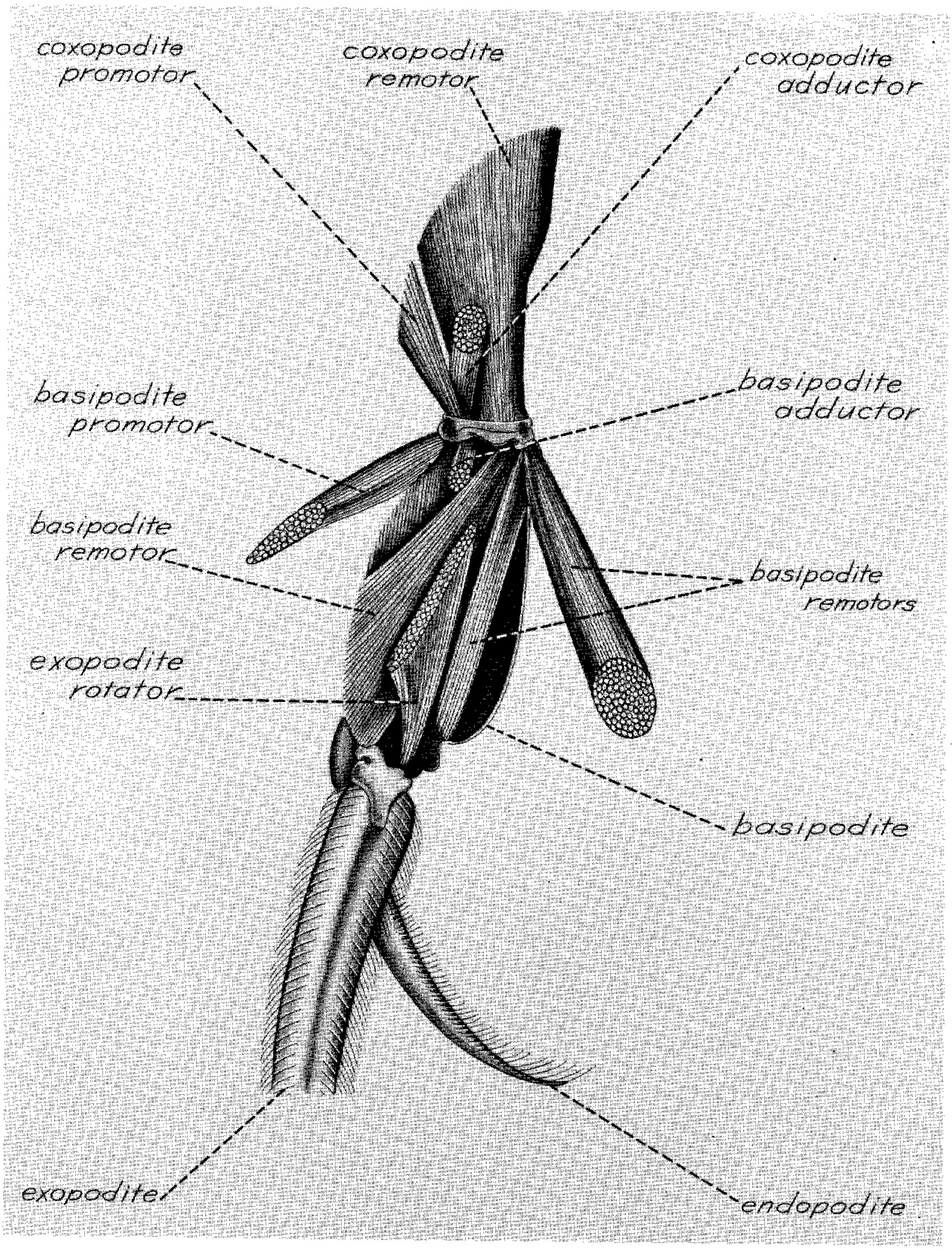

FIGURE 66.—Lateral view of left third pleopod showing basipodite and coxopodite musculature.

