Schmidt describes them as reductors. A single meropodite reductor is shown in the study of *Callinectes*. The muscle is unopposed by an extensor or productor in *Penaeus* and the other forms considered here.

CARPOPODITE EXTENSOR MUSCLE OF FIRST PEREIOPOD

FIGURE 49

The fibers of the carpopodite extensor muscle take origin over very nearly the whole of the lateral side of the meropodite. The apodeme upon which they insert extends proximally from the lateral edge of the carpopodite and runs almost the length of the meropodite. The carpopodite extensor straightens the carpopodite on the meropodite in a horizontal plane. The muscle is represented in *Astacus* and *Callinectes* as the carpopodite abductor muscle.

CARPOPODITE FLEXOR MUSCLE OF FIRST PEREIOPOD

FIGURE 49

Somewhat like the carpopodite extensor, the carpopodite flexor muscle is a long muscle inserting on a long apodeme. The muscle origins occur about the medial and ventral surfaces of the meropodite. The carpopodite flexor apodeme arises from the proximal margin of the carpopodite, mesad of the dicondylic axis. A pull on this apodeme turns the carpopodite and chela deeply on the meropodite, for this joint is a free one. The same muscle is found in the first pereiopod of *Astacus* and *Callinectes*, but named the carpopodite adductor muscle.

CHELA PRODUCTOR MUSCLE OF FIRST PEREIOPOD

FIGURE 49

The fibers of the chela productor muscle arise from lateral, proximal, and medial regions of the dorsal part of the carpopodite and insert on the long productor apodeme of the propodite. Since the joint between the carpopodite and propodite is a free one, tension on the productor apodeme tends to straighten the chela with respect to the carpopodite and even to levate the chela. The propodite productor muscle of *Penaeus* is found in much the same form in *Astacus* and *Callinectes*, under the name of propodite productor muscle.

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CHELA REDUCTOR MUSCLE OF FIRST PEREIOPOD

FIGURE 49

Directly ventrad of the chela productor muscle lies the chela reductor muscle, a structure also attaching by several slips to a long apodeme. The reductor apodeme arises from the ventral rim of the propodite. The chela reductor muscle turns the chela ventrad. The same muscle appears in the first pereiopod of *Astacus* and *Callinectes*, and in the second pereiopod of *Pandalus*, as the propodite reductor muscle.

CHELA EXTENSOR MUSCLE OF FIRST PEREIOPOD

FIGURE 49

As mentioned above, the joint between the carpopodite and propodite affords free movements of the latter on the former. The chela extensor muscle straightens the chela with respect to the carpopodite in the horizontal plane. The muscle originates in the distolateral part of the carpopodite and inserts on an apodeme projecting proximally from the lateral margin of the propodite. Exact counterparts of the chela extensor are missing in the first pereiopod of *Astacus* and *Callinectes*. Berkeley describes, however, 2 extensors and 2 flexors of the propodite in the second pereiopod of *Pandalus*. Homologies of these muscles without information about their innervations is not feasible.

DACTYLOPODITE ADDUCTOR MUSCLE OF FIRST PEREIOPOD

FIGURE 49

The dactylopodite adductor muscle originates throughout the medial part of the pod-shaped propodite and inserts on a heavy apodeme of the dactylopodite. Contractions of this large muscle close the dactylopodite on the distal gnathal process of the propodite. The dactylopodite adductor muscle is found in the first pereiopod of *Astacus* and *Callinectes*.

DACTYLOPODITE ABDUCTOR MUSCLE OF FIRST PEREIOPOD

FIGURE 49

Functioning in opposition to the dactylopodite adductor muscle, the fibers of the dactylopodite abductor muscle originate about the lateral surfaces of the propodite and insert on the abductor

apodeme attached to the lateral margin of the dactylopodite. The muscle opens the jaws of the chela. The dactylopodite abductor muscle of *Penaeus* is fully homologous with the muscle of the same name in the first pereiopod of *Astacus* and *Callinectes*. The first pereiopod chela of *Pandalus* is reduced.

5b. Fifth Pereiopod

The fifth pereiopod has been chosen as an example of a nonchelate limb. It is truly ambulatory, slender and very long, much longer than the first pereiopod, mainly due to pronounced lengthening of the meropodite and carpopodite. Dorsad of the fifth pereiopod projects a single pleurobranchia.

SKELETAL ELEMENTS

The coxopodite (fig. 54) is a rounded box whose lateral corner projects dorsally to a point. This point makes contact with the dorsal condyle of the article. The ventral condyle is located on the sternal plate between the limbs. The arrangement of these coxopodite dicondyles permits this article great freedom of movement. A large region of thin cuticle, the articular cuticula (fig. 54), lying caudad of the coxopodite, presents little resistance to posterior movements of the segment. A second articular cuticula associated with basipodite movements is found on the lateral surface of the coxopodite.

The strong basipodite (fig. 54) is hinged to the ventral surface of the coxopodite in the typical way, allowing for extensive movements of this article and of the distal segments in the vertical plane. With the dorsolateral surface of the basipodite is articulated a small exopodite. The ischiopodite (fig. 52) makes an oblique connection with the basipodite. The joint is slightly movable. The ischiopodite may be bent ventrad on horizontally located condyles. The articulation point between the short ischiopodite and the long meropodite is a transverse one capable of limited motion. By means of the joint the meropodite may be turned ventrad.

The carpopodite articulates with the meropodite by means of a complex "knee" joint made up of a pair of heavy condyles so arranged that the joint has considerable freedom of action. Similarly oriented, but not so freely movable, is the articulation between the carpopodite and propodite. The propodite is not so long as the carpopodite. The slender, tapering dactylopodite makes contact with the propodite by a simple dicondylic joint. Chemoreceptor tufts and other sensory and mechanical setae are arranged in rows on the dactylopodite and to some extent on the propodite.

MUSCLE ELEMENTS

The arrangement of the muscles of the fifth pereiopod is typical of the true supporting limbs of the thorax. The ambulatory muscles are light by comparison with those of the heavy reptant crustaceans and the terrestrial arthropods. In response to the support function of this appendage, the depressor musculature of the basipodite is especially well developed. The only anatomical account of the fifth pereiopod of a crustacean known to the present writer is that of Cochran on *Callinectes*. However, the fifth leg of the blue crab is the swimming leg and hence its muscles, particularly the basal ones, have diverged from the typical pattern. A remarkable uniformity of endopodite musculature between *Penaeus* and *Callinectes* still remains, however. The fifth pereiopod of *Penaeus* is operated by 24 muscles grouped into 13 functional types.

COXOPODITE PROMOTOR MUSCLES OF FIFTH PEREIOPOD

FIGURES 52, 53, 55 to 57

Two coxopodite promotor muscles are found in the fifth pereiopod of *Penaeus*. The smaller lateral promotor originates by its broad, dorsal, fan-shaped portion on the laterotergal plate of the segment (figs. 55, 56) and inserts on the anterior rim of the coxopodite. Lying medial to the latter muscle is a larger promotor muscle mass originating somewhat dorsad of the smaller promotor on the pleural region. Contractions of these muscles turn the coxopodite forward on its condyles.

COXOPODITE REMOTOR MUSCLES OF FIFTH PEREIOPOD

FIGURES 52, 53, 55, 56

The fifth pereiopod of *Penaeus* has two coxopodite remotor muscles. These are large, flat muscles (fig. 55) situated beneath the thin material of the articular cuticula (fig. 54). Both originate by broad margins on the pleural plate and insert on the caudal margin of the coxopodite.

