similar form in *Astacus* and *Pandalus.*

VENTRAL TELSON FLEXOR MUSCLE

FIGURE 74, *B*

The ventral telson flexor muscle is located within the sixth abdominal segment dorsal to the anterior oblique muscle apodemes. The muscle occupies a scoop-shaped depression in the posterodorsal part of anterior oblique muscle 6 (fig. 74, *B*) where it takes its origin. The muscle passes directly caudad to insert on an apodeme arising from the anterior margin of the telson sternum. The muscle turns the telson ventrad in the vertical plane. A counterpart of the ventral telson flexor muscle of *Penaeus* is found in *Pandalus.* The muscle is missing in *Astacus.*

ANAL COMPRESSOR MUSCLES

FIGURES 71, 72

The anal compressor muscles lie ventral to the rectum and alongside of it and insert into the lateral side of the anal opening. Contractions of the muscles flatten the sides of the anal opening in the long axis and thereby tend to close it. A similar muscle is found in *Astacus*, but not, according to Berkeley, in *Pandalus.*

ANAL DILATATOR MUSCLE

FIGURE 72

The anal dilatator muscle runs at right angles to the anal compressor and slightly above it (fig. 72, *A*), connecting into the lateral tergum of the telson by a tendon. Contractions of the dilatator open the anal aperture. The same muscle is found in the other crustaceans to which we have made reference.

RECTAL ATTRACTOR MUSCLES

FIGURE 74, *B*

The rectal attractor muscles are two small muscles of doubtful affinity not described by Schmidt in *Astacus* or Berkeley in *Pandalus.* The muscles lie in the midline of the sixth abdominal segment, between the uropod rotators. Both are attached to the median dorsal edge of the telson. The small, dorsal attractor passes rostrad to a tendinous fascia associated with the uropod rotators. If this muscle were larger it might better be named a telson extensor, but its size argues against this interpretation. The larger, ventral attractor muscle inserts in connective tissue on the dorsal surface of the rectum and undoubtedly draws the rectum caudad in movements associated with defecation.

II. THE NERVOUS SYSTEM

To the comparative morphologist, the nervous system is of fundamental importance. Of all the systems—skeletal, muscle, alimentary, reproductive, etc.—the annulate nervous system has most nearly retained its generalized form during the evolution of the group. That is, the nervous systems of any two annulates are remarkably similar. Nervous systems of Annulata, then, as has been amply shown by Snodgrass (1938), Ferris (1953), and others, are singularly conservative of form in

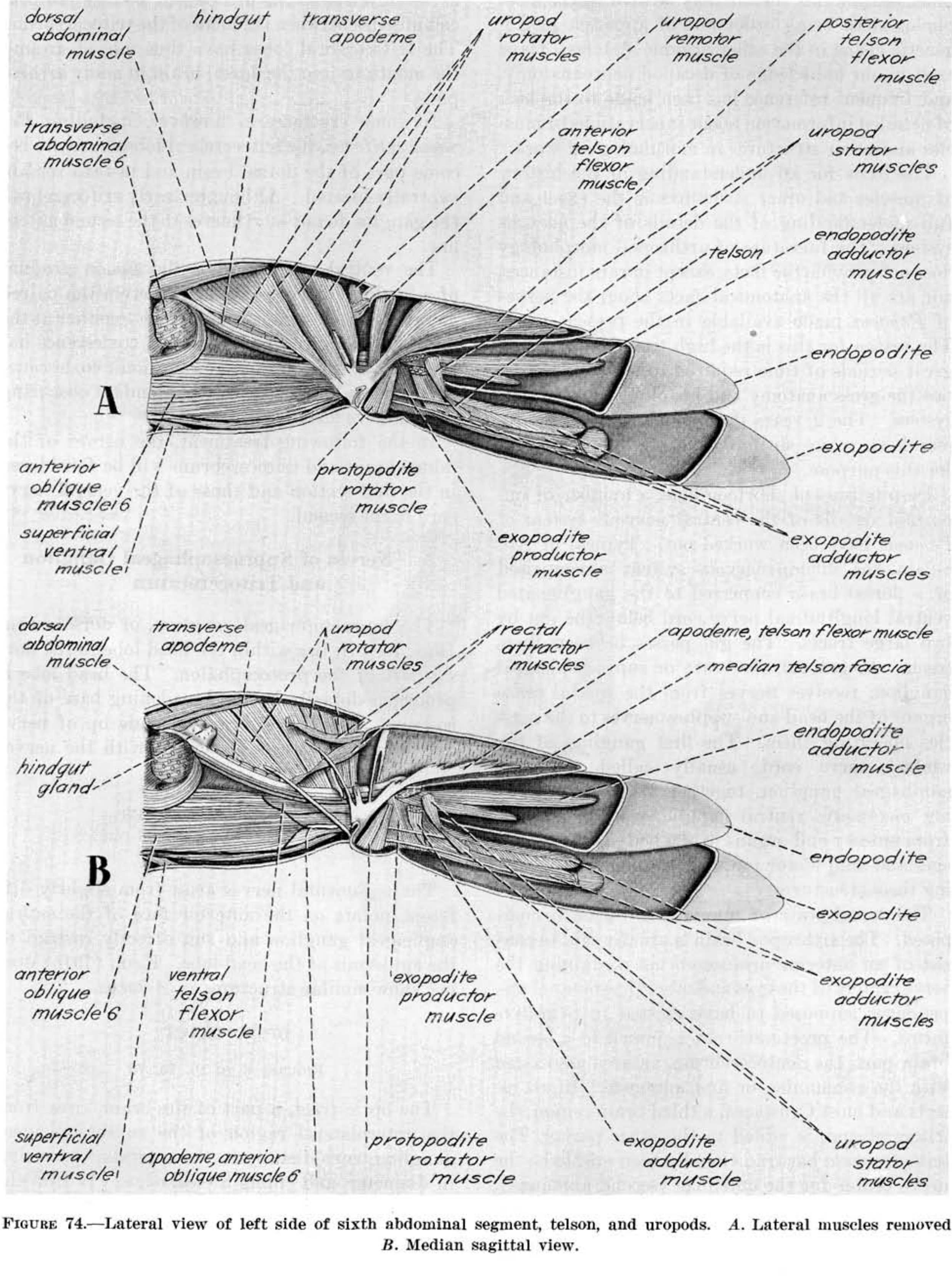

FIGURE 74.—Lateral view of left side of sixth abdominal segment, telson, and uropods. *A.* Lateral muscles removed. *B.* Median sagittal view.

time, and for this reason, may be used by the morphologist to bring order out of apparent phylogenetic chaos in the other organic systems. Gaps exist in our knowledge of decapod neuroanatomy, and frequent reference has been made to the lack of detailed information about innervations of muscles and other structures in morphological work.

The basis for an understanding of the history of muscles and other structures is the exact and full understanding of the details of the nervous system. The literature of arthropod morphology does not provide the facts, except in rare instances, nor are all the anatomical facts about the nerves of *Penaeus* made available in the present work. The reason for this is the high technical skill and great periods of time required to work out in detail the gross anatomy and histology of a nervous system. The 2 years devoted to the present research on white shrimp have not been sufficient for this purpose.

Despite present shortcomings, a number of important details of the central nervous system of *Penaeus* have been worked out. Typical of Annulata, the shrimp nervous system is comprised of a dorsal brain connected to the ganglionated ventral longitudinal nerve cord below the gut by two large tracts. The gut passes between these tracts. In general, the brain or supraesophageal ganglion, receives nerves from the special sense organs of the head and supplies nerves to the muscles operating them. The first ganglion of the ventral nerve cord, usually called the subesophageal ganglion, together with the following metameric ventral ganglia, receive impulses from sensory end organs of the body and appendages and send motor impulses to the muscles moving these structures.

The dorsal brain of annulates is variously composed. The arthropod brain is usually said to consist of an anterior protocerebrum containing the nerve centers of the eyes and other preantennal appendages supposed to have existed in primitive forms. The protocerebrum is joined to a second brain part, the deutocerebrum, an area associated with the antennules, or first antennae. In all insects and most Crustacea, a third brain region, the tritocerebrum, is added to the other parts. The tritocerebrum has traditionally been said to be the nerve center for the antennae (second antennae), although Ferris (1953) presents evidence opposing this view. Classically, the tritocerebrum has been considered the first ganglion of the ventral nerve cord due to the presence of a large postoral commissure between the lobes of the tritocerebrum. The tritocerebral lobes have thus moved around the mouth to join the dorsal brain in many arthropods.

In some crustaceans, however, including *Penaeus setiferus*, the tritocerebral lobes have not become part of the dorsal brain and instead remain ventrally located. Although clearly tritocerebral, the ganglia do not send nerves to the second antennae.

The ventral nerve cord is the fusion product of a "ladder" nervous system, wherein the paired ganglia of each segment have come together at the midline. Longitudinal segmental coalescence has frequently been followed by ganglionic coalescence in the ventral nerve cord with attendant obscuring of primitive metamerism.

In the following treatment, the nerves of the dorsal brain and tritocerebrum will be considered in the first section and those of the ventral nerve cord in the second.

A. Nerves of Supraesophageal Ganglion and Tritocerebrum

The supraesophageal ganglion, or dorsal brain (figs. 75, 76), lies within the head lobe in the dorsal part of the protocephalon. The head lobe is protected dorsally by the broadening base of the rostrum. The dorsal brain is made up of nerve cell bodies and tracts associated with the nerves running out of it.

TEGUMENTAL NERVES

FIGURES 75, 76

The tegumental nerves arise from slightly different points on the anterior face of the supraesophageal ganglion and run directly rostrad to the epidermis of the head lobe. Keim (1915) does not show similar structures in *Astacus*.

OPTIC TRACT

FIGURES 6 TO 10, 75, 76

The optic tract, a part of the brain, rises from the anterolateral region of the supraesophageal ganglion, runs distally in the eyestalk, increasing in diameter, and enters the calathus. Within the calathus, the optic tract enlarges to incorporate the various distal optic ganglia and makes contact with the nerves from the ommatidia (figs. 9, 10).

