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MORPHOLOGY OF THE WHITE SHRIMP
Penaeus setiferus (Linnaeus 1758)

BY JOSEPH H. YOUNG

FISHERY BULLETIN 145
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ABSTRACT

In this illustrated morphology of the commercially important white shrimp of the Gulf of Mexico the muscle, nervous, circulatory, excretory, reproductive, and respiratory systems are compared with those of the blue crab, *Callinectes*, a European crawfish *Astacus*, the "coon-stripe" shrimp, *Pandalus*, and other decapod crustaceans. The major portion of the comparative work deals with the muscles, since the muscle systems of a few Decapoda have been reported in much greater detail than other systems.

The comparative studies of muscles and nerves indicates that the Penaeidae represent a generalized anatomical condition in the Crustacea Decapoda, thus verifying the systematic research in this area. Evidently the Penaeidae are relatively close to the decapod stem in the Malacostraca. The generalized condition of Penaeidae is shown again and again by the repetition of functional muscle units. The same units have become simplified in the higher decapods, having been lost, presumably, by the fusion of separate parts. Adhering to the morphological principle that the nerves tend to retain their ancient innervations despite coalescence of parts, shifting of muscle origins, etc., and can therefore be considered as morphologically conservative, the nerves to the repeating muscle units of *Penaeus* are found to have kept their innervations to the same muscles, now fused, in higher Decapoda. The comparative morphology of decapod nerves and circulatory elements is treated only to the extent that research on these systems in other decapods has been published.

Several structures are found in *Penaeus setiferus* which have not been reported previously in the literature. A fibrous circulatory element, the capillary arbor, penetrates the distal optic ganglia. One or more hard concretions embedded in the substance of the antennal portion of the excretory gland are described. Although two pairs of muscles are associated with the labrum of Insecta, muscles have not been described in the labrum of Crustacea. The labrum of *Penaeus* has at least 12 pairs of muscles. A structure, the hindgut gland, is found in the anterior part of the sixth abdominal segment lying dorsal to the rectum. Its function is unknown. Some of the blood vessels of the heavily vascularized branchiostegal region of the carapace run parallel to the margin of the carapace, suggesting "growth rings" by their appearance.

MORPHOLOGY OF THE WHITE SHRIMP *PENAEUS SETIFERUS* (LINNAEUS 1758)

By JOSEPH H. YOUNG, *Department of Zoology, Tulane University*

Penaeus setiferus, the white shrimp of the Gulf of Mexico, represents an important component of the commercial shrimp catch throughout the northern, western, and southern margins of that body of water. With the rise in importance of the commercial shrimp industry to the economy of the Gulf States in the past two decades, information about the life history, morphology, physiology, and behavior of the edible shrimps has become necessary, and even critical, to the continued well-being of the industry.

We know very little about the diet of the penaeid shrimps, how far they travel in search of food and mates, or what constitute barriers to their activities. Our knowledge of digestion, of nervous and glandular control of the processes of molting, reproduction, and coloration is limited for the most part to distant relatives of the Penaeidae. Despite numerous efforts (Müller 1863; Kishinouye 1900; Hudinaga 1935, 1942; Pearson 1939; Johnson and Fielding 1956), the stages of the life cycle of penaeids are not certainly known and consequently we have very little exact ecological information about the larvae. Opinions vary on the life span of adult penaeid shrimps. Whether the adult females reproduce once and then die at the end of a year or reproduce more than once a season, or again, live for 2 years and reproduce each season is not known. The answers to such questions will have a profound effect on the future conduct of the commercial shrimp industry.

This study sets forth in detail the anatomy of *Penaeus setiferus*. Anatomical work as such does not answer the problems suggested above, but as a map to the explorer, anatomy provides the experimental biologist with a guide to the "lay of the land," thereby facilitating his progress. And as a map, the value of an anatomical study to its users hinges upon its accuracy and clarity. To these ends all efforts were bent, the illustrations are large and the structures shaded to give a sense of depth. The anatomical parts are labelled with full words, rather than disguised with cryptographic abbreviations listed below the illustrations or hidden in the text. The plates are defined as diagrams whereby important features may be emphasized by artwork without sacrificing accuracy.

P. setiferus is an omnivorous scavenger dwelling on or near mud-sand bottoms in the littoral zone. The animal is probably restricted to the euphotic stratum in which the light intensities are fairly high. The shrimps are gregarious and move about in large schools. The character of the bottom is probably important to the white shrimp. Evidence from various sources suggests that the animals make use of mud or mud and sand by burrowing into this soft substrate for protection during molting and possibly for other purposes. The white shrimp is a powerful swimmer and capable of migrating great distances. These and other aspects of the life habits of *P. setiferus* have been considered in terms of functional anatomy in the present study.

Several people have made significant contributions to the progress of this study. Credit for initiating the project belongs perhaps most of all to Albert Collier, United States Fish and Wildlife Service, Galveston, Tex. His unfailing cooperation, together with that of T. J. Costello of the same laboratory, contributed greatly to the completion of the anatomical work. Help and encouragement has also come from Dr. Fred R. Cagle, Dr. Royal D. Suttkus, and Dr. George H. Penn, all of the Department of Zoology, Tulane University. Percy Viosca, Louisiana Wildlife and Fisheries Commission; Charles Dawson, of

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the Bears Bluff Laboratories, Wadmalaw Island, S. C.; and Dr. Milton Fingerman, Department of Zoology, Tulane University, have all made useful comments about various aspects of the work. I am indebted to Prof. L. B. Holthuis, Rijksmuseum van Natuurlijke Historie, Leiden; Dr. Andre Mayrat, Laboratoire de Zoologie de l'Ecole Normale Superieure, Paris; and Jerome E. Stein, Texas A. and M. College, Galveston, Tex., for helpful criticism of certain parts of the study.

Heartfelt thanks go to the project artist, Raymond Bollinger of New Orleans, La., for the high quality of the plates making up the anatomical study of the white shrimp. Of the 136 figures in this work, all but 10 were finished by Mr. Bollinger from tracings made by the investigator.

METHODS

The anatomical study of *Penaeus setiferus* was made for the most part on white shrimps purchased alive from bait shrimp fishermen. The animals were fixed in Zenker's fluid, dehydrated to 70 percent ethyl alcohol and there stored. Despite difficulties in its use in the field, Zenker's fluid was found to have several advantages over formalin. Zenker's fluid softens or removes the calcareous deposits and leaves the cuticle in a condition similar to thick cellophane. This mixture quickly penetrates to and fixes the internal organs, and in so doing prevents internal maceration caused by the post-morten enzymatic activity of the hepatopancreas. Formalin-fixed material is useless for the study of internal organs. The fixative greatly hardens the cuticle and the external muscles and fails to penetrate to the internal organs.

Dissections were performed under a stereomicroscope. Dissecting needles which were sharpened to fine points in mixtures of strong nitric acid and ethyl alcohol were employed. Locations of muscles and attachments, and other skeletal details were studied on specimens of white shrimps cleared in strong alkali and stained with Van Gieson's Triple Stain (Curtis' Modification). The outlines of whole structures were used as templates within which muscles and other organs were sketched in layers on tracing paper as the dissections progressed. The tracings were transferred to drawing papers on a light box. The drawings were finished in ink and carbon pencil.

PENAEUS AS COMPARATIVE MATERIAL

For purposes of comparative morphology, the Penaeidae enjoy a unique position. Evolution has brought them down to us in an apparently generalized decapod condition. Naturally, we must view with caution any attempt to force a given structure or organ into the generalized category, for all extant animals must be highly specialized in specific instances, if unspecialized in others, for life today. Furthermore, the so-called generalized structure may be the superficies of a well-hidden specialization. Bearing in mind, then, that there may be no such thing as a generalized structure in a modern species, the comparative morphologist can proceed to draw homologies between structures which look alike on phylogenetic and ontogenetic grounds. Information shedding light on the evolution of the decapod crustaceans will be advanced here wherever supporting studies are available.

Unfortunately, very few complete anatomical works exist on decapod crustaceans, and none of these complete works deal with members of the Penaeidae. The present work will have reference to the studies of many workers, but in particular to the extensive studies of Berkeley (1928) on the "coon stripe" shrimp, *Pandalus danae* Stimpson 1857, of Schmidt (1915) and Keim (1915) on *Astacus astacus* (Linn. 1758), and of Cochran (1935) on the blue crab, *Callinectes sapidus* Rathbun, 1896. Other, frequently important, studies will be alluded to in the applicable sections. The greatest handicap to the establishment of a comparative morphology of the Decapoda is our ignorance of the details of the nervous system, the innervations of muscles and other organs. Despite widespread morphological change such as shifting of muscle origins, coalescence of metameres, and other distortions to the primitive body plan, structures tend to retain their ancient innervations. A muscle may move from one segment to another in the evolution of a group. The same nerve will usually continue to innervate it. For the nervous system is morphologically conservative and thus the most informative element in the historical study of metazoan structure. Until a substantial groundwork of neurological facts exists on the decapod crustaceans, homologies between many of the less obvious structures will rest on weak grounds.

When compared externally with the crustaceans mentioned (figs. 1, 2, 3), *Penaeus setiferus* is most similar to *Pandalus danae*, a caridean prawn, and less like *Astacus astacus*. The relationship with the blue crab is obviously distant. The Penaeidae are classed in the Sub Order Natantia together with the Caridae and the Stenopidae. All of these are relatively strong swimmers with light cuticles. Although *Astacus* displays many similarities in form to *Penaeus*, the crawfish is a reptant form with a heavy cuticle. With the lobster, the crawfish has an extensively developed chela on the first walking leg, whereas the white shrimp bears a small chela similar in size to those on the other chelate legs. The antennal scale and the pleopods of the crawfish are much smaller than those of the white shrimp. The former are large in the white shrimp. In other general details, superficially, the white shrimp and the crawfish are substantially similar in structure.

In general, the present anatomical study indicates that the Penaeidae are relatively generalized decapod crustaceans. Compared with the higher decapods, the penaeids tend to have several parts to accomplish a functional end that is carried out by a single part in a higher representative. Expressing this in terms of phylogeny, the lower decapod has lost fewer structures by the fusion of parts than has the advanced form. Since the present study of *Penaeus* is largely grounded upon earlier work on higher decapods, the process of homologizing the structures tends to be reversed from the phyletic order. Homologies must therefore be drawn from the specific to the general. Among the problems thus raised is the matter of functional nomenclature, in particular, of the muscles.

The historical base for the naming of decapod muscles is, for all practical purposes, the work of Schmidt (1915) on *Astacus*. This investigator employed a system of Latinized functional names, handed down to him by earlier anatomists, for the muscles he encountered in the European crawfish. With minor exceptions Schmidt's nomenclature accurately describes the actions of the muscles of *Astacus*. However, the functional muscle names of Schmidt do not describe the actions of the same muscle having a different function in another form. The investigator is therefore faced with the decision either to transfer to a muscle in another animal the functionally inaccurate name of Schmidt, which will simplify comparisons, or to rename the muscle in each case in accordance with its specific function, which will tend to compound the existing confusion in morphological nomenclature. With no great pride I have chosen the latter course in the present study. Until such time as a system of nomenclature having universal validity can be devised, the dilemma is inescapable.

Included in this paper is a section of bibliographical references. These items are primarily systematic, morphological, and experimental papers on Crustacea which contain valuable anatomical information used in the preparation of the present study, but not cited specifically. Since workers in many fields have to resort to anatomical studies in the course of their research, the anatomical information is necessarily disguised under titles which reflect the primary objects of their research. The student of crustacean morphology therefore, finds bibliographical compilations of works from diverse sources very helpful. The bibliography is in no sense complete.

I. SKELETAL AND MUSCLE SYSTEMS

The great mass of the shrimp body is comprised of skeleton and, in particular, muscle; accordingly, the bulk of the present anatomical study is devoted to a consideration of these elements. The description is presented in the order of the three natural body regions of the animal, the simple head, or protocephalon, the gnathothorax, and the abdomen. The skeleton falls easily into these divisions. The muscles, of course, do likewise, but not so obviously, since many of them cross skeletal subdivisions for mechanical reasons. In some anatomical works, the arthropod appendages are treated separately, as if these organs were attached to the animal in a kind of evolutional afterthought in the arthropod line. The appendicular muscles would, indeed, so indicate, but the skeleton, the nervous system, and the innervations of the muscles tell us that the arthropod appendage is an ancient structure. The appendages, then, will be taken up with the tagmata to which they belong.

A. Protocephalon

The protocephalon is that morphologically separable pregnathal group of segments so designated by Snodgrass (1951). This simple head includes, in the order of their occurrence in the adult, the eyes, antennules, antennae, and labrum.

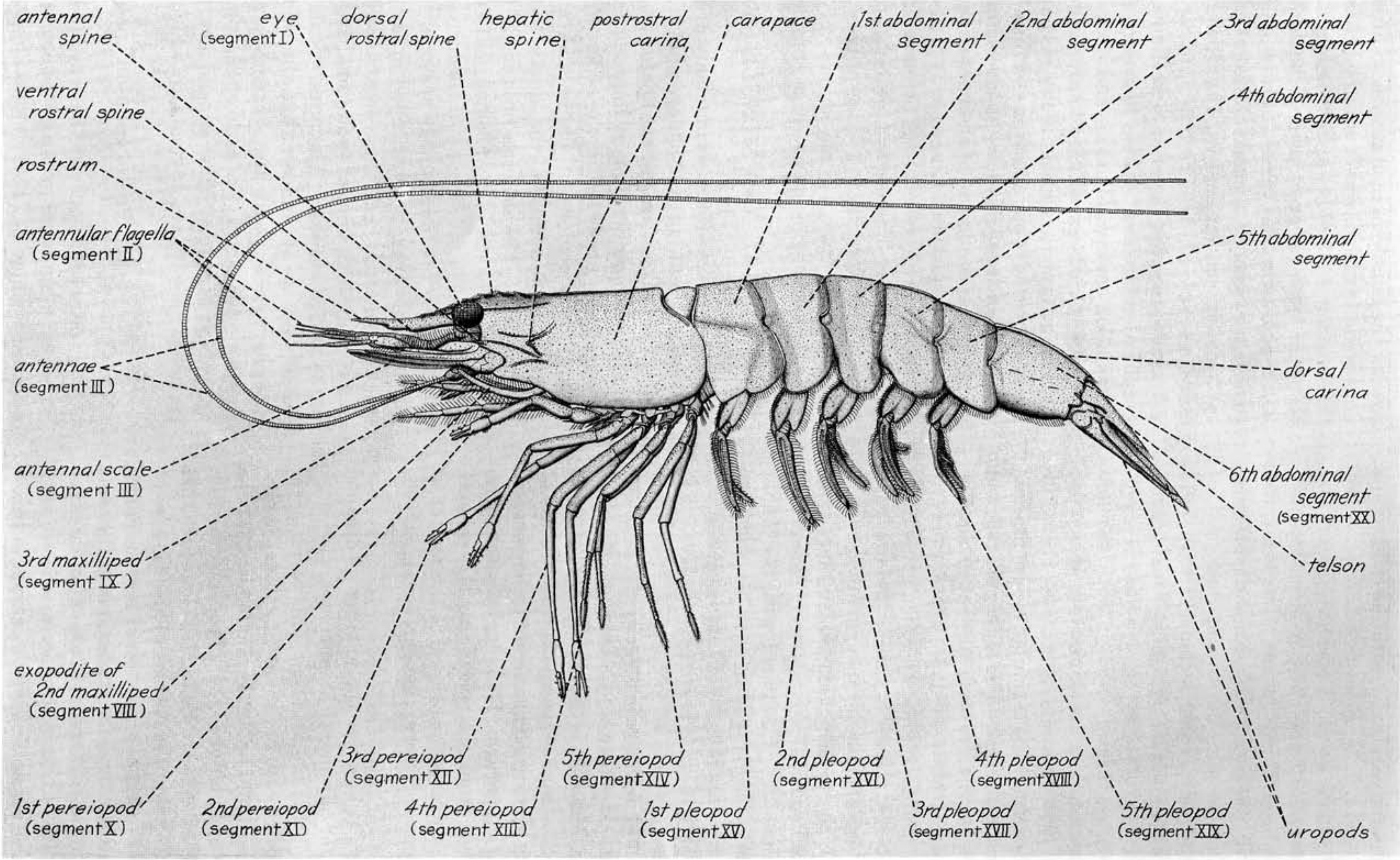

FIGURE 1.—***Penaeus setiferus.*** **Lateral view of adult female.**

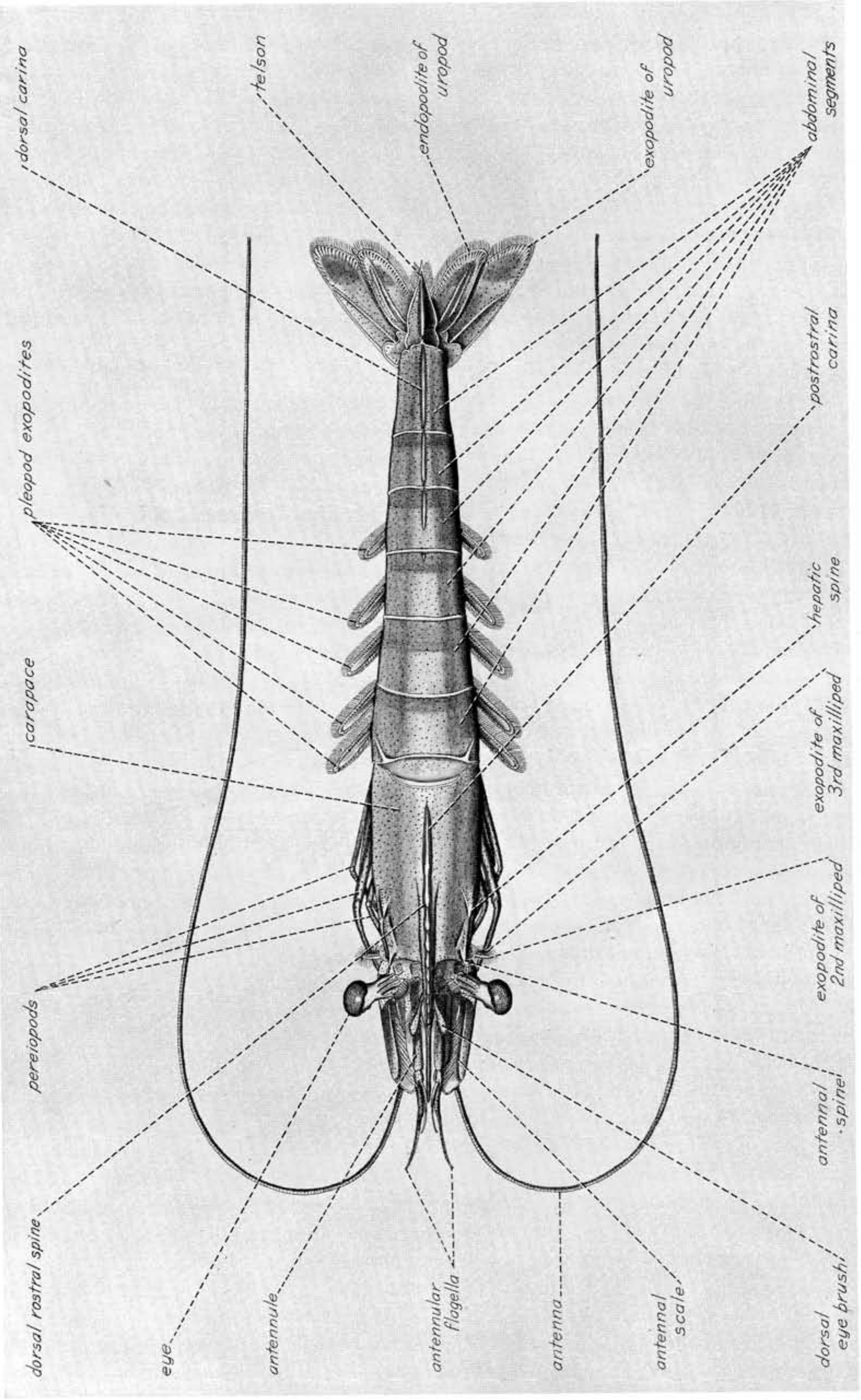

Figure 2.—Dorsal view of adult female.

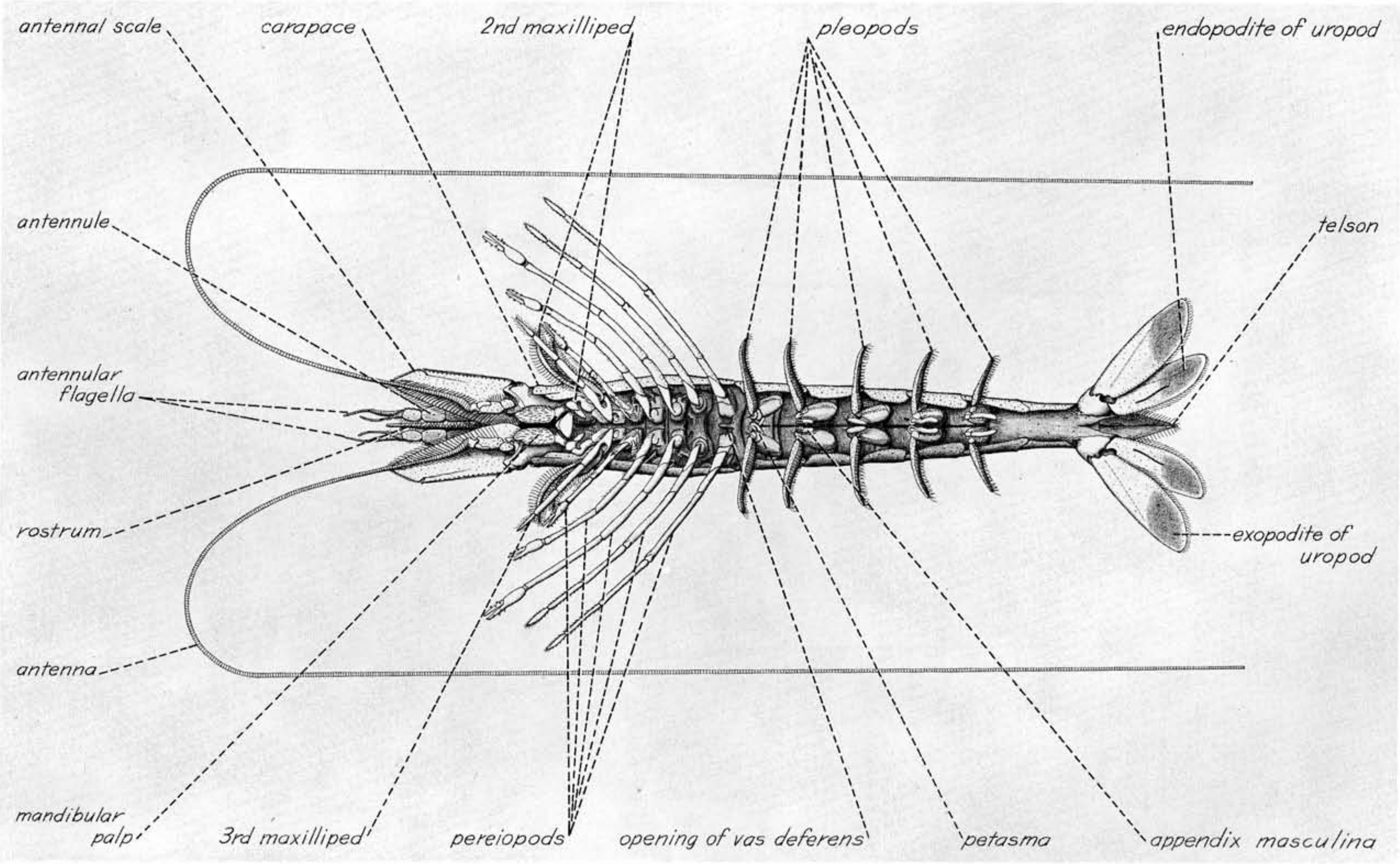

FIGURE 3.—Ventral view of young male.

The protocephalon is clearly distinct from the succeeding gnathothoracic and abdominal tagmata, and in *Penaeus setiferus*, and other species of the genus (Grobben 1917) is independently movable. Grobben, incidentally, described the area as the "sincipit," a term apparently discarded by Snodgrass in favor of the term, "protocephalon." In the section below on the eyestalks, a consideration of the muscles which move the protocephalon on the gnathothorax will be found. A discussion of the primitive order of the head segments follows in the section on the labrum.

SKELETAL ELEMENTS

The protocephalon is constructed roughly on the plan of a vertically placed hemisphere confluent posteriorly with the gnathothoracic hemocoele. The skeleton is flattened dorsally in the region of the ocular plate (fig. 4) or lobe from which the foramina of the eyestalks are perforated. The large, paired foramina of the antennules and antennae and the mesal foramen of the labrum occupy almost the entire anterior and ventral surface of the protocephalic skeleton. The latter regions are heavily sclerotized and deeply indented between the antennular and antennal foramina by the medial stem of the **Y**-shaped epistome (figs. 28, A; 30). The top, or posterior portion of the epistomal **Y**, divides across the anterior face of the labral foramen and the posterior side of the large antennal foramina. Upon the lateral epistomal bars, as shown by Snodgrass (1951), the medial mandibular condyles are located.

1. EYESTALKS

Most of the following section on the eyestalks was previously published by the writer (Young 1956).

In some of the lower and in many of the higher Crustacea, the compound eyes are set upon movable stalks or peduncles. Their presence at the ends of extensions has excited speculation for many years. Carcinologists have long discussed the reasons for the eyestalks, their similarity with other appendages (Calman 1909), and the nature of vision in a stalked-eyed animal, among other things. Yet little has been written about the mechanics of the eyestalk with respect to vision. No one has proposed any useful explanation for the fine adjustments presumably available to a compound eye which has as numerous oculomotor muscles as the crustacean stalked eye.

The presence of a set of muscles to move the corneal surface of the compound eye on the eyestalk, and of muscles to move the eyestalk about with respect to the body suggests the importance of the position of the corneal surface relative to the environment. By contrast, adjustments of corneal position in an arthropod without eyestalks suggests a function of head and "neck" muscles for activities other than feeding, if we assume any importance to the arthropod of corneal position adjustments.

Recently, the eyestalk nerves of a few crustaceans have been shown to contain neurosecretory elements which evidently proliferate hormone systems controlling such processes as molting (Passano 1953), retinal pigment migration (Welsh 1941), and chromatophore movements (Perkins 1928). In view of the concentrated attention currently being paid to matters of neurohormonal control of physiological functions in the arthropods, an understanding of the relation of vision to neurosecretion appears to be near at hand.

The white shrimp, *Penaeus setiferus*, carries its eyestalks at an angle of about 75° to the median sagittal plane and at an angle of about 10° to 15° to a frontal plane at the ocular plate (fig. 4). Only rarely are the eyes brought forward to lie in the optic depressions of the antennules, and then but for an instant for protection or possibly cleaning against the long plumules surrounding the depressions. Normally, therefore, in *P. setiferus* and many other species of shrimps, the eyes and stalks are widely spread and slightly upturned, a situation not understood by morphologists who, working with preserved materials, have described the eyestalks as projecting anteriorly. Had previous workers taken into account the lateral position of the eyestalk in the shrimps, and for that matter in the crawfishes, a certain amount of confusion in the naming of eyestalk musculature might have been avoided. For in fact, medial muscles are anterior and lateral muscles are posterior. In the interests of uniformity, however, certain of the incorrect names are here employed.

P. setiferus is a bottom feeder. According to an unpublished observation by Charles Dawson, Bears Bluff Laboratories, Wadmalaw Island, S. C., schools of penaeid shrimps are frequently found on muddy bottoms. This worker describes placing several *P. aztecus* Ives, 1891, in aquaria with an inch or two of mud on the bottom, into which the animals immediately burrow, except for the eyes. Such behavior suggests that the long eyestalks are among the organs enabling the penaeid shrimp to make use of mud for protection, especially after molting.

In the past, observers have described square corneal facets in the eyes of several species of decapod crustaceans (Huxley 1906; Calman, 1909). A study of slides made of the corneal cuticle shows that the corneal facets in the compound eye of *Penaeus setiferus* are also square. Likewise, the underlying crystalline cone cells are square in the white shrimp and total four per ommatidium, as determined by the study of tangential sections of the eye from which the corneal cuticle had been removed. Ramadan (1952) reports a similar situation in a species of *Metapenaeus.* In longitudinal section the ommatidium of *P. setiferus* is like that of *Astacus*, as described by Bernhards (1916), with comparatively elongate crystalline cone and short rhabdom cells. If anything, the cone cell is longer in the white shrimp than in the crawfish. A light pink substance which gives the dark-adapted shrimp eye its bright color in strong light is the tapetum (Ramadan 1952). It is associated with the proximal or retinal pigment of the ommatidia.

SKELETAL ELEMENTS

The ommatidial surfaces arise from a sclerotized cup, previously named the optic calathus, or basket (Young 1956), to avoid confusion with the optic cup of the vertebrate embryo (fig. 4). The optic calathus rests upon the elongate stalk segment in a structural relation permitting universal movements, although the degree of movement varies in different planes.

Two points of articulation in the dorsoventral plane allow the optic calathus considerable horizontal movement around the distal end of its supporting stalk. These dorsoventral hinges are, however, sufficiently loose to permit vertical and rotational calathus movements, but to a lesser extent than horizontal movements. The long stalk is comprised externally of several longitudinal sclerotized bars which are separated by pliable cuticle. Two of the bars give support to the dorsoventral points of articulation (fig. 11) and others to less well-defined points of articulation between the stalk and calathus, and between the stalk and basal segment.

The stalk is movable upon the short, boxlike, basal segment in the horizontal plane. Vertical movements between the basal segment and the stalk are restricted. With respect to the structure here labelled the median tubercle (fig. 4), Anderson and Lindner (1943) and Voss (1955) state that shrimps of the subfamily Penaeinae have no distinct median tubercle on the ocular peduncle. However, many of the shrimps of this group do possess large, blunt, median tubercles, similar to those in *Penaeus setiferus.*

Set between the basal segments is the ocular plate or lobe, a broad, roughly rectangular sclerotized structure which encloses laterally the medial parts of the basal segments (fig. 4). The ocular plate is the dorsal-most region of the protocephalon. Movements between the basal segment and the ocular plate are similar in extent to those between the stalk and the basal segment. Horizontal movements are limited to an arc of about 15° or 20°.

MUSCLE ELEMENTS

PROTOCEPHALON MUSCLES OF THE OCULAR REGION

Taking origin from either the epistomal invagination or the dorsal surface of the carapace and inserting upon basal parts of the eyestalks are four pairs of muscles. The basal regions of the eyestalks will be assigned here to the dorsal part of the protocephalon.