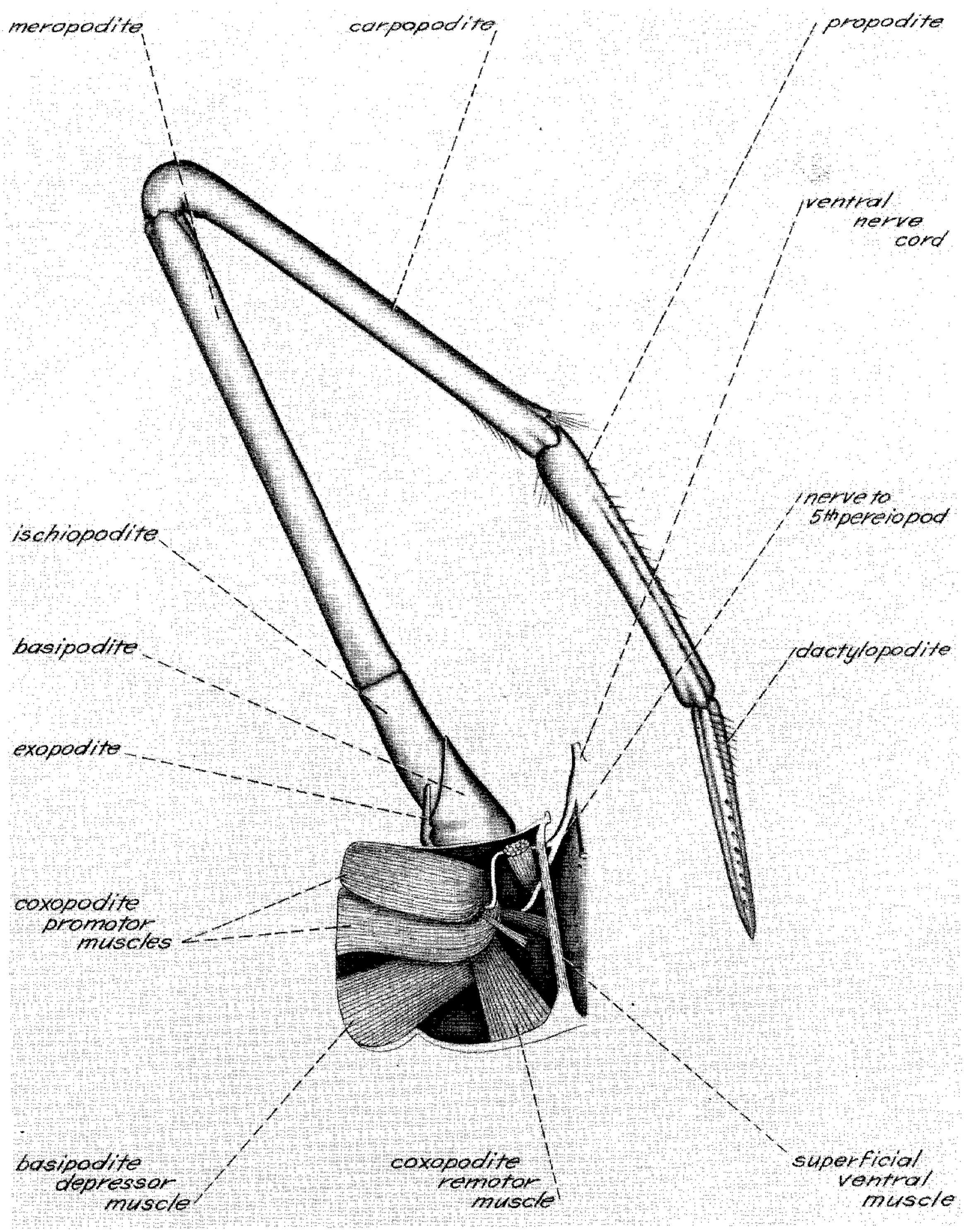

FIGURE 52.—Dorsal view of left fifth pereiopod showing protopodite muscles.

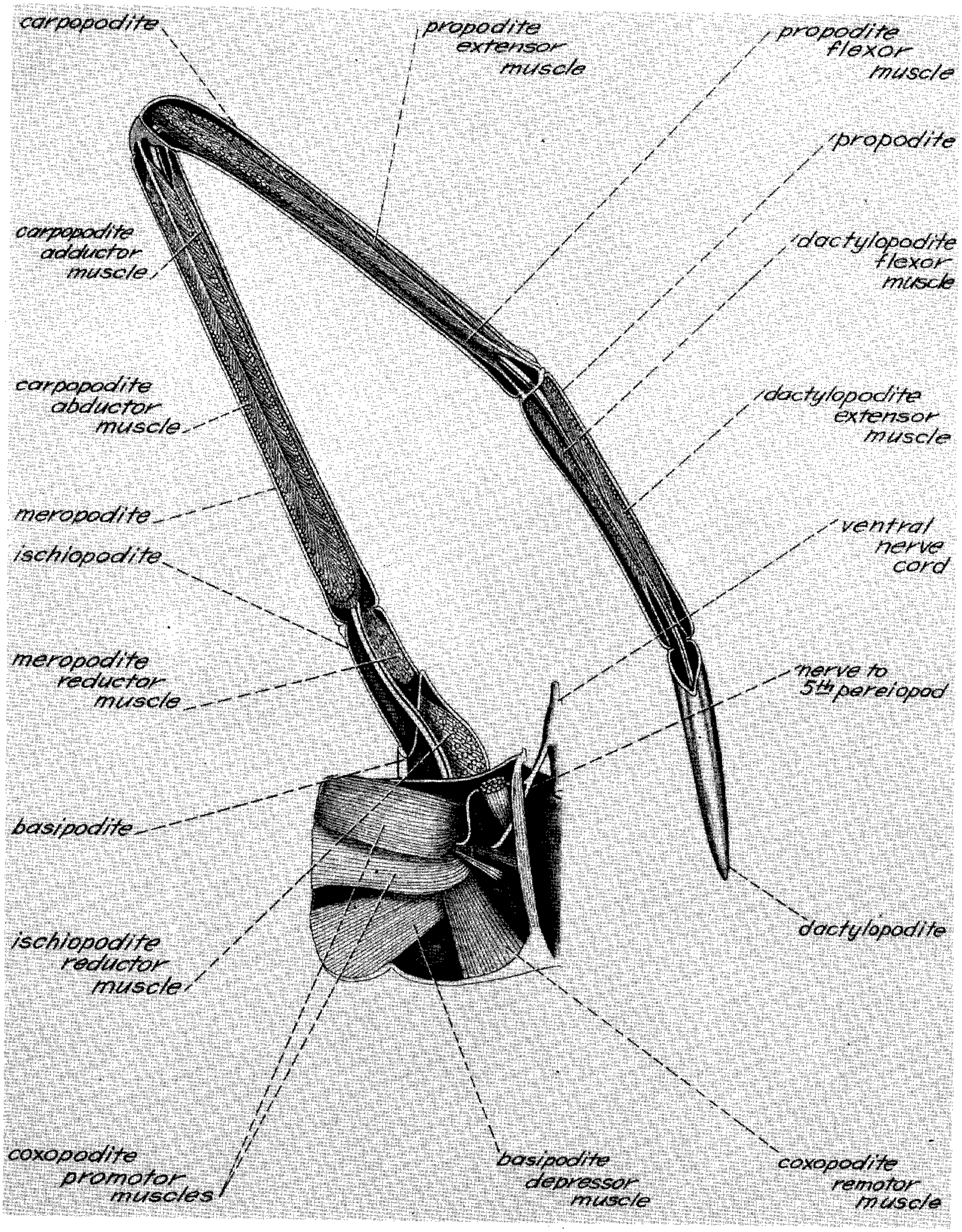

FIGURE 53.—Dorsal view of left fifth pereiopod. Dorsal cuticle removed to show muscles of protopodite and endopodite.

The coxopodite remotor muscles act with some power to turn the coxopodite rearward.

COXOPODITE DEPRESSOR MUSCLE OF FIFTH PEREIOPOD

FIGURE 58

The coxopodite depressor muscle arises from phragmal material on the medial margin of the ventral skeletal foramen entering the coxopodite and runs to the medial margin of the coxopodite (fig. 58). Apparently the muscle is able to lift slightly the medial margin of the coxopodite, and for this reason the structure has been named the coxopodite depressor muscle.

BASIPODITE LEVATOR MUSCLES OF FIFTH PEREIOPOD

FIGURES 55, 56

Four basipodite levator muscles are seen in the fifth pereiopod of *Penaeus*. The two lateral levators constitute together a broad fan (fig. 55) originating along the caudal margin of the coxopodite. They become narrow as they run to their insertions on the lateral rim of the basipodite. Two longer levators lying mesad of the lateral levators originate in the dorsal apex of the coxopodite and run to heavy apodemal material common to the levator muscles. The basipodite levator muscles raise dorsally the basipodite and with it the distal elements of the limb.

BASIPODITE DEPRESSOR MUSCLES OF FIFTH PEREIOPOD

FIGURES 52, 53, 55 TO 58

The most important muscles of the fifth pereiopod of *Penaeus* are the depressors of the basipodite. Seven basipodite depressor muscles exist in the limb. The first and second depressor muscles are lateral (fig. 56). They take origins on areas of the caudal margin of the coxopodite and insert on the large common depressor apodeme of the basipodite. The third depressor (figs. 55, 56) is a large fan which originates broadly on the laterotergal plate of the body segment. The fourth basipodite depressor (fig. 57), also fan-shaped but narrower than the third, lies just mesad of the third depressor muscle. It, too, has a broad origin on the pleural area. The fifth depressor is a rather small muscle (fig. 58) which takes its origin on medial phragmal material of the ventral skeleton. All of the foregoing five muscles insert on the basipodite depressor apodeme. The sixth and seventh depressor muscles (fig. 58) arise on phragmal material on the medial side of the ventral skeletal foramen and insert for some length along the posteromedial rim of the basipodite. The function of the basipodite depressor muscles is to turn the fifth pereiopod ventrad, providing support for the body.

ISCHIOPODITE REDUCTOR MUSCLE OF FIFTH PEREIOPOD

FIGURE 53

The ischiopodite reductor muscle has multiple origins over a substantial area on the dorsal and medial parts of the basipodite. It inserts on an apodeme projecting from the ventral surface of the ischiopodite. The muscle bends the ischiopodite ventrad slightly and to some extent rotates it, due to the oblique angle by which the basipodite and ischiopodite are connected (fig. 52). The muscle is not opposed by any other muscle.

MEROPODITE REDUCTOR MUSCLE OF FIFTH PEREIOPOD

FIGURE 53

Arising by multiple origins on the dorsal and medial half of the ischiopodite, the meropodite reductor muscle fibers insert on a small apodeme on the ventral surface of the long meropodite, proximally. The meropodite reductor bends the meropodite ventrally a short distance.