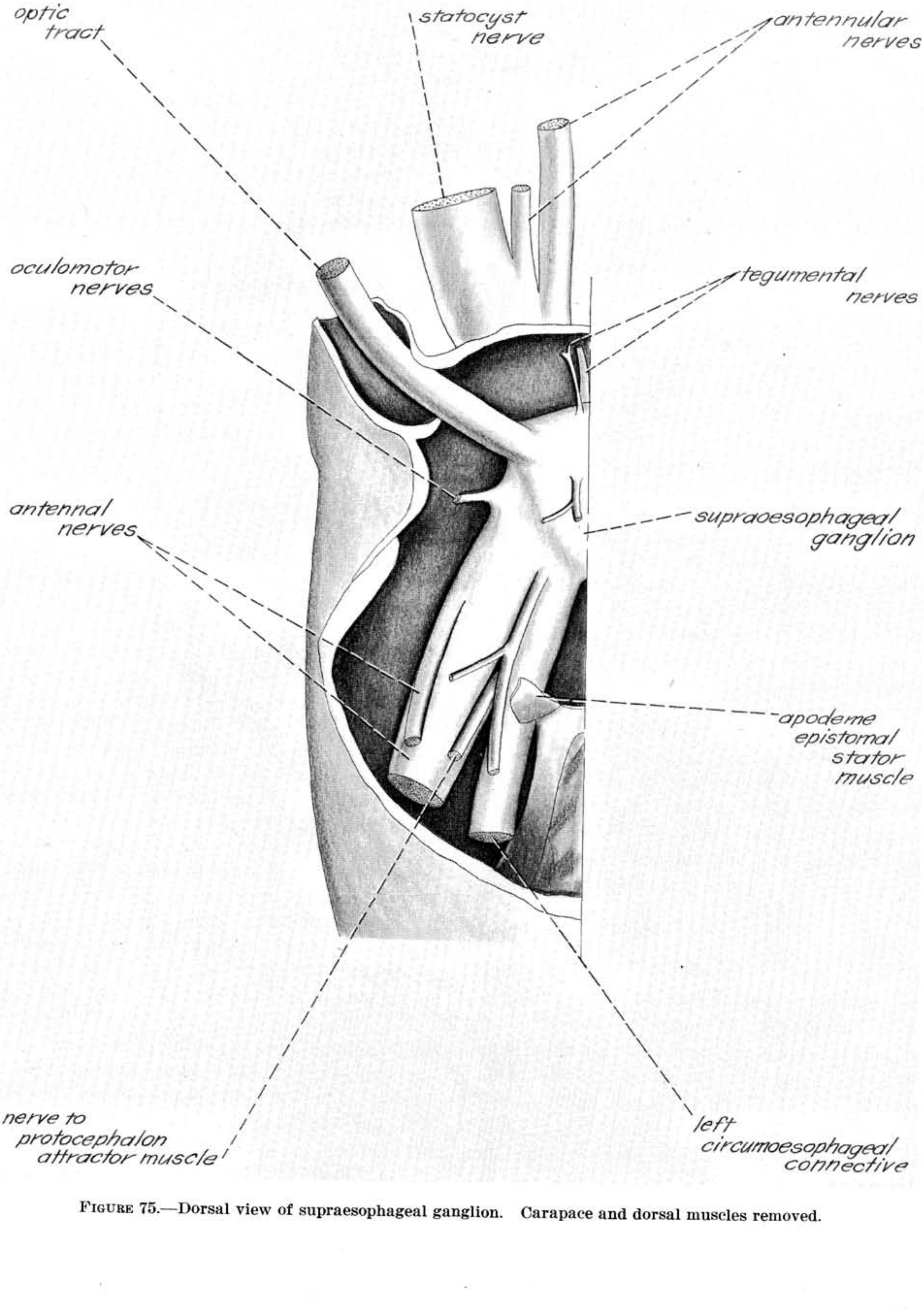

FIGURE 75.—Dorsal view of supraesophageal ganglion. Carapace and dorsal muscles removed.

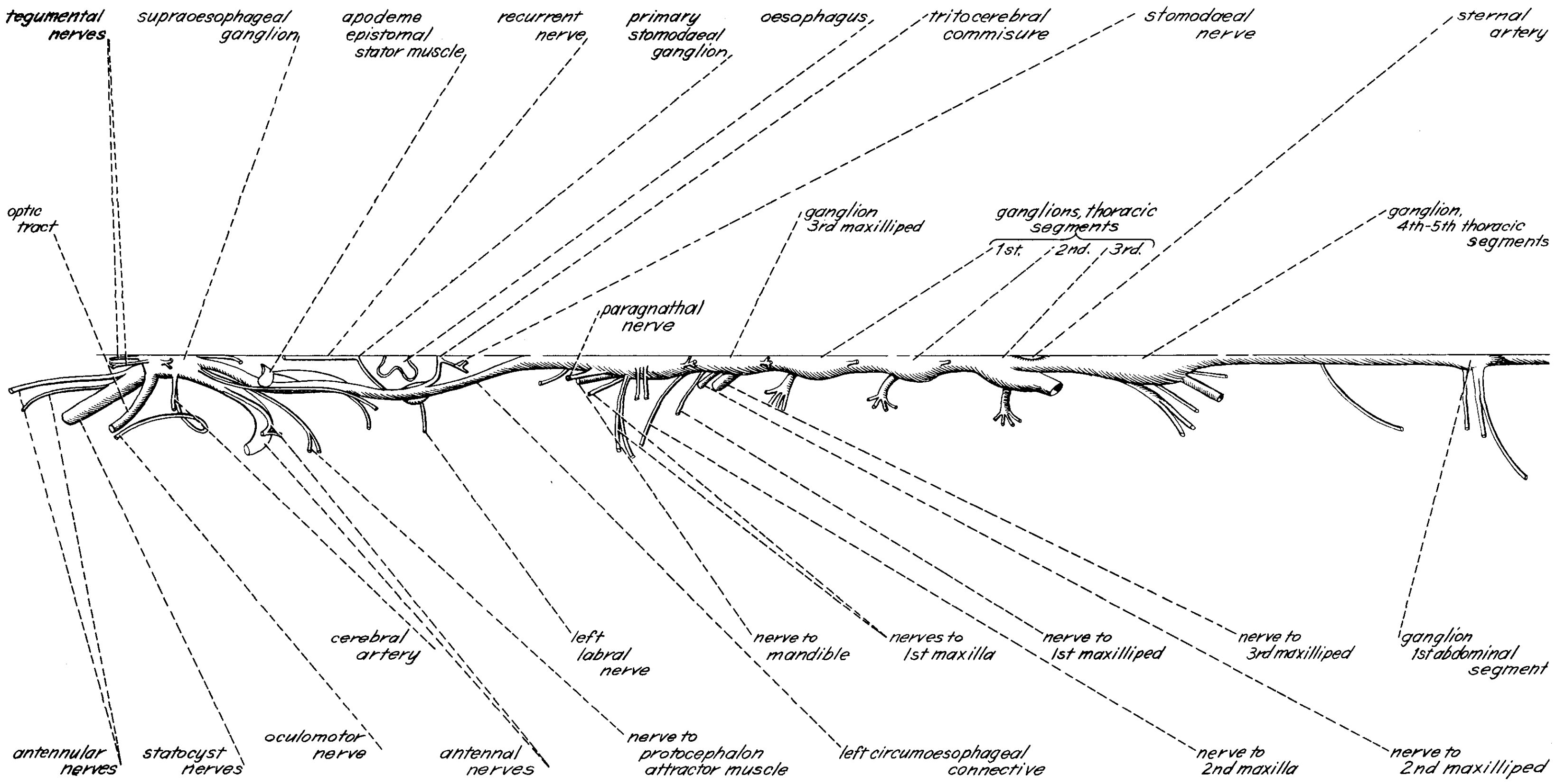

FIGURE 76.—Dorsal view of left half of brain and ventral nerve cord to ganglion of first abdominal segment.

These distal optic ganglia do not show superficially; however, longitudinal sections indicate very clearly the presence of a proximal, medial, and distal ganglion. If the distal optic ganglionic mass is pulled away from the dioptric elements of the eye, the tearing is confined to natural lines of weakness representing a deep concavity. Lining the concavity so produced is the capillary arbor (fig. 9), a structure which will be treated more fully in the section on the circulatory system.

NEUROHORMONAL ELEMENTS

FIGURE 10

Along the lateral side of the optic tract, and embedded in the perineurium in the proximal region of the optic tract, is a small nerve which branches out of the perineurium distal to the basal segment of the eyestalk. This nerve puts out several tiny branches to muscles and then enters a glandlike structure previously identified by Young (1956) as the X-Organ (fig. 10) of Hanström (1948), and which should be referred to as the pars ganglionaris X organi (Carlisle and Passano, 1953) rather than the X-Organ of Hanström.

From the pars ganglionaris X organi, a nerve continues along the optic tract distally to enter another, and larger, glandlike organ termed the "sinus gland" (fig. 10). The sinus gland lies against and sends branches into the optic ganglionic mass at the distal end of the optic tract. A second part of the X-Organ, that described by Hanström, is associated with the anterior eyestalk pore, or sensory pore (fig. 10). Knowles and Carlisle (1956) have proposed the term sensory pore X-Organ for the structure, to distinguish it from the ganglionic part. The identification of the parts of the X-Organ and of the sinus gland was made on doubtful grounds, since no supporting histological or experimental evidence was presented (Young 1956).

Confusion surrounding the identification of the X-Organ may be found in the literature of neurosecretory experiments (Knowles and Carlisle, 1956). Evidently the European and American workers have used the term "X-Organ" for different structures. The reason may lie in a weakness in communications, for the illustrations in some works of this literature are, to say the least, circumscribed (Passano 1953), however important the textual material may be to the experimental biologist. Welsh (1941), on the other hand, has taken pains to illustrate clearly his experiments on retinal pigment migrations in *Cambarus bartoni* (Fabricius 1798); unfortunately his identification of the X-Organ appears to be in error.

Keim (1915) in his account of the nerves in *Astacus* does not illustrate the sinus gland or the parts of the X-Organ.

OCULOMOTOR NERVE

FIGURES 8, 9, 10

The oculomotor nerve originates on the lateral side of the dorsal brain, slightly posterior to the optic tract, and, beginning ventrally, describes an almost complete loop around the protocephalon attractor muscles. It proceeds to the dorsolateral region of the protocephalon attractor, between the muscle and the outer epidermis. From the latter position the nerve turns sharply anterior and runs into the eyestalk, giving off branches to various of the eyestalk muscles. The nerve in *Penaeus* is the same as the eye muscle nerve described by Keim (1915) in *Astacus*.

Regrettably, very little can be said of homologies between the nerves serving the eyestalk of the various Crustacea, since so little information exists on the subject. Certainly, optic tracts, oculomotor nerves, and eyestalk neurohormonal elements in *Penaeus*, *Astacus*, and *Cambarus* are likely to be homologous structures. Further anatomical information on the nerves will have to be provided before the comparative morphology of this region of the brain and eyestalk will be in any way a satisfactory story.