ANTERIOR PROTOCEPHALON LEVATOR MUSCLES

FIGURES 34, 35

The tiny anterior protocephalon levator muscles are probably the muscles designated by Grobben (1917, 1919) as the protocephalon levators (musculus levator sincipitis) in a European penaeid and in other species of higher Crustacea. These muscles are difficult to make clear, either by dissection, or by illustration, since they take origin on the carapace, on the nearly vertical sides of the rostral base. During removal of the carapace and the underlying layers of tough, fibrous epidermis and connective tissue, these muscles are torn away. The anterior protocephalon levators insert in the heavy connective tissue associated with the posterior edge of the protocephalon. Their actual levation of the protocephalon is negligible, since they are not only minute in cross section, but

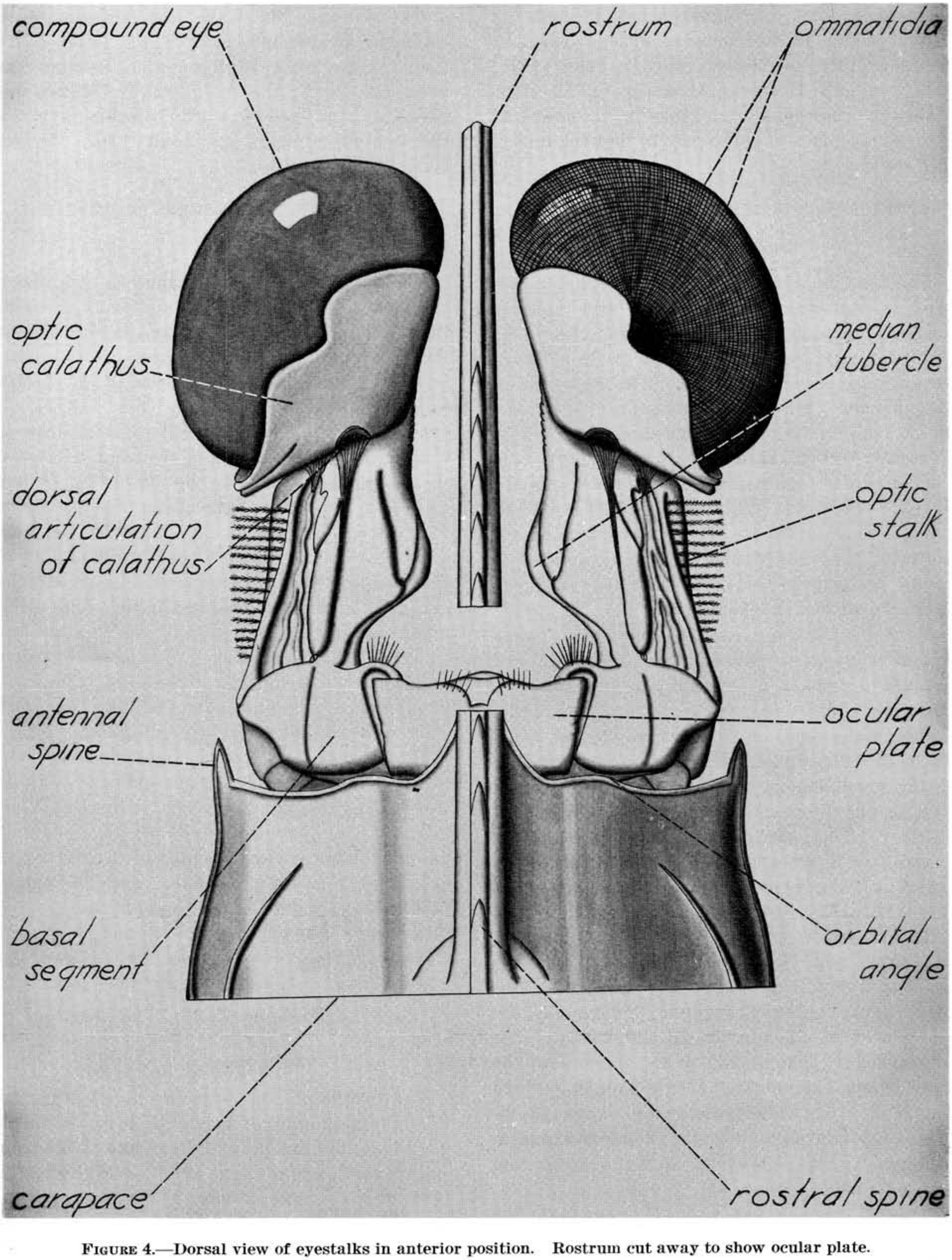

FIGURE 4.—Dorsal view of eyestalks in anterior position. Rostrum cut away to show ocular plate.

short in length. No counterpart of the anterior protocephalon levator muscles was described by Schmidt (1915) in *Astacus*, or by Berkeley (1928) in *Pandalus*. However, Grobben (1917) illustrates a protocephalon levator in *Astacus* and theoretically one would expect to find the muscle in *Pandalus*.

POSTERIOR PROTOCEPHALON LEVATOR MUSCLES

FIGURES 5, 6, 34

The function of moving the protocephalon dorsally is performed by a pair of large muscles, the posterior protocephalon levator muscles, which originate close together at the dorsal midline of the carapace somewhat posterior to the origin of the anterior protocephalon levator muscles and which run forward and downward to attach on a nearly vertical transverse plate, posterior to the postocular region of the eyestalk base (fig. 6). The muscle inserts ventrally to the insertion of the anterior levators. The contraction of the posterior protocephalon levators may also act to rotate posteriorly the eyestalk base and hence raise the extended eyestalks.

Possible homologs of the posterior protocephalon levator muscles are the median dorsal muscles designated as the musculus oculi basalis posterior. In *Astacus*, Schmidt (1915) found that these muscles arise on the median dorsal surface of the carapace and are attached by short tendons to the much longer tendons of other, more anteriorly placed muscles, the musculus oculi basalis anterior. The anterior eye base muscles, to anglisize freely, are attached to the median dorsal region of the eyestalk base (Schmidt 1915). More will be said of the latter muscles below.

The posterior eye base muscles, it should be emphasized, do not attach to the eyestalk base in *Astacus*, but if the assumption is made that, due to the immovable protocephalon in *Astacus*, the attachment of the muscles to the eyestalk base has moved in that animal to the tendons of the anterior eye base muscle, then a homology with the posterior levators in the white shrimp may be proposed. However, the extensive rearrangement of muscle attachments upon which the assumption is based weakens the proposal.

Even more significant, muscles exist in *Penaeus setiferus*, as will be shown later, which are more likely to be the homologs of the anterior and posterior eye base muscles in *Astacus*, *Pandalus*, and *Callinectes* than are the posterior protocephalon levator muscles. If the latter is true then the posterior protocephalon levators have been lost during the evolution of *Astacus*, *Pandalus*, and *Callinectes*, in which forms nc trace of the muscles appears (Schmidt 1915; Berkeley 1928; Cochran 1935).

OCULAR PLATE DEPRESSOR MUSCLES

FIGURES 5, 6, 7

The ocular plate depressor muscles originate on the posterior surface of the epistomal invagination. They run anterodorsally, passing beneath the insertions of the posterior protocephalon levator muscles, and insert broadly on the posterior edge of the ocular plate (figs. 5, 6, 7). On contraction, the ocular plate depressors draw the ocular plate posteriorly and ventrad. Based on the attachment points of the muscles in *Penaeus setiferus*, they may have given rise by partial fusion to the anterior eye base muscles (musculus oculi basalis anterior) as they are found in the European crawfish, where the muscles are attached ventrally to the epistomal region by a long tendon and run dorsad to the edge of the eyestalk base. Cochran (1935) describes in *Callinectes* a pair of anterior eye base muscles which arise from a kind of epistomal invagination rather like that in the white shrimp, but instead of fusing as in the European crawfish, they diverge slightly laterad in the blue crab in probable accompaniment with the general broadening of the body in the Brachyura.

The ocular plate depressor muscles apparently are homologous with the musculus oculi basalis anterior in *Pandalus*, the name for which Berkeley (1928) has taken from Schmidt (1915). In *Pandalus*, these muscles are similar to those in *Penaeus*, except that they are slightly separated, whereas in *P. setiferus* they are close together.

PROTOCEPHALON ATTRACTOR MUSCLES

FIGURES 5, 6, 7, 8

The protocephalon attractor muscles are two very large muscles which take broad **L**-shaped origins on the carapace and run anteriorly to insert on two pairs of large apodemes and on other parts of the protocephalon. The largest apodeme, on which the ventral-most part of the protocephalon attractor muscles inserts, arises from the ventral surface of the antennular foramen, broadening posteriorly into a large vertical sheet

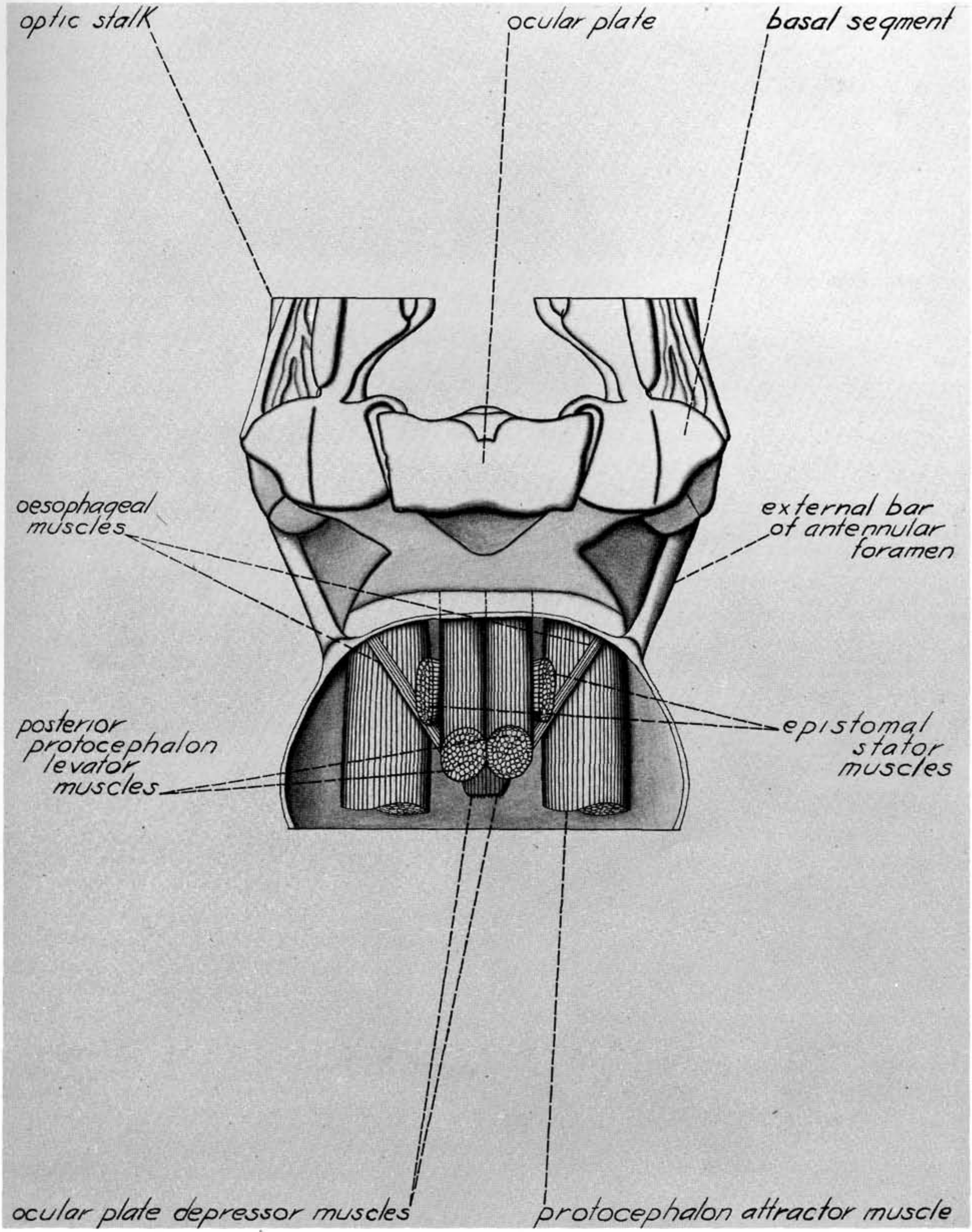

FIGURE 5.—Dorsal view of protocephalon, carapace removed, to show muscles of postocular region.

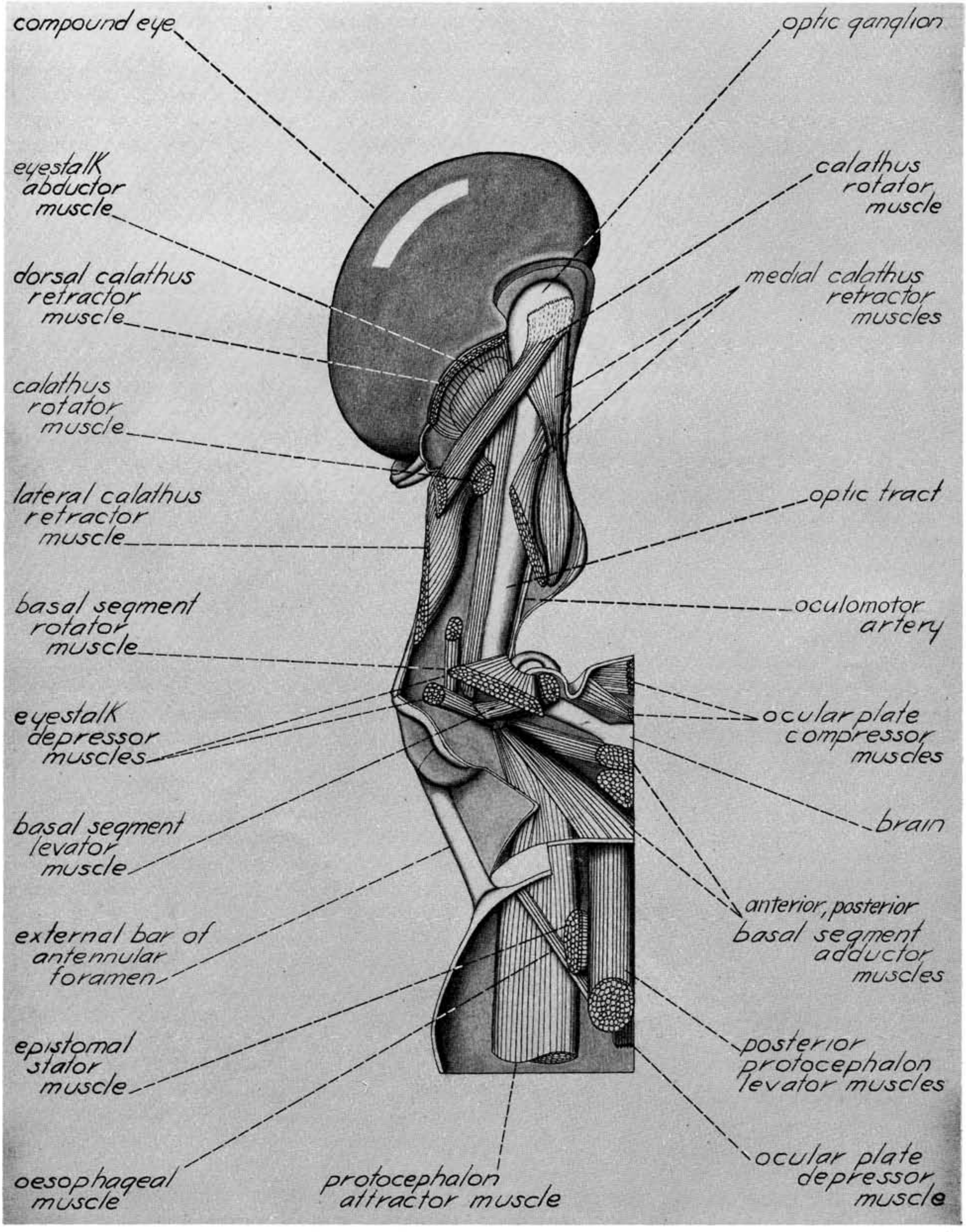

FIGURE 6.—Dorsal view of left eyestalk. Dorsal cuticle and carapace removed to show muscles.

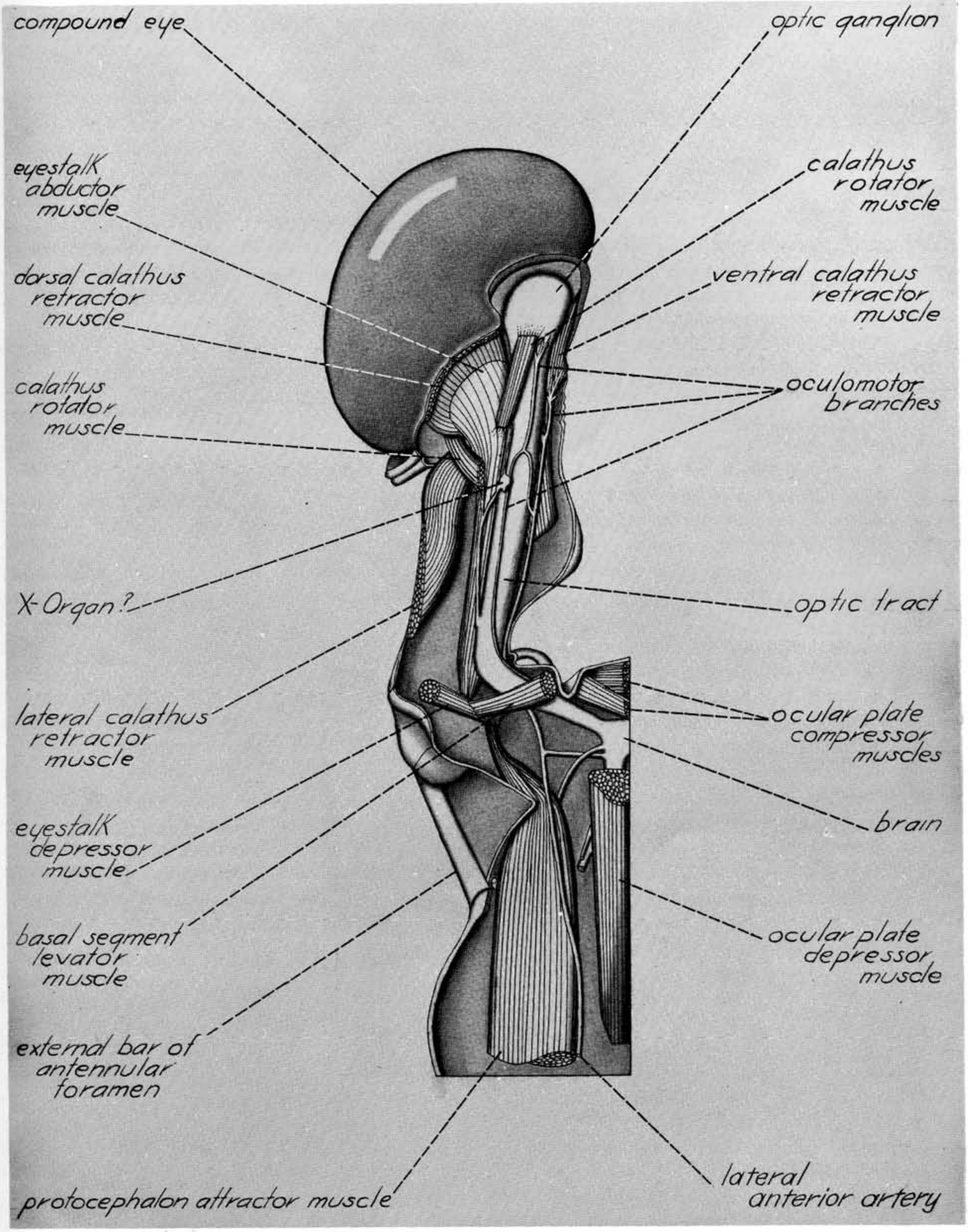

FIGURE 7.—Dorsal view of left eyestalk. Dorsal muscles removed to show branches of nerves and arteries.

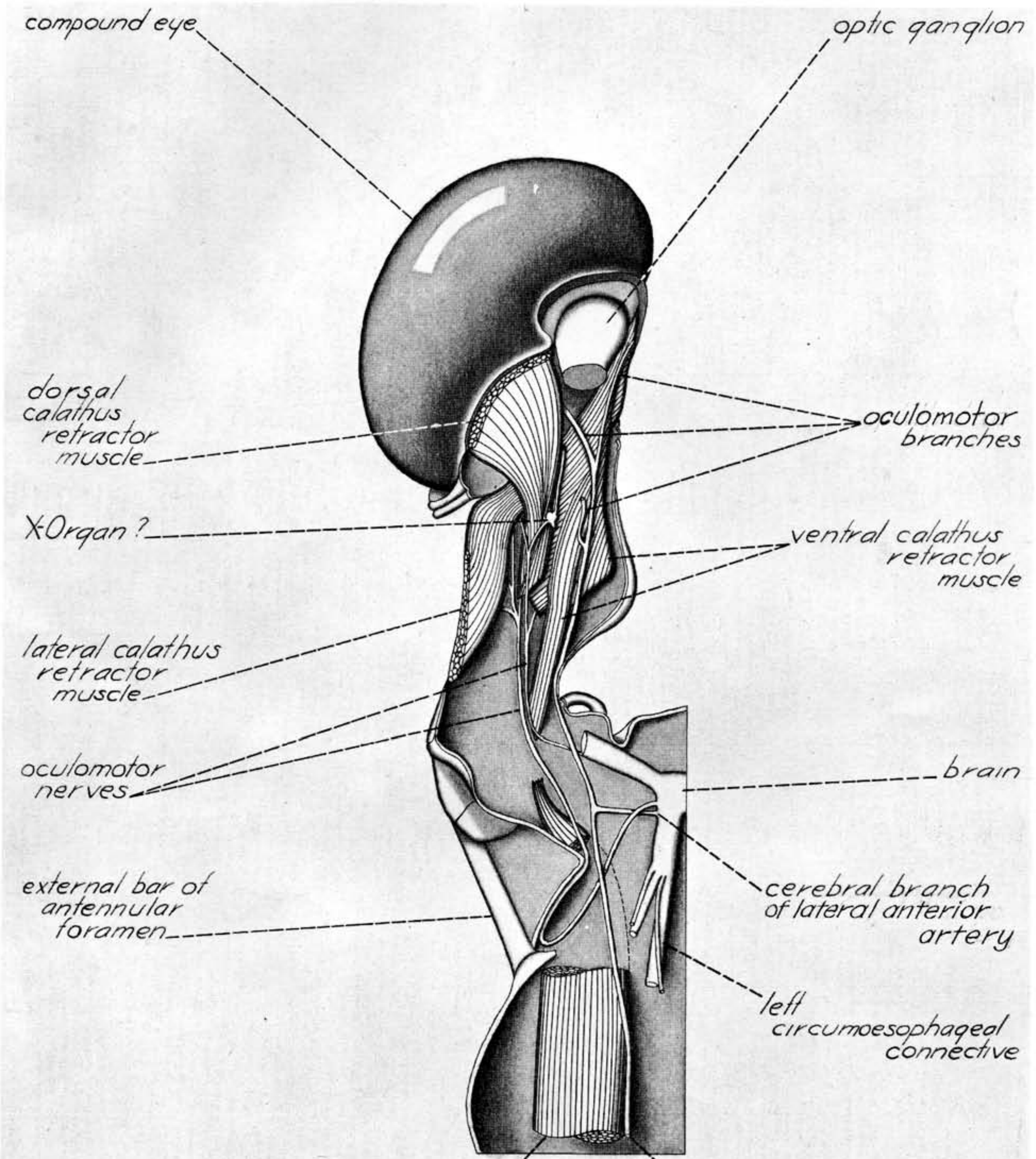

FIGURE 8.—Dorsal view of left eyestalk. Dorsal muscles and optic tract removed to show ventral muscles and branches of nerves and arteries.

of cuticular material. Slightly anterodorsal to the antennular apodeme, in the same parasagittal plane, is an apodeme which invaginates from the ventral floor of the basal segment of the eyestalk and projects through the ventrolateral side of the eyestalk foramen into the thoracic hemocoele. This apodeme, like that near the antennule, broadens vertically. By virtue of apodemal position, that part of the protocephalon attractor muscle attaching upon the eyestalk apodeme is somewhat longer than is the part inserting on the antennular apodeme.

The longest and most dorsal part of the protocephalon attractor muscle extends anteriorly beyond the antennular and eyestalk apodemes, to insert slightly laterad in connective tissue at the ventral surface of the basal segment of the eyestalk (figs. 7, 8).

To these comparatively huge protocephalon muscles we may ascribe at least two functions, namely, (1) attraction of the protocephalon, and (2) adduction of the eyes. The largest of the three inserting bodies of the muscle is the ventral-most part inserting on the antennular apodeme, described above. From a study of the points of articulation between the carapace and the protocephalon, dorsally, and the mandibular segment and the protocephalon, ventrally, the primary result of contraction of the ventral muscle body would be to draw the protocephalon directly posterior. The muscle was described as a protocephalon depressor (musculus depressor sincipitis) by Grobben (1917) in a number of Decapoda and in the stomatopod *Squilla*. This worker has shown that the protocephalon attractors, or depressors, are missing in those forms, like *Astacus*, in which the protocephalon is immovably fused to the thorax. The point of Grobben's discussion, that the protocephalon is movable on the gnathal tagma in the generalized crustacean, is not changed by a difference of opinion over the function of the muscle under consideration.

Furthermore, these muscles are not antennular in any way, having, as brought out by Snodgrass (1951), origins on the carapace. They are also, to say the least, not strictly antennal, since a portion of the muscle inserts in the eyestalk. Although the protocephalon attractor muscles in *Penaeus brasiliensis* Latreille, 1817, may be widely different from those in *P. setiferus*, the statement of Knowles (1953) that the two muscles lying just beneath the anterolateral side of the carapace are antennal is probably in error. From his figures the external-most muscle is properly a remotor of the antennal scale, while the large inner muscle is the protocephalon attractor muscle.

The two anterodorsal parts of the protocephalon attractor muscles which find insertions in the eyestalks have, in addition to attraction, the function of eyestalk adduction. Upon contraction of the whole muscle, these dorsal fibers in the eyestalk draw the ocular plate and attached eyestalk segments posteriorly toward the carapace. The posterior side of the basal segments makes contact with a condylic thickening on the anterior edge of the carapace, at a point known as the orbital angle (fig. 4), thereby swinging the eyestalks forward in a horizontal plane into the ocular depressions on the antennules. As suggested in introductory comments, the movement is a quick one, much faster than the return of the eyes to the spread position. In *Penaeus setiferus* other muscles exist which function to adduct the eyes, but their effect is negligible when compared to that of the much larger protocephalon attractor muscles.

The protocephalon attractor muscles appear in *Pandalus*, designated by Berkeley (1928) as the depressor muscles *c* of the antennae, on grounds of their attachment to the basipodites of those structures. At the same time this worker ascribes to the depressor muscles *c* the function of adduction and rotation, rather than the depression of the antennae. Berkeley's name for the muscles obviously was taken from the work of Schmidt (1915) on *Astacus*, in which form the antennal depressor muscles *c*, while small, nonetheless depress the antennae. Although proof must wait upon a study of the nerves in *Penaeus* and *Pandalus*, Berkeley has homologized the so-called depressor muscle *c* of *Pandalus* and *Astacus* on the basis of their dorsolateral origins on the carapace and their insertions on the mediodorsal edge of the antennal basipodite (in *Pandalus*) and coxopodite (in *Astacus*).

That the depressor muscles *c* in *Pandalus* and the protocephalon attractors in *Penaeus* are homologous seems fairly certain, despite the apparent change of insertion in the former. A review of cleared and stained exoskeletons of *Pandalus* might show multiple insertions of the muscle as in *Penaeus*. The homology of the protocephalon attractor muscles in *Peneaus* with the depressor muscles *c* in *Astacus* is less certain. In *Callinectes*, Cochran (1935) figures a pair of ocular attractor muscles which originate on the carapace. Their phylogenetic relation to the protocephalon attractor muscles in *Penaeus* is unlikely.

OCULAR PLATE MUSCLES

Arising in the ocular plate or postocular region dorsal to the brain are several pairs of muscles and a muscle group. Some of these muscles insert inside and some outside of the ocular plate.

OCULAR PLATE COMPRESSOR MUSCLES

Figures 6, 7

Attached about the shallow anterodorsal groove of the ocular plate is a group of muscles which runs to the lateral wall of the ocular lobe (figs. 6, 7), the ocular plate compressor muscles. They function to draw the sides of the head lobe and ocular plate mesad, and to depress slightly the center of the ocular plate.

ANTERIOR BASAL SEGMENT ADDUCTOR MUSCLE

Figure 6

The anterior basal segment adductor muscle originates on the ocular plate dorsal to the brain and attaches to connective tissue and apodemal material in the ventral part of the basal segment (fig. 6). Contractions of the muscle turn the basal segment toward the ocular plate in a horizontal plane.

POSTERIOR BASAL SEGMENT ADDUCTOR MUSCLE

Figure 6

The posterior basal segment adductor muscle inserts in the basal segment at the same point as the anterior basal segment adductors, but originates on the anterior side of the vertical transverse plate posterior to the postocular region (fig. 6). It, too, draws the anterior edge of the basal segment toward the ocular plate. The origins of these muscles are so widely separated that we may conclude that they have never been the same muscle. How the basal segment adductors may be homologized with muscles in *Pandalus* and *Callinectes*, in which forms no knowledge of muscle innervations exists, will be speculation. The ocular adductor muscles of *Astacus* and *Pandalus* may well be the homologs of the anterior adductor muscles of *Penaeus*, but hardly with the ocular adductors of *Callinectes*, in which animal the muscles are located in the distal end of the long stalk segment. Phylogenetic relationships of the posterior basal segment adductor muscle are even more uncertain, although possibly it is the same muscle as the ocular attractor muscle in *Pandalus* and *Astacus*. The basal segment adductor muscles do not appear in *Callinectes*.

BASAL SEGMENT LEVATOR MUSCLE

Figure 6

The basal segment levator muscle originates at the anterodorsal corner of the ocular plate and runs ventrally to the connective tissue and apodemal cuticle on the ventral surface of the basal segment (fig. 6). In the normal spread condition of the eyestalk, contraction of the muscle tends to raise the basal segment and with it the extended eyestalk.

BASAL SEGMENT MUSCLES

In the functional descriptions of the muscles which follow, the eyestalks will be considered as in their lifelike, lateral positions.

BASAL SEGMENT ROTATOR MUSCLE

Figure 6

The basal segment rotator muscle is a short, broad structure originating on the anterodorsal edge of the basal segment and inserting on the anteroventral edge of the same segment. Upon contraction, the muscle pulls the dorsal surface of the basal segment anteriorly, thus rotating the entire eyestalk forward.

EYESTALK DEPRESSOR MUSCLES

Figure 6

Two very small muscles, the eyestalk depressor muscles, one slightly lateral to the other (fig. 6), function to draw the eyestalk ventrally.

EYESTALK MUSCLES

EYESTALK ABDUCTOR MUSCLE

Figure 6

All of the muscles of the eyestalk and optic calathus are associated with retraction and rotation of the optic calathus on the eyestalk, except the long eyestalk abductor muscle (fig. 6). The proximal end of the eyestalk abductor muscle is attached in connective tissue in the ventral region of the basal segment. The muscle runs the length of the eyestalk to insert in connective tissue near the dorsal calathus retractor muscle. Contraction of the muscle swings the eyestalk horizontally to a lateral position. The eyestalk abductor muscle of *Penaeus* is very likely homologous with the abductor muscle described for *Astacus* and *Pandalus*, and possibly with the lateral branch of the ocular abductor muscle in *Callinectes*.

CALATHUS RETRACTOR MUSCLES

The muscles in *Penaeus* which retract the optic calathus appear to be clearly represented by the retractor muscles of the eyes of *Astacus*, *Cambarus bartoni* (Fabricius 1798), *Pandalus*, and *Callinectes*. Phylogenetically, the situation in *Penaeus* is somewhat more generalized than in the other forms which we are considering, in that several of the calathus retractor muscles in *Penaeus* have more than one part. In addition, *Penaeus* has a number of apparently independent rotator muscles, none of them previously described, which function to twist the optic calathus about a longitudinal axis through the eyestalk.

DORSAL CALATHUS RETRACTOR MUSCLE

FIGURES 6, 7, 8

The dorsal calathus retractor muscle arises in connective tissue near the ventral surface of the eyestalk and attaches to the dorsal edge of the calathus.