CARPOPODITE ABDUCTOR MUSCLE OF FIFTH PEREIOPOD

FIGURE 53

The fibers of the carpopodite abductor muscle originate over most of the dorsal half of the meropodite and insert on an extremely long apodeme running nearly the whole length of the meropodite along the midline. The length of pull of this muscle and of its opponent, the carpopodite adductor, is very great. The long apodeme to which it attaches arises from the proximal end of the carpopodite, lateral to the condylic axis. The muscle thus turns the carpopodite to a position in which the axes of the meropodite and carpopodite are in line. The carpopodite abductor muscle easily could be described as an extensor.

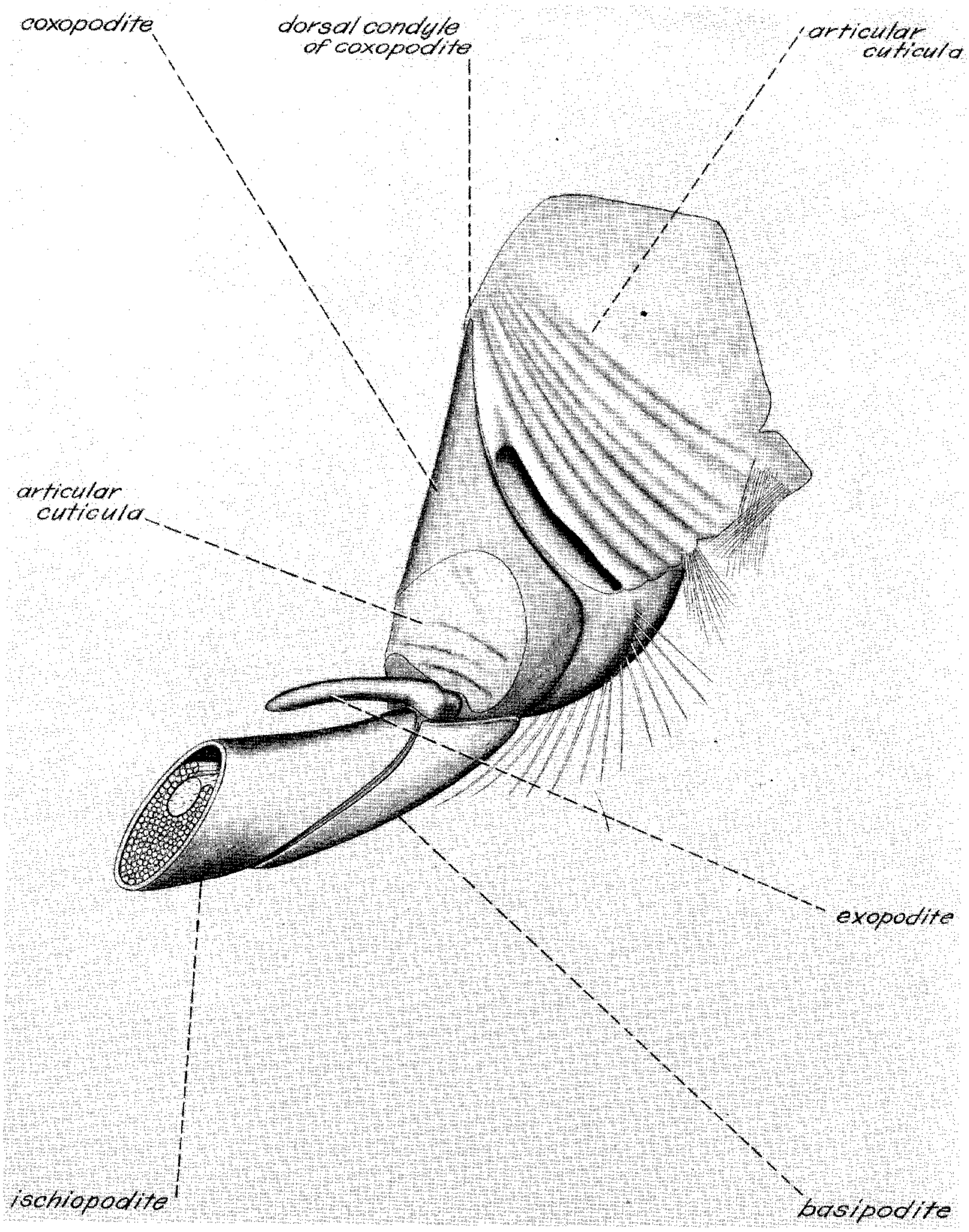

FIGURE 54.—Lateral view of leg base of left fifth pereiopod.

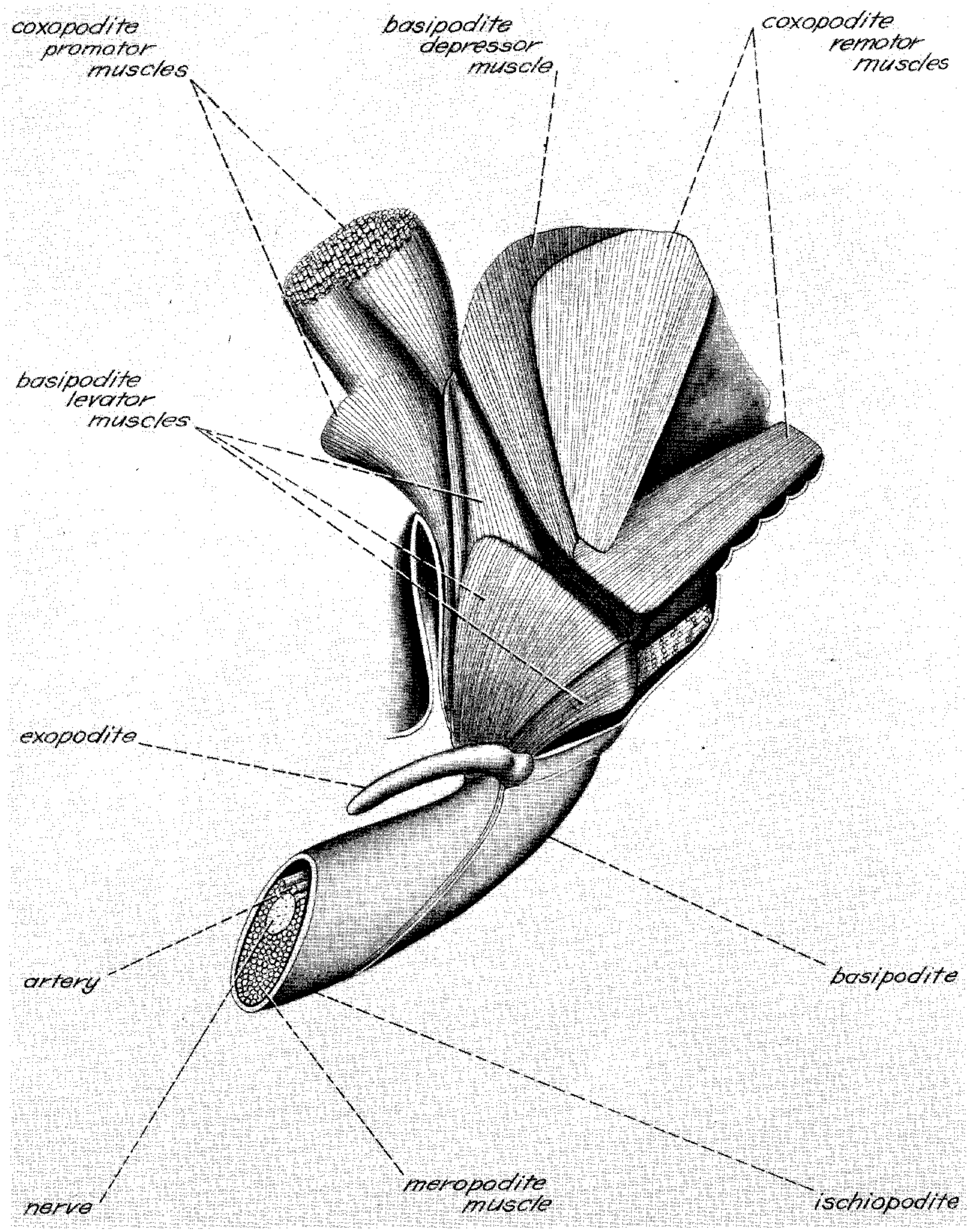

FIGURE 55.—Lateral view of leg base of left fifth pereiopod. Lateral cuticle removed to show superficial lateral muscles.