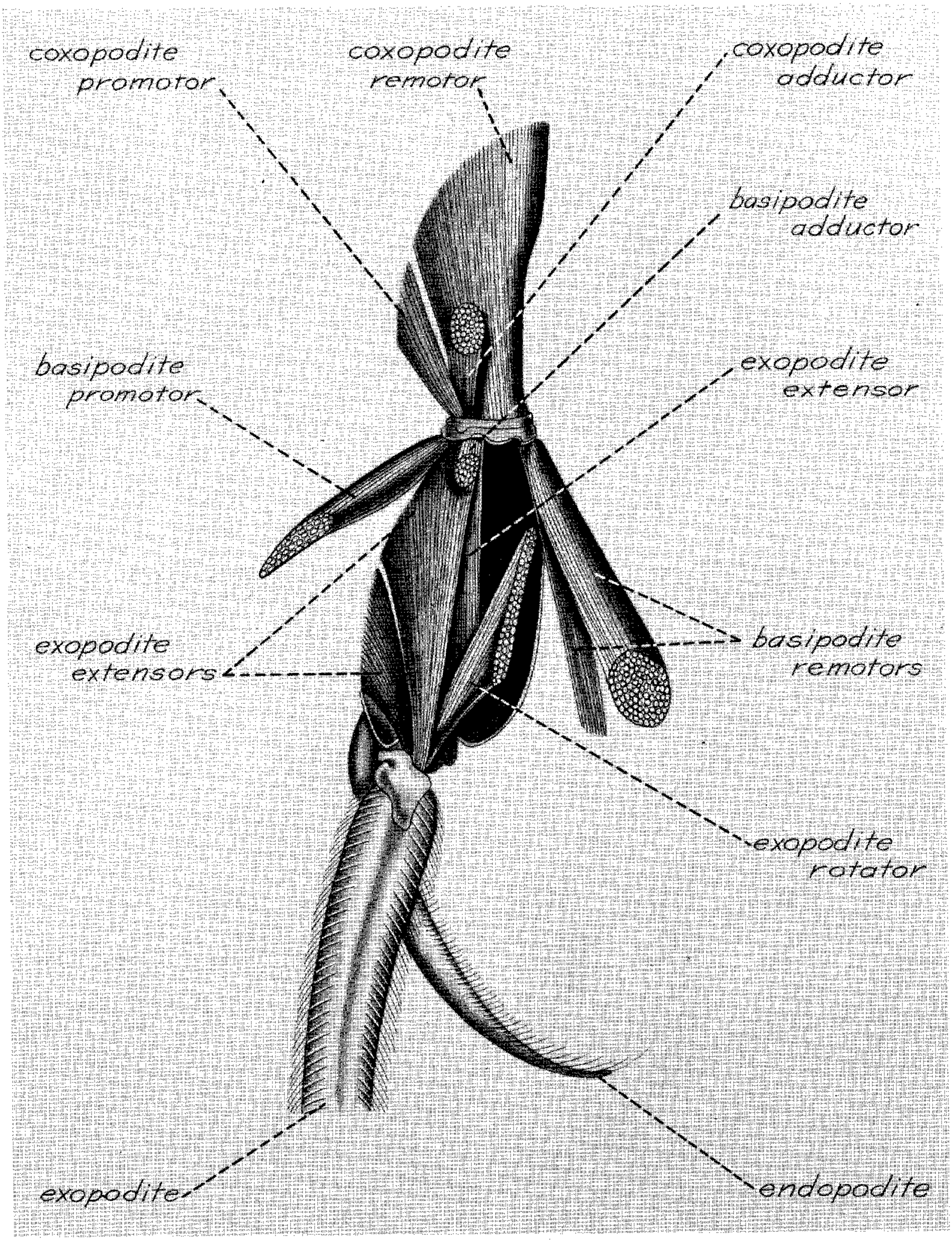

FIGURE 67.—Lateral view of left third pleopod showing basipodite and coxopodite musculature.

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

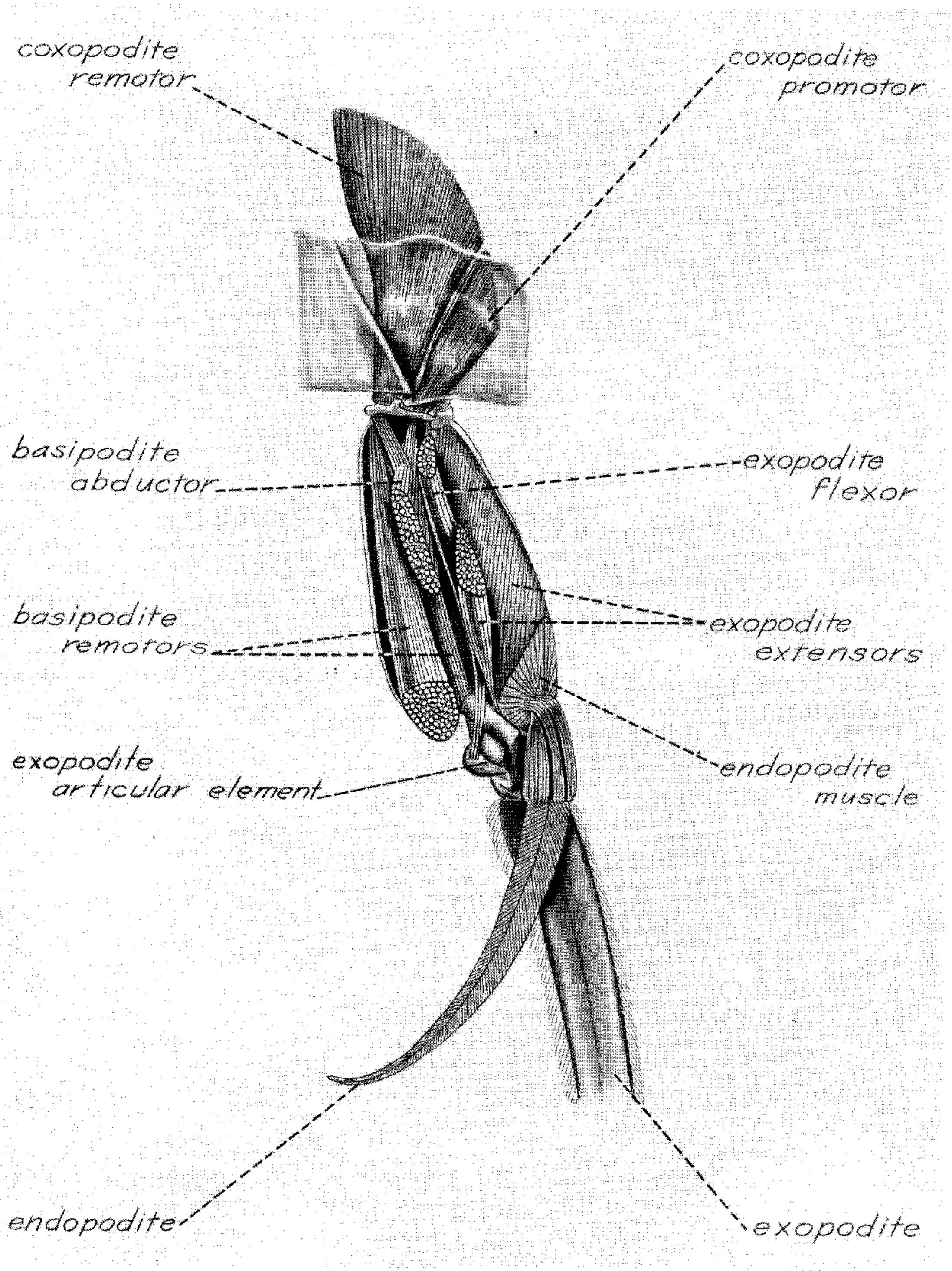

FIGURE 68.—Mesial view of left third pleopod showing coxopodite, basipodite, and endopodite musculature.