ANTENNULAR NERVES

FIGURES 14, 15, 75, 76

The nerves of the antennule pass rostrad from the anteroventral region of the supraesophageal ganglion within a single perineurium. Inside the antennule the single tract divides into three nerves. The largest is the short, flat statocyst nerve which runs anterolaterally and spreads widely on the ventral surface of the first antennular segment beneath the statocyst. This nerve is presumably the sensory nerve of the statocyst. The smaller antennular nerves parallel the statocyst nerve in the proximal region of the antennule, then turn anteriorly and run the length of the antennule including the flagella. This nerve is probably mixed, since it sends off branches to the muscles as well as to the sensory flagella.

Except for the work of Keim (1915) on the nerves of *Astacus*, little information exists on the innervation of the crustacean antennule. The situation in *Penaeus* appears to be roughly comparable to the arrangement of the antennular nerves in *Astacus*. The most striking difference is the size of the nerve innervating the statocyst. That of *Penaeus* is very much larger than the statocyst nerve of *Astacus*.

ANTENNAL NERVES

FIGURES 24, 75, 76

The antennal nerves pass out of the supraesophageal ganglion posteroventrally, from a point laterad of the circumesophageal connective. The antennal nerves proceed ventrocaudally for a short distance and then turn anteriorly to run into the antenna through its large foramen, or into the mass of the antennal muscles. Within the body of the antenna, the nerves give off branches to various muscles and sensory endings in the antenna and scale. One branch enters the antennal flagellum (fig. 24, *B*) and is extensively subdivided. Small groups of neurons are thus split off to each of the many sensory elements in the flagellum (fig. 25).

The antennal nerves of *Penaeus* appear to be similar to those described by Keim in *Astacus*.

NERVE TO PROTOCEPHALON ATTRACTOR MUSCLE

FIGURES 75, 76

This structure comes out of the dorsal brain between the antennal nerves and the circumesophageal connective and passes into the substance of the protocephalon attractor muscle. I have previously offered objections to assigning the protocephalon attractors to the "antennal" segment, on grounds of multiple insertions of the muscle. However, the position of the protocephalon attractor nerve origin on the brain tends to suggest that at least part of the muscle has affinities with the antenna.

LABRAL NERVE

FIGURES 27, 76

Each lateral half of the superficially unpaired labrum is supplied with a labral nerve descending from the tritocerebral ganglia (illustrated as the labral ganglion in fig. 27). Upon entering the labral sac, the nerve divides into parts which go to many labral muscles, to glands, and to sensory endings in the epidermis. From the work of Schmidt and Keim on the muscles and nerves of *Astacus* one receives the impression that this European crawfish does not posses a labrum, since no muscles or nerves are listed, nor in fact is the labrum mentioned. Henry (1948a) finds that the labral nerve of *Palaemon paucidens* de Haan and other Crustacea arises from the region of the primary stomodaeal ganglion, a stomatogastric ganglion connected to the tritocerebrum.

TRITOCEREBRAL GANGLIA AND NERVES

The tritocerebral ganglia or lobes represent the ganglia of the first ventral segment. As has been previously mentioned, the tritocerebral lobes are reflected into the dorsal brain in many arthropods, but not in *Penaeus*. In the latter the ganglia remain in the primitive, divided condition, connected by a transverse commissure, the tritocerebral (or stomodaeal) commissure (fig. 76), passing below the gut. The tritocerebral commissure sends a small nerve, the stomodaeal nerve, posteriorly from each side of the midline. The experimental workers evidently prefer the somewhat meaningless term, postcommissural nerve, for the structure (Knowles 1953). Keim makes no mention of the postcommissural, stomodaeal nerves in *Astacus*.

Associated with the tritocerebrum are the nerves of the stomodaeal system. So far as this system has been worked out in *Penaeus*, it appears to be simple. A primary stomodaeal ganglion lying on the anterior surface (primitive dorsal surface) of the esophagus is joined to each tritocerebral lobe by a nerve passing round the gut. From the primary stomodaeal ganglion another nerve, the recurrent nerve, passes dorsally along the dorsal surface of the esophagus to the gastric mill where it becomes subdivided. Keim finds a similar situation in *Astacus*. Henry (1948a) describes a secondary stomodaeal ganglion connected independently to the tritocerebrum, and from her work on lower Crustacea we may conclude that the presence of two stomodaeal ganglia is the more typical situation.

Posterior to the tritocerebral ganglia the circumesophageal connectives passing around the gut anastomose to form the ventral nerve cord.

Ventral Nerve Cord

FIGURES 36, 61, 63, 76

The ventral nerve cord of *Penaeus* is a longitudinal series of ganglia interconnected by fused pairs of intersegmental nerve tracts. A certain amount of longitudinal coalescence has taken place in the ventral cord, notably in the anterior, thoracic regions and less so in the abdomen. The ganglia of the gnathal appendages are conspicuously fused.

PARAGNATHAL NERVE

FIGURE 76

The element termed the nerve to paragnath arises from the ventral cord anterodorsad of the mandibular nerve. In *Penaeus* the paragnathal nerve is in no way posterior to the mandibular nerve as shown by Henry (1948a) for various crustaceans. However, whether the nerve is histologically anterior to the nerve to the mandible, as Chaudonneret (1956) holds, is not known. If Chaudonneret is correct in his claim that the paragnatha are anterior to the mandibles, then we are faced with the necessity of explaining the segmental interrelationships suggested by this view. Chaudonneret escapes from the dilemma by homologizing the paragnatha with the insectan superlinguae, a theory that has been advanced in the past (Snodgrass 1935). At the same time, Chaudonneret stoutly defends the morphological independence of the paragnathal nerve from that of the mandible. He thus arrives at a paradox, since the superlinguae arise from the hypopharynx and appear to belong to the mandibular segment (Snodgrass 1935). If, on the other hand, the superlinguae are not mandibular, and their homology with the paragnatha holds good, we must assign the paragnatha to some other segment, perhaps pre-mandibular and almost certainly postoral.

MANDIBULAR NERVE

FIGURES 36, 76

The large nerve to mandible is given off the ventrolateral surface of the anterior ventral nerve ganglion and runs into the heavy muscles of the mandibular segment. A branch of the nerve enters the mandibular palp.

MAXILLARY NERVES

FIGURES 36, 76

The nerves to the first and second maxillae depart from the ventral nerve cord and pass into the maxillae. The nerves to the first maxilla are much smaller than the one to the more active second maxilla. These nerves are very likely mixed since they separate into branches which run to muscles and to sensory end cells in the appendage extremities.

MAXILLIPEDAL NERVES

FIGURES 36, 43 TO 48, 76

The nerves to the first and second maxillipeds leave the anterior ventral nerve ganglion ventrolaterally from its caudal portion and run into the maxillipeds. The nerve to the third maxilliped arises from its own ganglion.

NERVES TO PEREIOPODS

FIGURES 36, 49, 51 TO 53, 56 TO 58

Beginning with the ganglion of the third maxillipeds, the thoracic ganglia are indicated for the most part by independent swellings in each segment. From the ventral surface of each ganglion a large nerve departs into each appendage. Between the ganglion of the third thoracic segment and the anterior portion of the coalesced fourth and fifth ganglia, the two longitudinal nerve tracts have been retained in the primitive divided condition to permit the sternal artery to pass through them. The thick ventral nerve cord of the thorax narrows posterior to the fused ganglia of the fourth and fifth thoracic segments and runs into the abdomen.

ABDOMINAL NERVES

FIGURES 61, 63, 71, 72, 76

The abdominal ganglia of the ventral nerve cord are all substantially similar, except for the terminal ganglion of the sixth abdominal segment. Two nerves arise from each of the first five abdominal ganglia. The anterior one enters the pleopod on that side and the posterior nerve sweeps laterally and dorsally to branch among the abdominal muscles of the segment.

The sixth abdominal ganglion lies in the posteroventral portion of the sixth segment (fig. 72, *B*). Four pairs of major nerves arise from it.

The first nerve is dorsolateral and runs beneath the apodeme of anterior oblique muscle 6 on its way to the muscles of the sixth abdominal segment. The second nerve serves the uropod exopodite, the third the endopodite, and the fourth, which arises posterodorsally, runs near the anal canal and enters the telson. These nerves are apparently mixed. The exopodite nerve (fig. 72, *B*) is easily observed. After giving off branches to the exopodite muscles, this nerve undergoes extensive subdivision to form a kind of sensory "cauda equina" in the distal regions of the exopodite.

III. CIRCULATORY SYSTEM

The typical blood circulatory system of Crustacea Decapoda is a closed arterial-open venous system. It consists of a heart and arteries by which blood is transported to arterial capillary beds throughout the body. Venous blood returns to the heart through conjoint blood sinuses in the appendages and body into which the capillaries empty. In general, the gills are served by the venous system. Although the circulatory systems of all decapods have marked similarities, the arteries display greater differences in detail than the nervous system or the muscle system. Furthermore, the circulatory elements are variable within the individual animal. The blood vascular system will be treated in two parts, the heart and pericardium and the blood vessels.

A. Heart and Pericardium

FIGURES 79, 80

The pericardium is a thin, contractile membrane surrounding the heart. The membrane is penetrated by passageways by which venous blood may enter the pericardial chamber. Slender muscle bundles inserted on the surface of the pericardium aid in its rhythmic contractions.

The heart of *Penaeus setiferus* is a many-sided structure lying within the muscular pericardium in the posterodorsal region of the carapace. Three pairs of valvular afferent ostia may be seen on the surface of the heart, two pairs dorsally and one pair placed laterally. By means of the valves in these pores, pericardial blood enters the heart during diastole and is prevented from escaping in the systolic beat. Structurally, the heart is more than a tubular expansion, and is, instead, comprised of a system of connected sinusoids. Microscopical sections indicate that the outer and intersinusoidal walls are made up of muscle fibers interspersed with connective tissue of a type strikingly reminiscent of the wavy elastic fibers in the tunica media of a vertebrate artery.

Although the details of cardiac innervation have not been worked out in the present study of *Penaeus*, the work of Alexandrowicz (1932) shows that considerable uniformity in the heart nerves of decapod crustaceans exists. Alexandrowicz has found that the decapod heart is well supplied with nerves. Restricted to the internal heart structures is a local system of heart neurons interspersed among the muscles of the sinusoidal septa. Alexandrowicz considers the local system inherently automatic.