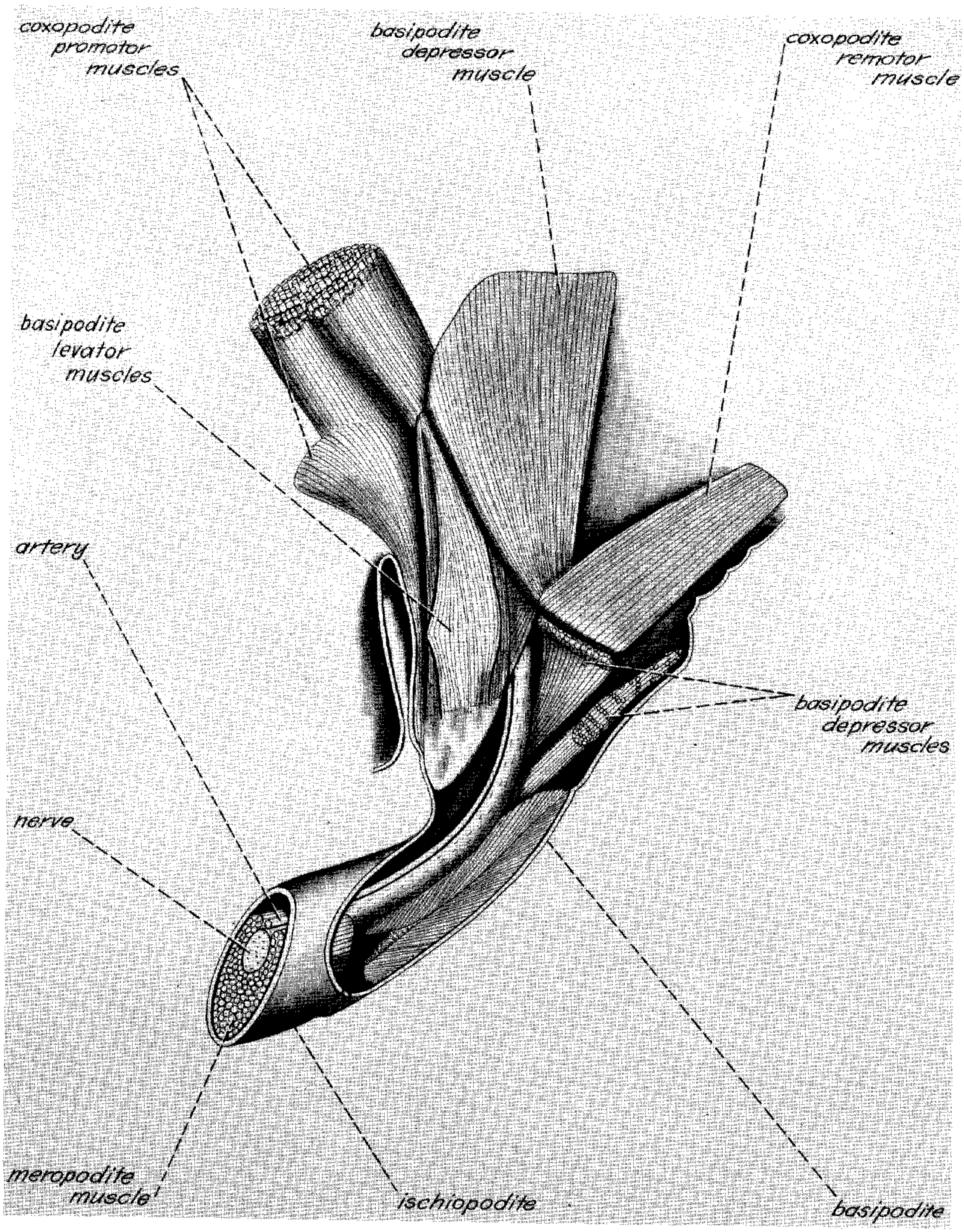

FIGURE 56.—Lateral view of leg base of left fifth pereiopod. Some superficial lateral muscles removed.

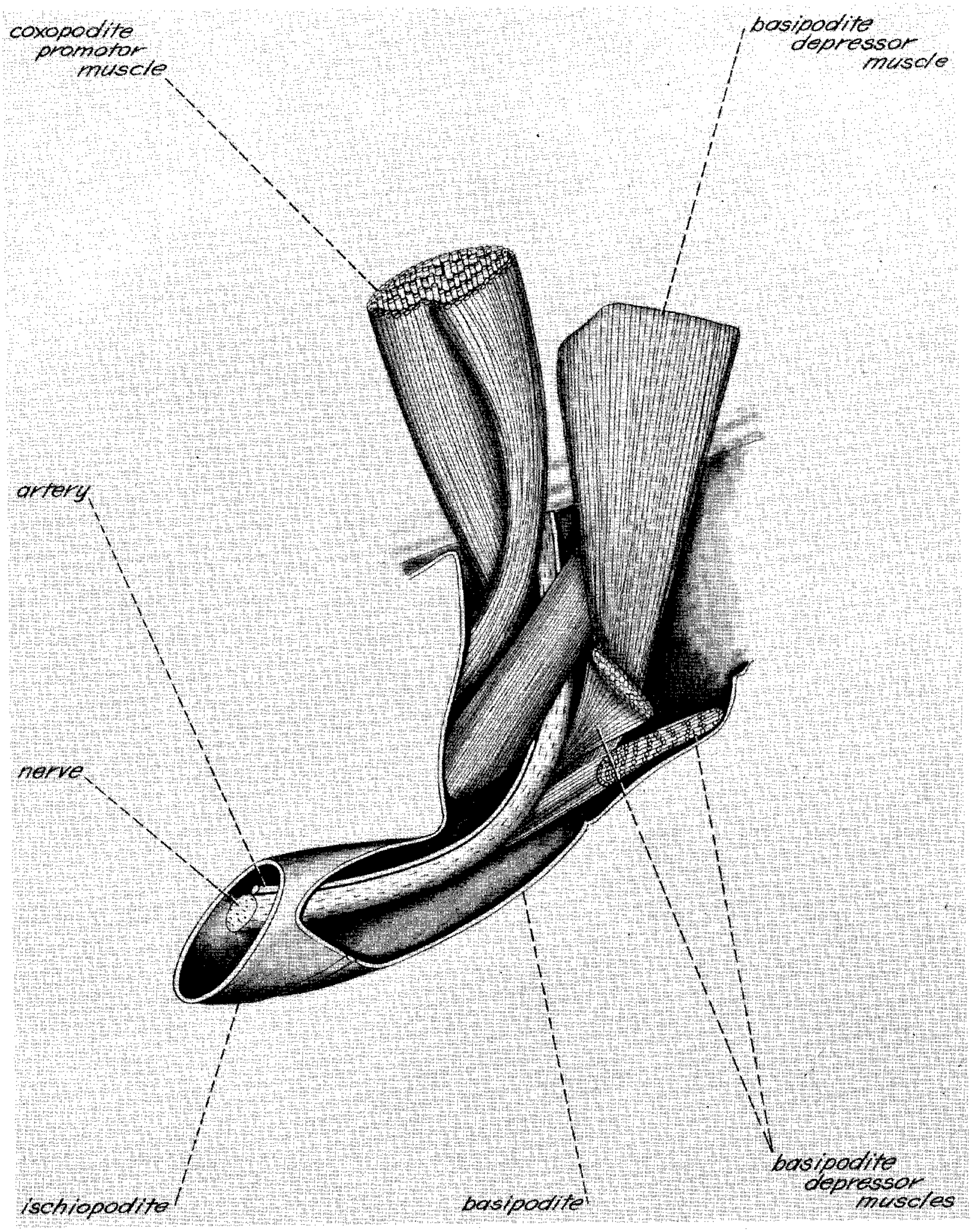

FIGURE 57.—Lateral view of leg base of left fifth pereiopod. Lateral muscles removed to show medial muscles.