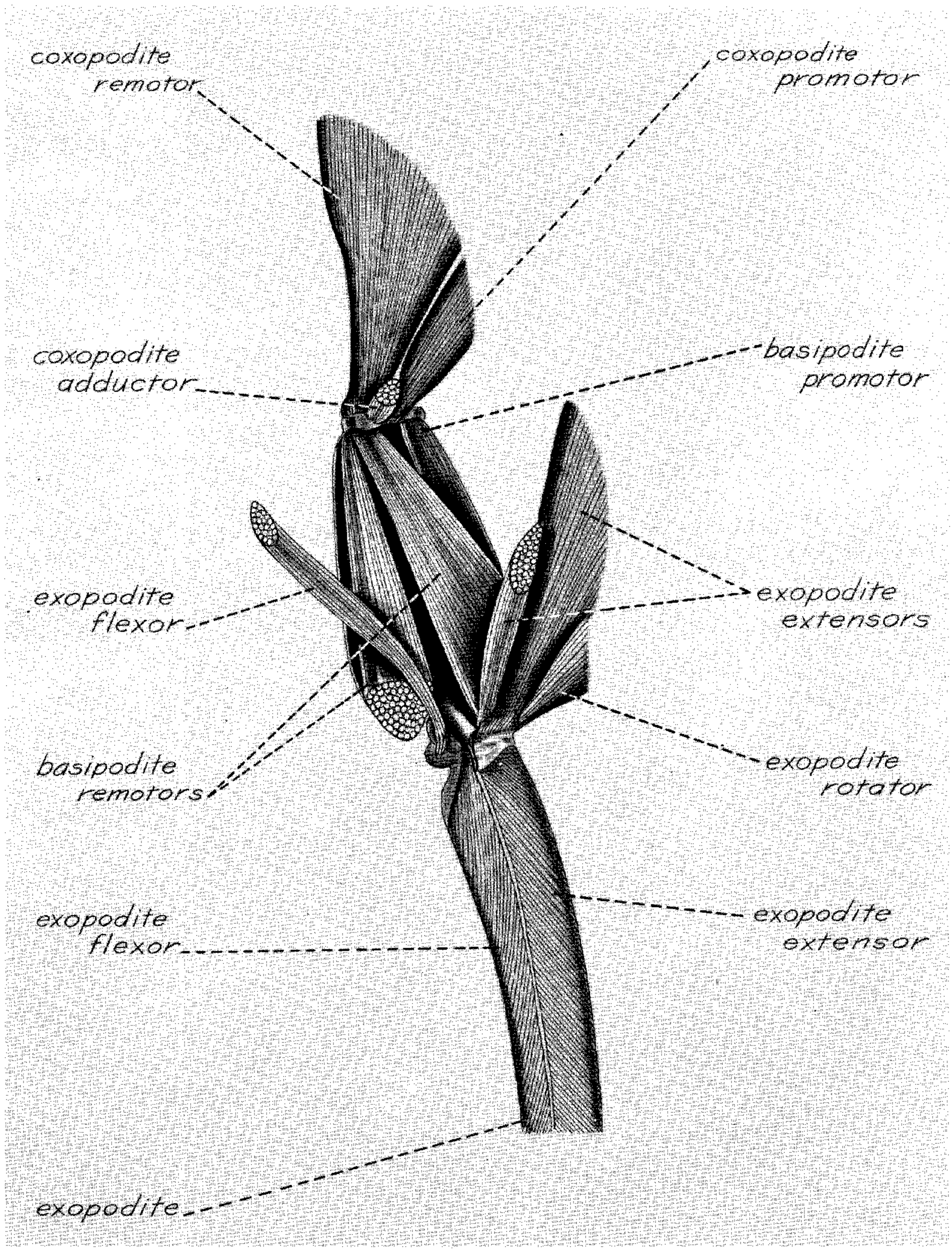

FIGURE 69.—Mesial view of left third pleopod showing muscles of coxopodite, basipodite, and exopodite. Endopodite removed.

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.

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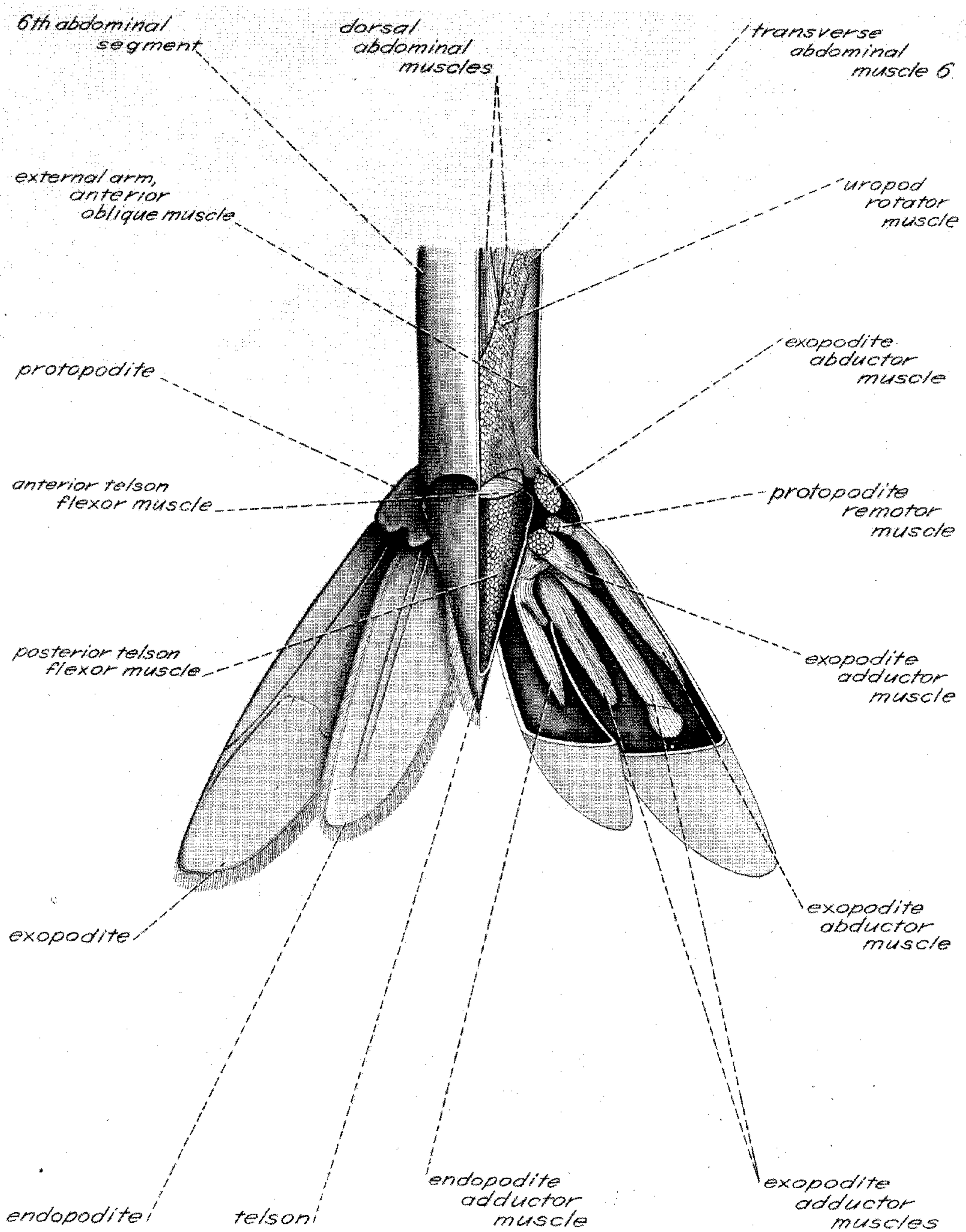

FIGURE 70.—Dorsal view of telson, uropods, and part of sixth abdominal segment. Left side intact. Dorsal cuticle of right side cut away to show muscles.