The heart neurons are connected to the central nervous system by a pair of dorsal cardiac nerves which arise from the subesophageal ganglion. The dorsal nerves Alexandrowicz believes to be regulatory and he subdivides them functionally into two groups of inhibitory and one of accelerator fibers. Distinct from the heart neurons and dorsal nerves is a third system serving the muscles of the pericardium and heart valves. The pericardial nerves are ventral and the ostial valve nerves are situated dorsally, and the two are interconnected with one another. Inexplicably, the pericardium-ostial valve system is not tied to either the heart neurons or the dorsal cardiac nerves. Consequently, Alexandrowicz states, the pericardium has its own rhythm.

B. Blood Vessels of the Body

LATERAL ANTERIOR ARTERY

FIGURES 79, 80

The narrow, apical end of the heart points rostrally. From this point in the midline a very small vessel extends a short distance anteriorly (fig. 80). This little artery may be the vestige of the ophthalmic artery (Huxley 1906), or the median aorta (Baumann 1919) found in *Astacus* and other crustaceans. In the opinion of Professor Mayrat (letter, May 3, 1957), ophthalmic (or median aortic) vascular function has apparently been taken over by a pair of lateral anterior arteries (figs. 79, 80) arising from the anterior end of the heart, laterad of the midline.

As the lateral anterior arteries run forward, they give off a number of branches, the first of which leaves just anterior to the heart. The

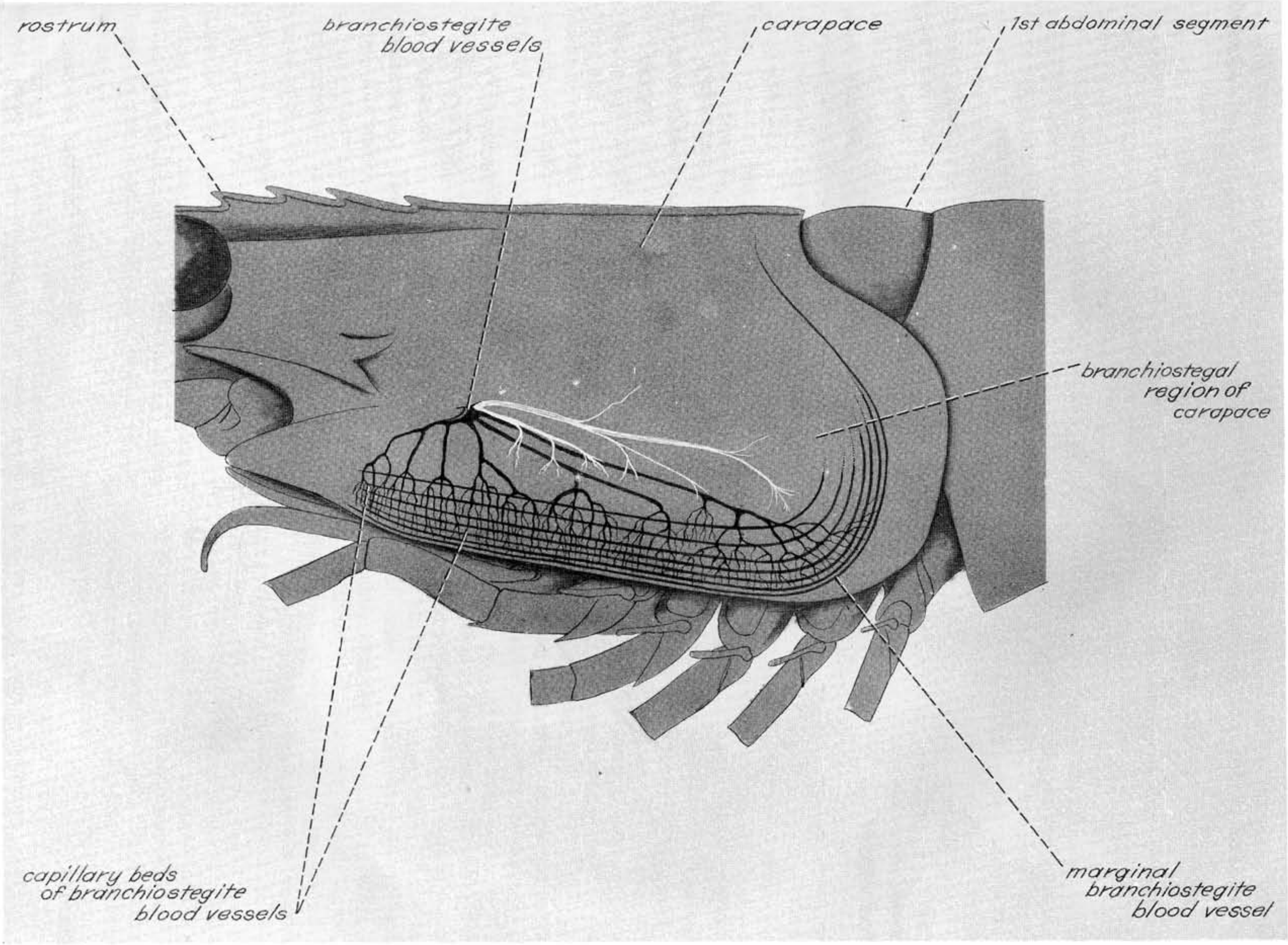

FIGURE 77.—Lateral view of gnathothorax showing blood vessels of branchiostegite epithelium.

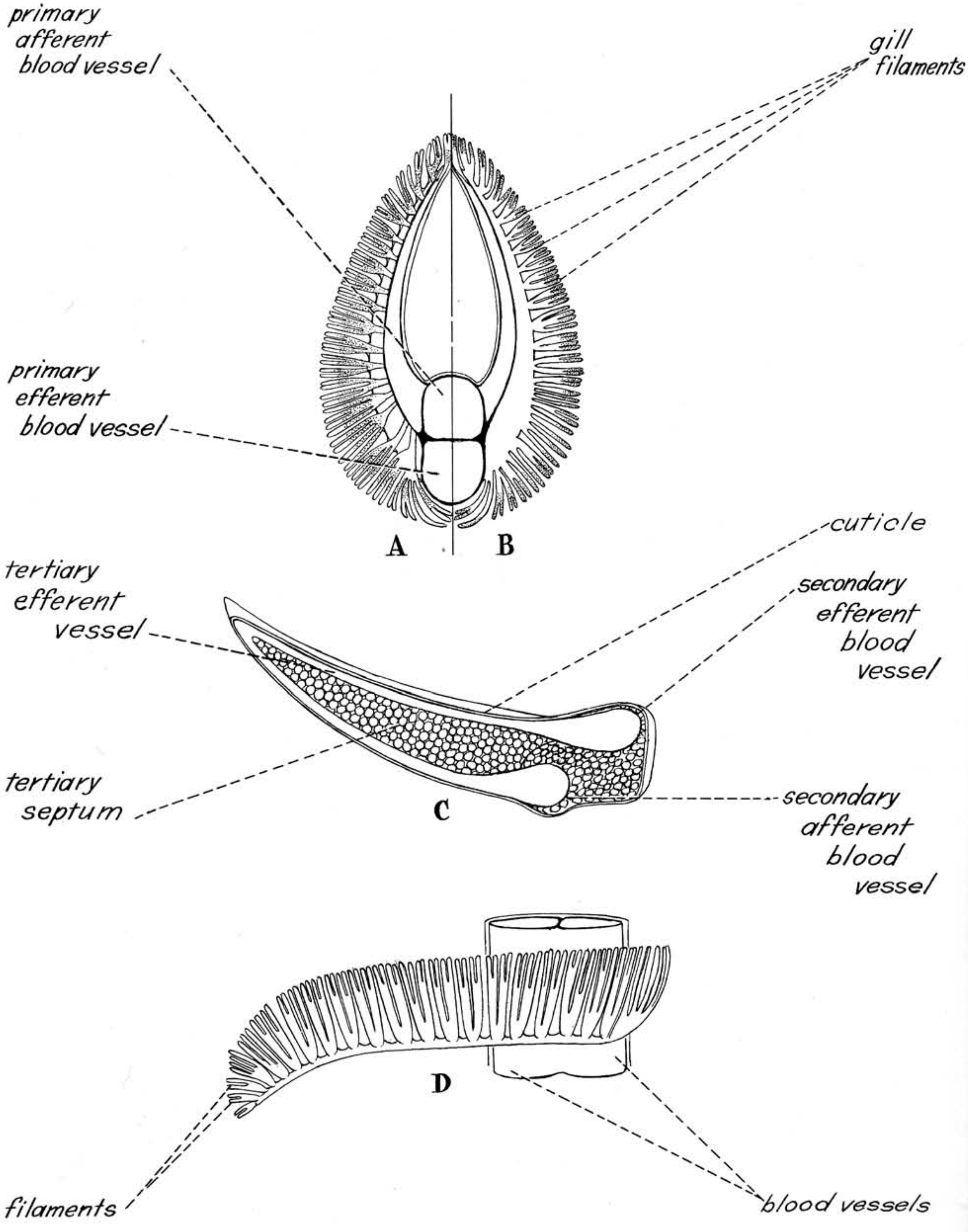

FIGURE 78.—Blood circulation of gills. *A*. Dorsal, and *B*. ventral views of single gill lamina. *C*. Lateral view of single gill filament showing circulation. *D*. Lateral view of single gill lamina.