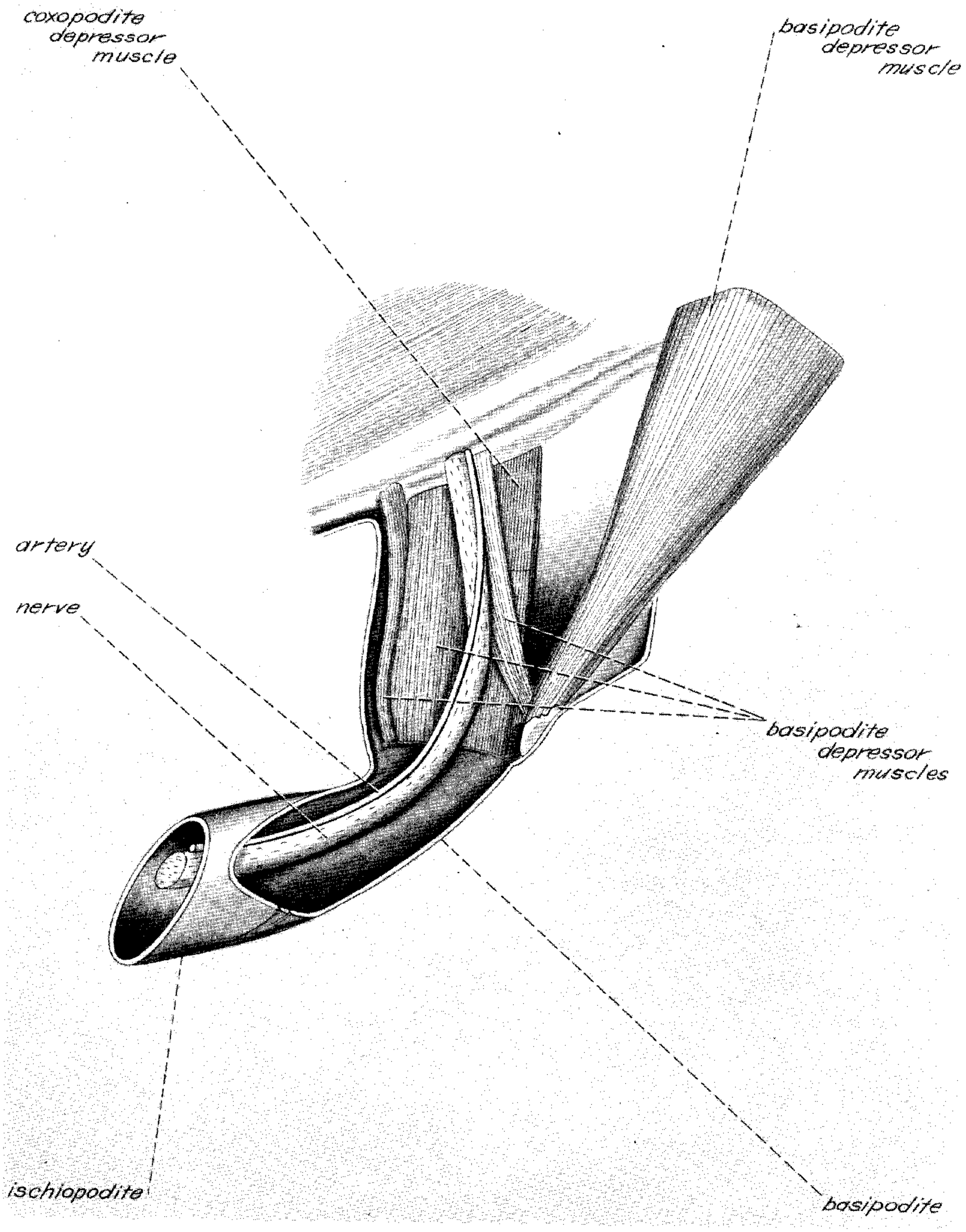

FIGURE 58.—Lateral view of leg base of left fifth pereiopod. Medial muscles.

CARPOPODITE ADDUCTOR MUSCLE OF FIFTH PEREIOPOD

FIGURE 53

In like fashion to the carpopodite abductor, the carpopodite adductor muscle fibers originate on a large area of the meropodite, but on the ventral half of the article. The muscle inserts on a long apodeme arising from the proximal portion of the carpopodite, medial to the axis of the dicondyles. Carpopodite adductor muscle contractions serve to turn the carpopodite toward the body, and in fact deeply on the meropodite. The muscle might better be considered a flexor of the carpopodite.

PROPODITE EXTENSOR MUSCLE OF FIFTH PEREIOPOD

FIGURE 53

The arrangement of the propodite muscles in the carpopodite is very similar to that of the carpopodite muscles within the meropodite. The propodite extensor muscle originates over much of the dorsal part of the carpopodite and inserts on a long apodeme projecting proximally from the base of the propodite. The apodeme is so connected to the propodite that a pull on it extends the propodite with respect to the carpopodite.

PROPODITE FLEXOR MUSCLE OF FIFTH PEREIOPOD

FIGURE 53

The propodite flexor muscle opposes the action of the propodite extensor muscle. The fibers of the flexor muscle arise from the ventral surface of the carpopodite and, like those of the extensor, attach to a long apodeme of the propodite. This apodeme arises from a position opposite to that of the extensor apodeme. Contractions of the propodite flexor muscle flex the propodite upon the carpopodite.

DACTYLOPODITE EXTENSOR MUSCLE OF FIFTH PEREIOPOD

FIGURE 53

The dactylopodite extensor muscle originates along the lateral side of the propodite and inserts on a long apodeme arising from the proximal end of the dactylopodite. The muscle straightens the dactylopodite on the propodite.

DACTYLOPODITE FLEXOR MUSCLE OF FIFTH PEREIOPOD

FIGURE 53

The dactylopodite flexor muscle bends the dactylopodite upon the propodite. Like the extensor muscle, the flexor has multiple origins upon the medial surface of the propodite. The muscle inserts on the long flexor apodeme of the dactylopodite.

C. Abdomen

Unlike the head and gnathothorax, the abdomen is almost entirely devoted to the propulsion of the white shrimp. Except for slender components of the gut, the gonads, and the nervous and circulatory systems, the space within the abdominal skeleton is filled with muscles, most of them concerned with the powerful flexion of which the animal is capable. The abdomen consists of six segments, all of which bear appendages, and a posterior telson which does not. The abdominal segments are attached to one another by deep folds of thin articular cuticle which allow each segment great freedom of movement with respect to its neighbors and with the thorax. Intersegmental connections in the abdomen are of several types. The simplest and perhaps most movable is that between the thorax and first abdominal segment (fig. 59). Here, cuticular folds of great depth reinforced by heavy muscles internally make ventral flexion possible between these body tagmata. The junction is without special, restrictive condyles, allowing extensive lateral movements of the abdomen on the thorax at this point.

The junctions of the first and second, and of the second with the third abdominal segments (fig. 59) are identical. Motion at these joints is limited to flexion and extension by lateral condyles of similar design. In contrast, the joint between the third and fourth adbominal segment differs from those between the first three segments. This connection is much simpler. The condyles are rather loosely connected, affording flexion and extension and a certain amount of lateral motion. The fourth, fifth, and sixth abdominal segments articulate with one another by means of two pairs of identical condyles similar in their rigidity to those between the first, second, and third segments, but different in structure (see enlargements of condylic structure, detail of articulation, fig. 59).

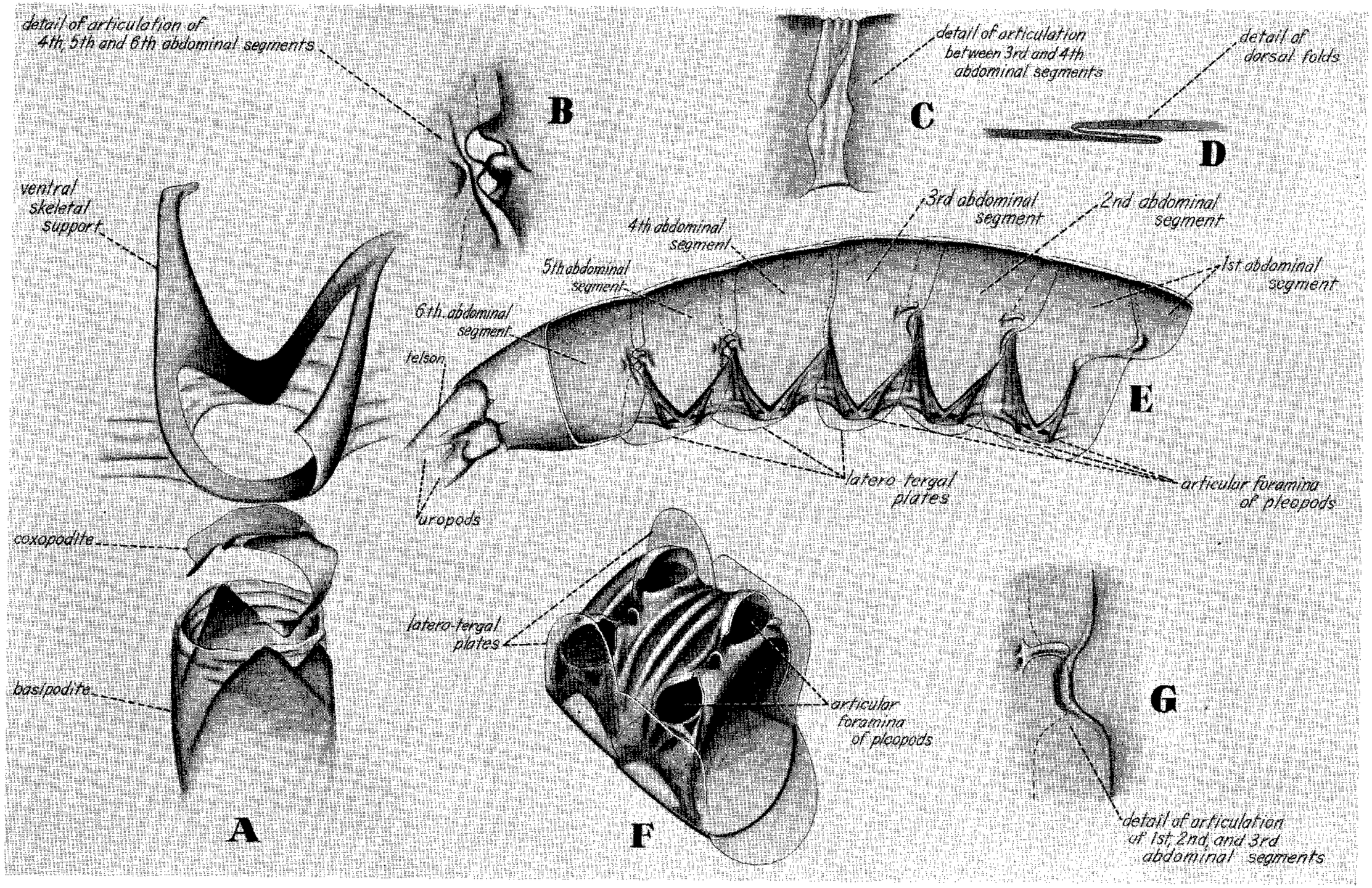

FIGURE 59.—Details of abdominal skeletal elements.