LATERAL CALATHUS RETRACTOR MUSCLE

FIGURES 6, 7, 8, 9

The lateral calathus retractor muscle, really the posterior retractor, originates on sclerotized material along the lateral, or actually posterior, blood sinus running the length of the eyestalk. The larger portion of this muscle attaches on the lateral edge of the calathus, the lesser part turning ventrally and running across the ventral edge of the calathus, just dorsal to the ventral retractor muscles (fig. 9). When this muscle contracts it not only retracts the calathus, but rotates the calathus about an axis longitudinal to the eyestalk.

VENTRAL CALATHUS RETRACTOR MUSCLE

FIGURE 9

The ventral calathus retractor muscle originates on several sclerotized regions on the ventral surface of the eyestalk. One part of the muscle is long and slender, while the others are short and arise from broad origins (fig. 9). The muscle is inserted over a wide area on the ventral edge of the calathus.

MEDIAL CALATHUS RETRACTOR MUSCLE

FIGURE 6

The medial calathus retractor muscle originates on two points in the region of the median tubercle, and actually is comprised of two muscles (fig. 6). The larger muscle originates in the median tubercle and inserts in connective tissue dorsal to the distal optical ganglionic mass. The smaller muscle originates dorsal to the larger muscle and inserts on a ventromedial point on the calathus. The contraction of both muscles results in medial retraction of the calathus; functioning in opposition, the muscles retract the calathus in a vertical plane, reinforcing the action of the dorsal and ventral retractor muscles.

CALATHUS ROTATOR MUSCLES

FIGURES 6, 7

At least three calathus rotator muscles may be seen in the eyestalk of *Penaeus setiferus*. Rotator muscles of this type have not been described for *Pandalus*, *Astacus*, *Cambarus*, or *Callinectes*. The calathus rotators bear a certain similarity to one another, in that they are all superficial in position and insert in the heavy connective tissue underlying the thick cuticle of the calathus.

2. ANTENNULES

The antennules, or first antennae, are said to belong to the second segment of the body of Crustacea, following the eyes. In the company of the eyes, the antennae, and the labrum, the antennules are attached to the body tagma that has been termed by Snodgrass (1951a; 1952) the protocephalon. Whereas the appendicular nature of the eyestalk generally has been questioned, the status of the antennules as true crustacean appendages has rarely been attacked, despite controversy over the homologies of the component segments.

The antennule of *Penaeus setiferus* is comprised of a proximal stem divided into three basal segments, called the protopodite by Huxley (1906), and two distal flagella. Proponents of theories such as Huxley's (1906) suggesting correspondence of parts between the segments of the anten-

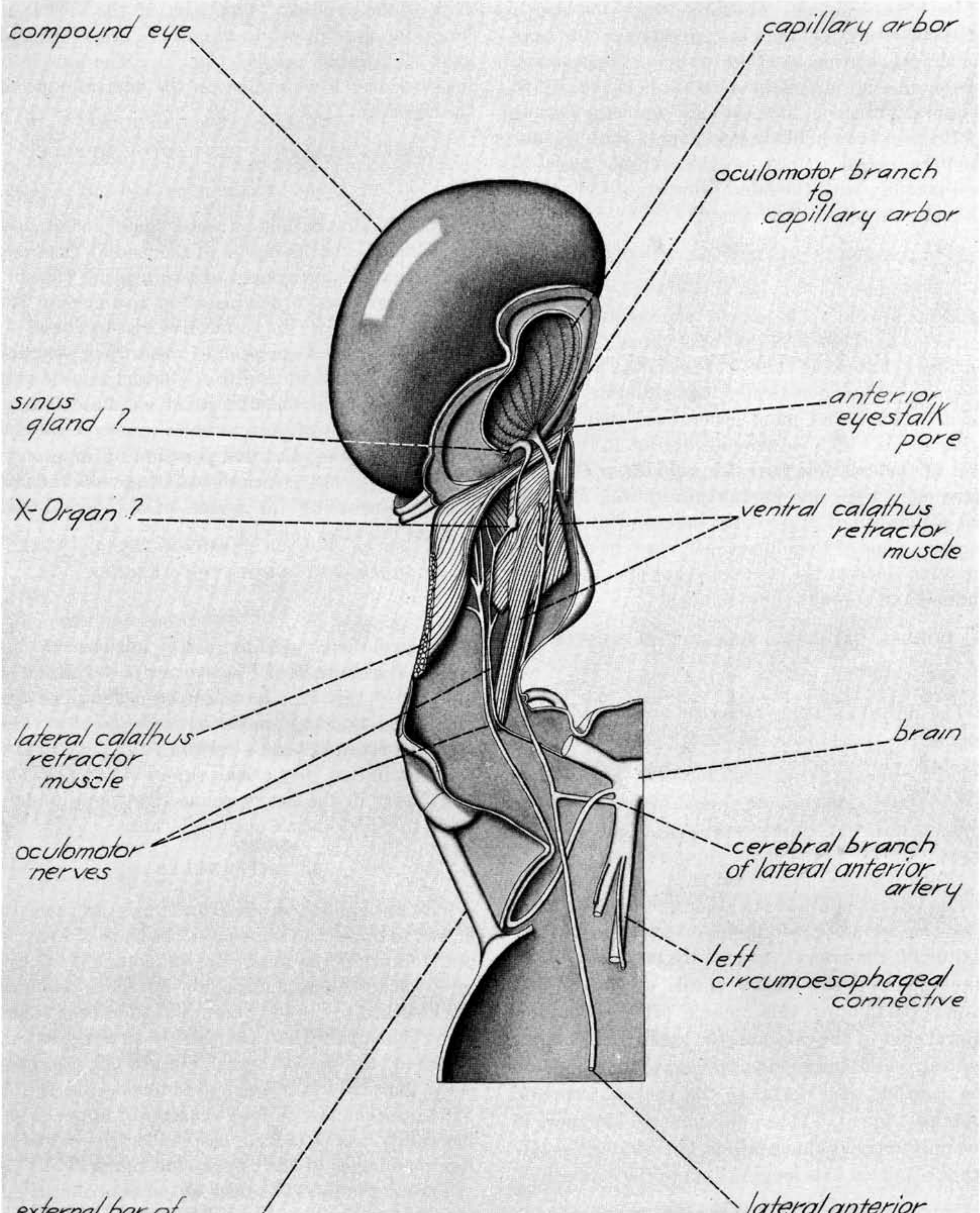

FIGURE 9.—Dorsal view of left eyestalk. Dorsal muscles and optic tract removed to show brain, branches of nerves, arterial capillary supply to distal optic ganglia, neurosecretory glands, and location of anterior eyestalk pore.

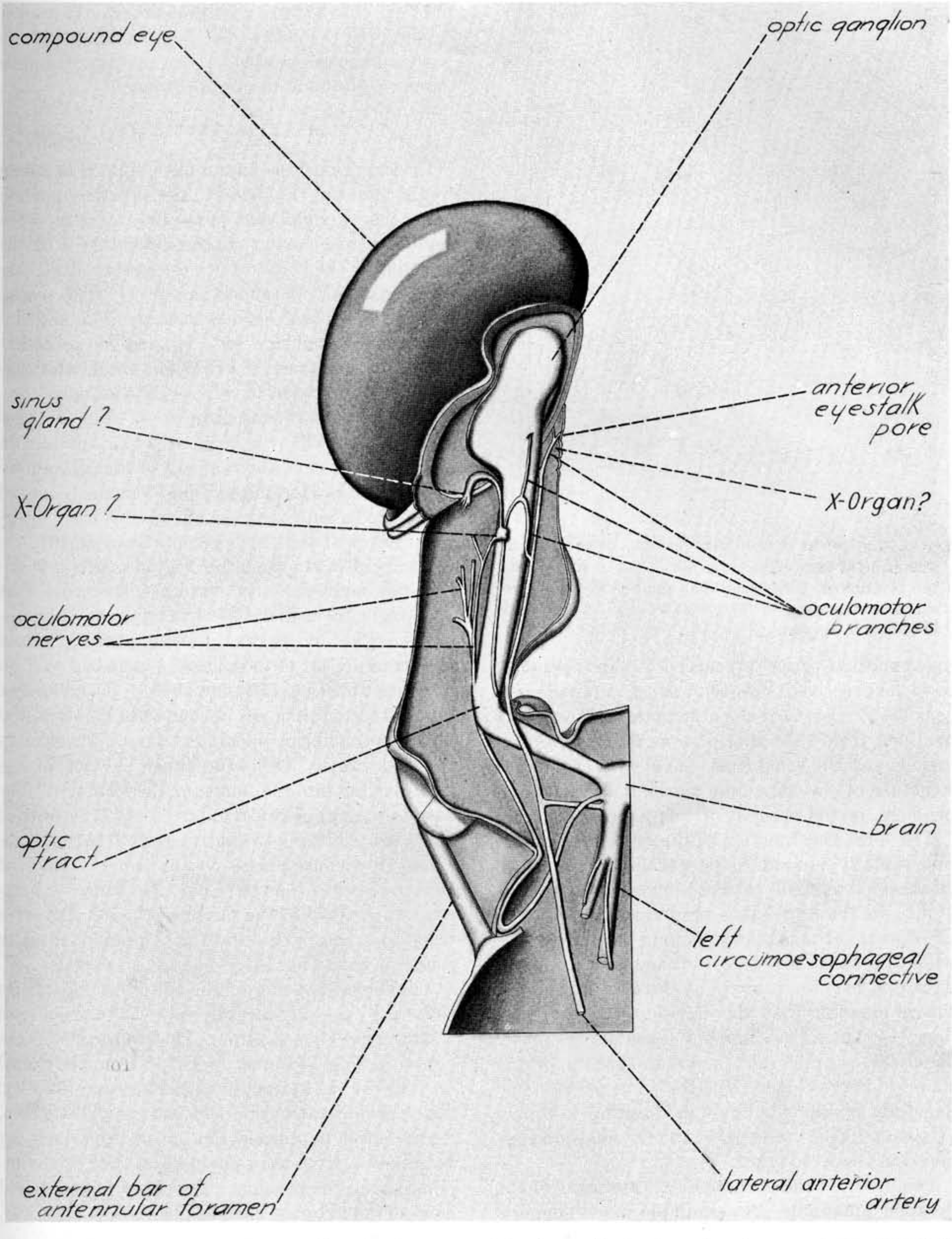

FIGURE 10.—Dorsal view of left eyestalk. Muscles removed to show optic tract, oculomotor nerves, neurosecretory glands, and branches of lateral anterior artery.

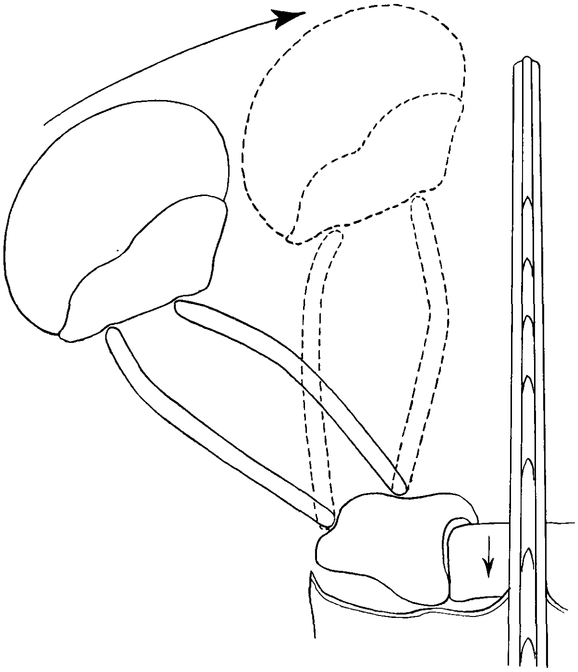

FIGURE 11.—Dorsal view of left eyestalk. Diagrammatic. The skeletal bars of the eyestalk are so arranged that the position of the ommatidial surface is maintained whatever the angle of the eyestalk with respect to the long axis of the shrimp.

nule and those of the typical crustacean appendage have not received support. Most carcinologists consider the parts of the antennule so extensively modified from the usual plan as to defy identification. At the same time, the clearly segmented structure of the antennule marks it as a true appendage, in the opinion of many workers.

The form and function of the crustacean antennule usually is said to be constant among the Decapoda, relative to the extraordinary variability in the appendage occurring in the lower Crustacea. Nonetheless, among the decapods wide differences are found. The outer or lateral flagellum is split in many of the Caridea, giving the impression that the antennule bears three flagella. Among the tribe Penaeidae, the outer flagellum is prehensile in certain genera of the Family Sergestidae. In the Solenocera each flagellum is semitubular, thus forming a siphon (Calman 1909). The antennule is small and reduced in the Brachyura.

Despite infrequent anatomical treatment of the decapod antennule, the available work suggests that a marked uniformity exists in the appendage and its parts over a broad spectrum of the Decapoda. From the standpoint of comparative morphology this feature of similarity would appear to simplify the process of homologizing part to part, and does, except for the matter of muscle names, a problem discussed earlier.

SKELETAL ELEMENTS

In dorsal view the antennule is shaped in a long wedge pointing anteriorly, the broadest portion being the proximal part of the first segment at the region of attachment of the antennule with the skeleton of the body. Each successive distal segment gradually becomes narrower. The mesial edge of the basal segments is straight and flat where the appendage rests against the other antennule. The first, or proximal, antennular segment (fig. 12) is relatively larger and more complex than the segments distal to it. The first segment is attached by a large articular foramen to the protocephalon, the tagma to which the antennules belong. Here, dorsal and ventral points of articulation, or condyles, afford the first antennular segment limited horizontal movement.

Centered in the posterior region of the first antennular segment is the statocyst, the organ that is thought to mediate the special sense of equilibration (figs. 12 to 16). Earlier workers termed the structure an otocyst, having ascribed to it an auditory function (Huxley 1906). The statocyst is constructed like an incomplete sac that has dorsal and anterior openings. Hairs, presumably sensory, project from the inner surface of the cuticular sac into the lumen of the statocyst. The hairs are arranged in regular rows. The rows of hairs are confined to oddly shaped patterns located at various places on the inner surface of the statocyst. Nerves from the sensory hairs coalesce ventrad of the sac into a broad, flat nerve tract that enters the brain at a point ventral to the optic tract (fig. 14).

The dorsal opening of the statocyst is partially covered by a fleshy, heavily setose lobe, the dorsal closing lobe (figs. 12, 15). In fresh material the dorsal closing lobe may be lifted from the dorsal opening of the statocyst without great difficulty. The saccular statocyst is shut anteriorly by a thin, curled sheet of cuticle that arises vertically by evagination from the ventrolateral floor of the antennular eye depression. The sheet is designated here as the anterior closing plate (figs. 12 to 15). Neither the dorsal closing lobe nor the anterior closing plate effect complete obturation of the statocyst. As a result, water circulates through

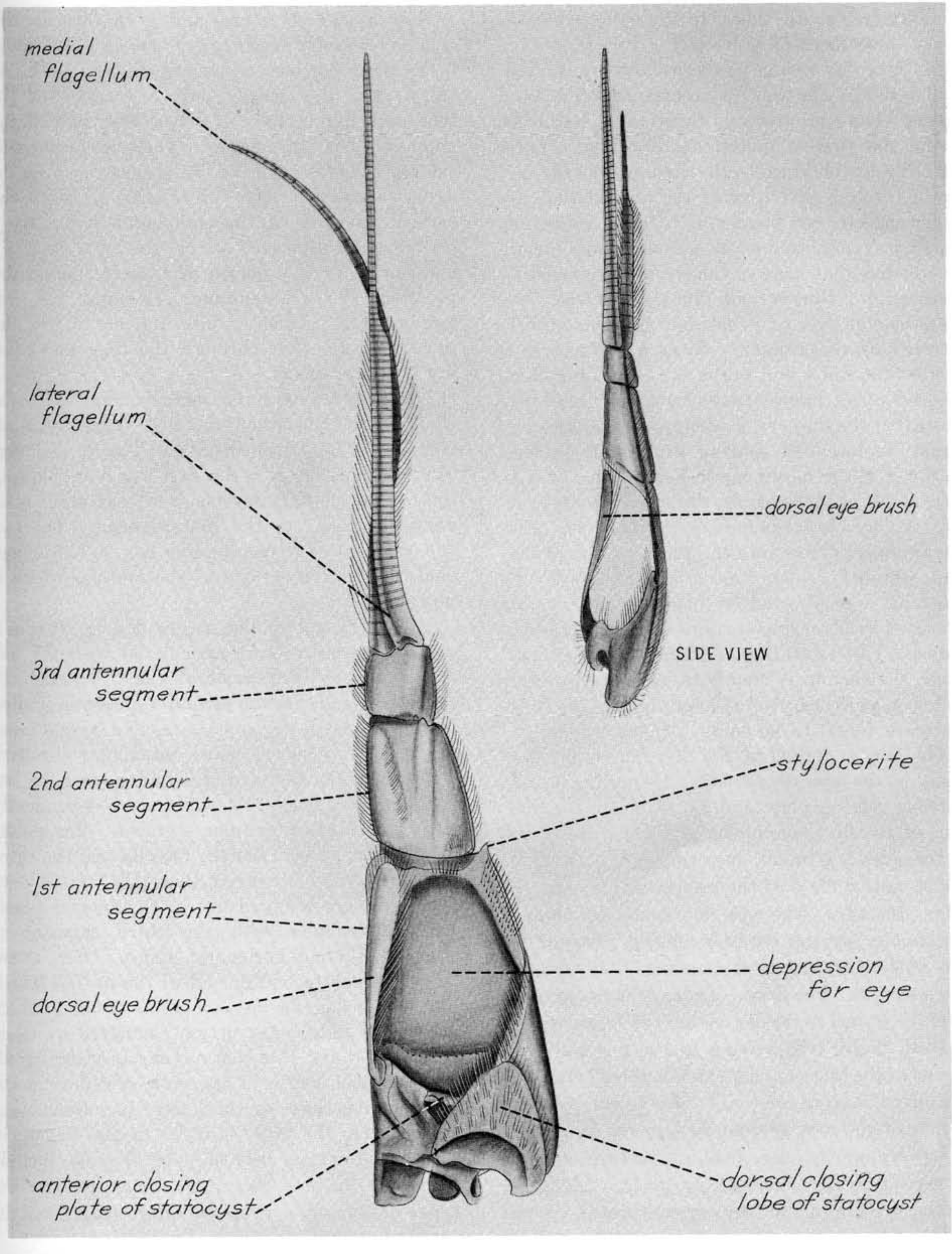

Figure 12.—The larger figure is a dorsal view of the right antennule, the smaller a lateral view of the right antennule.

the statocyst at all times, to the extent that the heavy investment of hairs in the area permits.

In living shrimps, as has been shown by Burkenroad (1939), the open statocyst contains sand grains. The sand probably functions as statoliths, if the statocyst is indeed equilibratory. These statoliths are obtained by the shrimp from the substrate through activities of the animal that are either directed or incidental to their collection. Cursory examination of the statocyst does not reveal bodies that have obviously been secreted by the shrimp. Burkenroad (1939), however, finds that the statocyst of penaeids contains statoliths secreted by the animals. Since the statocyst is open to the water and to the substrate into which the shrimp is known to burrow, the possibility exists that the statocyst contents may undergo continual replacement during intermolt periods. However, since the shrimp loses the statocyst with its contents at each ecdysis, the statoliths are probably replaced in large measure at the time. That the animals burrow into the substrate for protection, statolith replenishment, and rest following the molt is supported by negative information provided by observing shrimps in clean aquaria at ecdysis. Upon shedding in this unnatural environment, the shrimp is unable to navigate properly and soon perishes, even if kept alone. The statocysts are found to be empty of statoliths.

The largest region of the first antennular segment is the eye depression. Beginning at the anterior closing plate and extending to the margins of the first antennular segment distally and to the sides is a broad, deep concavity into which the corneal surface of the compound eye may rest (figs. 12, 13). The eye depression is confined proximally by the anterior closing plate of the statocyst and the skeletal structures that surround the statocyst. The dorsal closing lobe projects out slightly, dorsal to the depression. A large, wedge-shaped, fleshy lobe arising in the posterolateral region of the first segment extends anteriorly along the lateral margin to a point. At the anterolateral corner of the first antennular segment is a small, sharp stylocerite (fig. 12), a structure common to the Tribe Penaeidae (Voss 1955). Along the mesial margin of the first segment lies the dorsal eye brush, or prosartema (figs. 12, 13), a long, thin lobe arising dorsally from the proximal region of the segment and extending anteriorly to the anteromesial corner of the segment.

Most of the structures lining the eye depression are heavily setose, to a degree that would make their outlines obscure if illustrated faithfully. For this reason only a fraction of the true covering in hair of the dorsal side of the antennule has been shown. The presence of this extensive investment of hair probably can be explained as a system of brushes to clean the corneal surfaces of the compound eyes. Many stalk-eyed crustaceans carry the eyes laterally and never for any length of time in the eye depressions of the antennules. However, the eyes are brought frequently into and out of the depressions, and thus through the long hairs lining the depression.

The second antennular segment (fig. 12), a far simpler structure than the first segment, is attached to the latter distally. The second segment articulates with the first segment allowing limited horizontal movements of the antennular segments distal to the first segment. The second segment is a rectangular box in shape and modified for the actions of the muscles which it contains.

The third antennular segment (fig. 12) is a small, square structure articulated with the second segment. Movement of the third segment and the flagella on the second segment is limited to an attenuated horizontal arc. No special sense organ appears in the third antennular segment.

Two flagella, the medial flagellum and the lateral flagellum (fig. 12), articulate independently with the third antennular segment. The points of articulation between the flagella and the third segment are so arranged that the flagella may move through a broad arc in the frontal plane. Each articulates with the third segment in slightly different horizontal planes. The lateral flagellum is attached dorsad of the medial flagellum. The flagella are composed of many short articles of light construction connected by rings of thin cuticle, thus permitting bending in all planes. The length of the articles differs in the two flagella, those of the lateral flagellum being shorter than the articles of the medial flagellum. Other differences between the flagella include variation in cross-sectional shape and in the types of setae and processes projecting from the articles.

Numerous studies have been made on the function of the antennular flagella and the variety of hairs and processes that they bear. These investi-

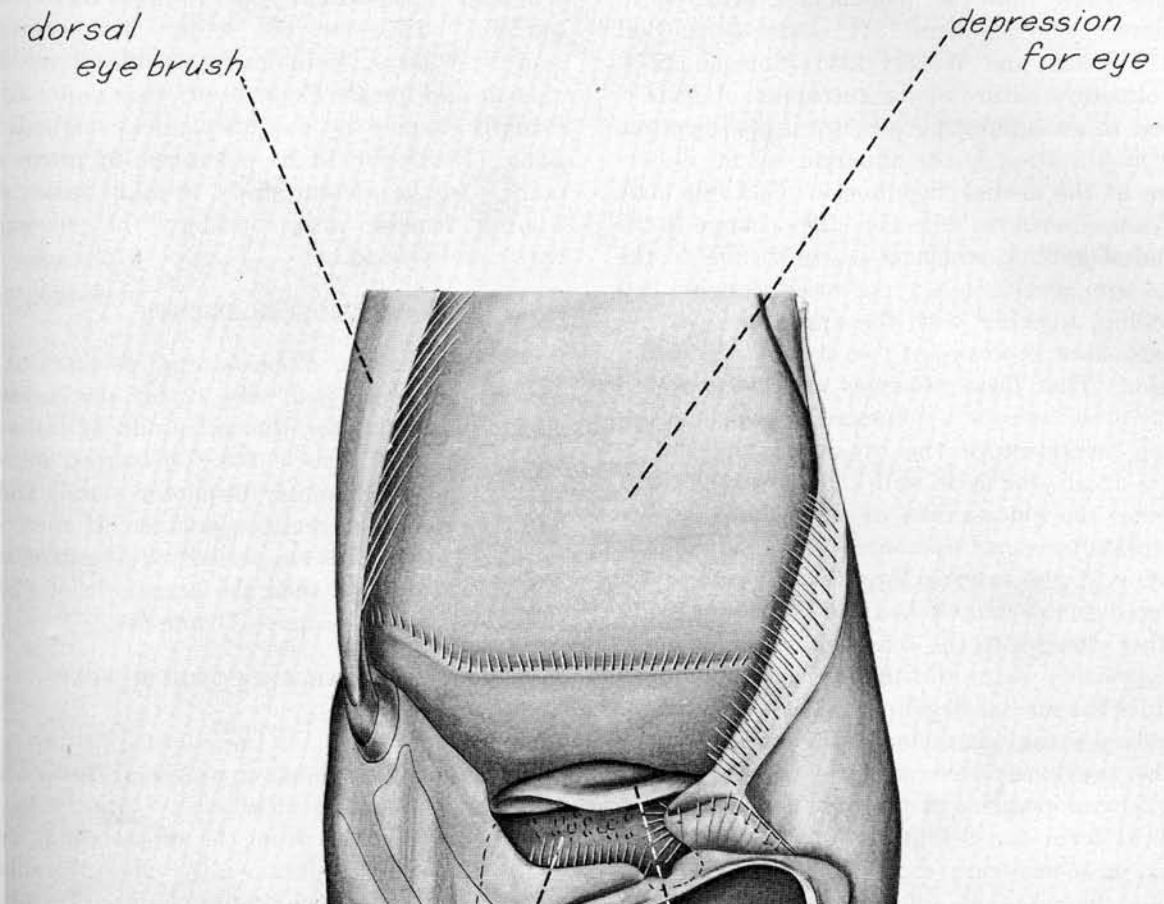

FIGURE 13.—Dorsal view of proximal region of first antennular segment, right antennule. Cleared specimen showing entrance to statocyst. Dorsal closing lobe removed.

gations show that the flagella are involved in chemoreception (Doflein 1911; Balss 1913; Bell 1906; Lissman and Wolsky 1935; Spiegel 1927). The olfactory nature of the antennular flagella is related to an interesting structural modification. This modification is the apparent sexual dimorphism of the medial flagellum in the adult male of *Penaeus setiferus* (fig. 17). The change to the medial flagellum, which is easily visible to the naked eye, results in a pronounced dorsoventral flattening, together with the appearance of numerous, stout processes of two sizes on the dorsal margin. That these processes may be predominantly proteinaceous is suggested by their loss following treatment of the preserved material in strong alkali, for as is well known strong alkali degrades the glucosamine of chitin but does not immediately remove it, whereas the alkali-soluble proteins of the internal organs and cuticle are rendered soluble and washed out (Richards 1951).

Other changes to the condition of adult maleness probably occur during the same molt that modifies the medial flagellum. The most obvious secondary sexual character is the mesial joining of the previously free wings of the modified pleopod endopodities of the first abdominal segment to form the definitive and functional petasma, or sperm-transfer organ.

Since the antennular flagella are olfactory, the sexually dimorphic medial flagellum of the male *Penaeus setiferus* probably functions to enable the male to find the sexually mature female during the time of mating. The occurrence of secondary sexual modifications of the antennular flagella are widespread among the Crustacea Decapoda. Meredith (1954) describes a modified outer antennular flagellum in the adult male of *Crangon vulgaris* and suggests that the structure may function in mating. This worker finds that the character is of use in identifying adult males in the field. The most extensive treatment of the subject of sexual dimorphism in Crustacea is that of Rioja (1939a, 1939b, 1940a, 1940b, 1940c, 1941a, 1941b, 1942a, 1942b), who has described in detail the sexually modified medial flagellum of *Penaeus setiferus* and several other species of penaeid shrimps. This worker considers the character to be constant in occurrence and sensory in function, and closely related to the sexual activities of the shrimps.

In the opinion of the present writer, the modified medial antennular flagellum is a constant character in the sexually mature male of *Penaeus setiferus*. However, the subject needs further study. A large, statistically significant number of male and female *Penaeus setiferus* shown to be sexually mature by the histological methods of King (1948) should be examined to prove the point. In the present study 10 adult males and 8 adult females were considered in connection with the character.

MUSCLE ELEMENTS

The antennule of *Penaeus setiferus* contains 13 muscles, as contrasted with 12 for the caridean *Pandalus*, and 9 for the antennule of *Astacus*. Cochran (1935) lists 9 for *Callinectes*, including a double antennular promotor muscle and a double antennular remotor muscle. If these divided muscle bodies are actually 2 promotor and 2 remotor muscles, then the antennule of *Callinectes* can be said to have 11 muscles.

ANTENNULAR ABDUCTOR MUSCLE

FIGURE 14

The antennular abductor muscle of the first antennular segment is attached posteriorly to an apodeme that arises from the ventrolateral margin of the articular foramen by which the antennule is connected to the protocephalon. The plane of orientation of this apodeme is vertical. The antennular abductor runs anteriorly a brief distance and divides into two large branches that attach to sclerotized bars supporting the posterior region of the first antennular segment in the neighborhood of the statocyst. Contraction of the first segment abductor muscle swings the first antennular segment, and with it the distal antennular segments, outward from the mid-sagittal plane of the body in the limited horizontal motion possible to the first segment. The antennular abductor of *Penaeus* is homologous with the musculus promotor I antennae of *Astacus*, *Pandalus*, and possibly to the first segment promotor muscles of *Callinectes*, judging from the origins, insertions, and arrangements of the muscles.

However, the functions of the homologous muscles are different, as often happens. The difference lies primarily in the restriction of antennular movement created by the presence of the antennal scales ventral to the antennules in *Penaeus*. In the white shrimp, the scales are relatively large and, when lying in their usual longitudinal posi-

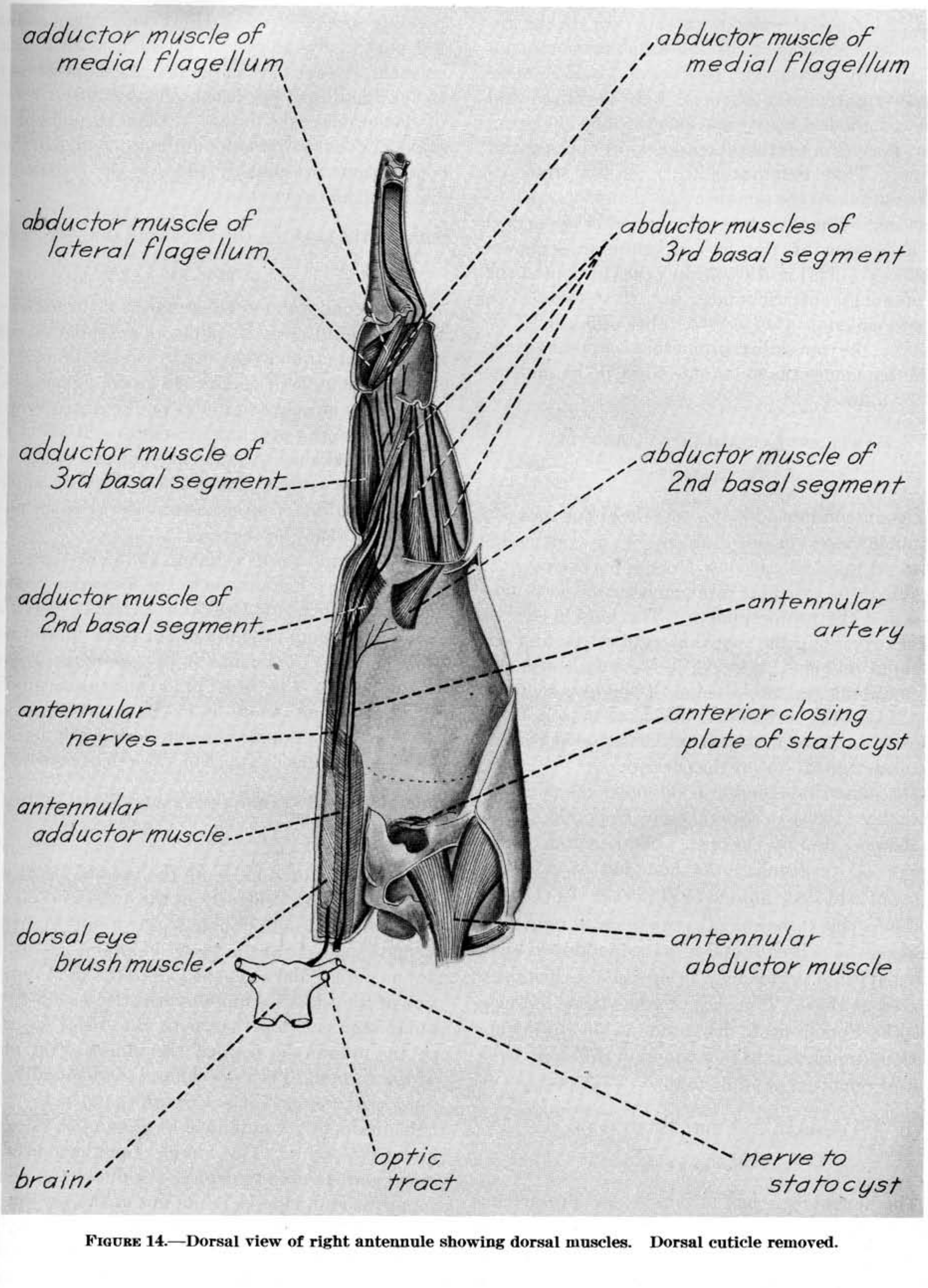

FIGURE 14.—Dorsal view of right antennule showing dorsal muscles. Dorsal cuticle removed.

tion, their mesial margins overlap beneath the antennules. Movements of the antennules ventrad are thereby prevented. In *Pandalus* and *Astacus* the first antennular segments may be raised and lowered about a transverse axis through the articular foramina of the antennules, in the sagittal plane. That Schmidt (1915) in his study of *Astacus* named the muscle a "promotor" is open to question. The muscle might better be described as a levator of the first antennular segment. Berkeley (1928) and Cochran (1935) adopted the terminology of Schmidt for this muscle in *Pandalus* and *Callinectes*, although, in *Callinectes* the musculus promotor I antennae apparently moves the antennule toward the midline of the animal.