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

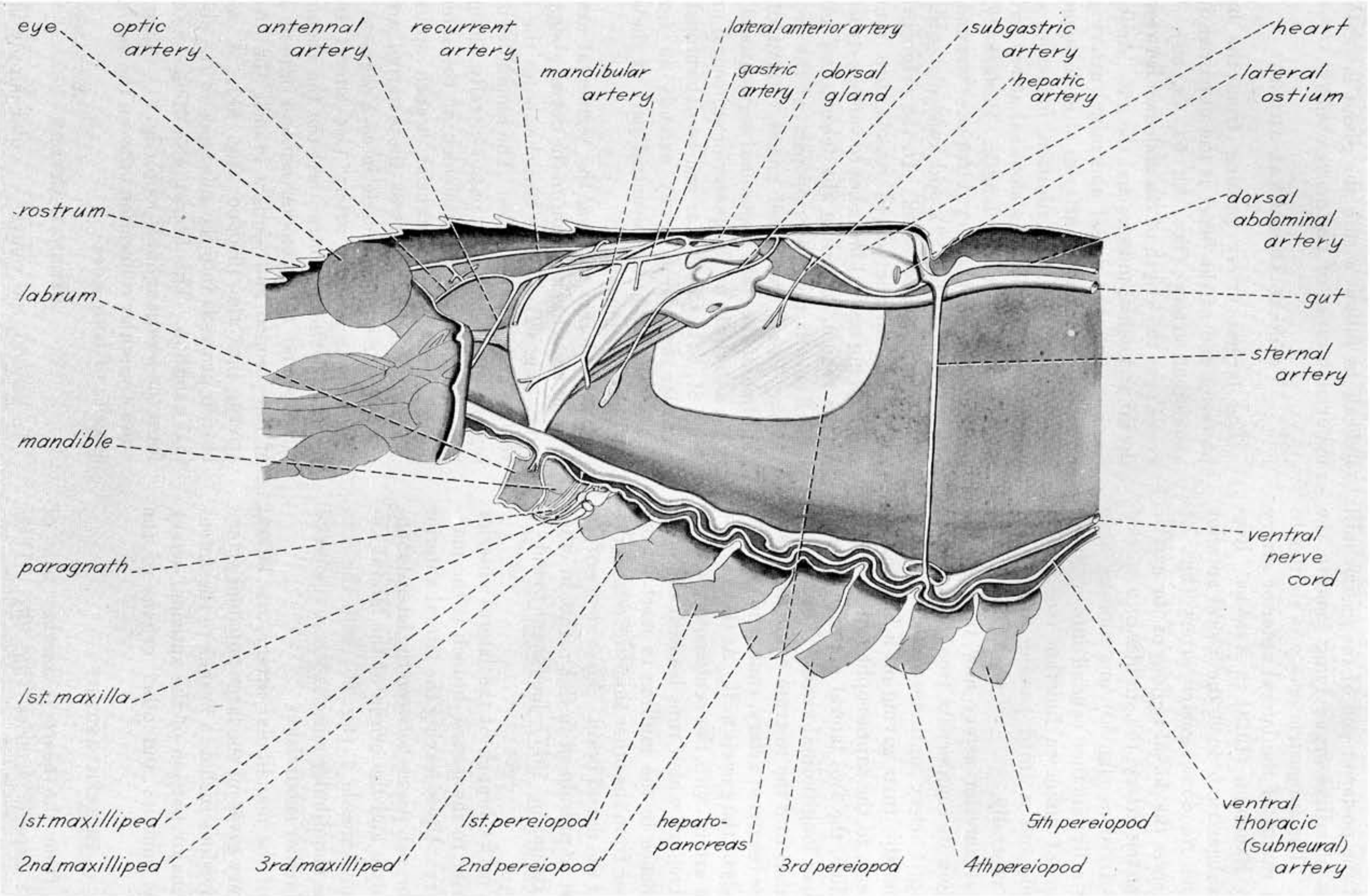

FIGURE 79.—Lateral view of gnathothorax showing circulatory elements.

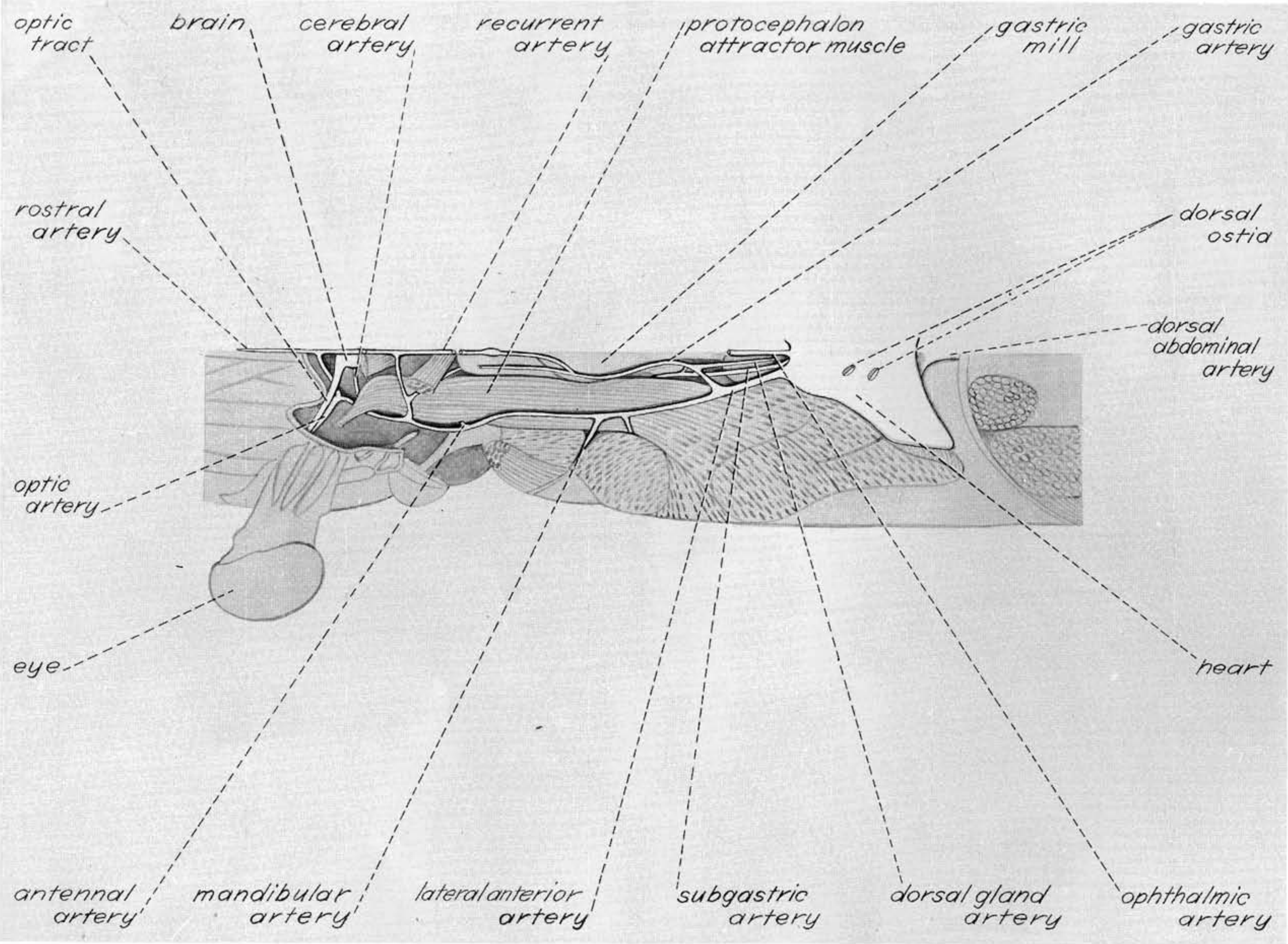

FIGURE 80.—Dorsal view of gnathothorax showing circulatory elements.

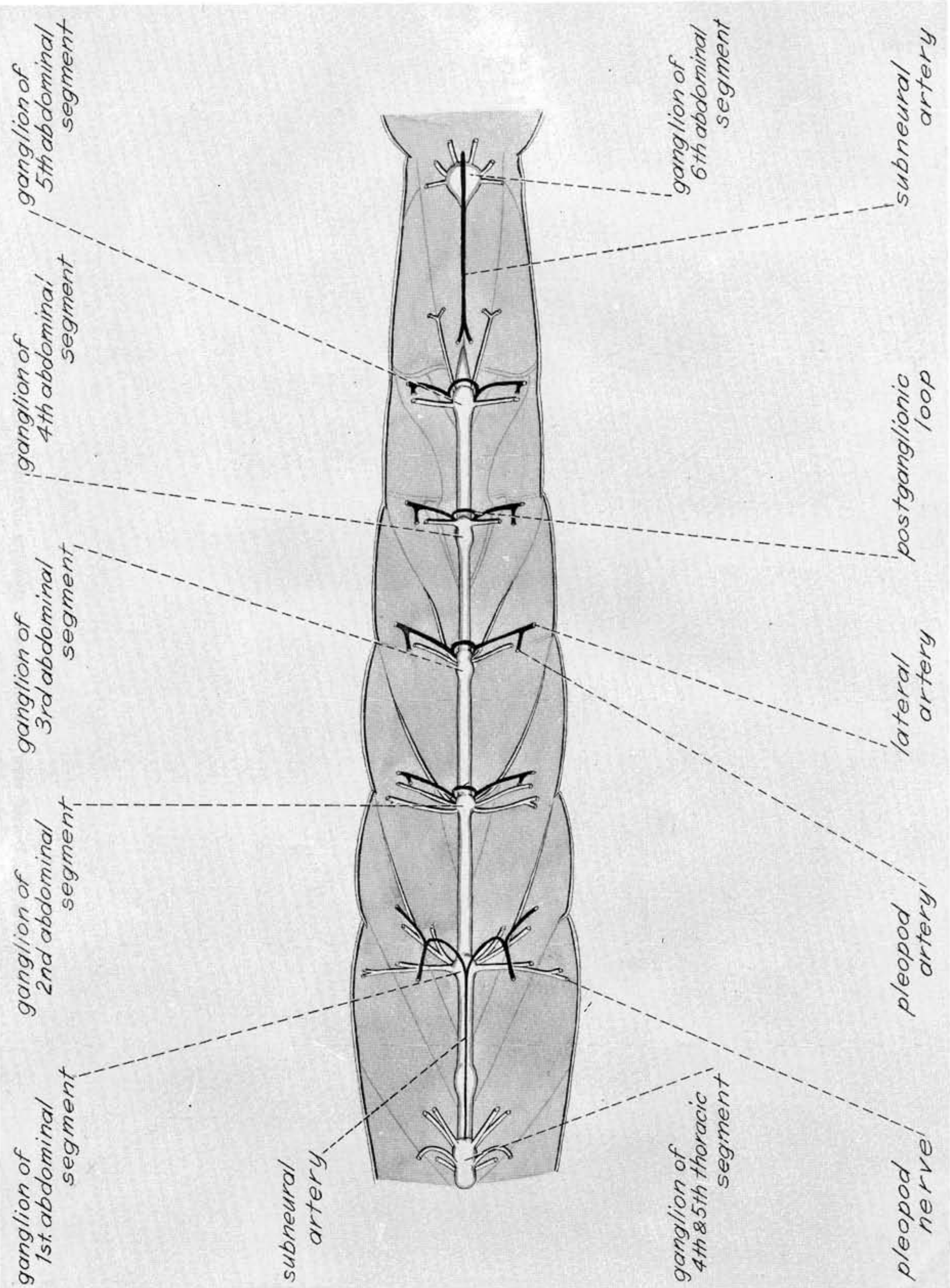

FIGURE 81.—Ventral view of abdomen showing neural and circulatory elements.