The posterior joints permit free extension and flexion, but probably resist lateral motion. We have, then, 4 kinds of intersegmental hinges functioning in 2 different ways. No reason for this multiplicity of structure in the hinges is readily apparent.

SKELETAL ELEMENTS

The abdominal segment of arthropods is comprised of a ring of cuticle. This ring, however, may be subdivided in parts. The abdominal somite in the Crustacea has usually been said to consist of an arched dorsal tergum and a flat, concave, or convex ventral sternum connected to the tergum by two lateral pleura, the latter often produced ventrad in a fold. The lateral pleuron has been variously interpreted. Snodgrass (1935) describes the pleural areas of arthropods as "typically membranous" to permit the movement of appendages arising from the pleuron. Pleural sclerites, when present, represent a contribution of the proximal parts of the appendages, according to this worker. He sets forth the fact also that the appendages articulate with the ventral margins of the pleural sclerites and with the lateral edges of the sternal sclerites. That this typical situation may not always obtain is shown by Hart (1952) who found that the first pleopod in *Cambarus longulus longulus* Girard, 1852, is connected to the abdominal venter entirely by sternal components.

Snodgrass (1935) apparently was of the opinion that the arthropod pleuron represented a distinct region of the segment. In a study of the Crustacea made at a later date, Snodgrass (1952) describes in *Anaspides tasmaniae* Thomson, 1892, a generalized malacostracan, a clearly demarked pleural sclerite with which the limb basis articulates. In the same study he refers to the pleural sclerite as a "laterotergal pleural plate" and states that the pleuron of the crustacean belongs to the tergum. Support of the more recent opinion of Snodgrass (1952) that the pleuron of crustaceans is tergal in origin may be found by a consideration of the abdominal segment of *Penaeus setiferus*.

The sternum and tergum are distinct regions in the white shrimp, but no line or suture can be seen which distinguishes a pleural component of the abdominal segment (fig. 59). From this we may conclude that the pleura are not needed in a morphological construct of the abdominal segment of the crustacean. That the term, "pleuron," for the laterotergal plates has become embedded ineradicably in the literature of crustacean systematics is therefore most regrettable.

Beyond what has been brought out about the general structure and articulation of the abdominal segments, little need be said further except for a brief mention of the modified posterior end of the sixth abdominal segment. Unlike the five anterior abdominal segments from which light appendages project, the sixth abdominal segment must be strong enough to bear the tail fan. For this reason the posterior end of the sixth segment is heavily sclerotized. In addition, the contents of the sixth segment are largely devoted to mediating the flexions of the tail fan which project caudad from the segment rather than ventrad as is the case with the preceding abdominal segments. The result is the visible difference in shape of the sixth segment compared to that of the typical abdominal segment. More will be said about the sixth abdominal segment when the tail fan is considered.

MUSCLE ELEMENTS

The characteristic of the abdominal muscles, apart from their great mass, is the unusual manner in which they are laid out. These muscle bodies are extraordinarily heavy and so intertwined with one another that their separation for study is difficult. In accordance with the system of Daniel (1931c), the abdominal muscles are divided into the following four functional muscle groups: (1) The superficial ventral muscles, (2) the lateral muscles, (3) the dorsal muscles, and (4) the main ventral muscles. They will be treated in that order.

SUPERFICIAL VENTRAL ABDOMINAL MUSCLES

FIGURES 61, 63

The superficial ventral abdominal muscles of *Penaeus* are attached between yokes of thin cuticle (fig. 63) lying transversely across the posterior portion of each abdominal segment beneath the ventral nerve cord. These yokes are associated with the folds of articular cuticle on the ventral surface, and they are so arranged that the superficial ventral muscles run from the posterior region of one abdominal segment to the posterior region of the next. The superficial ventral abdominal muscles are of course a continuous sys-

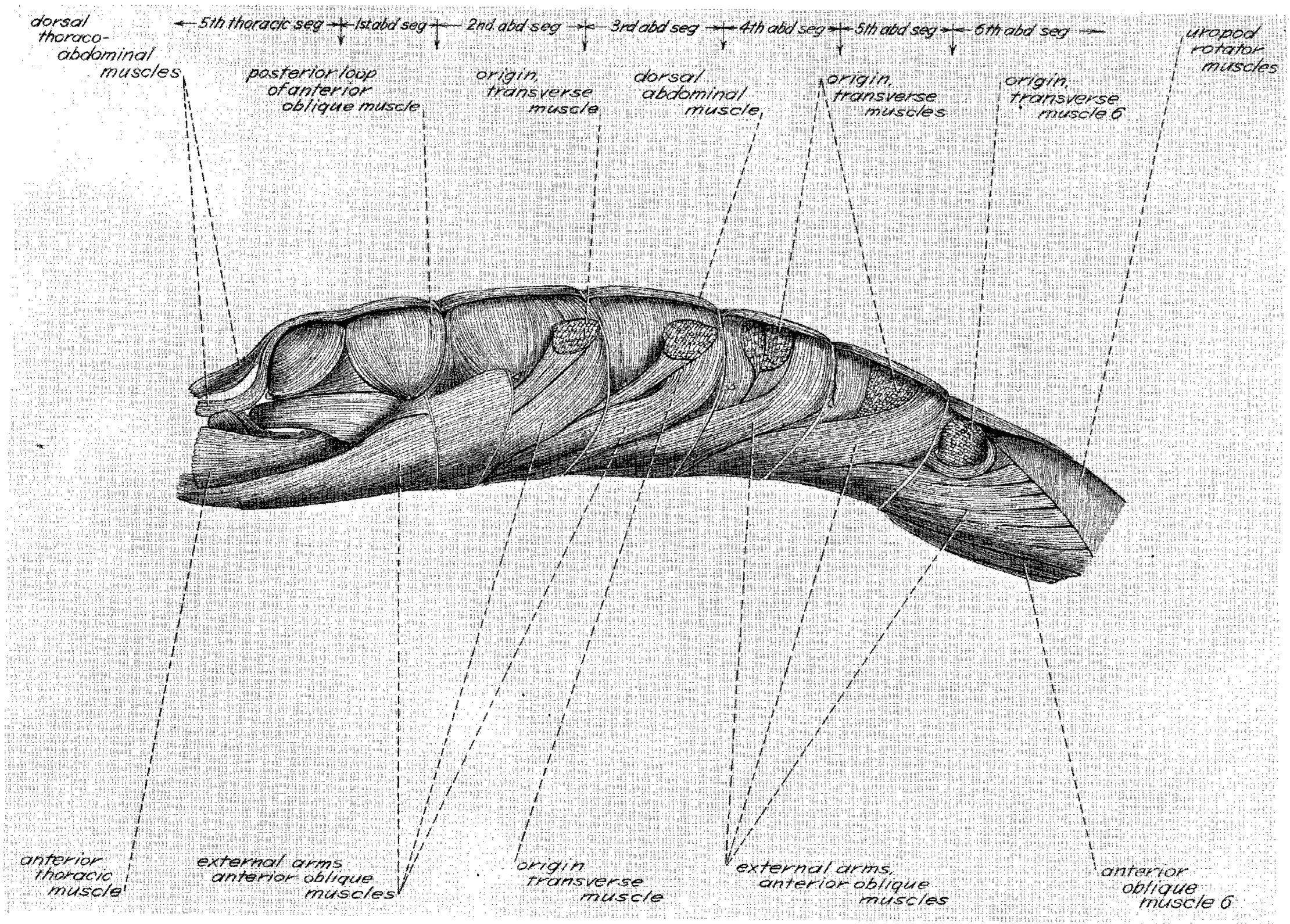

FIGURE 60.—Lateral view of left side of abdomen showing superficial abdominal muscles.