ANTENNULAR ADDUCTOR MUSCLE

FIGURE 14

The antennular adductor muscle of the first antennular segment originates on a vertically-oriented apodeme arising from the ventromesial region of the articular foramen between the antennule and the protocephalon. The muscle courses anteriorly along the mesial margin of the first antennular segment, inserting in the cuticle at many points along the mesial edge of the first segment (fig. 14). The antennular adductor muscle functions to turn the first antennular segment toward the mid-sagittal line of the shrimp.

The musculus remotor I antennae described by Berkeley (1928) in *Pandalus*, by Schmidt (1915) in *Astacus*, and by Cochran (1935) in *Callinectes* are in all probability the homolog of the first segment adductor muscle in *Penaeus*. In the case of the former three animals, two musculi remotor I antennae have been found in the antennule of each, a remarkable uniformity in animals as distantly related as these. *Penaeus*, too, has these muscles, but the dorsal-most, discussed in the following section, appears to have a function different from that of remotion or adduction.

DORSAL EYE BRUSH MUSCLE

FIGURE 14

The dorsal eye brush muscle, or prosartema muscle, lies upon the adductor muscle of the first antennular segment, and is almost certainly the homolog of the musculus remotor *b* I antennae found in the antennules of *Pandalus*, *Astacus*, and possibly of *Callinectes*. However, instead of taking part in the adduction of the first antennular segment, the eye brush muscle in *Penaeus* serves to stiffen the dorsal eye brush (figs. 12, 13). Fibers of the muscle enter the eye brush at its point of attachment to the first antennular segment, and their contractions presumably enhance the function of the brush as an eye cleaner.

ABDUCTOR MUSCLE OF SECOND BASAL SEGMENT

FIGURE 14

The second antennular segment is turned away from the midline on its points of articulation with the first antennular segment by contractions of the abductor muscle of the second basal segment (fig. 14). This muscle originates on the anteroventral part of the first antennular segment at about the midpoint between the anterior margins of the segment. The muscle runs a short distance anterolaterally to insert on a posterolateral apodeme of the first antennular segment.

The second basal segment abductor muscle of *Penaeus* has a homologue in the musculus productor$_2$ I antennae of *Pandalus*, *Astacus*, and *Callinectes*, although the use of the term "productor" for the action of the muscle in *Callinectes* is questionable. In the blue crab musculus productor$_2$ I antennae is said by Cochran (1935) to pull the second antennular segment downward, indicating that the muscle functions as a depressor.

ADDUCTOR MUSCLE OF SECOND BASAL SEGMENT

FIGURES 14, 15

The adductor muscle of the second basal segment originates ventrally in the anteromesial corner of the first antennular segment and inserts on a small apodeme at the posteromesial corner of the second antennular segment (figs. 14, 15). Contraction of the adductor muscle turns the second antennular segment, together with the distal elements of the antennule, toward the mid-sagittal plane of the animal. The second basal segment adductor muscle of *Penaeus* has a counterpart in the musculus reductor$_2$ I antennae of *Pandalus*, *Astacus*, and *Callinectes*. The muscle functions in *Pandalus* and *Astacus* to depress the distal antennular segments and flagella, while in *Callinectes* the distal elements are raised toward the midline by the action of the musculus reductor$_2$. The muscle might better have been called a second segment levator in the blue crab.

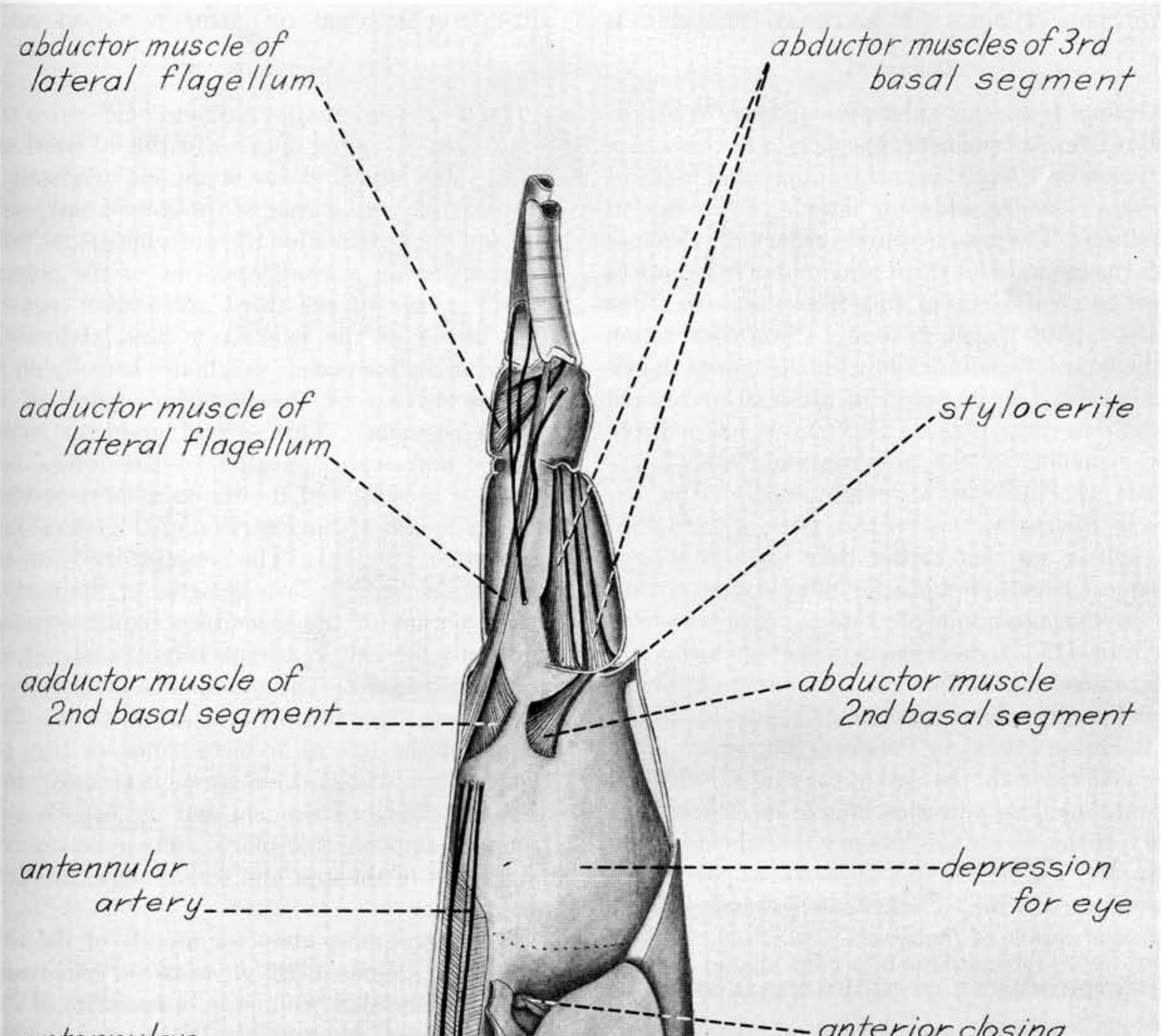

FIGURE 15.—Dorsal view of right antennule showing ventral muscles.

ADDUCTOR MUSCLE OF LATERAL FLAGELLUM

FIGURE 15

Arising from the anteromesial margin of the first antennular segment, just dorsal to the origin of the second basal segment adductor muscle, is the long, slender adductor muscle of the lateral flagellum. The muscle courses anteriorly through both the second and third antennular segments to insert on an apodeme arising from the mesial edge of the lateral flagellum base. Upon contraction of the lateral flagellum adductor the lateral flagellum is turned on its points of articulation toward the mid-sagittal plane. The muscle has a probable homolog in the musculus adductor I antennae of *Pandalus*, although in the latter the muscle inserts in the ventral part of the third antennular segment rather than on a flagellum. A lateral flagellum adductor muscle does not occur in the antennule of *Astacus* or *Callinectes.* Cochran (1935) describes a musculus adductor$_2$ I antennae for *Callinectes* that functions somewhat like the musculus adductor I antennae found by Berkeley (1928) in *Pandalus*, but which is not homologous with the latter muscle or with the lateral flagellum adductor muscle in *Penaeus.* A study of the nerves might show that the musculus adductor$_2$ I antennae in *Callinectes* is part of the musculus reductor$_2$ I antennae (second segment adductor muscle of *Penaeus*).

ADDUCTOR MUSCLE OF THIRD BASAL SEGMENT

FIGURE 14

The relatively large adductor muscle of the 3d basal segment originates in the posteromesial corner of the second antennular segment and runs directly anterior to insert on an apodeme in the posteromesial corner of the first antennular segment. Contractions of this muscle turn the third antennular segment and the flagella mesad, reinforcing the action of the proximal antennular adductors. The third basal segment adductor of *Penaeus* has homologs in the musculus reductor$_3$ I antennae of *Pandalus*, *Astacus*, and *Callinectes.* Cochran's (1935) use of the name "reductor" for the muscle in *Callinectes* is unfortunate. The reductor muscle of the third antennular segment in the blue crab appears to function virtually opposite to the muscle of the same name in *Pandalus* and *Astacus*, a situation that underlines the impropriety of transferring functional muscle names from one animal to another.

ABDUCTOR MUSCLES OF THIRD BASAL SEGMENT

FIGURES 14, 15

The second antennular segment of *Penaeus* contains three abductor muscles of the 3d basal segment. The lateral abductor muscle originates in the posterolateral corner of the second antennular segment and runs directly anterior to its point of insertion on a small apodeme of the posterolateral corner of the third antennular segment. Just mesad of the lateral, or first, abductor, a second abductor muscle originates broadly on the ventral surface of the posterior region of the second segment. This second abductor muscle courses anteriorly, parallel to the lateral-most abductor muscle, and inserts on a short apodeme slightly mesad of the insertion of the lateral-most muscle (figs. 14, 15). The mesial third basal segment abductor muscle originates in the posteromesial corner of the second antennular segment dorsal to the origin of the third basal segment adductor muscle. The mesial abductor runs diagonally to the anterior to insert on the apodeme of one of the lateral abductor muscles (fig. 14). Contractions of the third segment abductor muscles turn the third segment and the flagella away from the mid-sagittal plane. Their action reinforces that of the first and second segment abductor muscles.

The lateral-most abductor muscle of the third antennular segment of *Penaeus* is homologous with the musculus productor$_3$ I antennae of *Pandalus*, *Astacus*, and possibly *Callinectes.* In *Pandalus* and *Astacus* the musculus productor$_3$ swings the third segment dorsally in the sagittal plane, while in *Callinectes* the muscle named by Cochran (1935) a "productor" appears to flex the third segment. The second lateral third-segment abductor muscle in *Penaeus* has homologs in the musculus abductor$_3$ I antennae of *Pandalus* and *Astacus.* The muscle has been lost in *Callinectes.* The mesial third-segment abductor muscle of *Penaeus* does not appear in the antennule of any of the crustaceans to which reference has been made here.

ABDUCTOR MUSCLE OF LATERAL FLAGELLUM

FIGURES 14, 15

The abductor muscle of the lateral flagellum has its origins along most of the mesial side of the third antennular segment. The muscle nar-

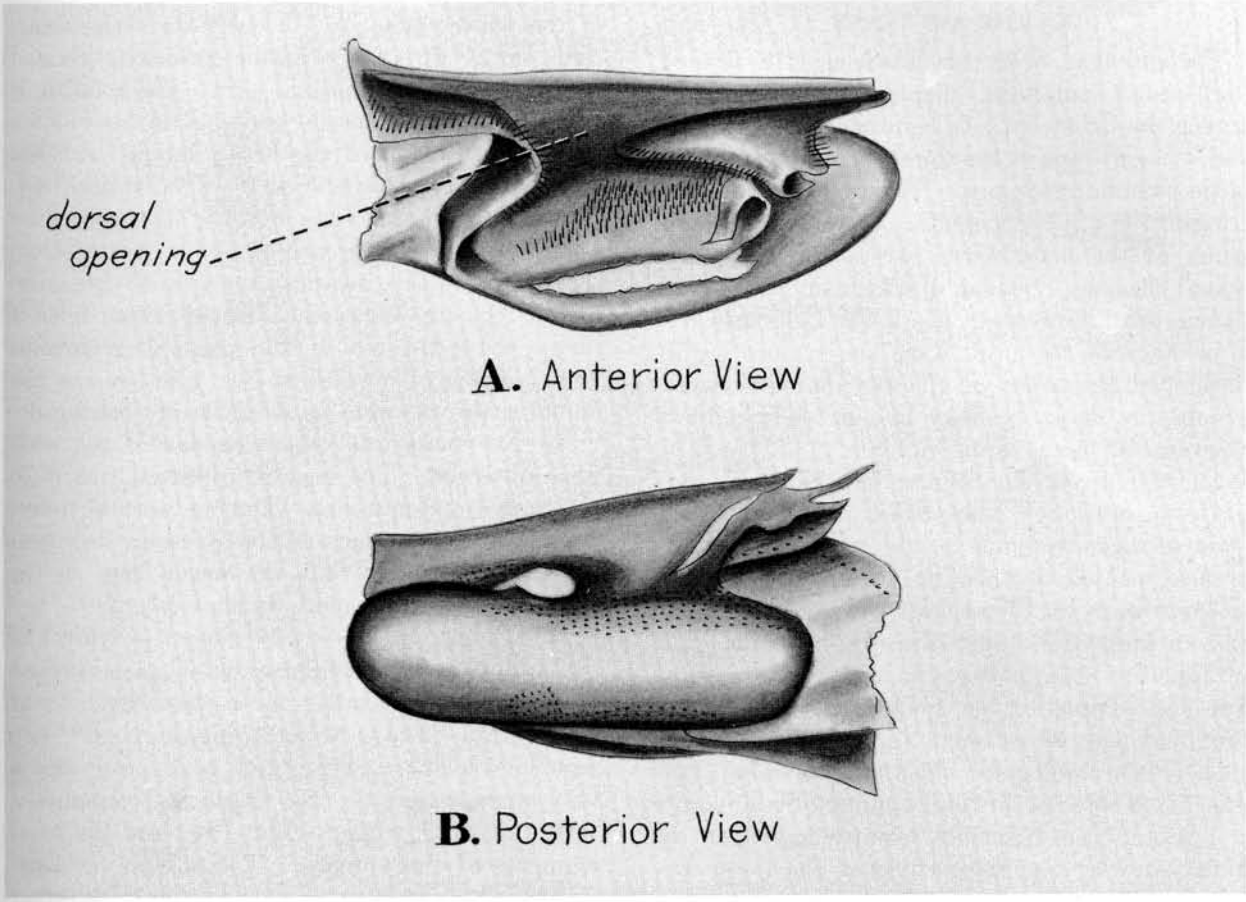

FIGURE 16.—Cleared statocyst. *A*. Anterior view. *B*. Posterior view.

rows as it runs anterolaterally, ventral to the lateral flagellum adductor muscle, to insert on an apodeme on the lateral edge of the base of the lateral flagellum (fig. 15). The lateral flagellum abductor muscle turns the lateral flagellum away from the midline in the horizontal plane. The muscle in *Penaeus* is very likely homologous with the musculus reductor$_4$ I antennae of *Pandalus*, *Astacus*, and *Callinectes*, although evolutional rearrangements have given rise to several changes. Berkeley (1928) describes the reductor$_4$ muscle in *Pandalus* as consisting of two parts, inserting on two opposite margins of the base of the lateral flagellum, and having at times an antagonistic action to one another. Such action suggests very strongly the existence of two muscles, rather than one with two functions.

ADDUCTOR MUSCLE OF MEDIAL FLAGELLUM

FIGURE 14

Originating in the posteromesial corner of the third antennular segment is the small adductor muscle of the medial flagellum. The adductor muscle courses anteriorly and inserts on an apodeme on the mesial edge of the flagellum base. Contractions of the muscle turn the medial flagellum toward the midline in the horizontal plane. No counterpart of this muscle in *Penaeus* is described for the antennule of *Pandalus*, *Astacus*, or *Callinectes*.

ABDUCTOR MUSCLE OF MEDIAL FLAGELLUM

FIGURE 14

The abductor muscle of the medial flagellum originates ventral to the origin of the medial flagellum adductor muscle and inserts on the medial flagellum by a short apodeme located at the lateral margin of the flagellum base. The muscle turns the medial flagellum outward from the midline in a horizontal plane. The medial flagellum abductor muscle of *Penaeus* has been lost in the antennule of the other crustaceans referred to in this study.

3. THE ANTENNAE

The antennae, or as they are frequently termed, the second antennae, display wide variations among the Crustacea. In certain of the Copepoda and other groups in the lower Crustacea they are large swimming organs. They are modified for clinging in other copepods. Frequently the antenna of the male crustacean is modified as a sexual clasper. Sexual dimorphism of the antennae is widespread in the lower Crustacea, the appendage of the adult male being more highly developed than that of the female. In several groups the structures may be extremely reduced or even lost in the adult animals.

The antenna of the higher Crustacea is fairly uniform, although exceptions do occur. The malacostracan antenna is said to consist of a 2- or 3-segmented protopodite, an endopodite of 2 or 3 segments, the distal-most bearing a flagellum, and an exopodite reflected into a flat scale. The protopodite usually is comprised of the coxopodite and basipodite, but some forms may have a proximal pre- or sub-coxa in addition (Calman 1909). Carcinologists use the expression "peduncle" to refer to the total number of endopodite and protopodite segments, usually 5 or 6, in the Malacostraca. Representatives of the lower Decapoda, like *Penaeus setiferus*, have a 5-segmented antennal peduncle, made up of the coxopodite and basipodite in the protopodite, and 3 proximal endopodite segments. The exopodite is scalelike. The scale is often missing or reduced to a spine in the higher decapods and the endopodite and flagellum may be relatively small.

Functionally, the antennae have always been thought to be sensory. More specifically, the antennal flagella are said to be centers of tactile sensation, whether pressure or simple touch is not known. No experimental data to support these contentions exist. The functions of the antennal scale would appear to be varied, in accordance with its great variation in size. The scale is missing in the Brachyura and small in the crawfishes and other Astacura, making its function somewhat difficult to determine by observational means. The organ is very large in the swimming decapods of the Natantia. The suggestion has frequently been made that the scale is an anterior swimming plane in the latter group.

Some attempt has been made to ascertain the function of the antennal scale in the swimming of the white shrimp. Normally the scale is carried in a directly anterior position, rotated slightly on its longitudinal axis. The rotation is such that the thin mesial margins of the scale lie somewhat ventrad of the heavy lateral margins. The effect produced is that of a ship's bow. Shrimps in an aquarium were lightly secured by a loop of string to the end of a rod. Lifted from the bottom in this position, the animals are stimulated to swim forward. Jets of water from a pump were directed at the motionless shrimps from various directions to see whether the antennal scale was used as an anterior steering device. No compensatory movements of the scale were observed. The organs appeared simply to cleave the water ahead. During normal movements about an aquarium, the scales are occasionally spread widely, but are never kept in the spread condition for more than a moment.

The antenna in *Penaeus setiferus* is typical of the natant Decapoda. The antennal scale is broad and strong and extends as far as the anterior tip of the rostrum. The protopodite is comprised of two segments, a short, incomplete coxopodite and a very large basipodite. To the large basipodite is articulated the exopodite, or scale, and the basal segments of the antenna. The size of the basipodite reflects its support of the heavy scale rather than that of the smaller antennal segments. The long antennal flagellum is carried laterally, from which position the movements of the shrimps through the water cause the flagellum to drag alongside and some distance behind the animal. The flagellum is approximately twice the body length in the white shrimp.

SKELETAL ELEMENTS

The first antennal segment, or coxopodite (fig. 18), is an incomplete ring by which the antenna is attached to the protocephalon. The foramen of the antenna at which the first antennal segment articulates with the protocephalon is by far the largest of the head foramina. At its broadest portions, muscles insert upon the first antennal segment.

The basipodite, or second antennal segment (figs. 18, 23), is a large, heavily sclerotized article connected firmly to the first antennal segment proximally and articulating distally with the third antennal segment, or ischiopodite, of the endopodite, and with the antennal scale, or exopodite. At

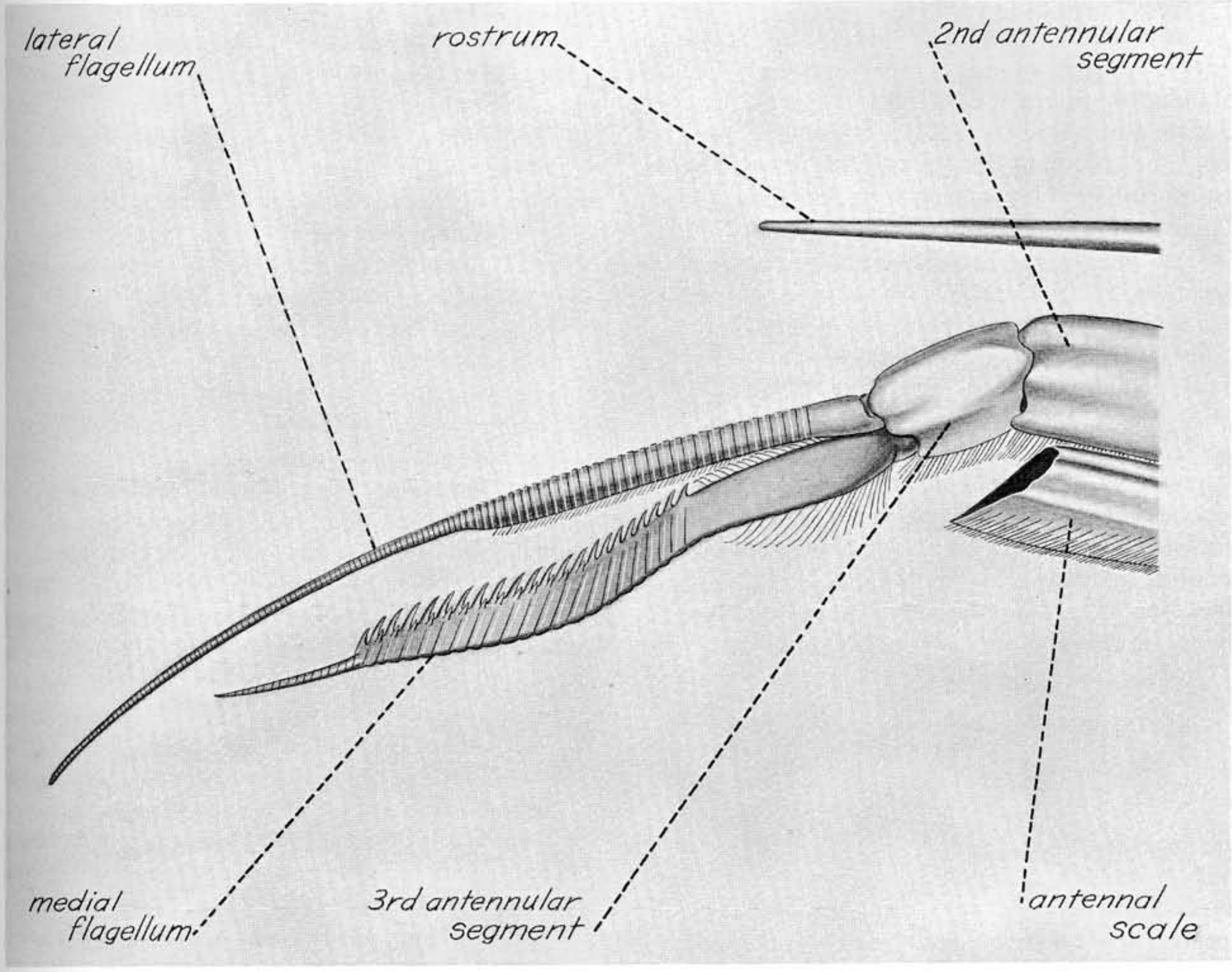

FIGURE 17.—Enlarged view of left antennular flagella showing sexual modification to medial flagellum in adult male.

the point of articulation with the antennal scale, the second antennal segment is deeply notched anteriorly providing an articular foramen for the large antennal scale. Strong dorsal and ventral points of articulation, or condyles (figs. 18, 22, 23) on the rim of the scale foramen permit the scale considerable horizontal movement. As brought out earlier, the great weight and strength of the second antennal segment exists as support for the antennal scale, rather than for the long, slender antennal flagellum. The second antennal segment articulates with the third antennal segment, or ischiopodite, by a small foramen located ventromesially (figs. 18, 23). The extent of movement between the second and third antennal segments is very limited.

The third antennal segment (figs. 18, 23) is a small, heart-shaped structure whose apex is directed posteriorly. Its small vertical movement, at right angles to its long axis, against the second antennal segment permits some rotation of the distal antennal segments. Movements of the little shield-shaped fourth antennal segment (figs. 18, 23) against the third antennal segment are, on the other hand, extensive. The fourth antennal segment attaches laterally to the third segment at about a 45° angle. By means of a dicondylic articulation, the fourth segment rotates through an arc of nearly 90°, and with it the distal antennal parts.

According to Schmidt (1915), the third antennal segment represents the fusion of the ischiopodite and meropodite and he evidently has morphological support for this view in *Astacus*. Curiously, no trace of a division is apparent in the third antennal segment of *Cambarus*, nor does Berkeley (1928) find one in the caridean *Pandalus*. No evidence for the fusion of the ischiopodite and meropodite can be seen in *Penaeus setiferus*.

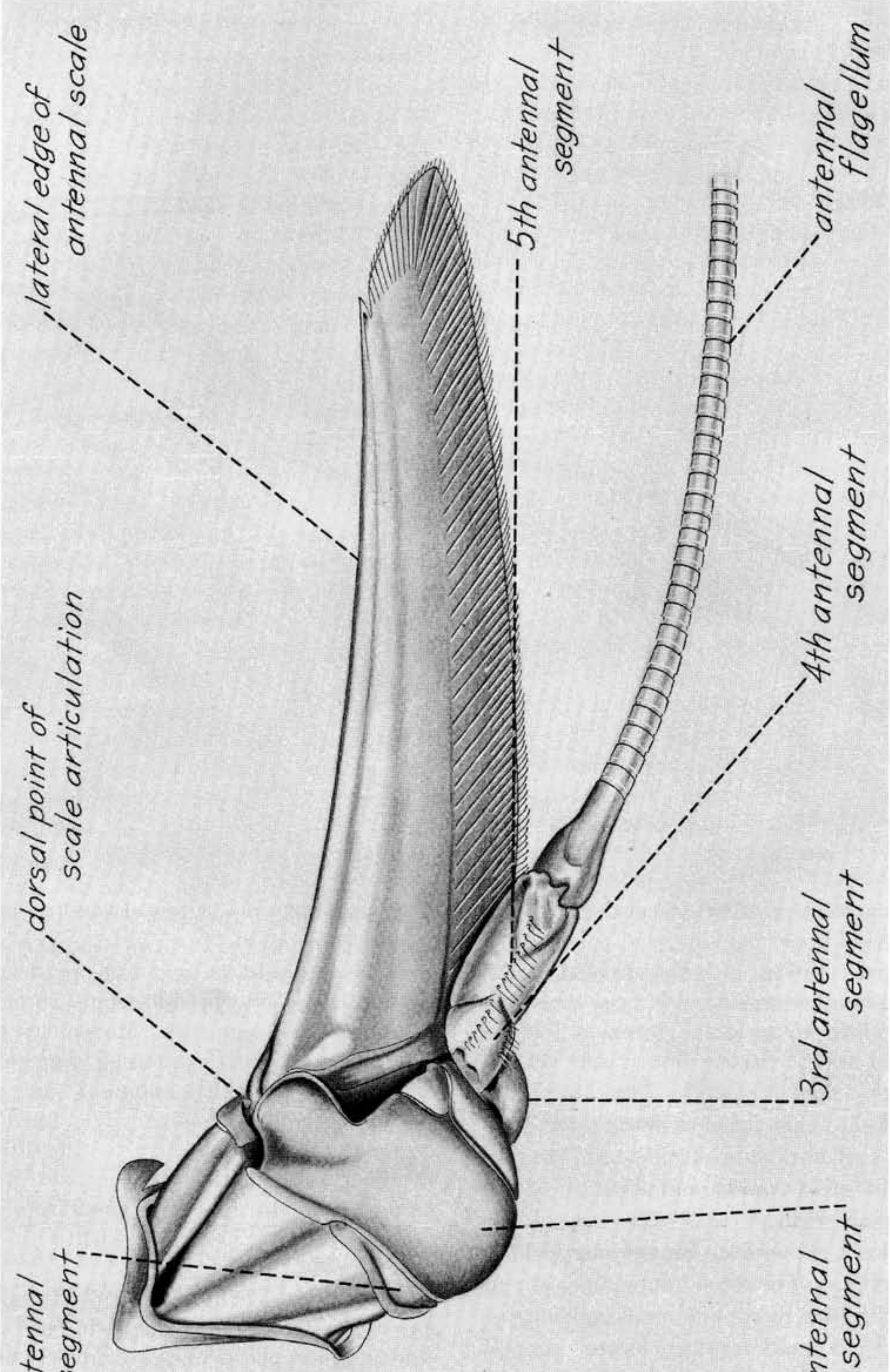

FIGURE 18.—Lateral view of right antenna.