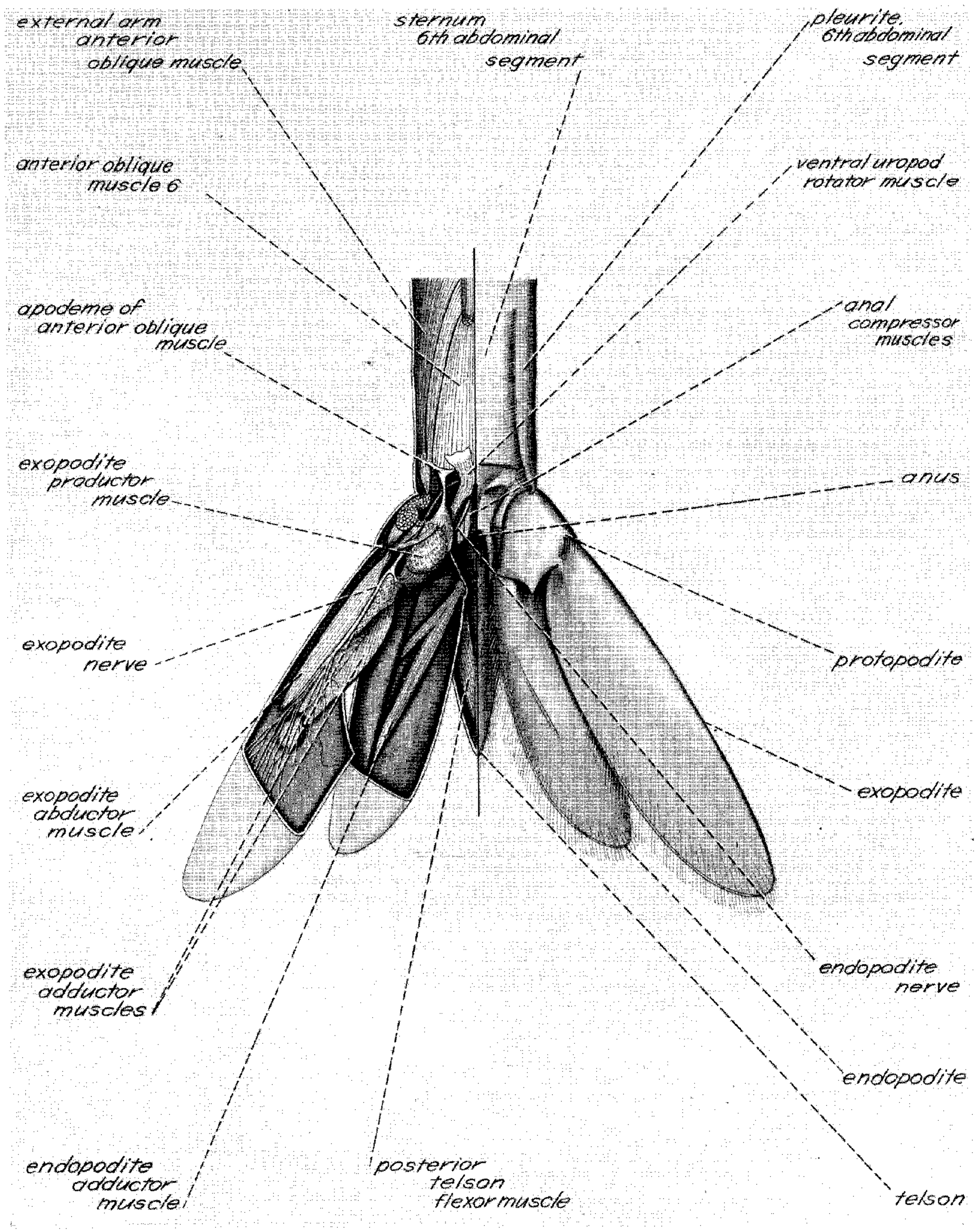

FIGURE 71.—Ventral view of telson, uropods, and part of sixth abdominal segment. Right side intact. Ventral cuticle of left side cut away to show muscles.