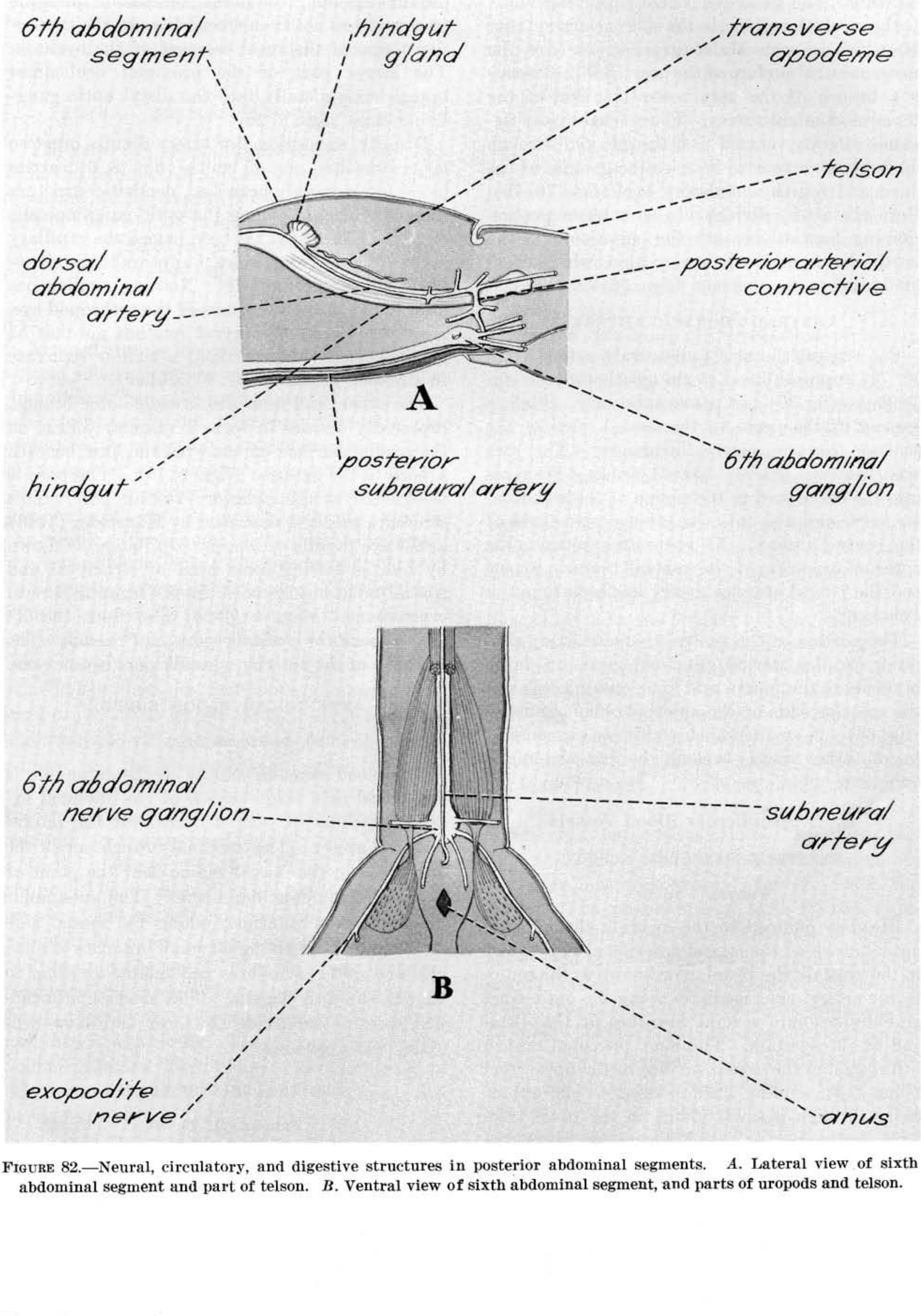

FIGURE 82.—Neural, circulatory, and digestive structures in posterior abdominal segments. *A.* Lateral view of sixth abdominal segment and part of telson. *B.* Ventral view of sixth abdominal segment, and parts of uropods and telson.

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

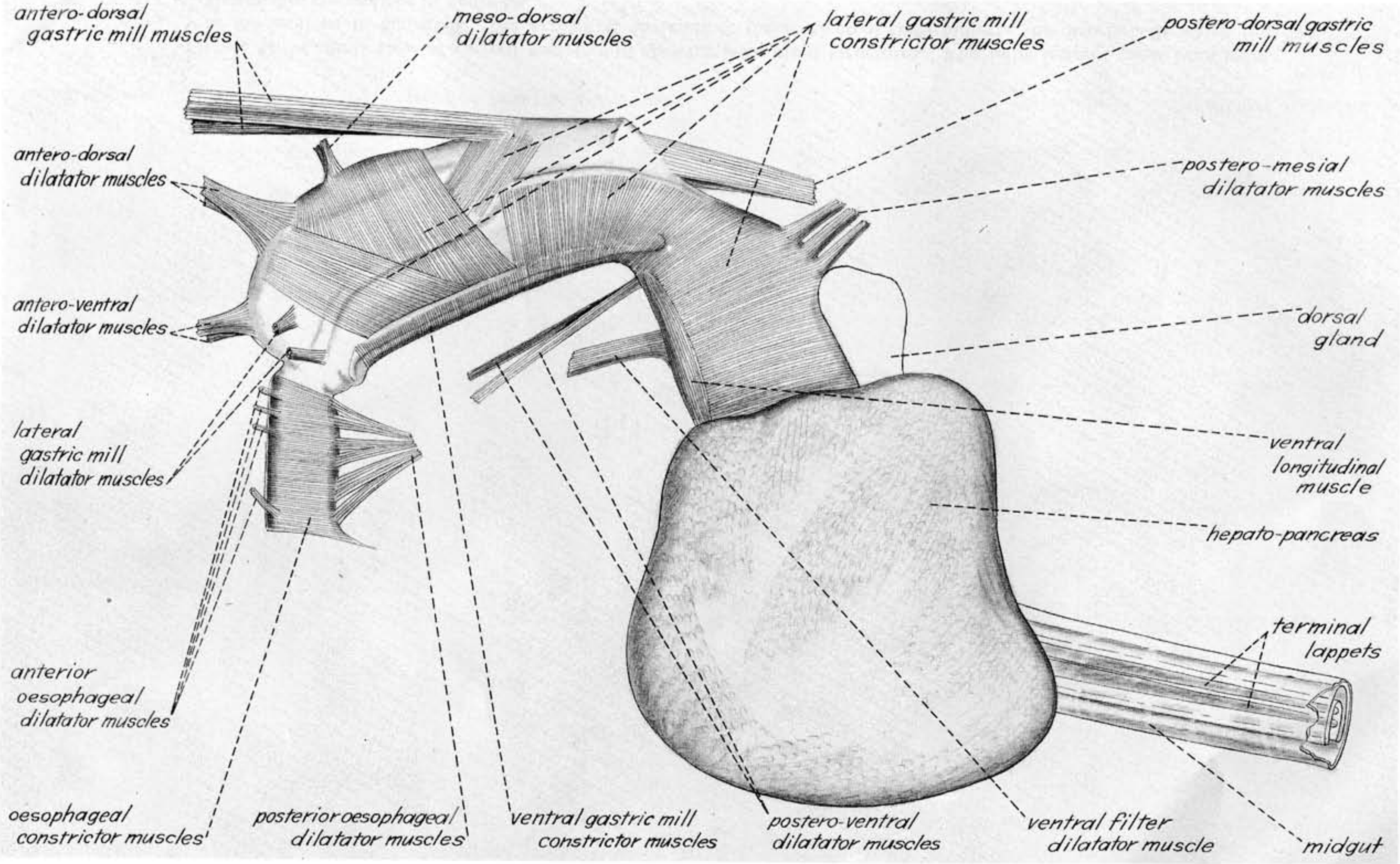

FIGURE 83.—Lateral view of left side of gastric mill and hepatopancreas.

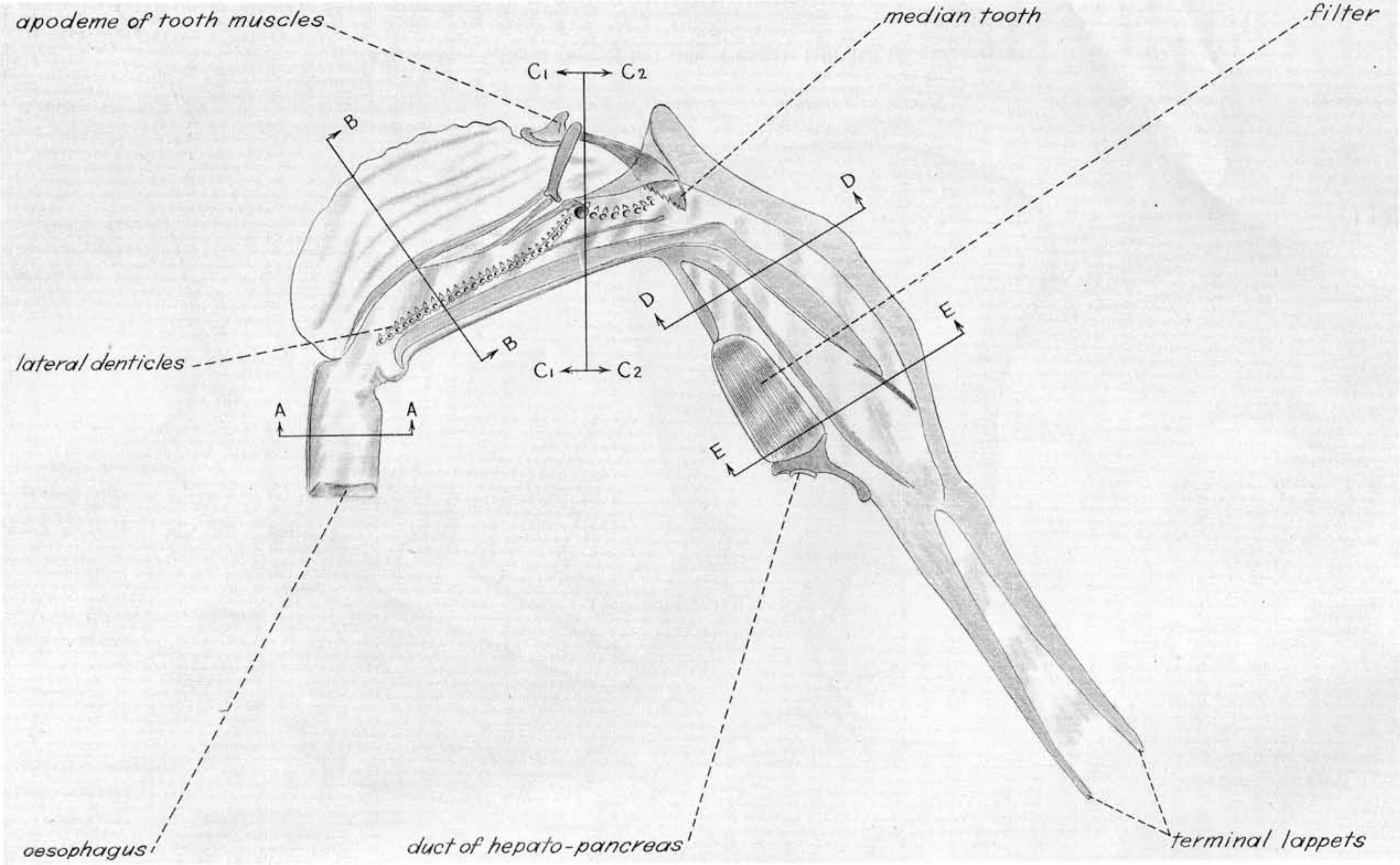

FIGURE 84.—Lateral view of cleared gastric mill showing sclerotized structures. The solid, lettered cross lines refer to the sections in figure 85. The arrows at the ends of the solid cross lines indicate the direction in which the viewer sees the sections in figure 85.