The fifth antennal segment (figs. 18, 23) lies on the axial line distal to the fourth antennal segment and is connected to the pointed fourth segment by a broad V-shaped surface in the proximal end of the fifth segment. Two condyles in the vertical plane located at the apex of the V-shaped surface permit limited horizontal movements of the fifth segment on the fourth antennal segment. The relatively large fifth antennal segment bears the base of the long flagellum on its distal end. Strong dorsoventral condyles allow the flagellum to turn through an arc of more than 90° and the size of the fifth segment is probably an evolutional response to the long muscles needed to operate the flagellum. In living shrimps, the distal part of the flagellum is carried at right angles to the fifth antennal segment, the rest of the long flexible flagellum floating behind the animals. The antennal flagellum (figs. 23, 25) owes its flexibility to its annular construction. Each small annulation is capable of a little movement with respect to its neighbors.

An enlargement of the flagellar rings (fig. 25) shows probable sensory structures. On the dorsal surface of each ring (fig. 25, *A*) may be seen a pair of dorsal setae. On the ventral surface (fig. 25, *B*) a pair of plumose ventral setae project anteriorly from the distal portion of each annulation. Between the bases of the ventral setae is a ventral pit. The interior of the flagellum consists of blood vessels and nerves.

MUSCLE ELEMENTS

The skeletal parts of the antenna of *Penaeus setiferus* are operated by 12 types of muscles, including at least 26 individual muscles. Berkeley (1928) describes 15 types of muscles in *Pandalus*. Schmidt (1915) lists 18 muscle types in the European crawfish, the appendage containing 21 separate muscles to carry out its complex movements. The reduced antenna of *Callinectes* has only 8 muscles (Cochran 1935). The evolutional trend of reduction of the number of muscles and muscle types has apparently been reversed in the case of the crawfish antenna, in which form much more complicated antennal activities are displayed by the living animals than in *Penaeus* or *Pandalus*.

FIRST ANTENNAL SEGMENT ADDUCTOR MUSCLE

FIGS. 21, 24

Attaching on the median rim of the coxopodite foramen, the first antennal segment adductor muscle inserts in the first antennal segment near the external opening of the excretory apparatus (fig. 21). Contractions of this short, powerful muscle turn the coxopodite and hence the antenna mesad. Homologs of this muscle in *Astacus* and *Pandalus* are difficult to determine without full information on the nerves. Allowing for functional differences in the antennae of the various crustaceans here considered, the most likely homolog of the first segment adductors in *Astacus* is the musculus depressor *a* II antennae. Berkeley (1928) designates two medial antennal base muscles as the musculus depressor *a* and *b* II antennae, after Schmidt (1915). From her illustrations of the antenna in *Pandalus*, the antennal depressor muscle *a* appears to be the same muscle as the first antennal segment adductor in *Penaeus*. The muscles in the latter two forms are similar, strongly suggesting an homology. The antennal depressor muscle *a* in *Astacus* is much less suggestive of phylogenetic similarity.

SECOND ANTENNAL SEGMENT PROMOTOR MUSCLES

FIGS. 19, 22

Far and away the heaviest musculature of the anterodorsal region of the white shrimp is that concerned with the antennae. The dorsal-most of these is a large, flat muscle originating in connective tissue slightly laterad of the postrostrum (fig. 19). This muscle, a second antennal segment promotor muscle, runs anteriorly and laterally to insert in what appears to be a free apodeme just beneath the dorsal rim of the coxopodite. This apodeme is not connected to the coxopodite, but instead (fig. 19) consists of a transverse fascia in which the distal second antennal segment promotor muscle originates. The presence of the free apodeme of the proximal second segment promotor muscle may indicate that the muscle is in reality a first antennal segment (coxopodite) promotor. The free apodeme, however, produces a functional second antennal segment (basipodite) promotor and the muscle is therefore so described. The proximal second segment promotor is evidently the homolog of the musculus promotor II antennae in *Astacus*, *Pandalus*, and *Callinectes*, although in these forms the muscle clearly attaches to the dorsal margin of the coxopodite.

The distal second antennal segment promotor muscle extends the functional connection of the muscle group to the dorsal edge of the second an-

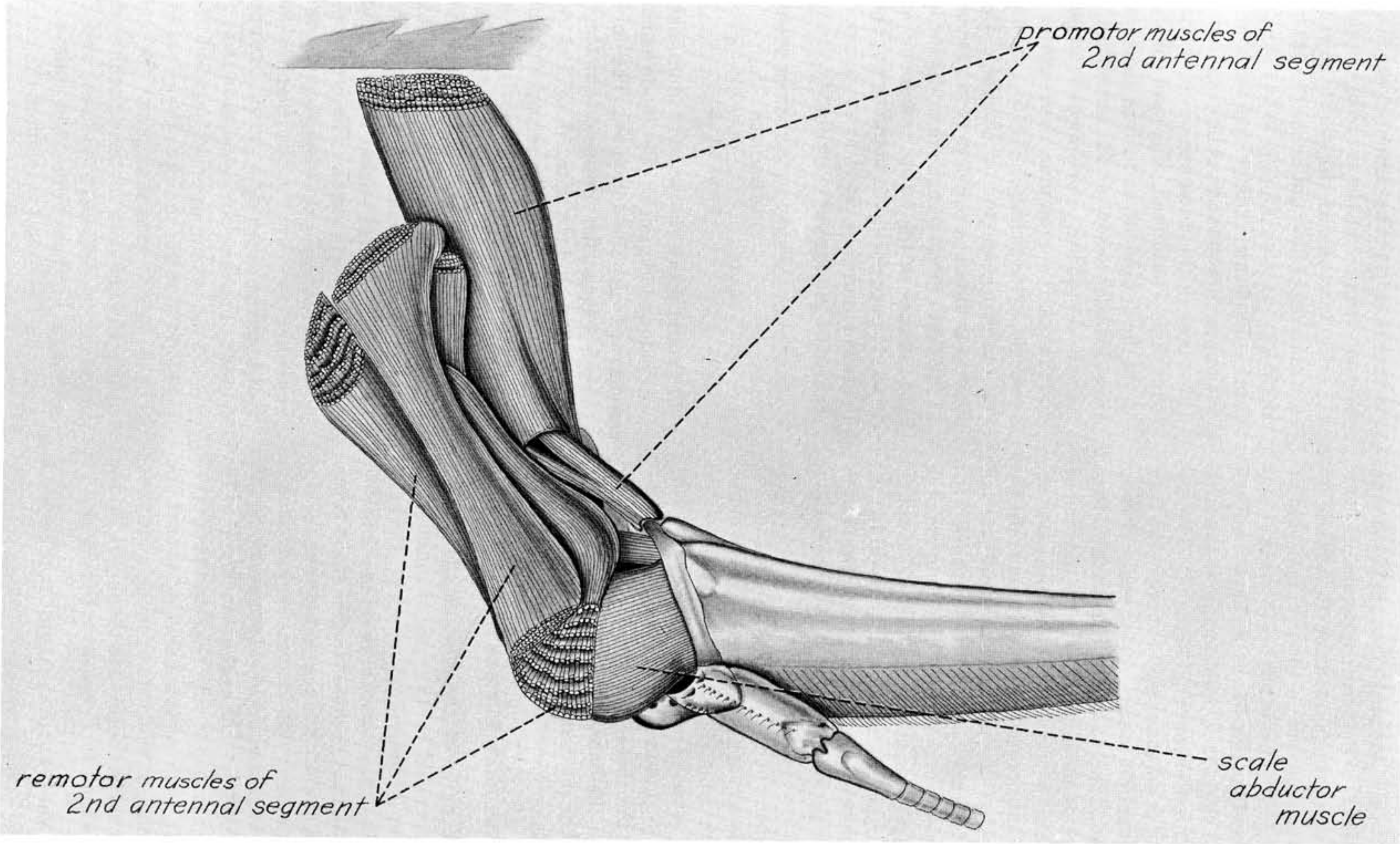

FIGURE 19.—Lateral view of right antenna, carapace and cuticle removed to show muscles.

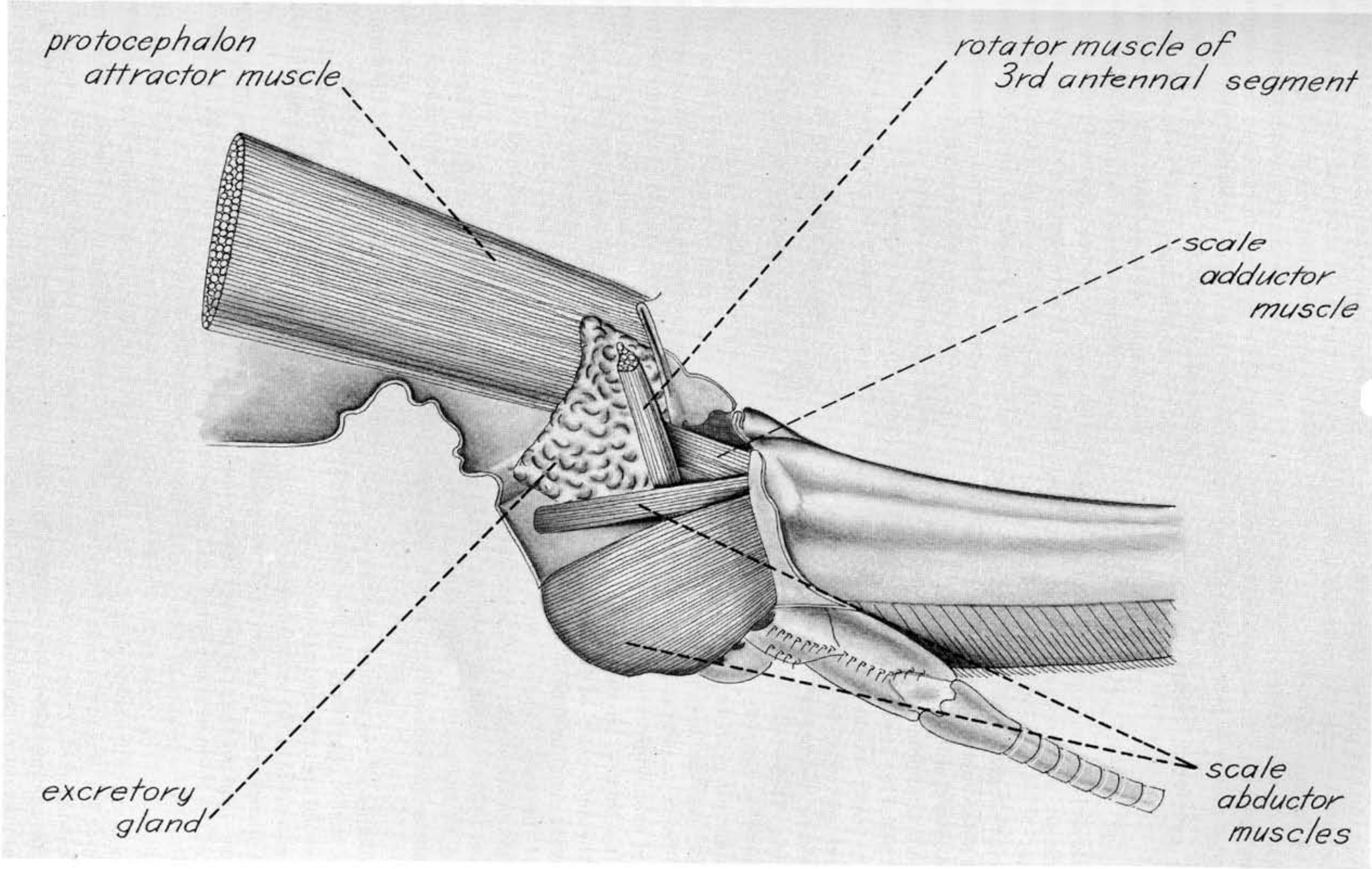

FIGURE 20.—Lateral view of right antenna. Lateral muscles removed to show excretory gland.

tennal segment, or basipodite. Upon contraction the promotor muscles raise the antennal scale and endopodite segments dorsally. The muscles actually function as levators. Without information about the innervation, no homolog of the distal promotor muscle is here suggested.

SECOND ANTENNAL SEGMENT REMOTOR MUSCLES

FIGS. 19, 24

At least three large antennal muscles arise on the dorsolateral carapace just anterior to the hepatic spine. These muscles, here considered the second antennal segment remotor muscles (figs. 19, 24), run anterolaterally to extensive insertion areas in the lateral and posterior regions of the second antennal segment (basipodite). The lateral- and posterior-most of these muscles might be thought to insert on the ventral margin of the first antennal segment, in which case the two muscles would be first segment, or coxopodite, remotor muscles. Repeated dissections in the area indicate otherwise, however, and for this reason the muscles are assigned to the basipodite. The posterior-most remotor displays a definite torsion as it passes from its lateral point of origin to a posterior and even slightly medial insertion area. While the function of all three remotor muscles is actually the depression of the large scale, that of the posterior remotor muscle may also include adduction of the scale, together with depression. Since the antennal scale of *Penaeus* bears a major portion of the weight of water striking the anterior end of the animal, large remotor (depressor) muscles are needed to maintain the scale in position.

The homologies of the second antenna segment remotors is made confusing by the functional muscle nomenclature. A comparison of the function of the antennae in the crawfish and *Penaeus* shows wide differences. The crawfish antennal segments are constructed to permit extension movements of the comparatively short, stiff flagellum. One kind of extreme of this modification has been achieved in the antenna of *Palinurus*, in which form movability is combined with great size and power for the protection of the animal. As has been suggested, the antennal movements of *Penaeus* are comparatively limited by virtue of segmental architecture, particularly in the segments of the protopodite. The heavy musculature of carapace origin is in reality associated with the simple movements of the scale; the muscles of the distal antennal segments of the endopodite are comparatively small.

As a consequence of the many antennal functions in different crustaceans, homologous muscles have different functions and nomenclature. At least part of the second antennal segment remotor muscle mass in *Penaeus* is undoubtedly homologous with the musculus remotor II antennae in *Astacus*, *Pandalus*, and *Callinectes*. Part also may be homologous with the musculus depressor *c* II antennae in *Astacus* and perhaps even with a part of the large musculus depressor *c* II antennae in *Pandalus*, although certainly the major part of the antennal depressor *c* in *Pandalus* is the protocephalon attractor muscle. The other antennal depressor muscles, *a*, *b*, and *d* (*d* is not found in *Pandalus*) in *Astacus* and *Pandalus* are not evident in *Penaeus*.

SCALE ABDUCTOR MUSCLES

FIGURES 19, 20, 24

Taking origin from large areas to the posterior, ventral, and medial region of the second antennal segment (basipodite), the proximal scale abductor muscles (figs. 19, 20, 24) insert on the lateral margin of the antennal scale (exopodite), lateral to the dorsoventral scale condyles. In addition to the huge ventral scale abductor, at least two and probably three small-scale abductors (figs. 20, 24) are found in the second antennal segment of *Penaeus*. A long, distal scale abductor muscle (fig. 24, *B*), originating in the distal part of the scale, runs proximally along the lateral margin of the scale to insert on the lateral margin of the basipodite foramen, lateral to the axis of the scale condyles. When the scale abductor muscles contract, the large scale is swung laterally some distance. The functional reason for this movement is not clear. Shrimps in an aquarium occasionally spread the scales, at times in association with cleaning activities of the head appendages and a sudden flushing out of the gill chamber.

The proximal scale abductor muscles of *Penaeus* are probably homologous with the second antennal exopodite abductor muscles *a*, *b*, and *c* in *Astacus* and with the single exopodite abductor in *Pandalus*. The scale is reduced in *Callinectes*. Schmidt (1915) does not show a distal scale abductor muscle in *Astacus* such as exists in *Penaeus*, and Berkeley (1928) makes no mention of the muscle

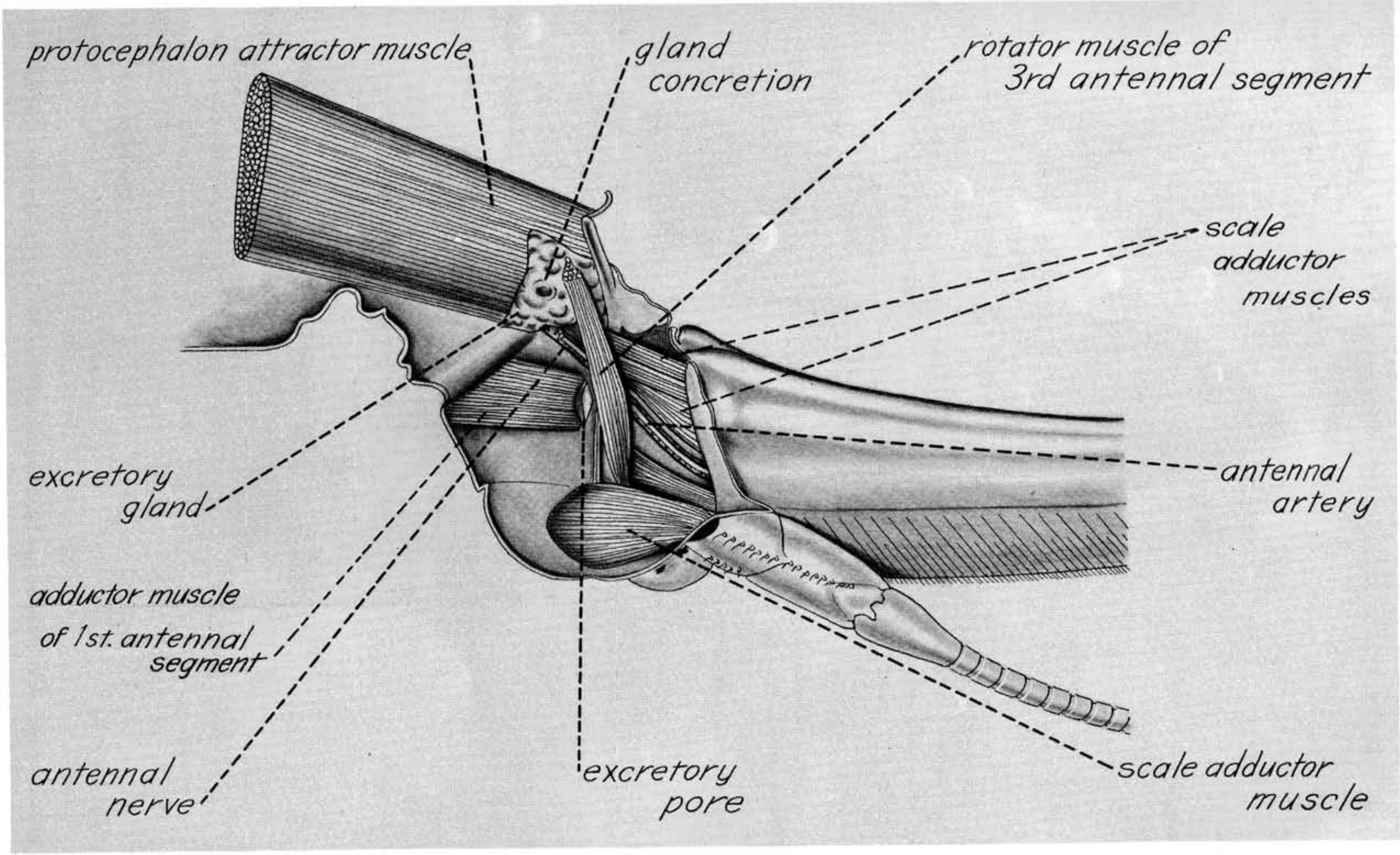

FIGURE 21.—Lateral view of right antenna. Lateral muscles removed to show medial muscles, nerves, and arteries. Part of excretory gland removed to show gland concretion.

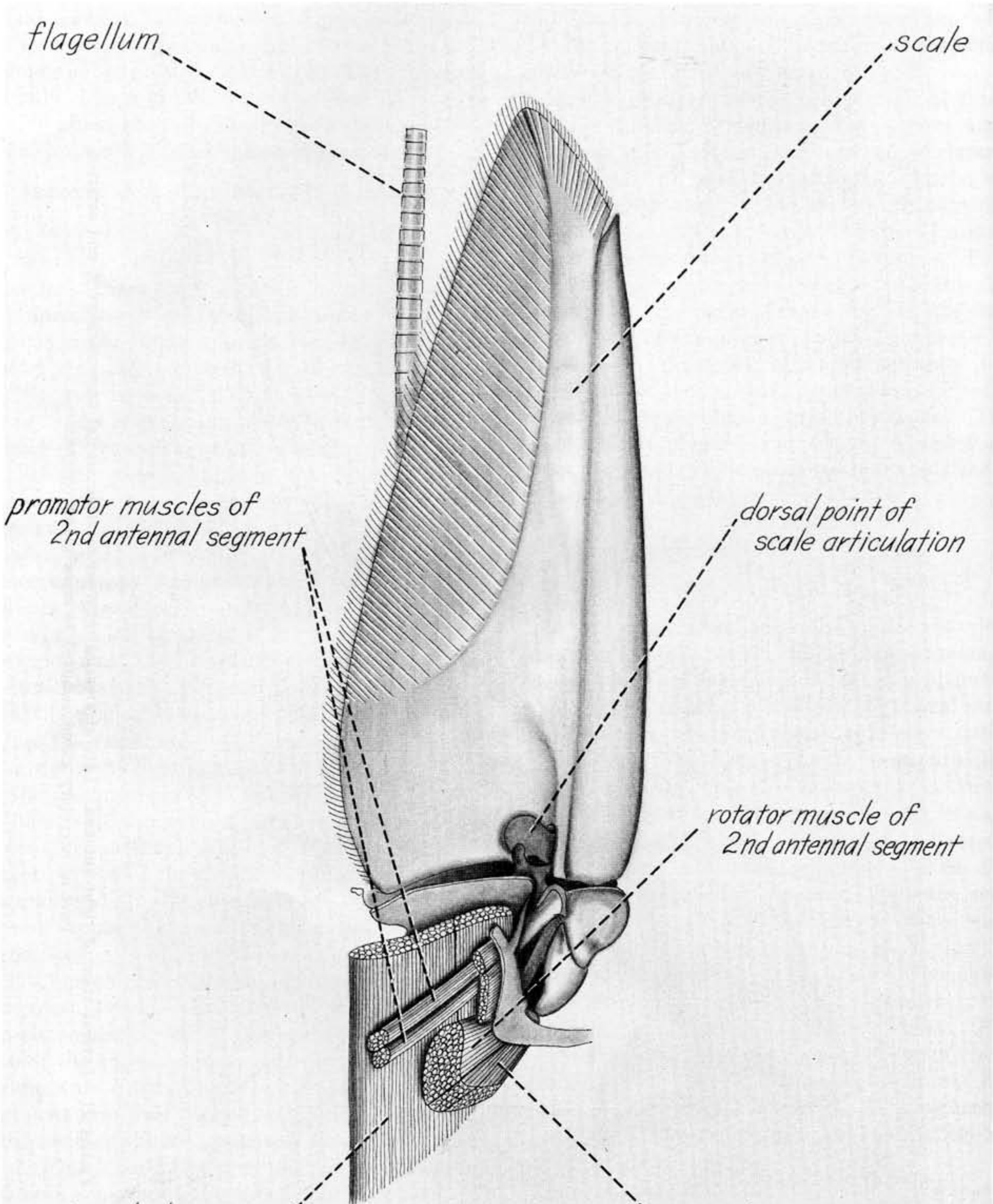

FIGURE 22.—Dorsal view of right antenna showing antennal scale and protopodite muscles. Carapace removed.

in *Pandalus*. However, Berkeley illustrates a distal scale muscle which she designates as the musculus adductor exopoditis *b* II antennae and which from the standpoint of its arrangement appears to be the distal scale abductor muscle in *Penaeus*. A careful review of the insertion of Berkeley's exopodite adductor muscle might show that it is in reality an abductor muscle.

SCALE ADDUCTOR MUSCLES

FIGURES 20, 21, 24

Two types of scale adductor muscles (figs. 20, 21, 24) are found in the antenna of *Penaeus*. At least two scale adductors originate on the medial wall of the second antennal segment ventral to the excretory pore (fig. 24, *B*), and run diagonally to insertion points on the ventral and medial margins of the scale foramen. Their insertions are mesad of the axis of the scale condyles. The distal scale adductor muscle (fig. 24, *B*), like the distal scale abductor, is located in the body of the scale. It originates in the distal region of the exopodite and runs caudad parallel to the distal scale abductor to insert on the margin of the basipodite foramen mesad of the scale articles. Upon contraction, the scale adductor muscles move the antennal scale inward toward the median line of the shrimp, in opposition to the action of the scale abductors.

THIRD ANTENNAL SEGMENT ROTATOR MUSCLE

FIGURES 20, 21, 24

Arising on the dorsomedial rim of the first antennal segment (coxopodite) foramen and running ventro-medially, the third antennal segment rotator muscle (figs. 20, 21, 24) inserts on an apodeme located on the lateral margin of the third antennal segment (figs. 23, 24). Contractions of the muscle accomplish the movement described in the section on the skeletal elements, namely, lateral rotation of the third antennal segment and the antennal parts distal to the third segment.

The homologs of this muscle in the other crustaceans referred to are not clear. The best possibility in *Astacus* is one or both of the meropodite muscles *a* and *b*. On the basis of area of insertion, the most likely homologs is the musculus meropoditis *a*, although the third segment rotator in *Penaeus* and the meropodite muscle *a* in *Astacus* have different origins, the latter being in the basipodite of the crawfish antenna. The meropodite muscle in *Pandalus* is more nearly similar to the situation in *Penaeus* than in *Astacus*. In both *Astacus* and *Pandalus*, Schmidt (1915) and Berkeley (1928) illustrate a muscle, the musculus reductor ischiopoditis II antennae, said to oppose the action of the meropodite muscles *a* and *b*. No similar muscle has been found in *Penaeus*, although the shrimp may have a functional analog in the fourth antennal segment adductors.

FOURTH ANTENNAL SEGMENT ADDUCTOR MUSCLE

FIGURE 24

The fourth antennal segment adductor muscle (fig. 24) originates in a broad fan on the ventral surface of the basipodite. The muscle runs anterodorsally, narrowing to its apex at its point of insertion on a small, movable article presumed to be a part of the fourth antennal segment. Certainly a muscle originating on the basipodite and inserting on the fourth antennal segment is unusual. Controversy could be avoided by assigning the small, movable article to which this muscle inserts to the third antennal segment; however, the movable article appears to be widely separated from the third segment and instead is lateral to the fourth segment and clearly connected to it. When the fourth segment adductor muscle contracts, the movable article is drawn posteroventrally with the result that the fourth antennal segment is rotated upon the third segment and turned a short distance mesad. As such, the fourth segment adductor represents in part an opposing muscle to the third segment rotator muscle. The homology of this muscle is uncertain.

FOURTH ANTENNAL SEGMENT ABDUCTOR MUSCLE

FIGURE 24

Originating from a broad area slightly posterior to the origin of the fourth segment adductor muscle, the fourth antennal segment abductor muscle (fig. 24) runs to an insertion on the same small movable article of the fourth antennal segment to which the fourth segment adductor attaches. The fourth segment abductor is much larger than the fourth segment adductor. Upon contraction the fourth antennal segment abductor reinforces the action of the fourth segment ad-

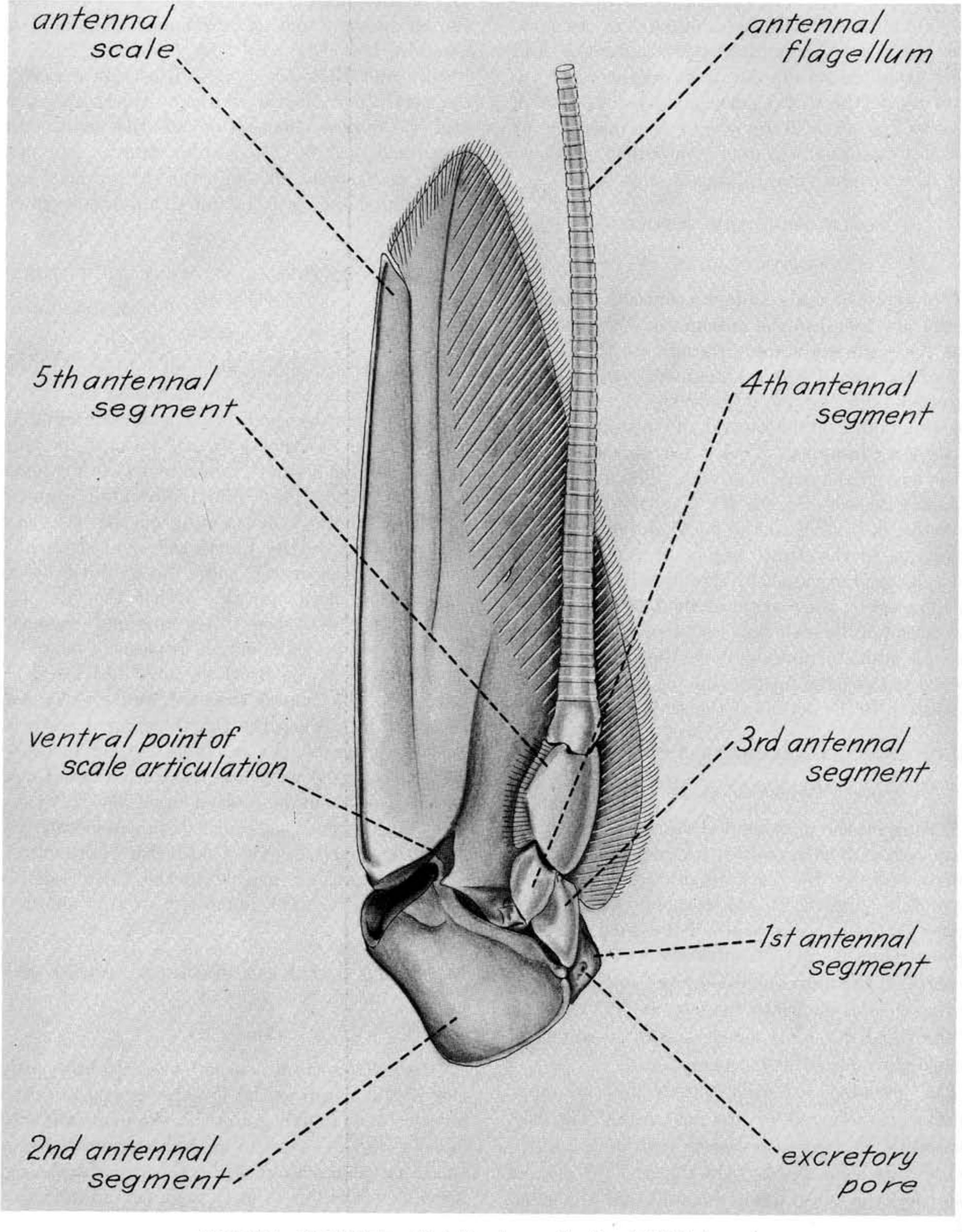

FIGURE 23.—Ventral view of right antenna showing skeletal elements.