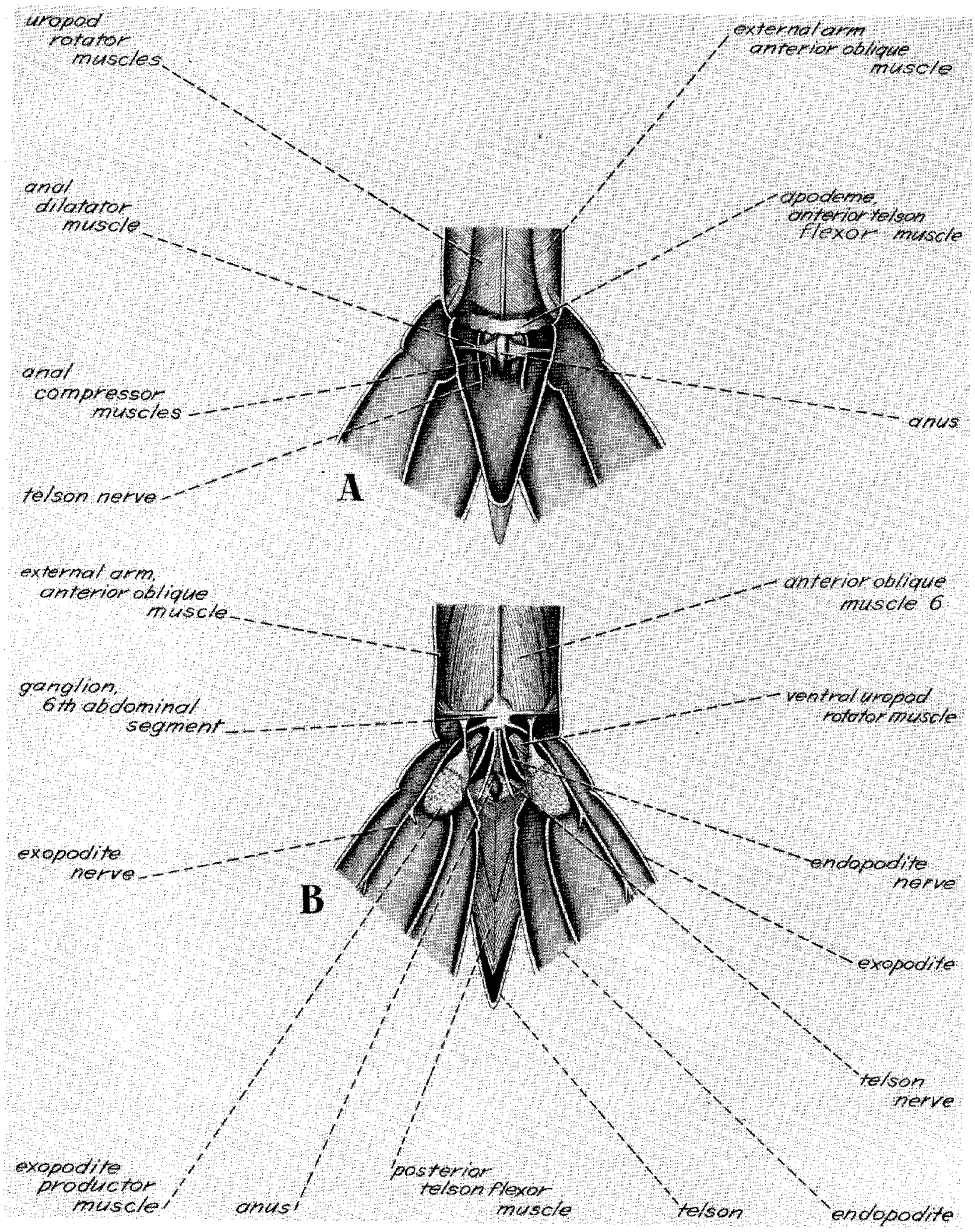

FIGURE 72.—Views of dissections of telson and uropods. *A*. Dorsal view. Muscles removed to show anus and posterior muscles of sixth abdominal segment. *B*. Ventral view. Muscles removed to show nerves.

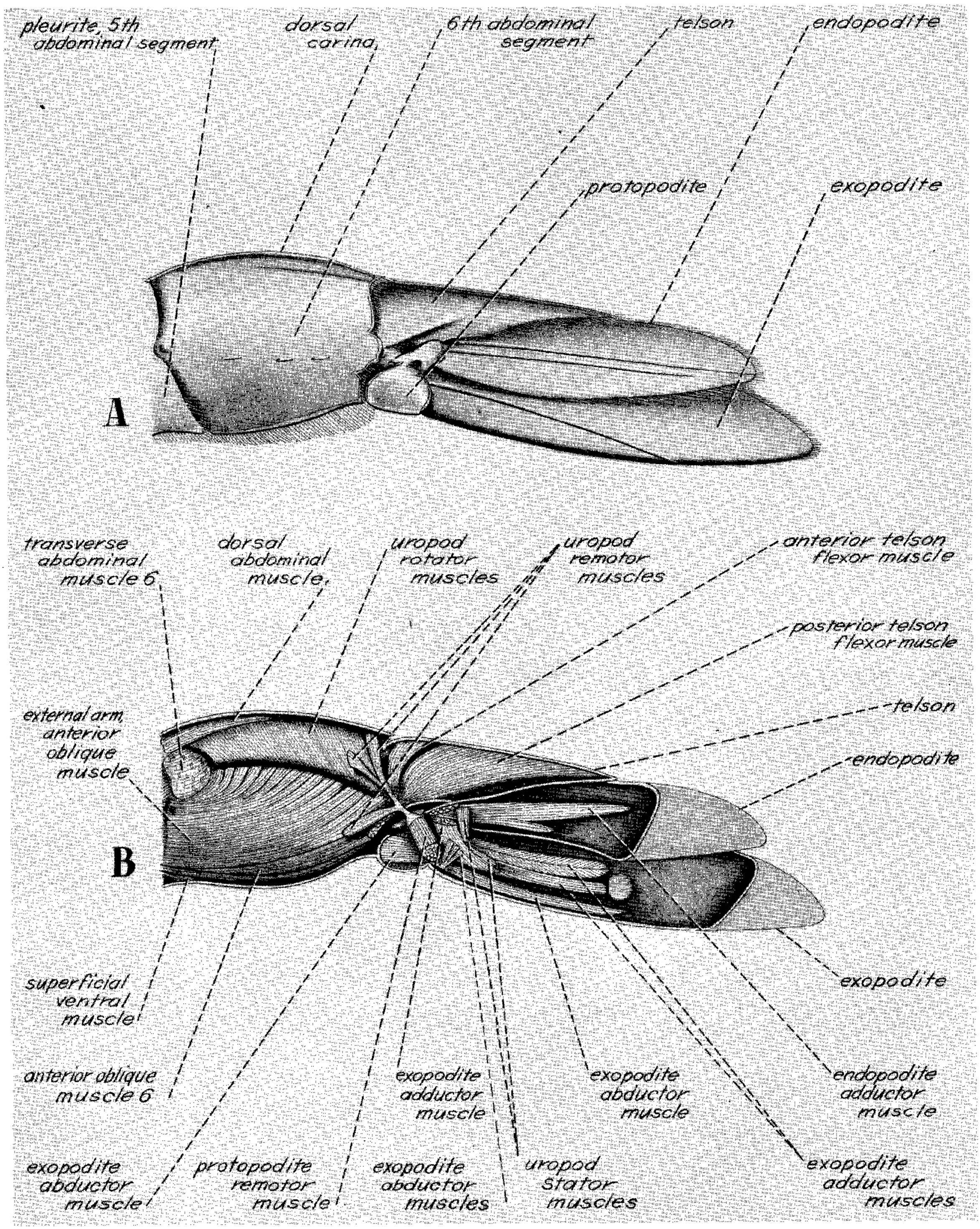

FIGURE 73.—Lateral view of left side of sixth abdominal segment, telson, and uropods. *A*. Intact structures. *B*. Lateral cuticle removed to show superficial lateral muscles.