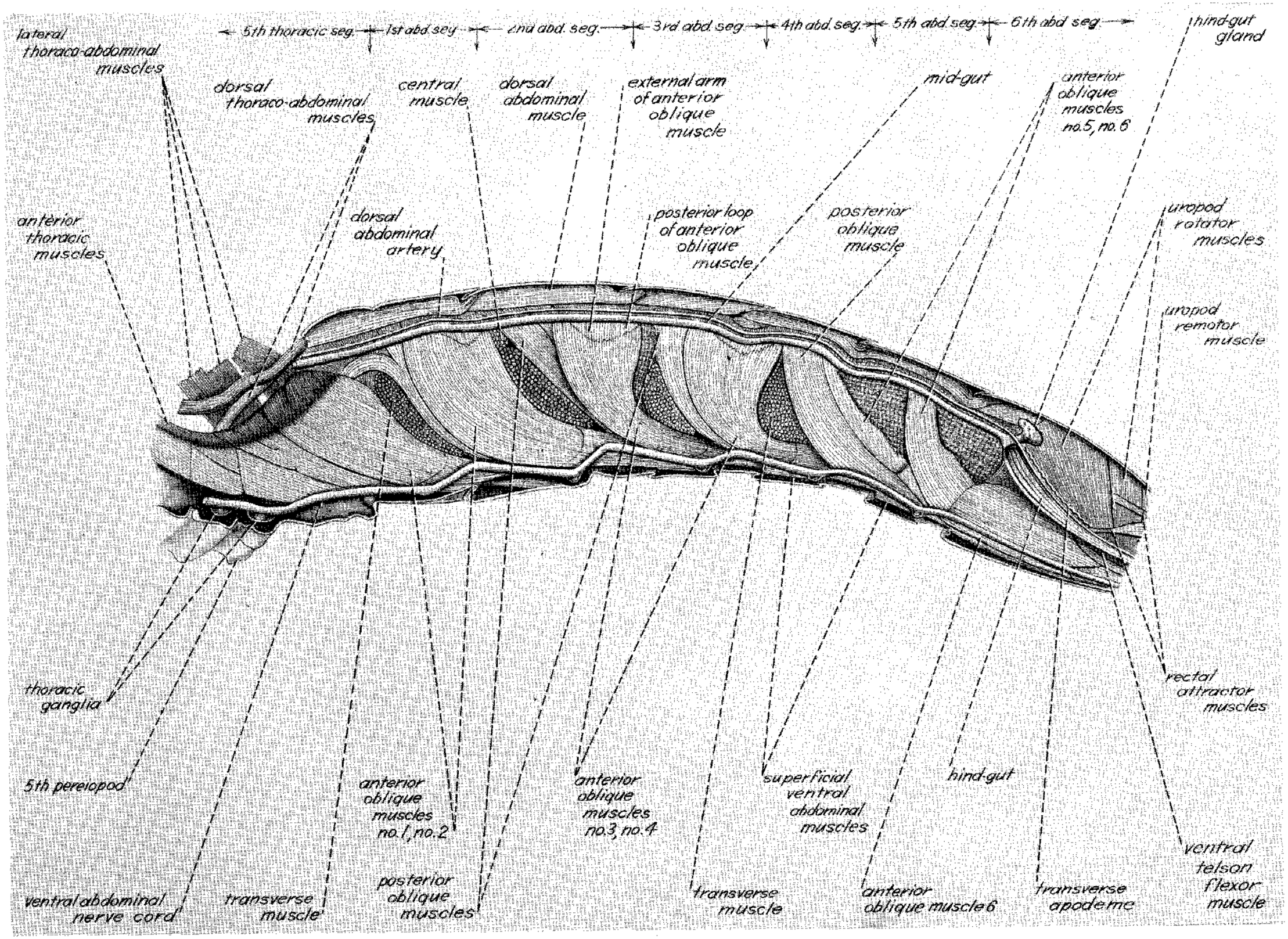

FIGURE 61.—Median sagittal cut through abdomen showing medial muscles.

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

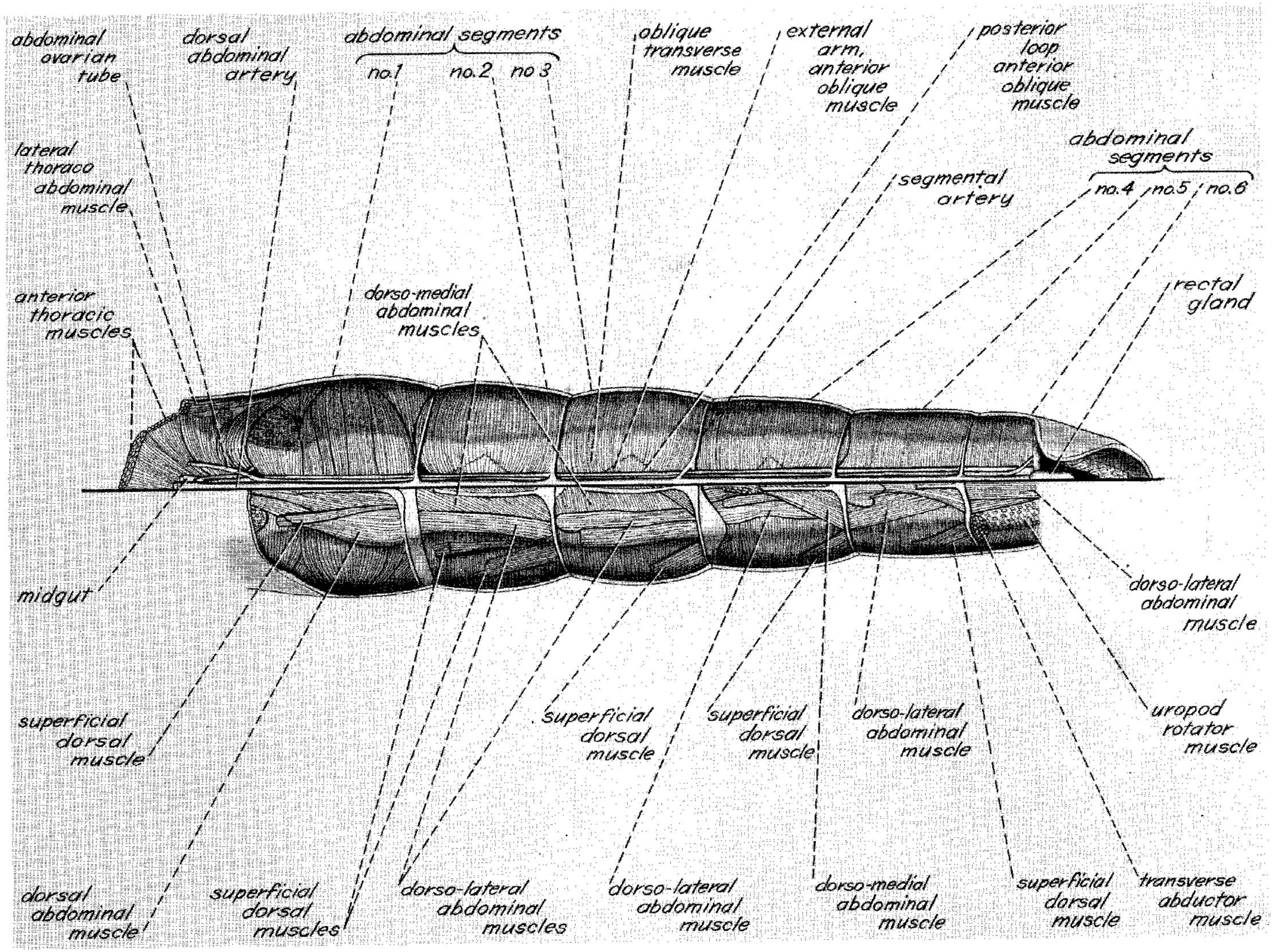

FIGURE 62.—Dorsal views of abdominal muscles. Lower section, intact musculature. Upper section, dorsal abdominal muscles removed.

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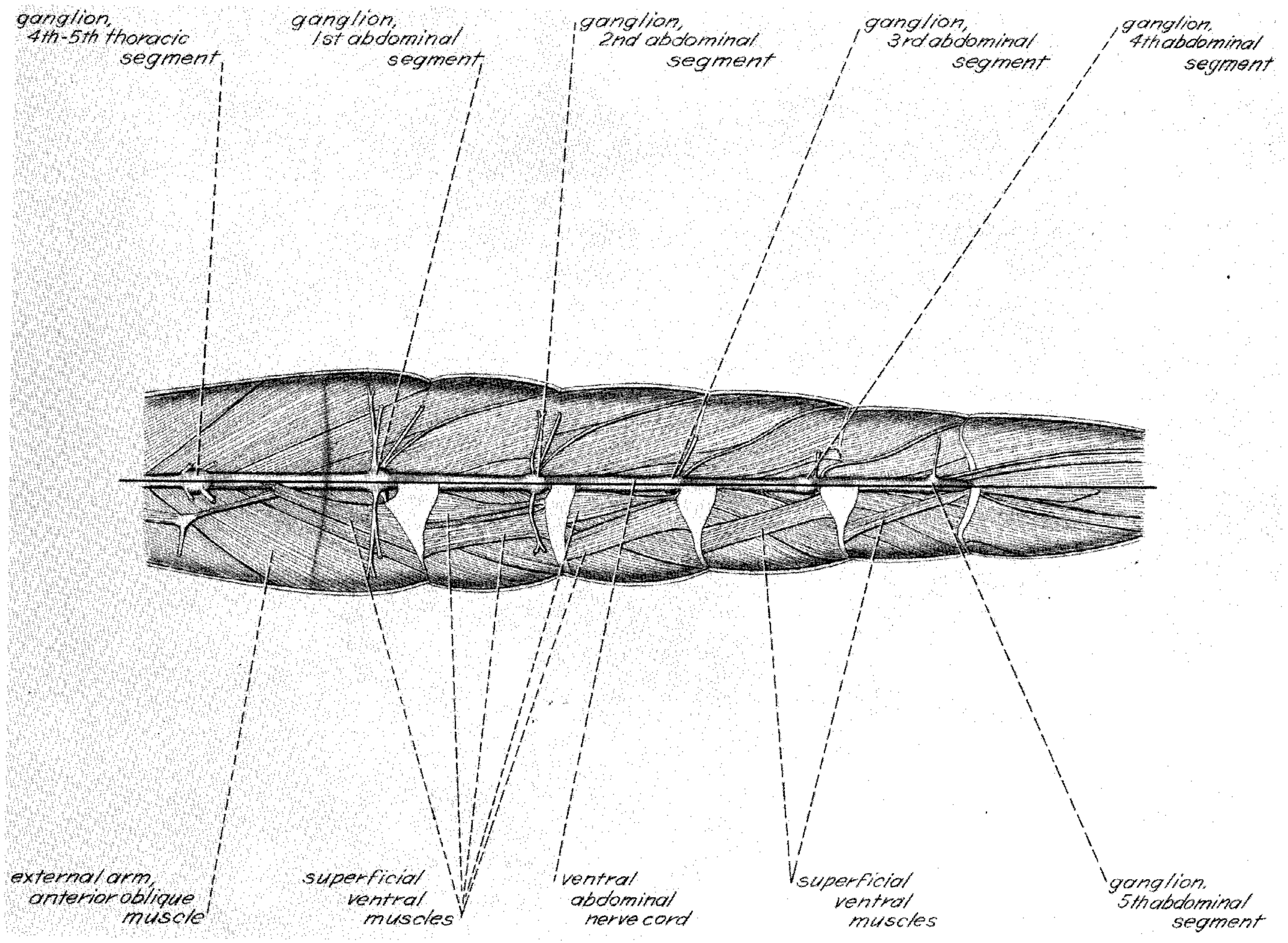

FIGURE 63.—Ventral views of abdominal muscles. Lower section, intact musculature. Upper section, superficial ventral muscles removed.