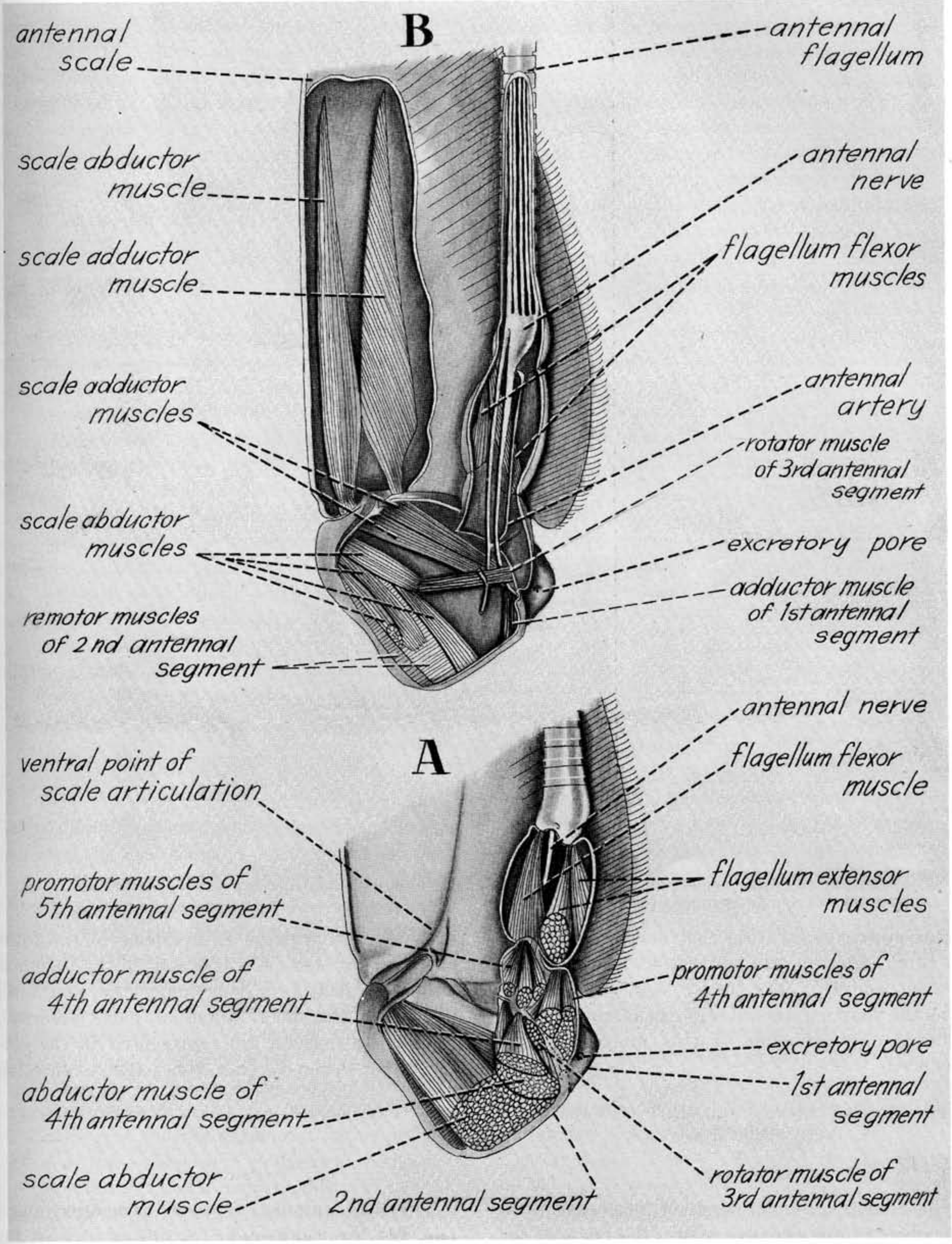

FIGURE 24.—Ventral view of right antenna showing ventral muscles, nerves, and blood vessels. Ventral cuticle removed. *A*. Superficial ventral elements. *B*. Dorsal elements.

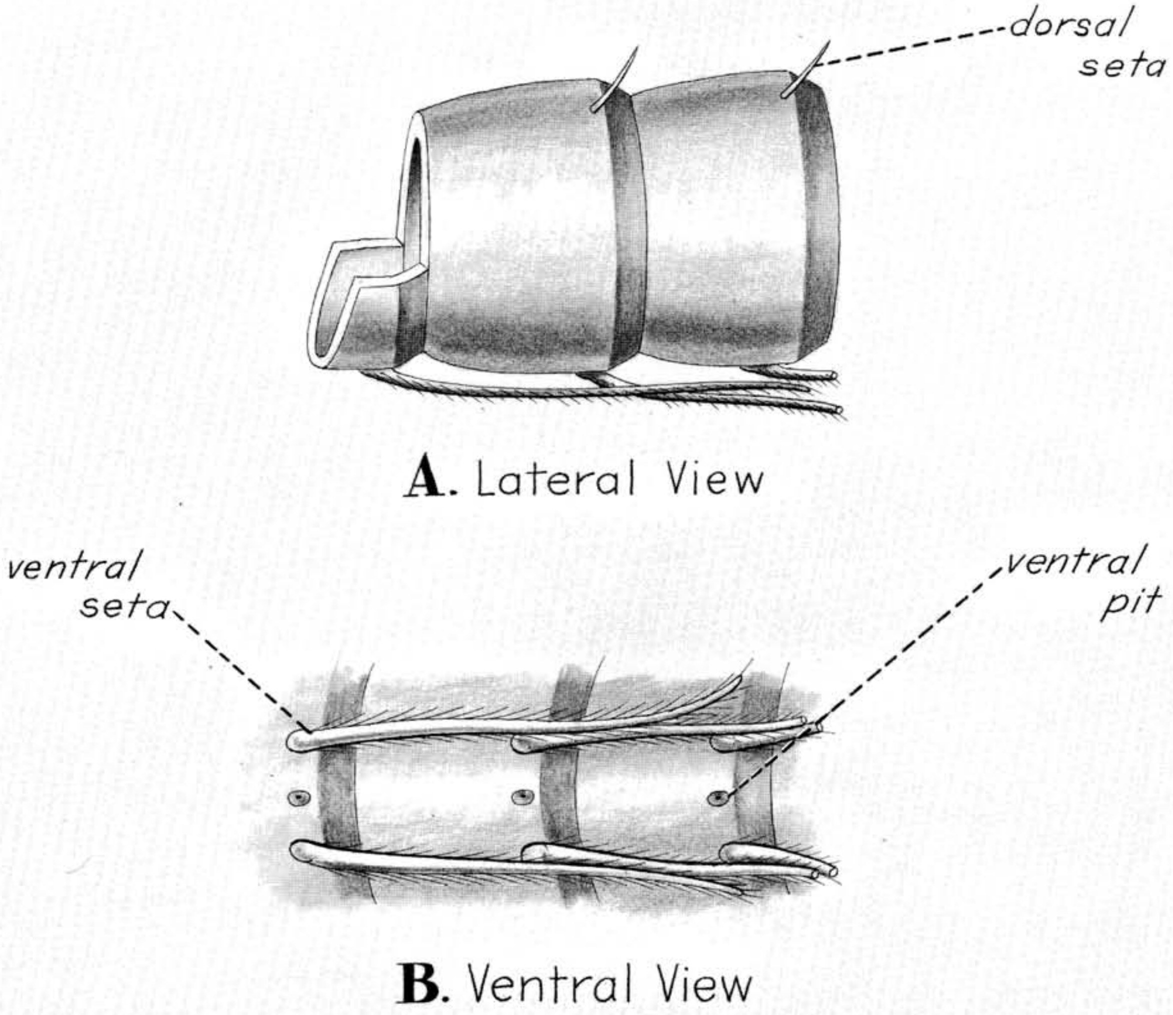

FIGURE 25.—Enlargement of proximal segments of antennal flagellum showing sensory structures.

ductor muscle in rotating the fourth segment on the third segment. In opposition to the fourth segment adductor, the fourth segment abductor turns the fourth antennal segment laterad a short distance. No homolog of this muscle is here advanced.

FOURTH ANTENNAL SEGMENT PROMOTOR MUSCLES

FIGURE 24

The fourth antennal segment promotor muscles (fig. 24) are situated within the body of the third antennal segment. At least three of these muscles occur in *Penaeus*. The short, thick promotors originate throughout the ventral surface of the third antennal segment and insert at their narrow apical tips on an apodeme of the fourth antennal segment. Contractions of the fourth antennal segment promotors move the fourth segment and the distal antennal parts anteriorly. How these muscles are represented in the other crustaceans referred to in this paper is uncertain.

FIFTH ANTENNAL SEGMENT PROMOTOR MUSCLES

FIGURE 24

The fifth antennal segment promotor muscles (fig. 24) are comprised of a tuft of at least four small muscles restricted to the fourth antennal segment. The muscles originate on the lateral and posterior margin of the fourth article and attach to an apodeme arising from the posterior groove of the fifth antennal segment. Contractions of the fifth segment promotors move the fifth antennal segment anteriorly in a limited way. The homolog of these muscles in *Astacus* is very like the musculus extensor propoditis II antennae. Berkeley (1928) does not find the muscle in *Pandalus*.

FLAGELLUM EXTENSION MUSCLES

FIGURE 24

The fifth antennal segment of *Penaeus* contains two flagellum extensor muscles (fig. 24), occupying the medial half of the segment. One of the flagellum extensors originates on the medial side of the fifth segment and runs distally to insert on the large extensor apodeme on the medial side of the flagellum base. The second extensor takes origin on the posteroventral region of the fifth segment, runs distally, and inserts on the large extensor apodeme on the flagellum. These muscles bring the base of the flagellum directly anterior to the proximal antennal segments. One or both of these muscles is undoubtedly homologous with the antennal dactylopodite extensor muscle as shown by Schmidt (1915) in *Astacus* and by Berkeley (1928) in *Pandalus*. The related muscle, if any, in *Callinectes* is uncertain without adequate information about the nerves.

FLAGELLUM FLEXOR MUSCLES

FIGURE 24

Three flagellum flexor muscles in the fifth antennal segment of *Penaeus* turn the antennal flagellum to its normal position at right angles to the proximal antennal segments. The largest and ventral-most of these muscles originates broadly along the proximal groove of the fifth segment and inserts on the flexor apodeme on the flagellum base. Dorsal to the large muscle, two flagellum flexor muscles insert on the same flexor apodeme on the flagellum. The dorsolateral flagellum flexor originates in the lateral corner of the fifth segment, the dorsomedial flexor originating in the medial corner of the fifth antennal segment. At least one of these muscles in *Penaeus* is the homolog of the musculus flexor dactylopoditis II antennae in *Astacus* and *Pandalus*. Whether homologs exist in *Callinectes* is not known.

4. LABRUM

The labrum is the final component of the protocephalon to be considered. In all arthropods the labrum is a lobe or sac suspended over the mouth from a sclerotized region of the head known as the epistome (the hexapod clypeus). Crustacean morphologists ordinarily do not consider the labrum an appendage. Most workers consider the labrum an unpaired structure. Some students of Crustacea place the epistome as the ventral element of a preoral, premandibular segment, behind the eyes, antennules, and antennae, in the order of their occurrence in many adult crustaceans. Others have even assigned the epistome to the sternum of the antennal or mandibular segments, giving the labrum an utterly indefensible postoral position.

The position of the epistome and labrum in adult arthropods is variable. In some crustaceans, like the adult isopods and amphipods, and in most insects, the epistome is anterior or facial (Snodgrass 1951). The labrum thus is ventral or anterior to it. However, in most crustaceans, some chilopods, and a few insects the head segments have thrust forward, overgrowing the epistome anteriorly. The result is a secondary ventral position of the epistome and labrum in some arthropods. In point of fact, the labrum is the anterior end of the arthropod. I am in full agreement with Snodgrass (1951) in this view. Furthermore, the labrum is here considered not only the most anterior part of the arthropod, but also the anterodorsal "upper lip" of these forms, and as such the dorsal part of the first segment. Considerable support for this interpretation has been adduced by Ferris (1947) and Henry (1948a), based on the study of the labral nerves.

If we accept the view of various workers, including Henry (1948a), that the tritocerebrum of arthropods is in reality the first ganglion of the ventral nerve cord, whatever its fate in the adult, then we are bound to regard structures innervated by tritocerebral nerves as primitively anterior. Since the labrum of *Penaeus* is clearly innervated by a pair of nerves from the tritocerebral ganglia (figs. 27, 76), similar to the situation in other Crustacea and Insecta (Henry 1948a, 1948b), then the labrum is segment 1 in *Penaeus*.

No evidence is here advanced to suggest that the labrum is a reduced appendage. Indeed, this ancient "upper lip" was probably never an arthroappendage in the true sense at any time in its history. The labrum is, however, very likely paired. In support of this is the morphology of the nerves and muscles. The labral nerves are paired and arise from the clearly bilateral tritocerebral ganglia. Each nerve enters the sac of the labrum and innervates only those sensoria and muscles in half the labrum from the medium sagittal plane laterad. In *Penaeus* no nerve can be seen crossing the median sagittal plane. Furthermore, the embryonic labrum of many higher arthropods (Johannsen and Butt, 1941; Young 1953) develops as a paired structure, with paired coelomic sacs.

SKELETAL ELEMENTS

FIGURES 26, 27

In *Penaeus setiferus* the labrum is a soft, lightly sclerotized sac attached between the widely spread posterolateral bars of the epistomal **Y** (fig. 28, *A*). It may be noted in passing that these lateral epistomal bars are morphologically anterior, although due to rearrangements of the head segments, discussed above, the position of the epistome is reversed in the head of many crustaceans. The anterior or medial bar of the epistome, dividing the antennal foramina, curves anterodorsally to form a deep ventral pit, best seen in lateral view (figs. 28, *A*; 30) of a cleared anterior skeleton cut along the median sagittal plane. To the epistomal invagination, or apodeme, is attached a pair of muscles to be discussed below.

The labrum is shaped to fit between the antennal bases anteriorly and the incisor and molar surfaces of the mandibles posteriorly (figs. 26, *A*, *B*). Various auricles and lobes project from the labral surface to enhance its function as an aid in feeding. A toothed structure, the posterior feeding process (figs. 26, 27), projects directly into the mouth aperture.

MUSCLE ELEMENTS

EPISTOMAL STATOR MUSCLES

FIGURES 5, 6, 30, 34

Originating on the dorsal surface of the carapace, lateral to the posterior protocephalon levator muscles, and converging on the anterior side of the epistomal invagination is a pair of small muscles which are named in the present work the epistomal stator muscles (figs. 5, 6). The name derives from the fact that contractions of the muscles would appear to hold the epistomal invagination in position during the contraction of other muscles in the area. The epistomal stator muscles are homologous with the musculus oculi basalis posterior in *Pandalus*, *Astacus*, and probably in *Callinectes*.

Giving the name, epistomal stators, to these muscles may be adding confusion to the morphological scene, since these muscles are undoubtedly the musculus attractor sincipitis described by Grobben (1919) in the stomatopod *Squilla mantis* and the muscle attracteur du synciput illustrated by Mayrat (1955, 1956a, 1956b) in *Praunus flexuosus* O. F. Müller. The "sincipit" (Mayrat spells it "synciput") of Grobben (1917) is of course the protocephalon of Snodgrass (1951) as applied to the Crustacea. No great objection is offered here to designating the muscles in *Squilla* and *Praunus* as the synciput attractors. The muscles are indeed synciput or protocephalon muscles apparently functioning in certain forms to draw the protocephalon posteriorly. However, the same muscles in *Penaeus* do not attract the protocephalon. Furthermore they insert on a specific region of the protocephalon, the epistome, and so deserve as special a name as possible. The problem can be resolved by a study of the nerves, for if the epistomal stator muscles belong to the epistome, they should be innervated by epistomal or clypeal nerves.

LABRAL MUSCLES

FIGURE 27

One of the most astonishing features of the anatomy of *Penaeus setiferus* is the musculature of the labrum. In the generalized insect labrum, the structure is moved by two pairs of extrinsic muscles, the anterior and posterior labral muscles arranged for production and reduction. To the intrinsic labral compressor muscles of insects may be assigned various functions. In contrast, a review of general and special accounts of the anatomy of Crustacea has shown no reference to labral muscles in this class. Yet the labrum of *Penaeus* (fig. 27) is operated by at least 12 pairs of intrinsic muscles, bilaterally situated, and at least 1 intrinsic muscle running across the entire lobe. From their arrangement, the labral muscles obviously distort the labrum in all sorts of ways in the function of the organ as a tongue. In addition, at least 2 pairs of extrinsic muscles insert on the edge of the labral foramen to move the entire organ. No attempt has been made here to assign functional muscle names to the individual labral muscles.

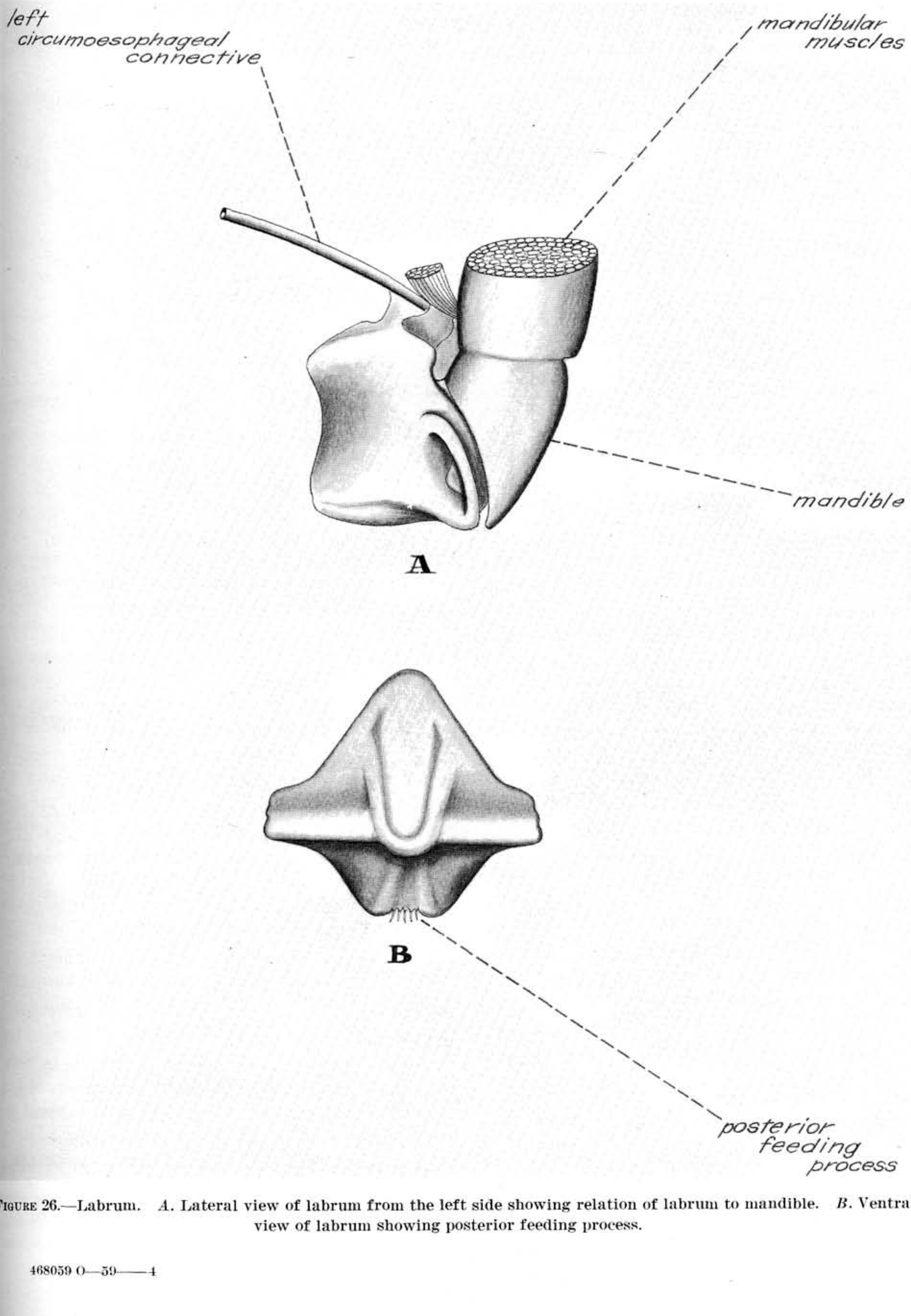

FIGURE 26.—Labrum. *A*. Lateral view of labrum from the left side showing relation of labrum to mandible. *B*. Ventral view of labrum showing posterior feeding process.

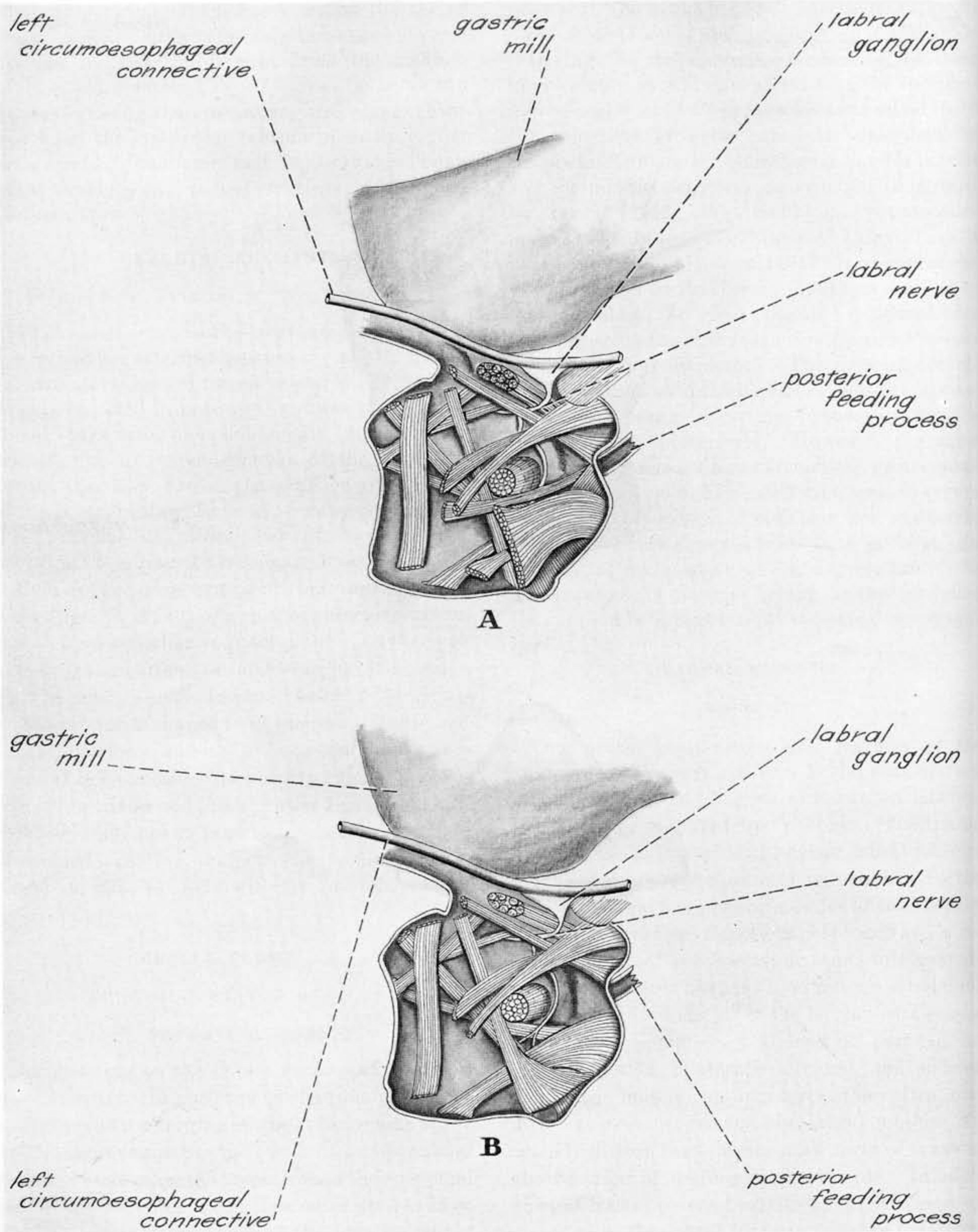

FIGURE 27.—Lateral views of labrum from the left side showing muscles and nerves. *A*. Cuticle removed to show superficial lateral muscles of left side. *B*. Interior muscles of labrum.

Although not shown in the illustrations of the labrum, material of a glandular nature is found in median ventral regions of the structure. Gland cells in the crustacean labrum have been described in the past.

B. Gnathothorax

The gnathothorax will be considered here as those segments following the protocephalon involved primarily with feeding and walking. The latter are not truly separable as body tagmata in the Crustacea, since after the mandibles and maxillae, varying numbers of walking legs may be adapted for feeding (Snodgrass 1951). Walking legs adapted for feeding are referred to as maxillipeds. In the Crustacea Decapoda, the gnathothorax is comprised of the mandibles, paragnatha, 2 pairs of maxillae, 3 pairs of maxillipeds, and 5 pairs of walking legs. In the present study, the gnathal segments will include the maxillipeds, and to the thorax will be assigned the five walking legs, without implying any morphological rigidity to the division. Above and to the sides, the gnathothorax is protected by the large dorsal shield, or carapace. Nearly all trace of segmentation has disappeared from the dorsal regions of the gnathothorax and the carapace. The few remaining sutures and markings of the carapace are not well understood in the Crustacea; consequently systematic nomenclature which has grown up around these devices is highly artificial.

The gnathothorax is constructed in the form of a rather special box arranged to provide both rigidity and movability. The immobile carapace is heavily sclerotized for protection of the internal organs and support of muscle origins, and extends ventrad in a deep fold of the tergum to cover completely the laterally placed gills (figs. 30, 31). The lateral carapace is called the branchiostegite, since the structure forms a chamber for the gills. The deep fold of the rigid carapace forming the branchiostegite permits movement between the carapace and the architecture of the ventral gnathothorax. The whole is reminiscent of a modern sedan in which a rigid body above is attached to a chassis able to respond to imperfections in the road surface. Upon the dorsal carapace orginate numerous important muscles, including some of those of the protocephalon appendages, the mandibles, maxillae, gastric mill, and dorsal and ventral abdominal muscles.

Compared to the ventral skeleton of Astacura and Brachyura, that of *Penaeus* is very lightly sclerotized (Snodgrass 1952; Huxley 1906). In the crawfishes, the median sternal elements are rigidly fused together, except for the sternum of the last thoracic segment, and thus provide a rigid keel from which the pleurosternal arms arise. Pleural (laterotergal) and sternal apodemes arise from the invaginations between the fused arms of two adjacent segmental units. Similar apodemes occur in the same locations in the ventral skeleton of *Penaeus*, but the ventral sternal element of each segmental unit is separated from its neighbors by a transverse slit of thinly developed cuticle (fig. 28). The slits permit movements between segments along the anteroposterior axis of the thorax, even though the lateral pleurosternal arms are fused.

The ventral skeleton of the gnathothorax in *Penaeus* (figs. 28, 30) consists of a series of sclerotized units which are slightly movable with respect to one another, but not articulated (fig. 28). Each unit bears the paired foramina and muscle apodemes of the jointed appendages attached thereto. The typical segmental unit contains contributions from two sources: The tergum, in the form of the dorsal tergum, and the vertical, laterotergal pleural plates (Snodgrass 1952), dorsal to the leg bases, and the sternum which comprises the ventral region between the leg bases. The dorsal condyles of the coxopodites are situated on the laterotergal plates while the ventral coxopodite condyles are sternal. In the anterior region of the gnathothorax of *Penaeus*, the pleural plates lie horizontally to become the roof of the gill chamber, similar to the arrangement in *Cambarus longulus* Girard as shown by Snodgrass (1952).

The delicate nature of the ventral skeleton in *Penaeus* is even more noticeable in lateral view (fig. 28, *A*). From here the pleurosternal arms may be seen to bifurcate in the pleural region and those of each segmental unit tend to unite dorsally in the form of a reverse-curve, or ogee, arch of the architect. Again, compared to the composite pleura of the crawfishes (Snodgrass 1952), those of *Penaeus* appear to have been retained in a somewhat more generalized condition, with 7 or 8 pleura clearly distinguishable from one another (figs. 28, 30).

Huxley (1906), Calman (1909), and other students of Crustacea often refer to the system

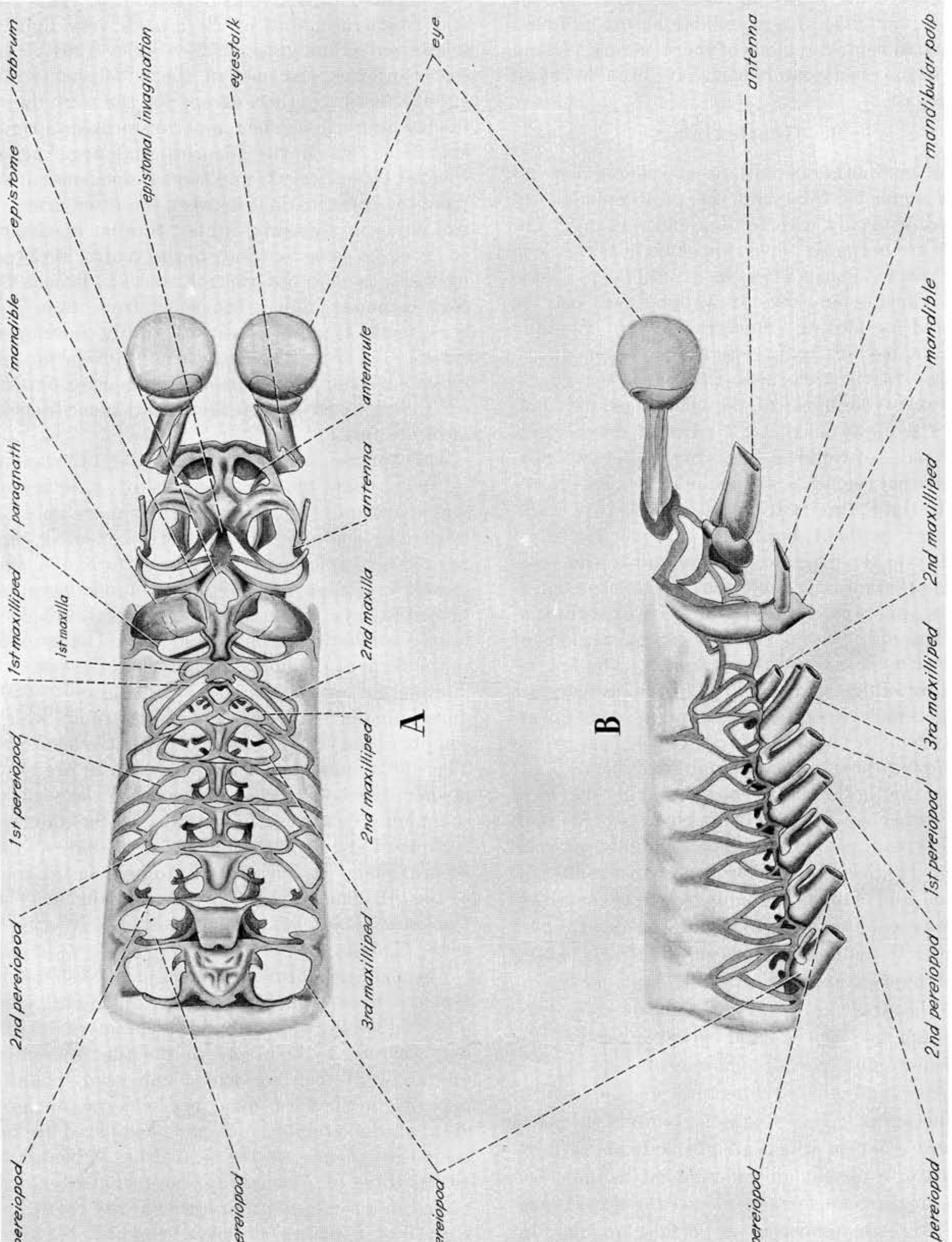

FIGURE 28.—Ventral skeleton of protocephalon and gnathothorax. *A.* Ventral view. *B.* Lateral view of right side.