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 in-

sertion 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

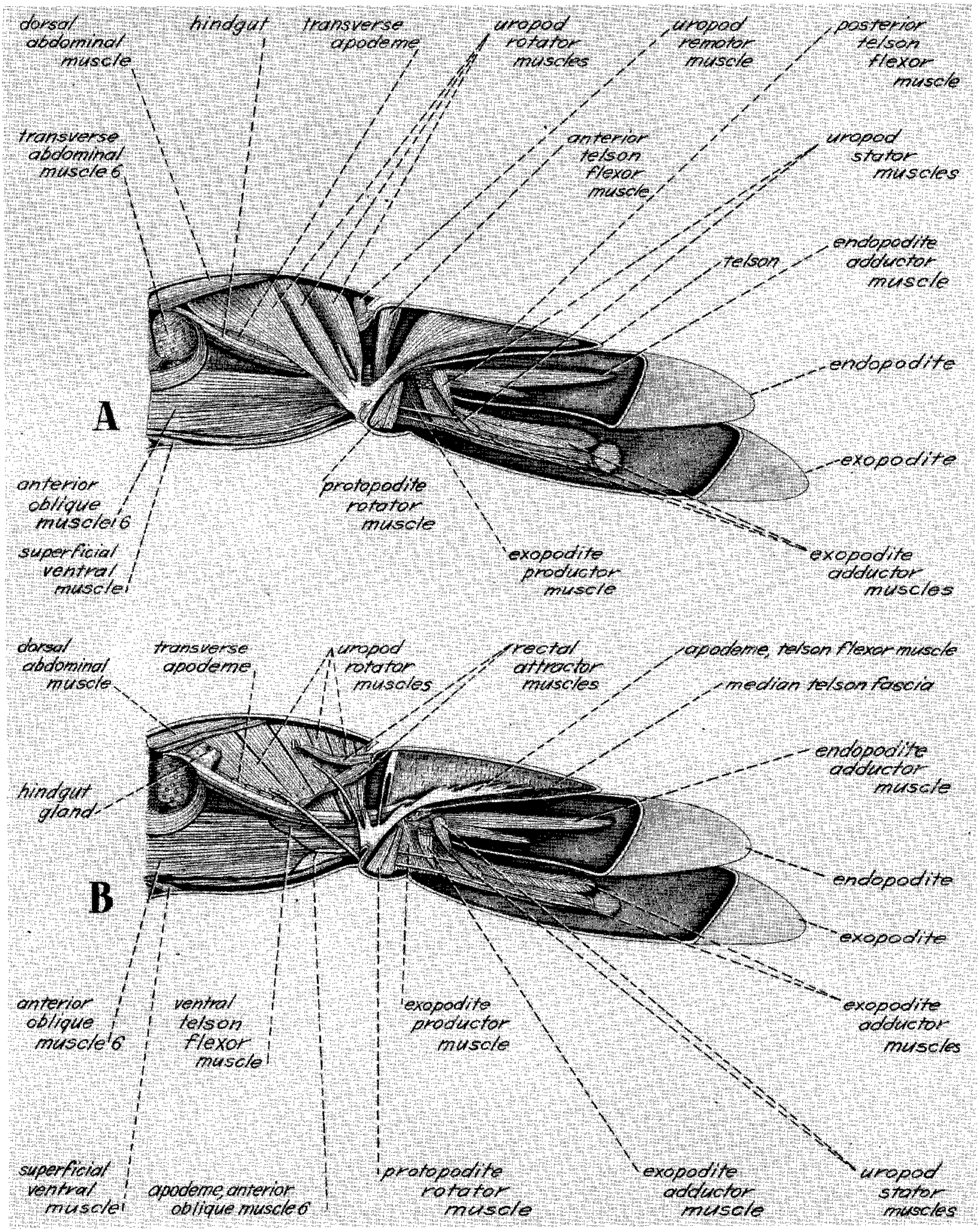

FIGURE 74.—Lateral view of left side of sixth abdominal segment, telson, and uropods. *A*. Lateral muscles removed. *B*. Median sagittal view.

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).

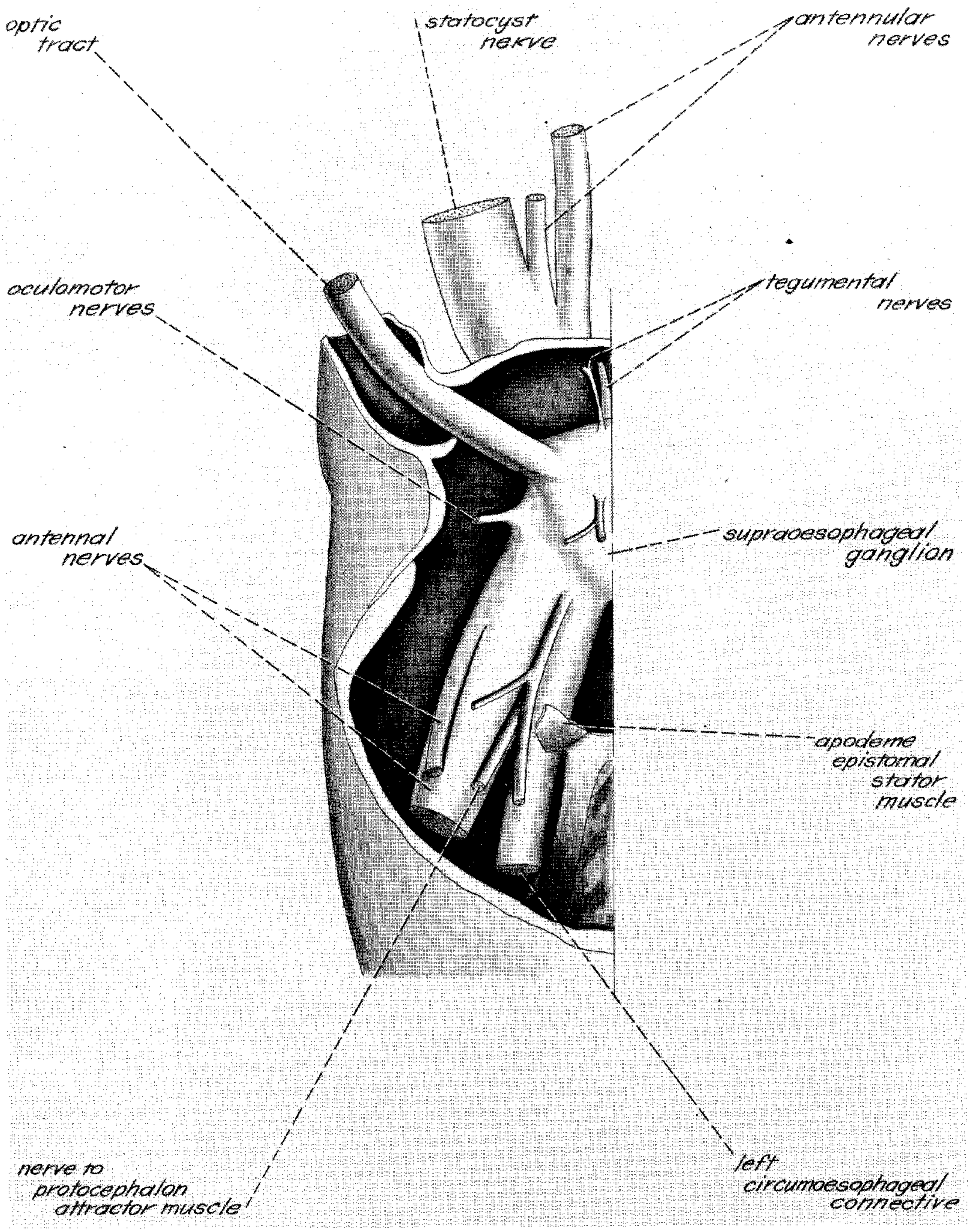

FIGURE 75.—Dorsal view of supraesophageal ganglion. Carapace and dorsal muscles removed.