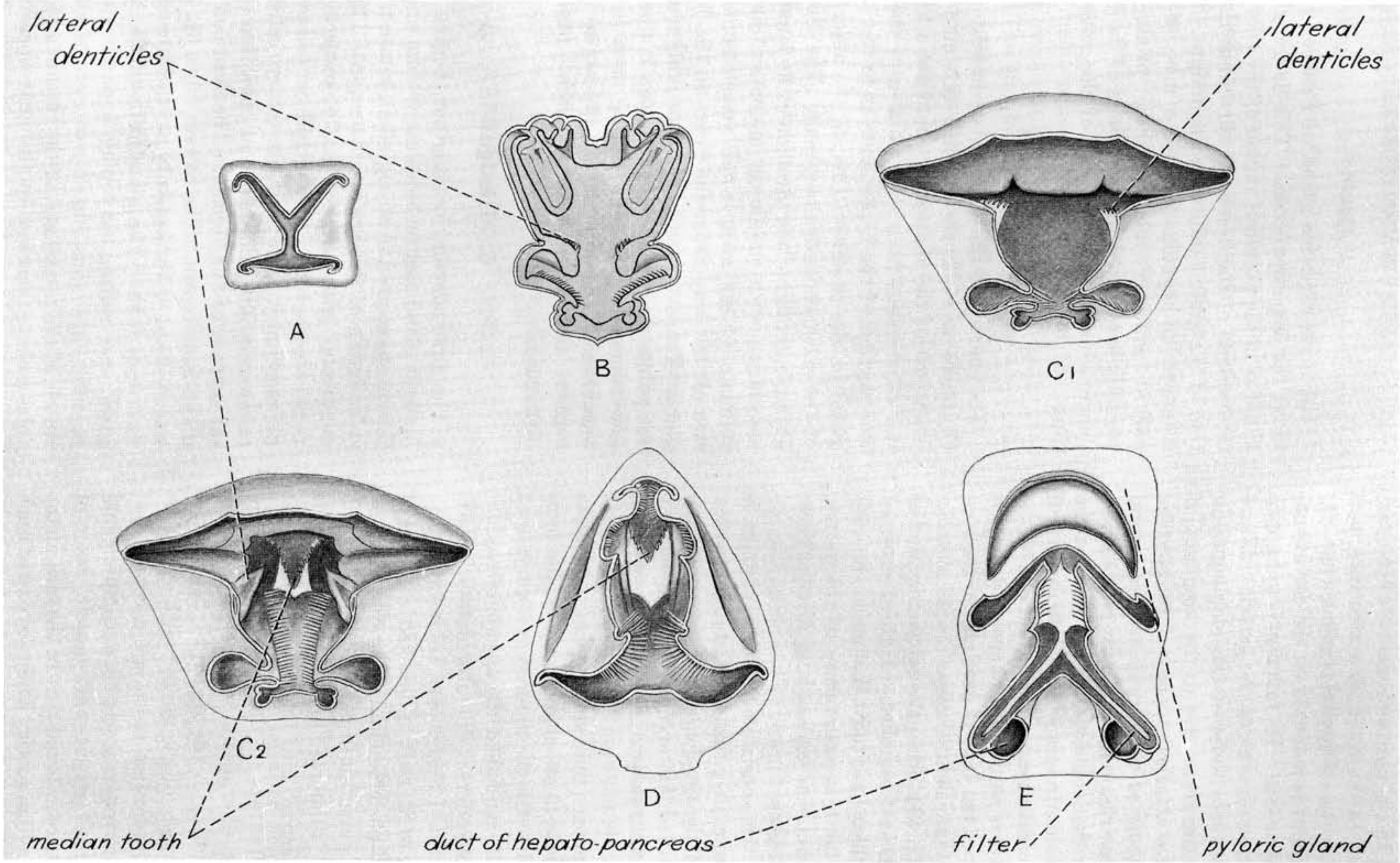

FIGURE 85.—Cross sections through the esophagus and gastric mill. The letters below the figures refer to the corresponding letters at the ends of the solid lines on figure 84.

(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

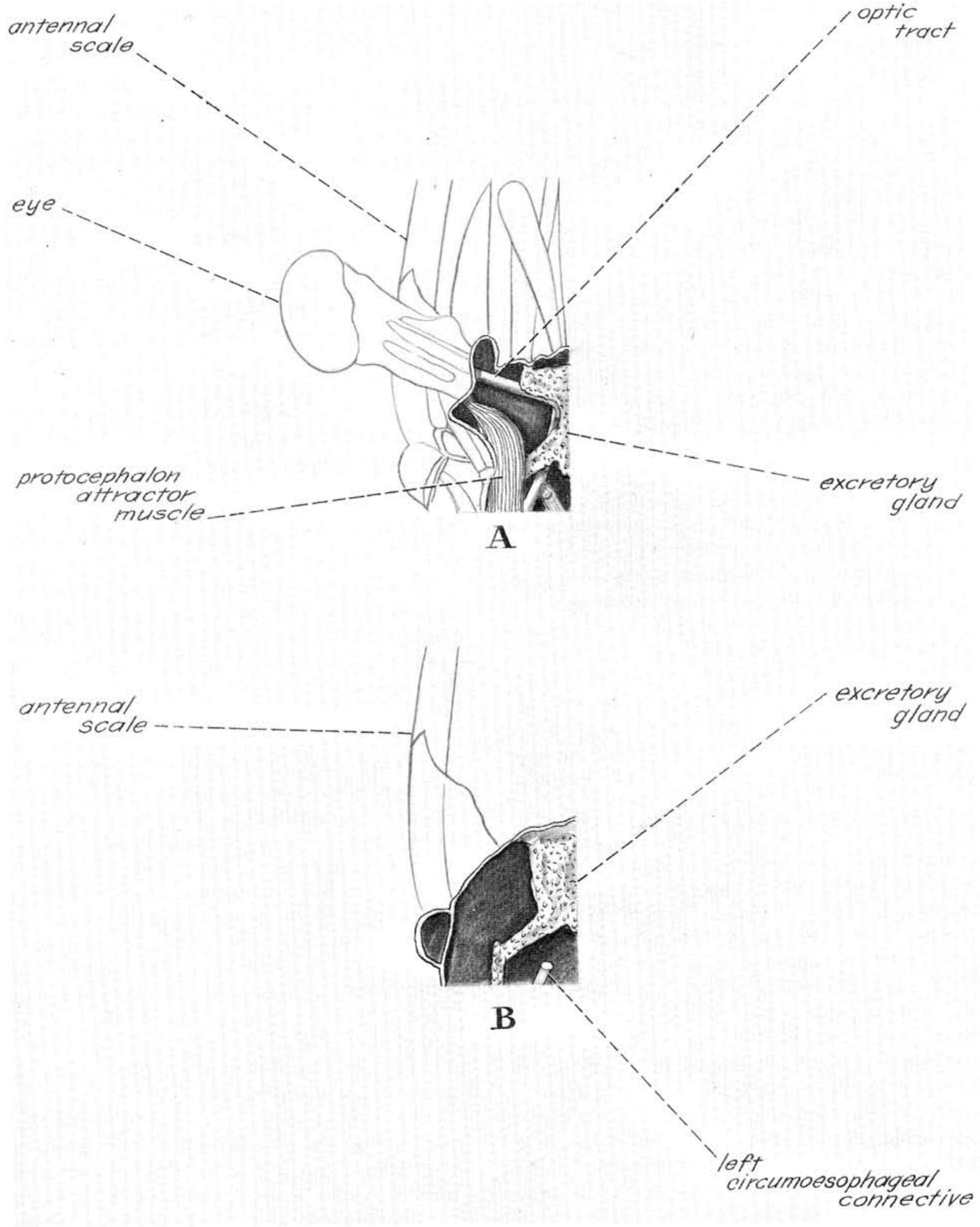

FIGURE 86.—Dorsal view of head region showing excretory gland. Carapace removed. *A*. Part of excretory gland dorsal to brain. *B*. Part of excretory gland ventral to brain.