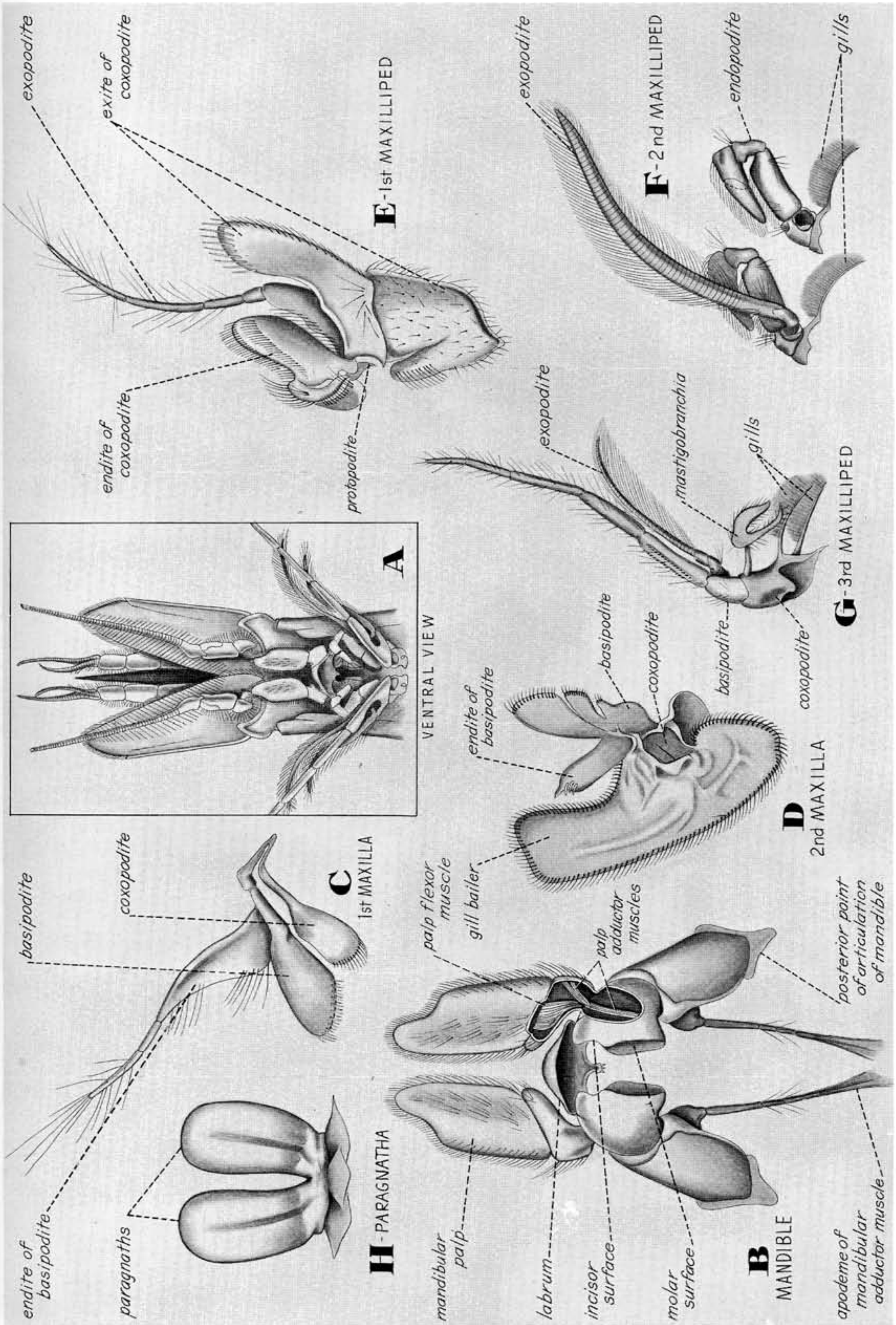

FIGURE 29.—Mouthparts.

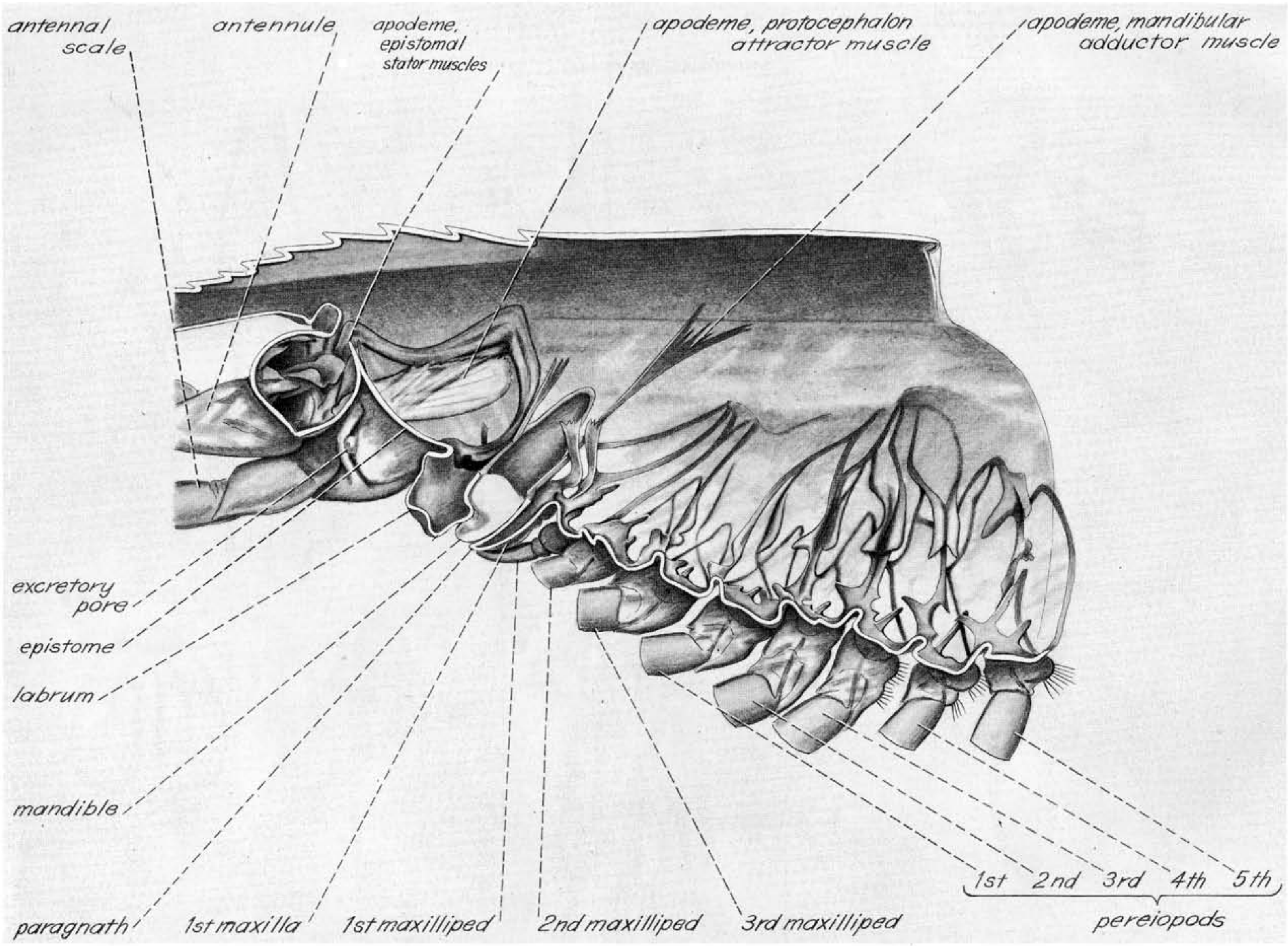

FIGURE 30.—Internal view of right half of protocephalon and gnathothorax.

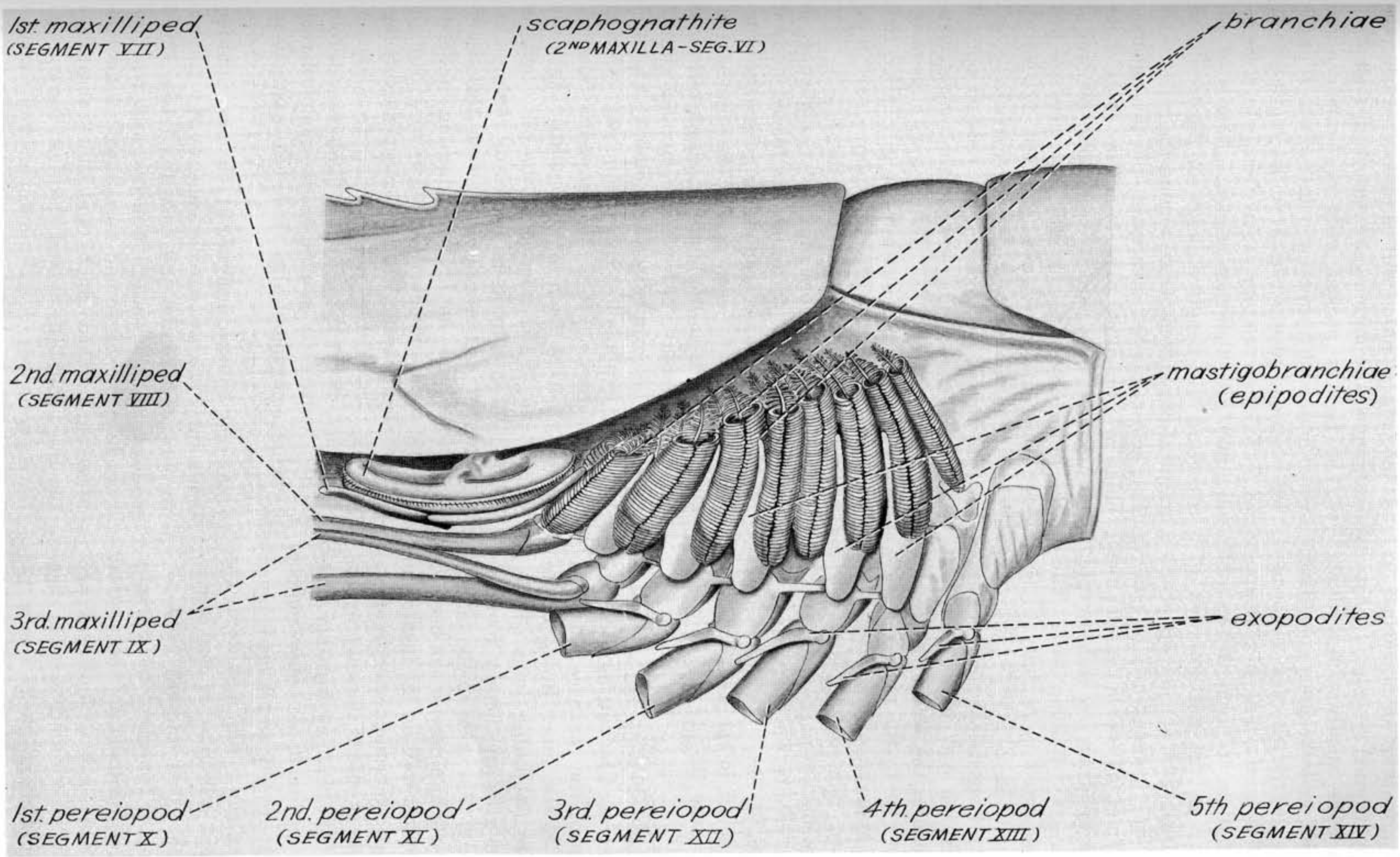

FIGURE 31.—Lateral view of left side of thorax, carapace cut away to show gill chamber, gills, and mastigobranchiae.

of pleurosternal invaginations or apodemes in decapods as the endophragmal system. In Astacura and Brachyura these apodemes fuse internally to form complex endoskeletons consisting of septate structures in the thoracic segments above the ventral nerve cord. The sternal apodemes fuse in the midline to form the sternal furca in the Insecta. In the gnathothorax of *Penaeus* the laterotergal and sternal apodemes are light and do not fuse, consequently no endophragmal system is found, unless we consider the transverse mandibular apodeme (see endosternite, fig. 38) an endophragm of some sort. This structure will be considered more fully in the treatment of the mandibles.

Although the ventral sternal elements of the penaeid gnathothorax are not coalesced into a rigid keel as in Astacura, the sternal plates do broaden from the anterior to the posterior ends of the gnathothorax, and abruptly so in the last three thoracic segments. The sternal plates of the last two thoracic segments are particularly modified in the female to receive the spermatophore from the male (figs. 28, *B;* 89). These structures will be discussed in detail in the section on the reproductive organs, page 155.

Gills

The gills may be exposed by cutting away the branchiostegal region of the carapace along the dorsal-most reaches of the inner lining of the branchiostegite, where the lining joins the laterotergal plates. The gills are thereby found to occupy a chamber (fig. 31), open to the outside ventrally and posteriorly by a narrow slot between the leg bases and thoracic wall on the inside and the extreme margin of the branchiostegite on the outside. The chamber is closed dorsally by the branchiostegal fold. The chamber is rather shallow transversely in its broad, posterior region, but becomes narrow anteriorly and is made much deeper in the region of the second maxilla by the lateral and horizontal reflection of the laterotergal, pleural plates. This narrow, deep, anterior chamber is thus a funnel, closed dorsally by the pleural bridges, medially by the vertical pleural wall, laterally by the branchiostegite, and ventrally by the large, flat coxopodite exites (figs. 29, *E;* 42) of the first maxilliped. Inside the funnel resides a pump, the scaphognathite of the second maxilla (figs. 29, *D;* 31; 41). Details of its mechanical action will be considered when the scaphognathite muscles are described, page 69.

The tightly packed gills or branchiae rise roughly dorsad from their points of origin on the leg bases and pleura (fig. 31). Each gill consists of an axial circulatory rachis from which the individual gill filaments branch. Details of gill structure will be given below in the section on respiration. Interspersed among the gills are six flat, setose, bilobed structures, the mastigobranchiae or epipodites. The lateral margins of the mastigobranchiae may be seen upon removal of the branchiostegite (fig. 31), but they are best seen if the gills are removed (fig. 32). If a shrimp whose branchiostegite has been removed is cooled so that the body processes are reduced but not stopped, the long, fine setae of the mastigobranchiae may be seen to beat in phase with the movements of the scaphognathite, or gill bailer, thus suggesting that the epipodites play a part in the water flow and cleaning of the gills.

The older literature of Crustacea abounds in so-called branchial formulae, the formal study of gill origins. In the decapods the generalized situation is 4 gills for each side of the segment (fig. 32); 1 arises from the laterotergal, pleural plates (pleurobranchia), 2 from an articular element dorsal to the coxopodite (arthrobranchia), and 1 from the coxopodite (podobranchia) (Calman 1909; Snodgrass 1952). The epipodite (mastigobranchia) arises from the coxopodite. As shown by Calman (1909), the use of the gill origins as evolutional landmarks is limited by the practical difficulty of distinguishing between the pleurobranchiae and arthrobranchiae in different species, since ontogenetic changes of gill origin are frequently seen. In fact, evidence exists suggesting that all the gills develop from the appendages, rather than from the limb bases or body wall. Apparently in *Penaeus* the podobranchiae develop embryologically from the mastigobranchiae.

As may be seen in figure 31, the branchial formula for *Penaeus setiferus* consists of 1 tiny arthrobranchia on the first maxilliped (fig. 42); 1 podobranchia, 1 mastigobranchia, and 2 arthrobranchiae on the second maxilliped; 1 mastigobranchia, 2 arthrobranchs, and 1 pleurobranch on the third maxilliped, and the first, second, and third pereiopods; 1 arthrobranchia and 1 pleurobranchia on the fourth pereiopod, and 1 pleurobranch on the fifth walking leg. In a European

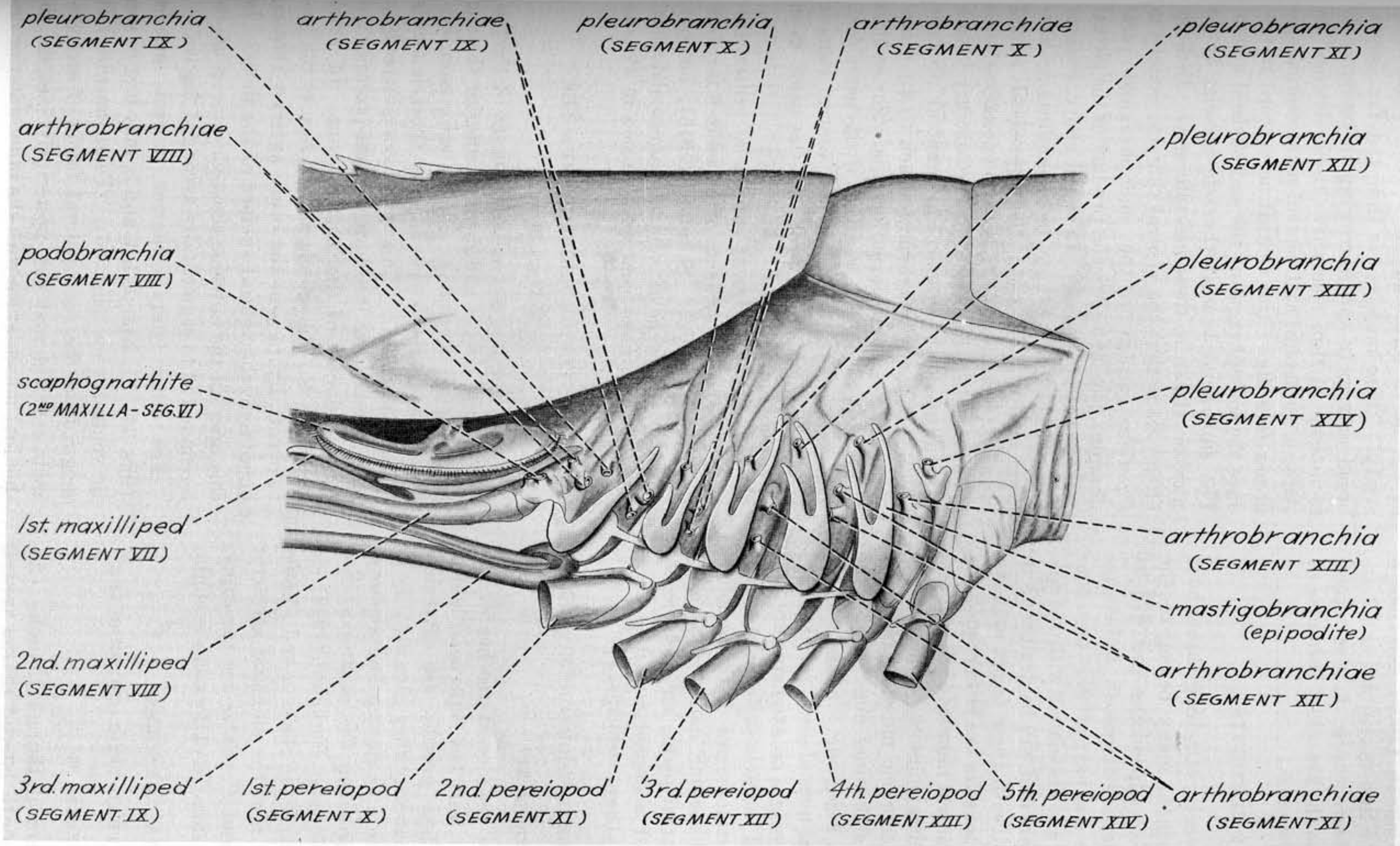

FIGURE 32.—Lateral view of left side of thorax, carapace, and gills removed to show mastigobranchiae and gill attachments.

species of *Penaeus*, Calman (1909) describes a mastigobranchia on the first maxilliped and 1 arthrobranch and 1 pleurobranch on the second maxilliped. Otherwise the branchial formulae of the two penaeids are the same.

MUSCLE ELEMENTS

Of the numerous muscles attaching throughout the gnathothoracic region, many belong to the mouthpart and thoracic appendages and will be taken up when the latter are discussed. Others are protocephalon muscles and have already been considered. Still others are associated with the alimentary canal and heart and will be dealt with in the sections concerned with these organ systems. The many remaining muscles are either small superficial lateral and ventral muscles of the thorax, or large dorsal and ventral muscles. Some of these are morphologically thoracic muscles, and some are morphologically abdominal muscles. In the functional sense, the foregoing muscles may be classified as abdominal musculature, for all of the large muscles taking origin on extensive areas of the dorsal and ventral thoracic skeleton represent the major muscular attachments of the abdomen to the thorax. Substantial movements, especially in the dorsoventral plane, are possible between the thorax and abdomen and it is these muscles which mediate the movements.

SUPERFICIAL LATERAL THORACIC MUSCLES

FIGURE 33

Stretching between the dorsal reaches of the pleural brachia are at least five superficial lateral thoracic muscles. These muscles are extremely thin and weak. Apparently they give rigidity to the thin cuticle of the area during lateral movements of the shrimp along the anteroposterior axis. Schmidt (1915) and Berkeley (1928) do not describe these muscles in *Astacus* and *Pandalus*. The possibility that the epimeral attractor muscles in *Astacus* and *Pandalus* are the superficial lateral thoracic muscles of *Penaeus* is slight.

VENTRAL MUSCLES

SUPERFICIAL VENTRAL THORACIC MUSCLES

FIGURE 36

The superficial ventral thoracic muscles (fig. 36) are situated slightly laterad of the ventral nerve cord. Their median parts are also ventrad of the nerve cord and the ventral (subneural) artery. These muscles are thin and fan shaped, broad anteriorly and narrowing to posterior attachments to thin connective tissue fasciae. In *Astacus* the lateral and ventral pleurosternal apodemes fuse above the ventral nerve cord to produce the mesophragm of the endoskeletal system. The superficial ventral thoracic muscles of the crawfish attach to these mesophragms. Berkeley (1928) finds that the ventral thoracic muscles in *Pandalus* attach to the endophragmal paraphragms, the lateral fusion product of the pleural and sternal apodemes. As stated above, *Penaeus* has neither paraphragm or mesophragm; however, one would expect the superficial ventral muscles to attach to the little pleurosternal apodemes near the limb foramina. Contrary to such expectations, the superficial ventral thoracic muscles in the white shrimp attach to small apodemes on the pleurosternal brachia. The result is to place these muscles ventrad of the nerve cord. Their function of drawing the ventral thoracic segments together is probably the same as in *Pandalus* and *Astacus*.

In *Penaeus* 7 pairs of superficial ventral thoracic muscles are evident compared to 6 for *Astacus* and *Pandalus*. Schmidt (1915), however, finds two superficial ventral thoracoabdominal muscles in *Astacus* compared to one in *Penaeus* and *Pandalus*.

ANTERIOR THORACIC MUSCLES

FIGURES 33 TO 36

By far the largest ventral muscles of the thorax are the lateral and median anterior thoracic muscles (figs. 33 to 36). The anterior-most muscle of these is the lateral anterior thoracic muscle 1 (figs. 33 to 36). This muscle originates by a large, lateral oval in the region just posterior and slightly dorsad of the hepatic spine. In dorsal view (fig. 35) the muscle may be seen to run posteroventrally to join the other anterior thoracic muscles on the ventral surface of the thorax. In this area all the anterior thoracic muscles are interconnected to segmentally arranged fasciae.

The other lateral anterior thoracic muscles (figs. 34, 35), Nos. 2, 3, 4, and 5, may best be seen in ventral view (fig. 36). These muscles take origin from the ventrolateral fascia of each thoracic segment and run posteriorly into the abdominal musculature with the other anterior thoracic muscles.

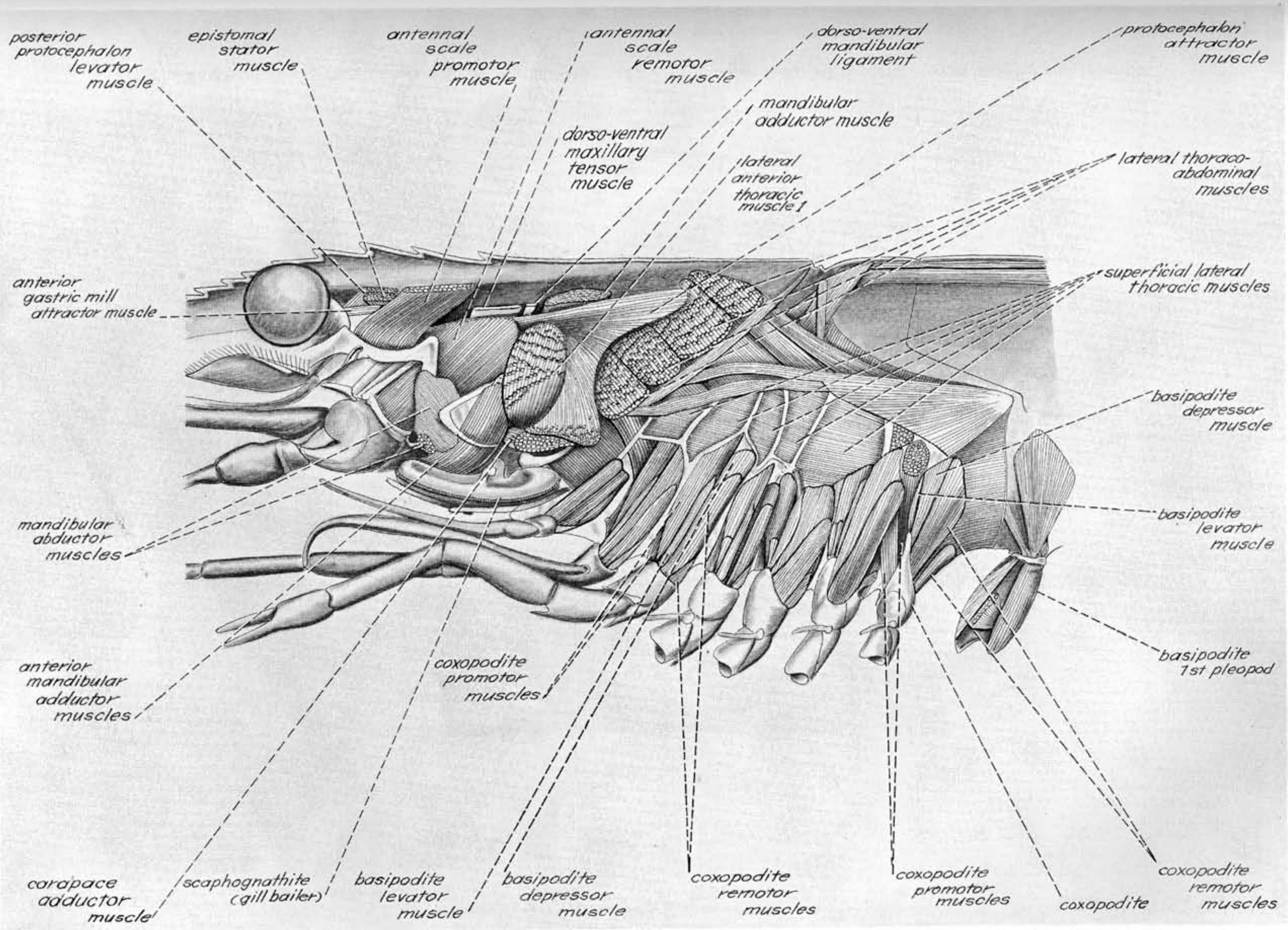

FIGURE 33.—Lateral view of left side of protocephalon and gnathothorax showing muscle origins. Carapace and left body wall removed.

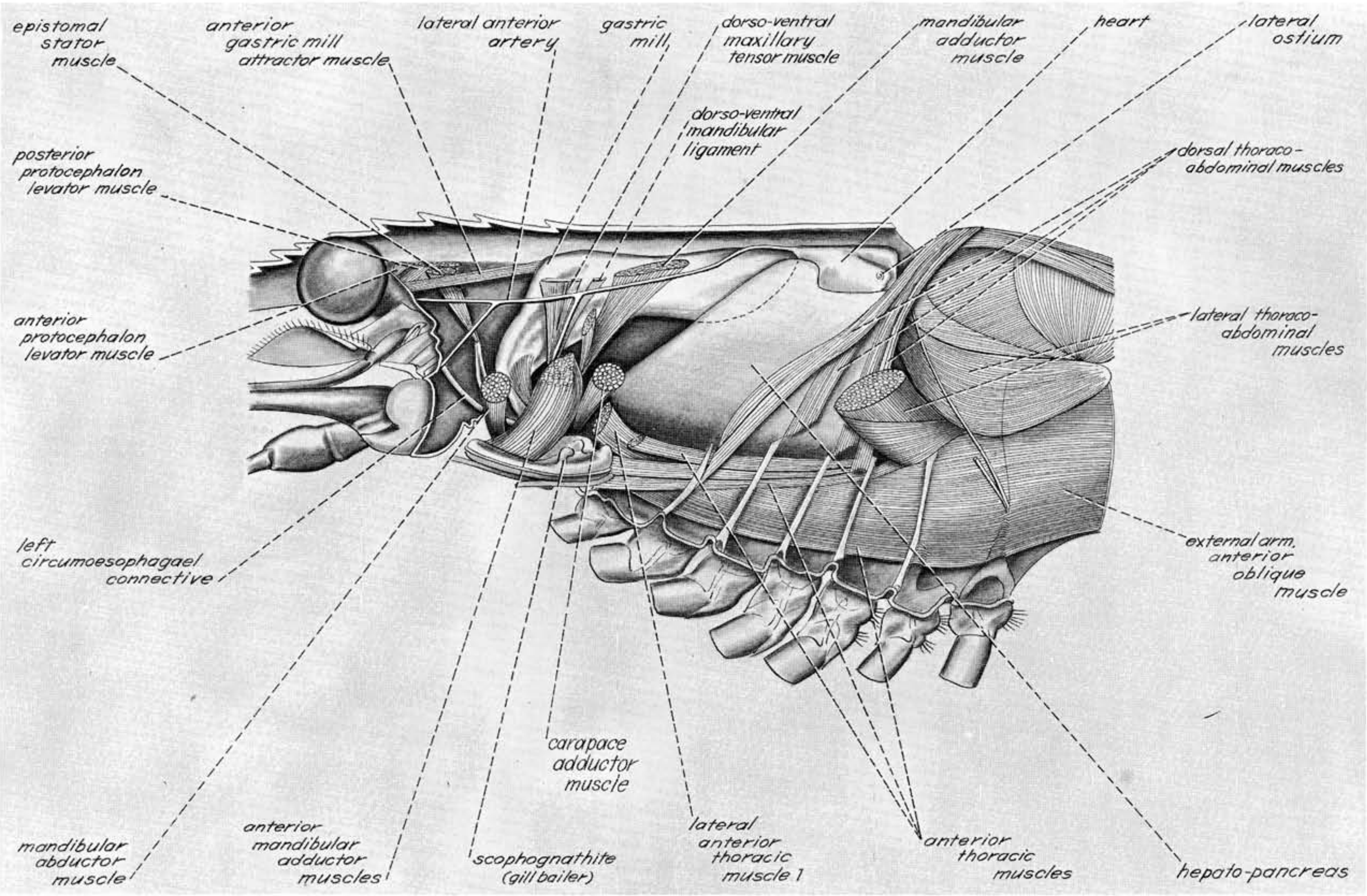

FIGURE 34.—Lateral view of left side of gnathothorax. Lateral muscles removed to show medial muscles and internal organs.