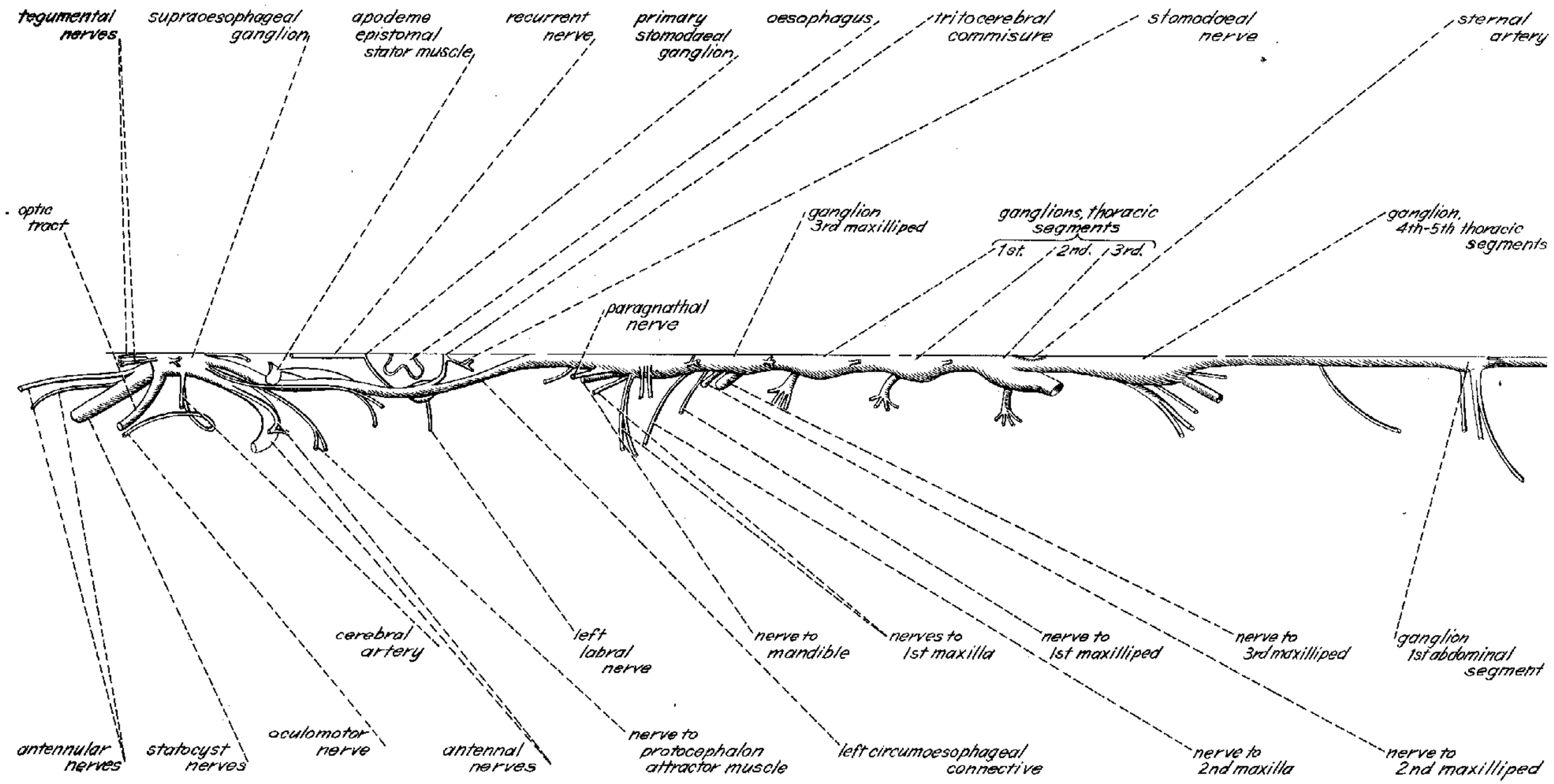

FIGURE 76.—Dorsal view of left half of brain and ventral nerve cord to ganglion of first abdominal segment.