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

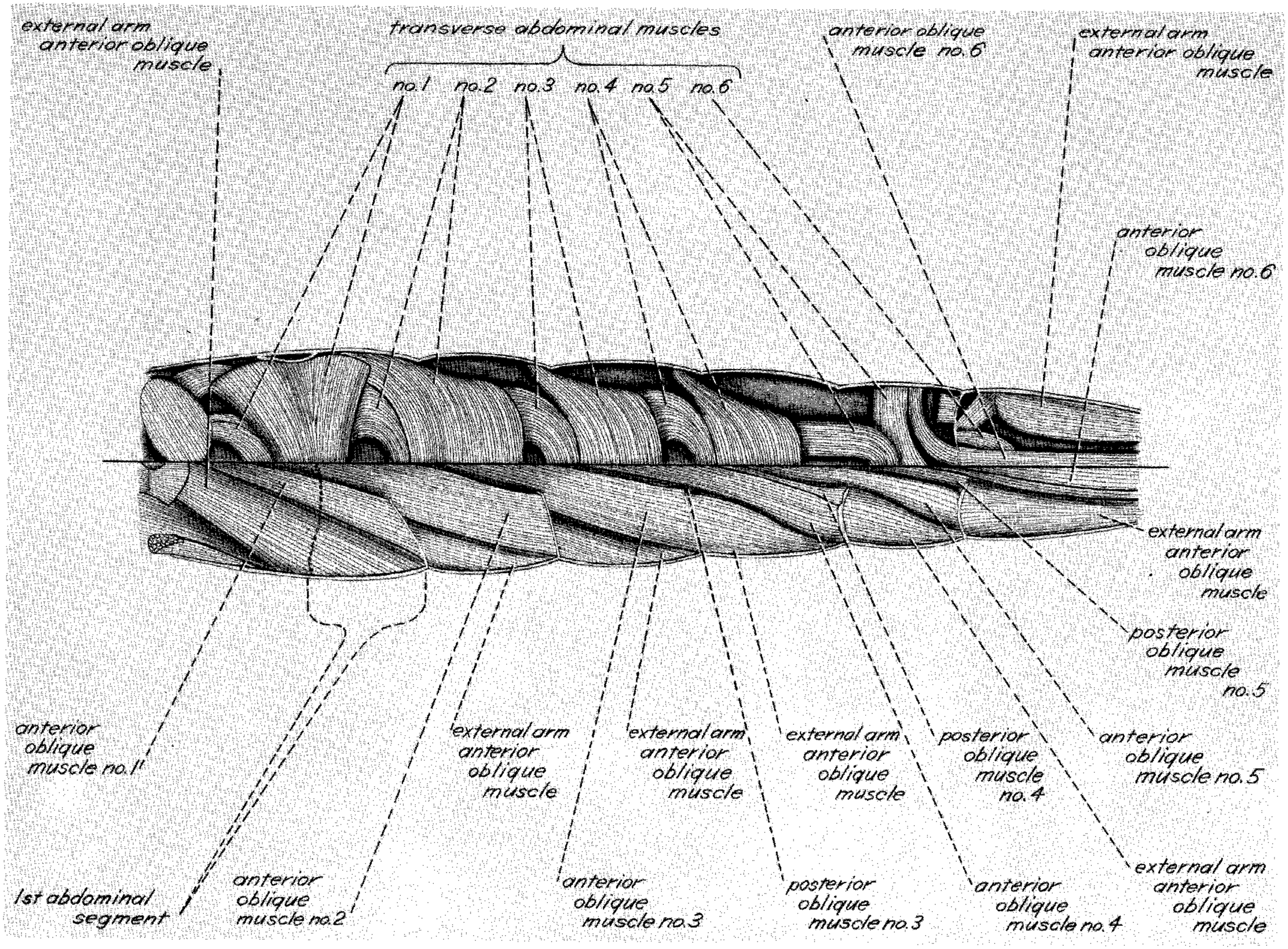

Figure 64.—Ventral view of abdominal muscles. The lower section shows the arrangement of the oblique muscles. The upper section shows the transverse abdominal muscles dorsad of the oblique muscles.

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

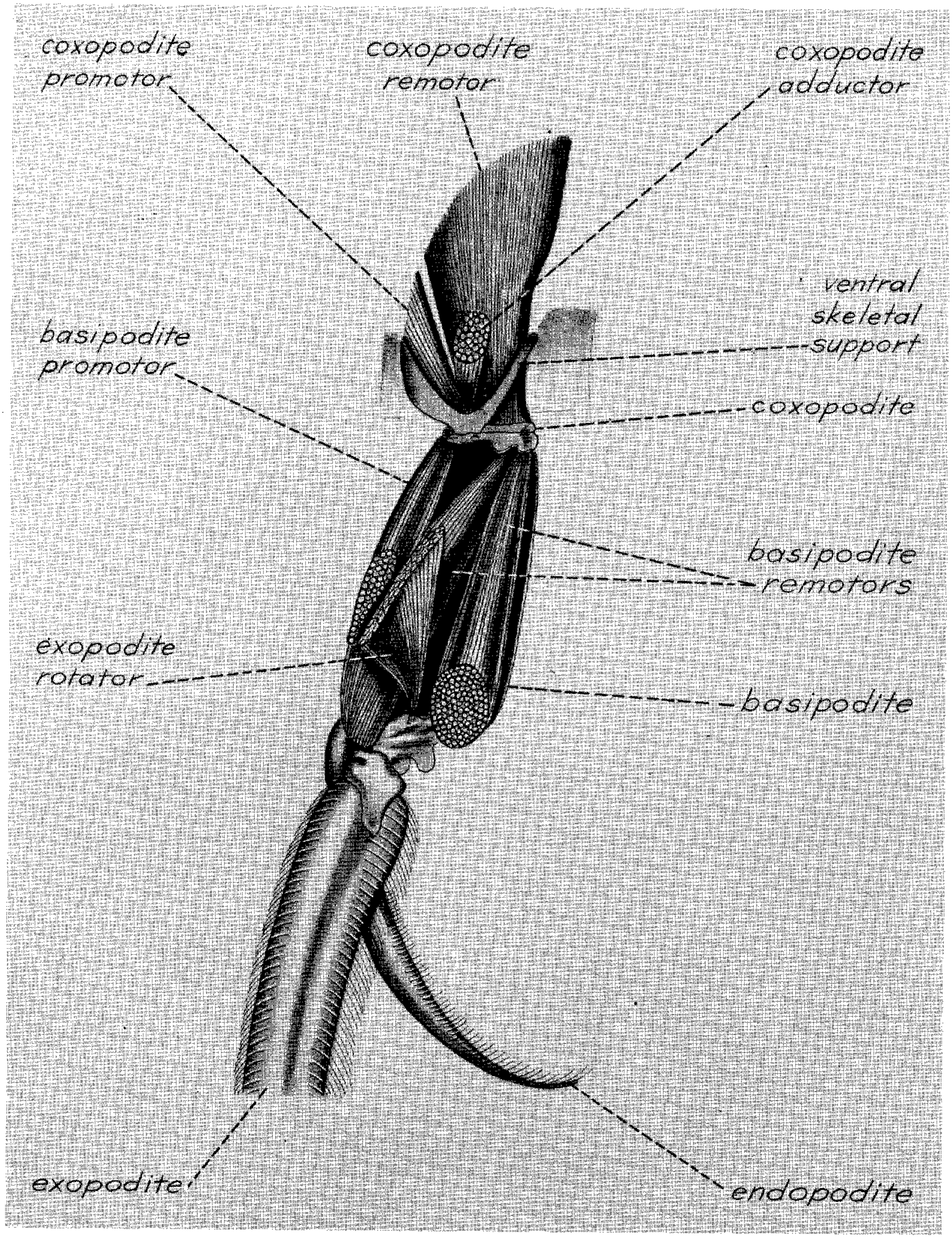

FIGURE 65.—Lateral view of left third pleopod showing basipodite and coxopodite musculature.

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*.