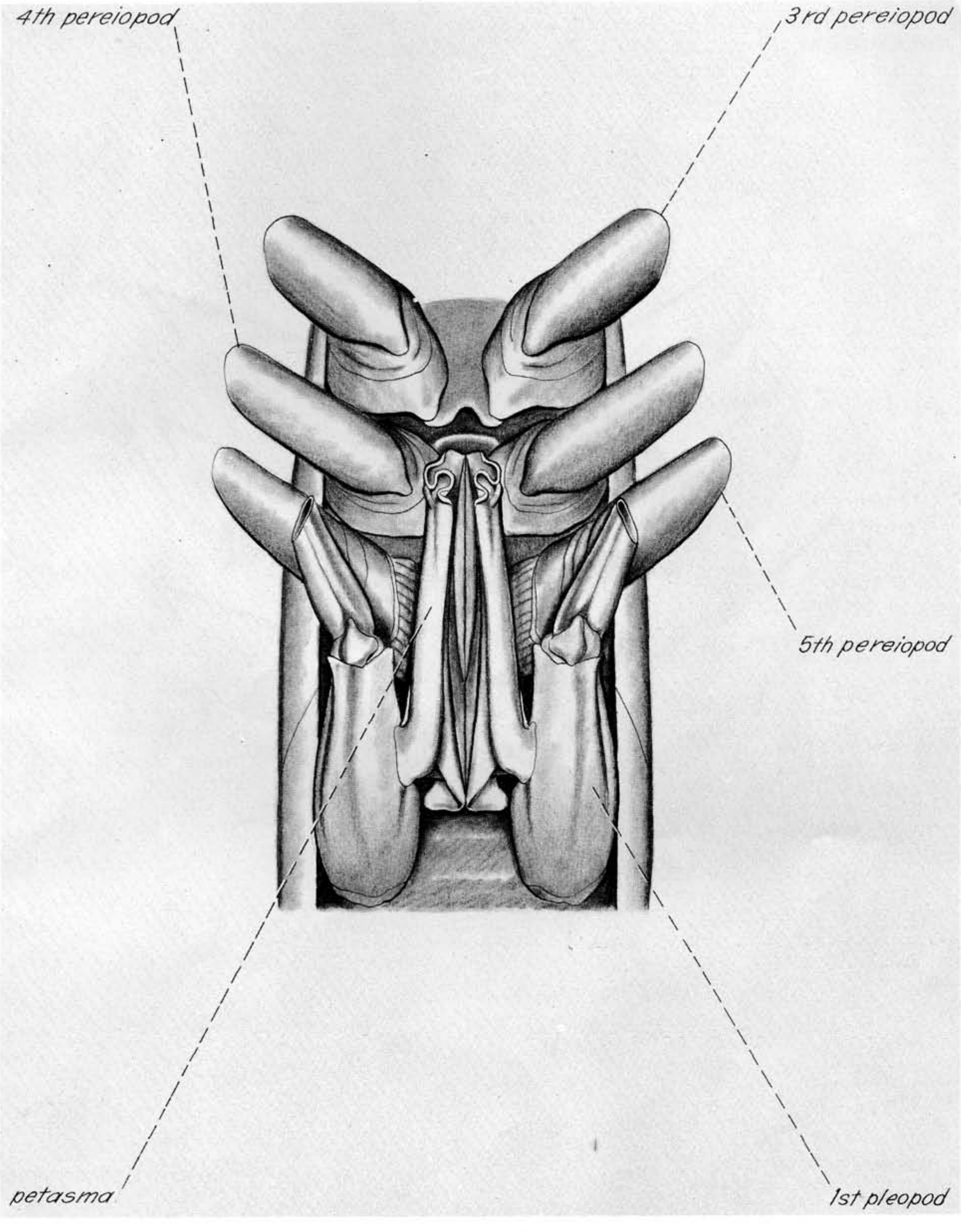

FIGURE 87.—Ventral view of parts of thorax and abdomen showing petasma of male.

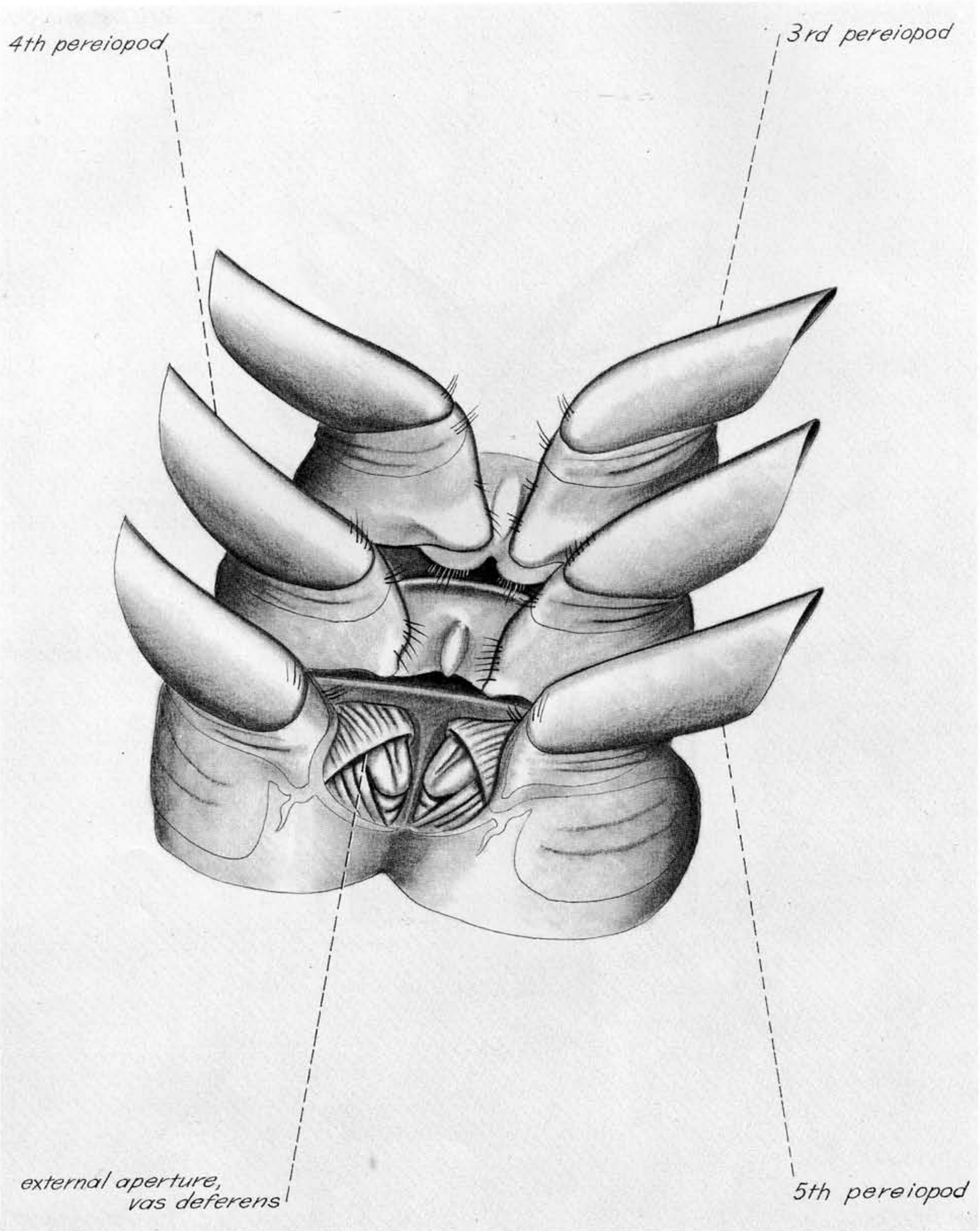

FIGURE 88.—Ventral view of parts of thorax in male. Petasma removed.

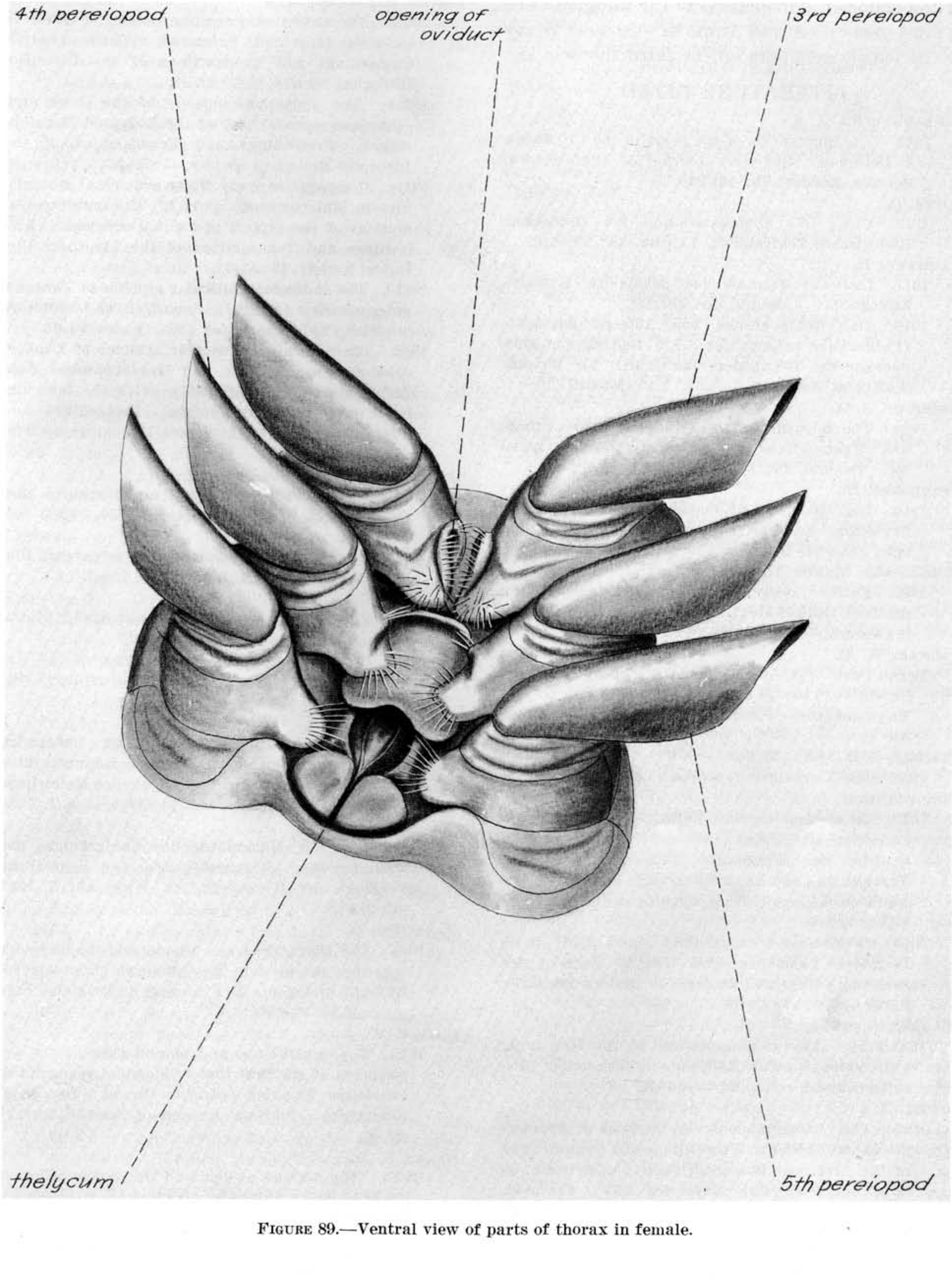

FIGURE 89.—Ventral view of parts of thorax in female.

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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