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 anten-

nule, 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

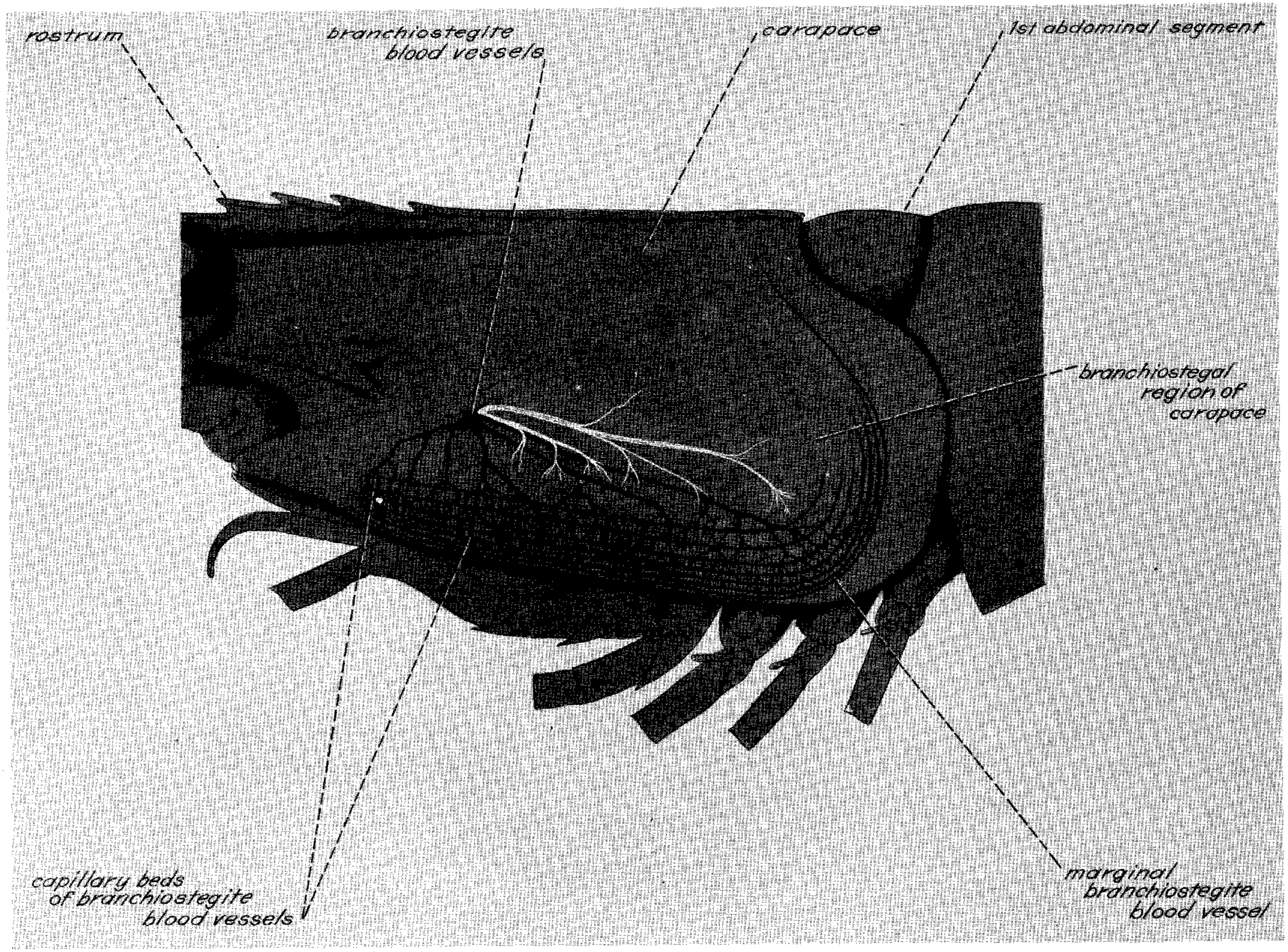

FIGURE 77.—Lateral view of gnathothorax showing blood vessels of branchiostegite epithelium.

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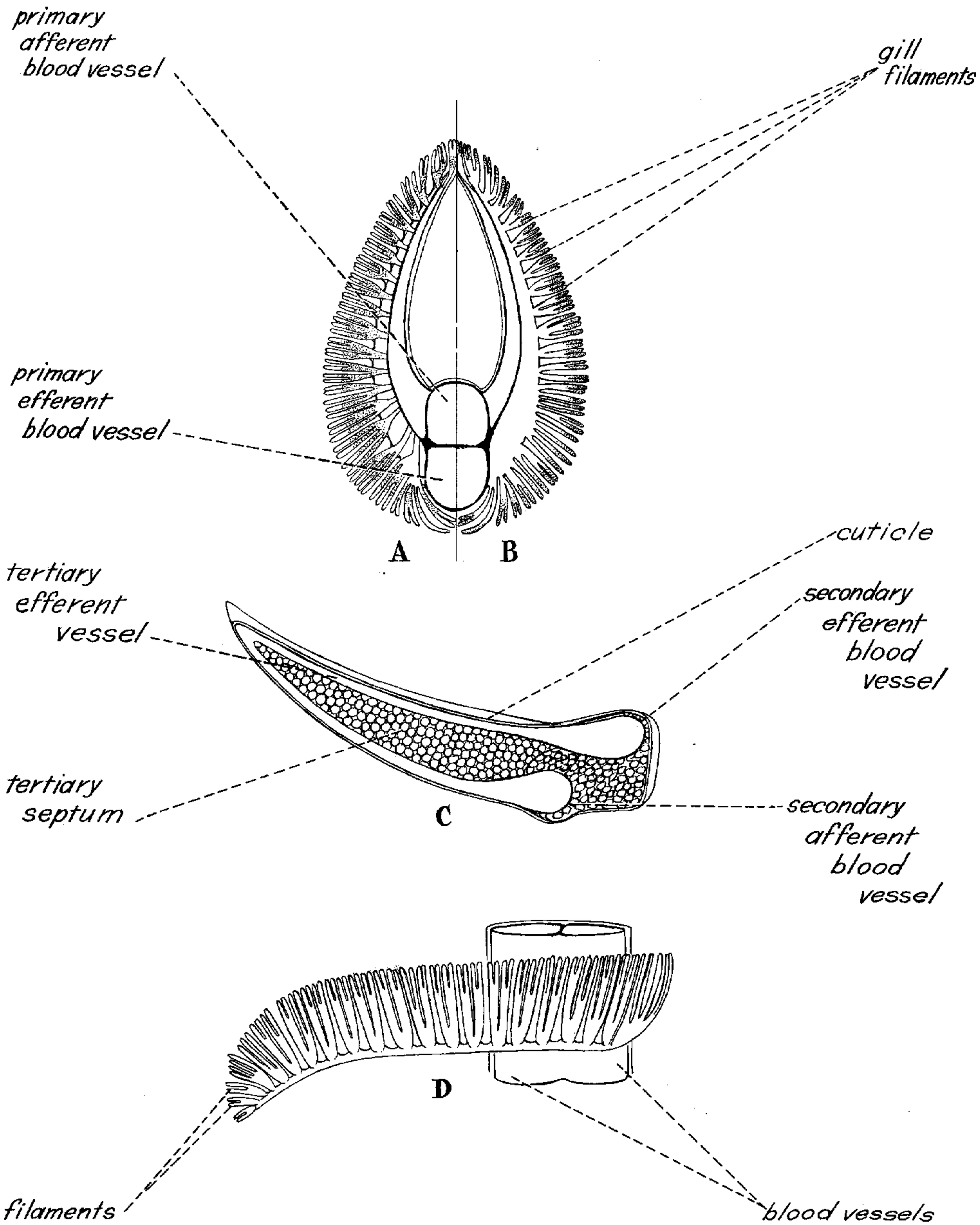

FIGURE 78.—Blood circulation of gills. *A*. Dorsal, and *B*. ventral views of single gill lamina. *C*. Lateral view of single gill filament showing circulation. *D*. Lateral view of single gill lamina.