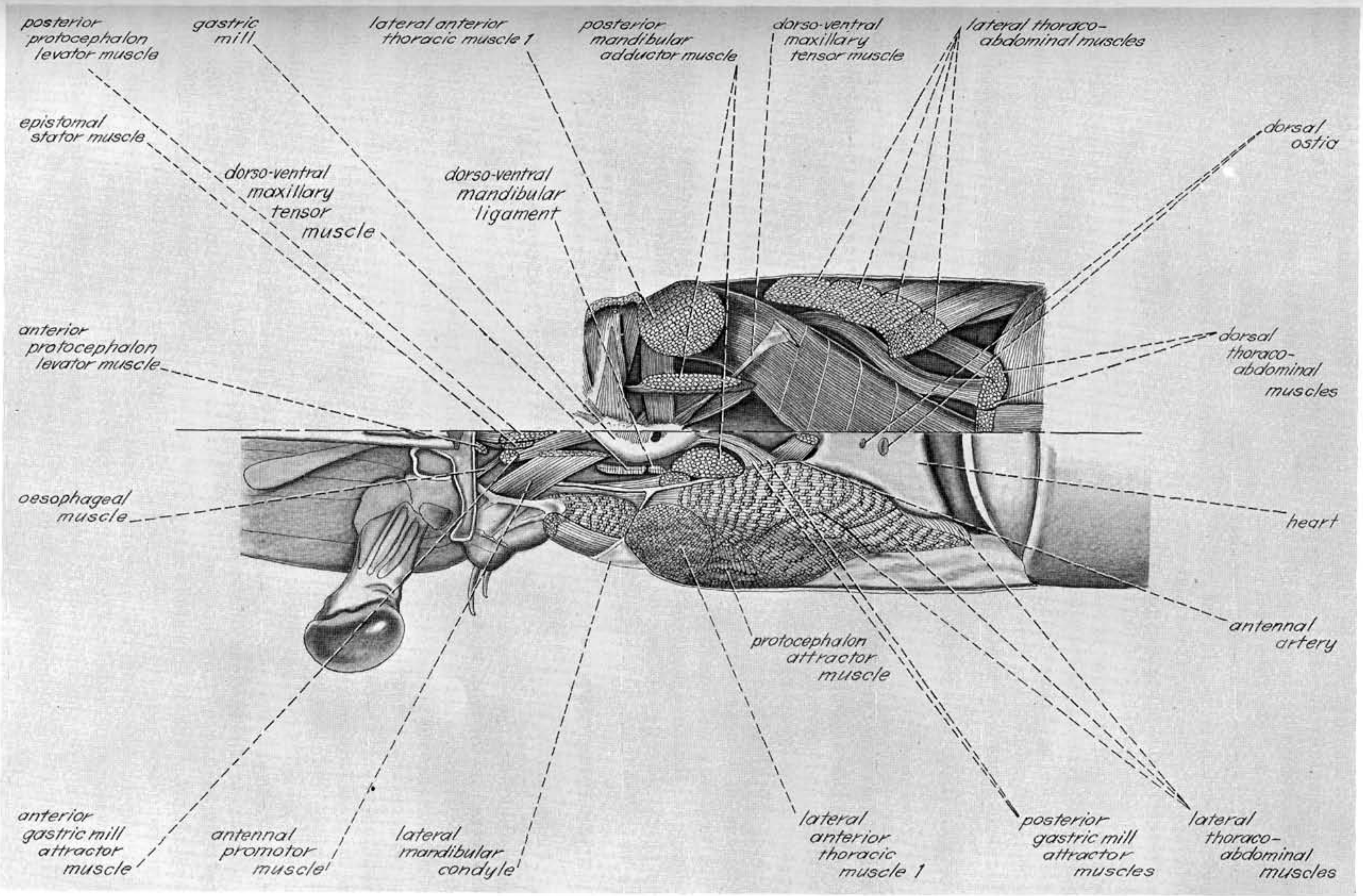

FIGURE 35.—Dorsal views of protocephalon and gnathothorax. Lower section, dorsal muscles. Upper section ventral muscles.

The median anterior thoracic muscles (fig. 36) also originate in segmentally arranged fasciae on the ventral surface. Joined by the other anterior thoracic muscles, the median anterior thoracic muscles pass caudad into the abdominal muscles.

The anterior thoracic muscles play an important part in the powerful flexion of the abdomen on the thorax made by the white shrimps when the animals withdraw suddenly from danger. The anterior thoracic musculature is similar to that in *Pandalus* and *Astacus*, except that in the crawfish these muscles are somewhat smaller. The anterior thoracic muscles are fully homologous in all the forms mentioned here.

VENTRAL HEAD LIGAMENTS

Figures 37, 38

The ventral head ligaments are small structures attached between the lateral wings of the epistome and the mandibular endosternite (fig. 37). Apparently they hold the endosternite in position anteriorly. Schmidt (1915) calls these ligaments the ventral head muscles in *Astacus*. Grobben (1917), however, denies the presence of muscle fibers in the structures and suggests the name ligament for muscle. Berkeley (1928) describes the organs as ventral head muscles in *Pandalus*.

CARAPACE ADDUCTOR MUSCLE

Figures 33, 34, 37, 38

The carapace adductor muscle originates on the carapace just ventrad of the most ventral part of the protocephalon attractor muscle (fig. 33). The origin point of the carapace adductor is slightly dorsal to the horizontally turned pleural plates, above the gill pump, or scaphognathite. The muscle runs directly mesad to insert on the posterodorsal midline of the endosternite (fig. 37). The carapace adductor muscle functions as the major position retainer of the endosternite. It may also play a part in necessary distortions of the carapace associated with feeding, molting, and the like.

The carapace adductor muscle appears in many crustacean groups (Grobben 1917). Schmidt (1915) describes it in *Astacus* as the musculus dorsoventralis posterior and Berkeley (1928) has adopted his terminology for the muscle in *Pandalus danae*. Grobben (1917) considers the carapace adductor a useful phyletic character, because of its frequent occurrence, and we are indebted to this worker for the name. Grobben described the carapace adductor muscle (Schalenschliessermuskel) in species of *Penaeus*, *Palaemon*, *Leander*, *Pandalus*, *Galathea*, and *Athanas*.

DORSAL MUSCLES

DORSAL THORACOABDOMINAL MUSCLES

Figures 34, 35

Inserting on the anterodorsal tergum of the first abdominal segment and running forward and down to the laterotergal brachia of the thorax are four pairs of long, slender muscles, the dorsal thoracoabdominal muscles (figs. 34, 35). In dorsal view (fig. 35) the area of attachment may be seen on the dorsal part of the first abdominal segment. The muscles divide around the heart and hepatopancreas as they go to the lateral wall of the thorax. Each muscle originates on its own pleural arm, suggesting that the muscles each belong to specific thoracic segments. Upon contraction the dorsal thoracoabdominal muscles extend the first abdominal segment with respect to the thorax, in opposition to the action of the anterior thoracic muscles.

The dorsal thoracoabdominal muscles are evidently the same muscles as those designated as the dorsal thoracoabdominal muscles in *Pandalus* and *Astacus*, although they appear to be relatively larger in size in the caridean shrimp.

LATERAL THORACOABDOMINAL MUSCLES

Figures 34, 35

From an area laterad of the heart and the dorsal thoracoabdominal muscles, the lateral thoracoabdominal muscles (figs. 34, 35) originate along a diagonal line just above the dorsal edge of the inner branchiostegal fold and run ventrally and caudad to junctions with abdominal muscles. Very likely the thoracoabdominal muscles are in reality abdominal muscles. Unlike the anterior thoracic muscles, the lateral thoracoabdominal muscles are not segmented. At least four pairs of these muscles covering a broad area laterally are found in *Penaeus*. Functionally, the lateral thoracoabdominal muscles are involved in the flexing of the abdomen, reinforcing the action of the anterior thoracic muscles. Berkeley (1928) suggests that contractions of the muscles on one side may bend the abdomen laterally in *Pandalus*, and such a movement may also take place in *Penaeus*. The lateral thoracoabdominal muscles of *Penaeus* are

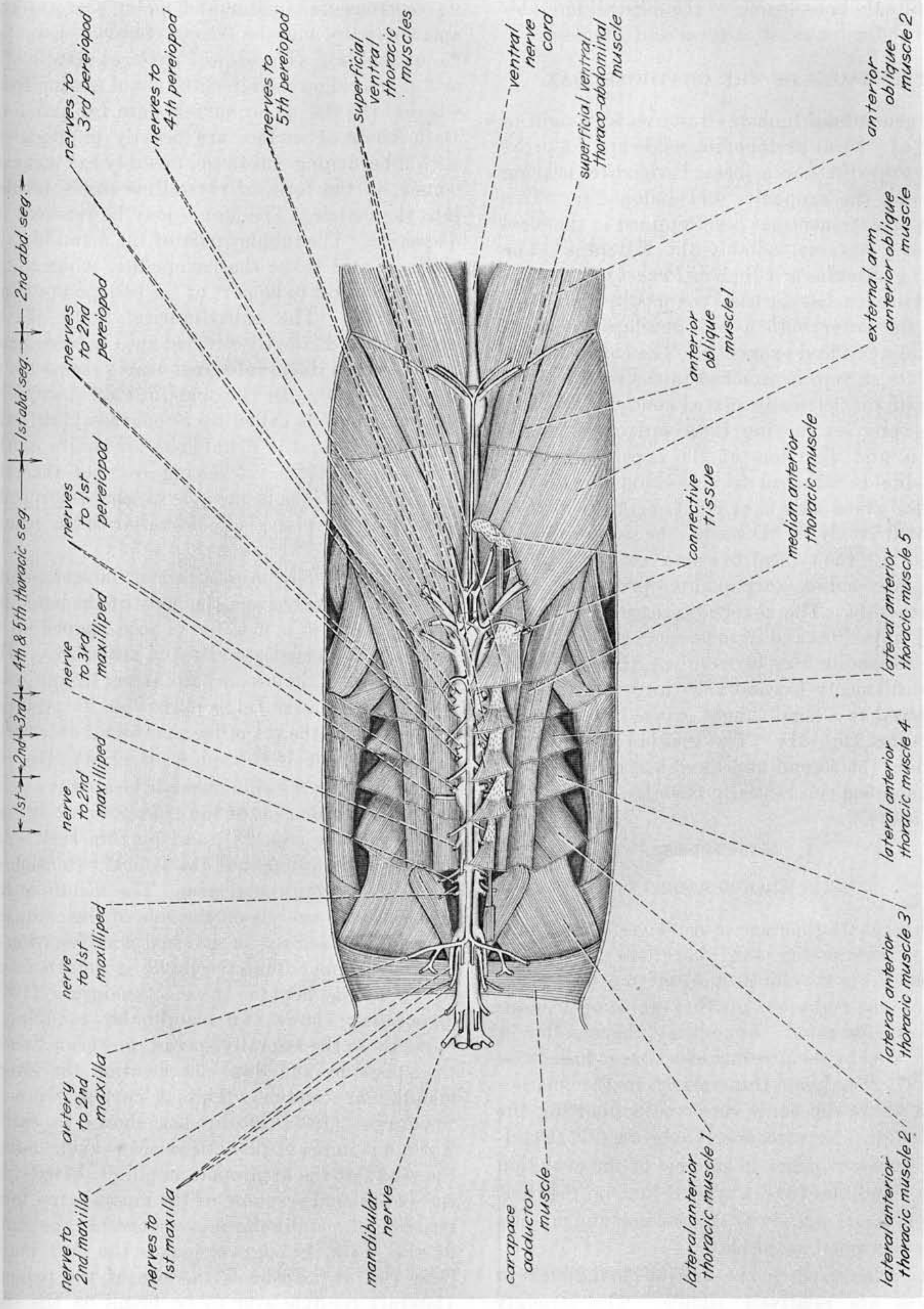

FIGURE 36.—Ventral view of gnathothorax showing muscles, nerves, and blood vessels.

undoubtedly homologous to the musculi laterales thoracoabdominales of *Astacus* and *Pandalus*.

APPENDAGES OF THE GNATHOTHORAX

The generalized limb of Crustacea is thought to consist of a basal protopodite, made up of a proximal coxopodite and a distal basipodite, bearing two rami, the exopodite and endopodite. This simple arrangement has been retained in the pleopods of Crustacea, notably the Natantia. The typical gnathothoracic limb of *Penaeus*, if one can be said to exist, has the basal coxopodite and basipodite, the latter with a well-developed endopodite and a reduced exopodite. The coxopodite of the white shrimp is attached to the limb base by means of diametrically placed condyles, the axis of the condyles varying in accordance with the location and function of the appendage. The basipodite is attached to the coxopodite by dicondyles whose axis is at right angles to that of the coxal condyles. Distally, the endopodite is divided into the typical five articles: the ischiopodite, meropodite, carpopodite, propodite, and dactylopodite. The coxopodite may give rise to lateral epipodites and in some cases gills.

The exopodite may be modified to long, frond-shaped filaments (second and third maxillipeds) or reduced to a small finger projecting from the basipodites (fig. 31). The gnathal appendages, excluding the second and third maxillipeds, tend to be modified substantially from the typical plan given above.

1. MANDIBLES

SKELETAL ELEMENTS

Of the gnathothoracic appendages, the mandibles are perhaps the most difficult to understand. For one thing the dorsal and internal manifestations of this and other gnathal segments are coalesced or obliterated. In addition, the mandible is complicated by the presence of a true endoskeleton (figs. 37, 38), lying transversely in the gnathothorax above the nerve cord and supporting the gastric mill. Nevertheless, Snodgrass (1951b) adduces strong evidence in support of the evolution of the mandibles from a typical limb on the basis of a comparative study of the skeleton and muscles of the arthropod mandible.

The sclerotized parts of the mandibles in *Penaeus* are relatively simple. The strongly sclerotized incomplete tube of the mandible, with its ventromedial incisor and molar surfaces and anterior palp, may be seen in ventral view (fig. 29, mandible). The incisor surfaces consist of 2 or 3 sharp ridges used in cutting and tearing food, whereas the flat molar surfaces are for grinding. Both kinds of surface are heavily impregnated with a hardening substance, possibly calcium carbonate, in the form of crystalline stones molded into the cuticle. The stones may be removed by dissection. The tubular part of the mandible, the body, is said to be the coxopodite, whereas the palp is thought to be part of the endopodite (Calman 1909). The subcylindrical body of the mandible is distinctly divided into a large basal portion and a distal lobe, immovably connected to the basal part. In the mandible of *Anaspides*, the basal part is called by Snodgrass (1952) the coxopodite and the distal lobe an endite of the coxopodite. It is interesting to note that the distal gnathal lobe is movable in some arthropods, notably the Diplopoda, and similar to the maxillary lacinia of insects.

The mandibular palp, a part of the endopodite, extends anteriorly from the body of the mandible in the form of a flat, setose lobe shaped to fit around the labrum laterally and anteriorly. The larger part of the broad palp arises from a basal segment, the latter being narrow at its posterior junction with the mandible and broad anteriorly.

The mandible of *Penaeus* is attached to the ventral skeleton by a medial condyle located at a point on the posterior arm of the epistome just laterad of the labrum (fig. 28), and by thin cuticle between the mandible and the lateral extension of the posterior epistomal arm. The mandible has also a lateral condyle on the side of the carapace. Among taxonomists the external manifestation of this lateral mandibular condyle is known incorrectly as the hepatic spine. Snodgrass (1951) erroneously shows two mandibular condyles in *Penaeus* on the laterally spread, posterior bars of the epistome, and does not mention the lateral mandibular condyle. This is curious since, as Snodgrass (1935, 1951b) has shown in earlier work, a significant phyletic series is evident from the study of the arthropod mandible, based upon the evolutional response of the musculature to restriction of mandibular movements. In the course of the work, Snodgrass makes the fact amply clear that in no case is the site of the primary (lateral) condyle ever to be found on the epistome. Rather, the generalized arthropod man-

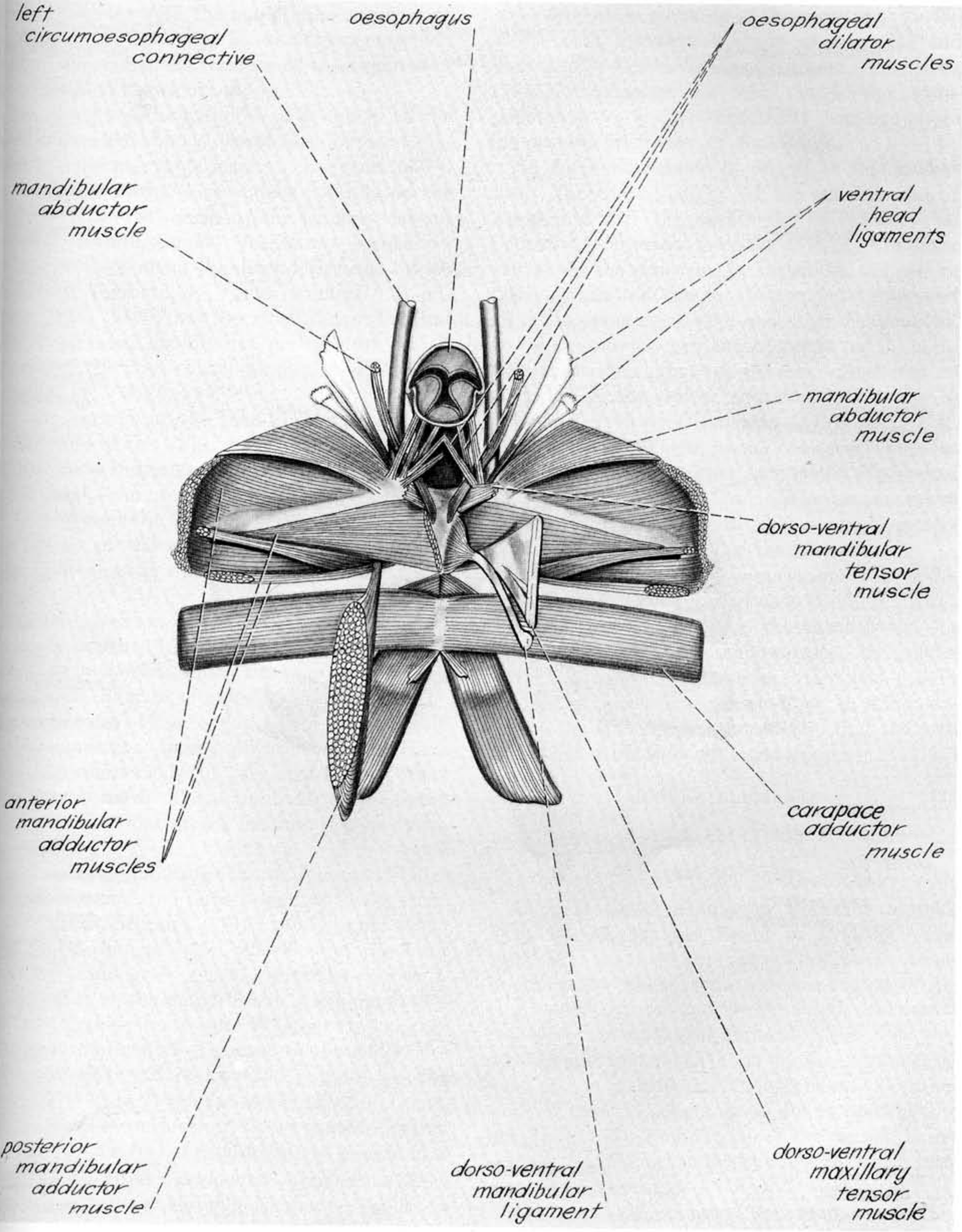

FIGURE 37.—Dorsal view of mandibular musculature.

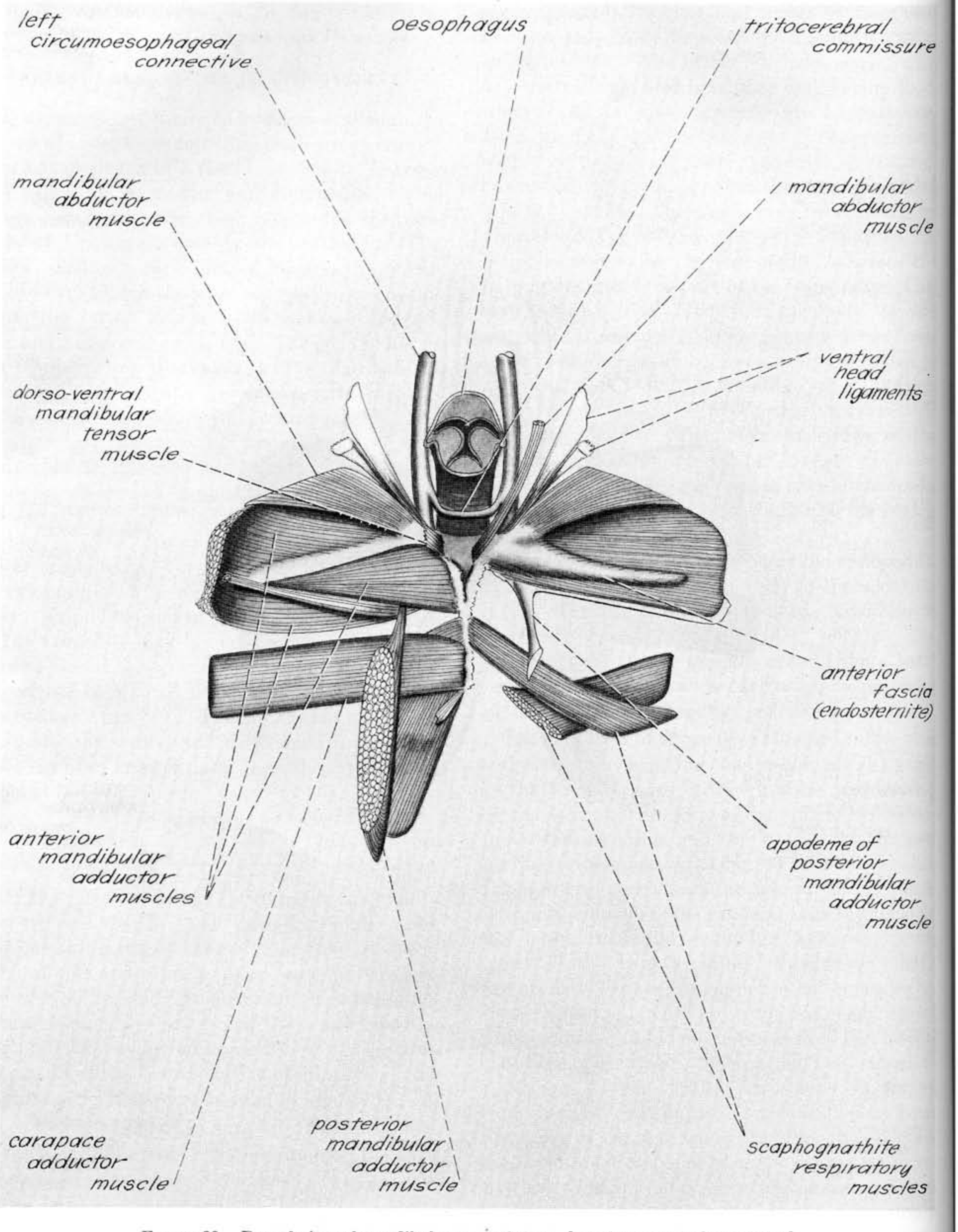

FIGURE 38.—Dorsal view of mandibular musculature, dorsal-most muscles removed.

dible articulates with the mandibular segment at a single point laterally, an arrangement which permits the varied movements of the organ seen at this stage of its evolution.

The monocondylic mandible is found in all the mandibulate arthropods except some higher Crustacea and the pterygote insects (Snodgrass 1935). In the latter forms, a secondary condyle on the epistome is added mesad of the primary lateral condyle. Mandibular movements now become restricted to those about the dicondylic axis. With simplicity, furthermore, comes strength. Snodgrass (1935, 1951b) has described the evolutional simplification of mandibular musculature which follows in groups developing the dicondylic mandible.

A comparison of the mandibular hinges and musculature of the white shrimp with the account of Snodgrass indicates that *Penaeus* represents a transitional form; for, although the shrimp mandible is dicondylic, its musculature is strongly reminiscent of the monocondylic musculature in apterygote insects, myriapods, and lower Crustacea.

The endoskeleton of the mandibles, mentioned above, is a thick tendon situated between the mandibles and upon which the heavy ventral adductor and abductor muscles insert (figs. 37, 38). The substance of the endoskeleton is extremely tough connective tissue, not sclerotized. Such cuticular components of the structure as may exist are not hard. The mandibular endoskeleton of Crustacea Malacostraca has been variously interpreted. In forms having a well-developed endoskeletal system in the thorax, the mandibular element is considered to be a part of that system.

In *Astacus*, Schmidt (1915) refers to the structure as the endoskeleton, specifically, the head apodeme. Snodgrass (1935), referring to a similar structure in the mandibles of a diplopod, uses the term median ligament. Whether this worker attributes the median ligament to the endoskeleton is not clear. Berkeley (1928) designates the same material in *Pandalus* as the anterior fascia. She evidently considers it to be endoskeletal in nature, and the fusion product of the mandibular and first maxillary segments. Grobben (1917) apparently believes the mandibular tendon to be endoskeletal, naming it the median transverse mandibular tendon. Snodgrass (1952) refers to an intergnathal ligament in *Anaspides tasmaniae* Thomson and an endosternum in *Cambarus longulus* Girard, in speaking of the structure. In the course of a histological study of muscular and skeletal elements in various Crustacea, Debaisieux (1954) emphasizes that the mandibular endoskeleton is an endosternite, fully homologous in his opinion with that of Arachnida.

No further evidence is offered in the present study for the homology of the endosternite of Arachnida with the mandibular endoskeleton of Crustacea. However, from the work of Debaisieux (1954) on the structure in Crustacea, we can be fairly certain that the mandibular endoskeleton of all crustaceans mentioned above are homologous. In response to the plethora of names for the mandibular endoskeleton, the present writer sees no objection to the terms "endosternite" or "endosternum" given by Debaisieux (1954) and Snodgrass (1952). These names are used here as equivalent to one another and to the expression, "mandibular endoskeleton." Whether an endoskeleton and an endosternite are morphologically equal is not made clear in the literature.

As a final word on the composition of the endoskeleton, it will be recalled that Schmidt (1915) describes two small medial muscles between the mesophragms of the endosternite, the endophragmal compressor muscles. Grobben (1917) denies the existence of muscle fibers in this material in the crawfish and establishes that the area is composed of connective tissue.

MUSCLE ELEMENTS

MANDIBULAR ABDUCTOR MUSCLES

FIGURES 33, 37, 38

At least three mandibular abductor muscles (figs. 33, 37, 38) are found in *Penaeus.* The smallest is the most anterior. This muscle arises in connective tissue in the anterior region of the gnathothorax, lateral to the esophagus and dorsal to the circumesophageal connective, and runs posteriorly and ventrad to insert on the anteromedial part of the mandibular endoskeleton. Contractions of these slender muscles aid in opening the mandibles. No counterpart of the muscle is described for the other crustaceans to which reference has been made.

The large and important mandibular abductors originate in connective tissue on the laterotergal plates (fig. 33) and run posteromedially to insertion areas on the mandibular endoskeleton (figs. 37, 38). Their contractions serve to open the gnathal elements of the mandibles. These two mandibular abductor muscles are fully homologous with the major and minor mandibular abductor muscles in *Astacus* and with the mandibular abductor muscle in *Pandalus*. Presumably the homology holds for the major and minor mandibular abductors of *Callinectes*.

DORSOVENTRAL MANDIBULAR TENSOR MUSCLE

Figure 37

The long tendon of the dorsoventral mandibular tensor muscle (fig. 37) originates in connective tissue on the dorsal carapace by an extremely thin band mesad of the origin of the antennal promotor muscle. The thin apodeme runs ventrad to the muscle body which inserts on the anterior part of the mandibular endoskeleton, slightly laterad of the small mandibular abductor muscle. The muscle pulls the mandibular endoskeleton dorsad, possibly as a minor adjustment of the mandible in feeding. The muscle was named by Grobben (1917), who described it in a number of crustaceans, including species of *Penaeus*, *Palaemon*, *Leander*, *Pandalus*, and *Nebalia*. The description by Berkeley (1928) of *Pandalus danae* does not include the dorsoventral mandibular tensor muscle, although it is almost certainly present in that species. The muscle is missing in *Astacus*.

ANTERIOR MANDIBULAR ADDUCTOR MUSCLES

Figures 33, 34, 37, 38

The anterior mandibular adductor muscles (figs. 33, 34, 37, 38) are the largest occupants of the subcylindrical mandibular body. At least three muscles are evident in *Penaeus*, although a study of the nerves may show that the muscle groups are actually parts of the same muscle. The adductors originate laterally throughout the body of the mandible and insert extensively over the tissues of the mandibular endosternite. Contractions of the anterior mandibular adductors draw the gnathal lobes of the mandibles together. The action is direct and efficient. The anterior mandibular adductor muscles of *Penaeus* are the homologs of the musculus adductor anterior mandibulae in *Astacus* and *Pandalus*.

DORSOVENTRAL MANDIBULAR LIGAMENT

Figures 33, 34, 35, 37

The dorsoventral mandibular ligament (figs. 33, 34, 35, 37) originates in the thick connective tissue of the dorsal carapace by a narrow, thin, apodeme between the dorsal edges of the protocephalon attractor muscle and the gastric mill (fig. 35). The apodeme runs anteroventrally to a thin, fan-shaped muscle inserting on the dorsal surface of the endosternite. It crosses over the tendon of the dorsoventral maxillary tensor muscle medially. The muscle is closely appressed to the fibers of the dorsoventral maxillary tensor, but may be separated readily from the latter in the sagittal plane. The dorsoventral mandibular ligament (or muscle) aids in retaining the endosternite in position.

The structure was found in a species of *Penaeus* and of *Palaemon* and named by Grobben (1917). Since the dorsoventral mandibular ligament actually ends in a small muscle, Grobben's name should be replaced with the name, "dorsoventral mandibular muscle." A muscle in *Pandalus*, designated by Berkeley (1928) as the musculus dorsoventralis anterior 2, is probably the dorsoventral mandibular ligament.

POSTERIOR MANDIBULAR ADDUCTOR MUSCLE

Figures 30, 33, 34, 35, 37, 38

Taking origin in an elongate ovoid on the dorsal carapace is a large, wedge-shaped muscle, the posterior mandibular adductor muscle (figs. 35, 37). Growing narrower as it passes ventrad, the posterior adductor attaches to a broad apodeme (figs. 29, *B;* 30, apodeme, mandibular adductor muscle). The adductor apodeme arises from the posterior margin of the semitubular mandibular body. The apodeme is so placed that a dorsal pull of the powerful muscle brings the gnathal lobe to the midline. The posterior mandibular adductor muscles are widely represented in the Arthropoda.

MANDIBULAR PALP FLEXOR MUSCLE

Figure 29

The muscles operating the mandibular palp are situated either in the gnathal lobe of the mandible or in the basal segment of the palp. The distal lobe of the palp contains no muscles. The mandibular palp flexor muscle (fig. 29) originates in the proximal region of the basal palp segment near the foramen between the gnathal lobe and the palp base. The muscle runs distally, becoming broad and flat, and inserts on the posteroventrad margin of the distal palp lobe. In action, the mandibular palp flexor turns the distal lobe ventrad. An apparently similar muscle in the palp of *Astacus* is called by Schmidt (1915) a palp flexor also. Berkeley (1928) describes both a palp flexor and a palp extensor in the body of the mandible of *Pandalus*.

MANDIBULAR PALP ADDUCTOR MUSCLES

FIGURE 29

The proximal, and larger, mandibular palp adductor muscle originates on the posterior wall of the gnathal lobe of the mandible and inserts on the medial margin of the basal palp foramen. The smaller palp adductor originates dorsad of the insertion of the larger palp adductor on the medial margin of the gnathal lobe foramen. Contractions of these muscles turn the palp segments toward the midline. The proximal mandibular palp adductor muscle is probably homologous with the musculus flexor *a* mandibulae of *Astacus* and either the palp flexor or extensor of *Pandalus*.

2. PARAGNATHA

The paragnatha (figs. 29, 39) are two rounded lobes suspended from small foramina in the ventral skeleton immediately posterior to the gnathal lobes of the mandibles. Their cuticle is very thin, except for a slightly thickened ridge along the posterior surface of each paragnath. No intrinsic muscles are found in the body of the paragnath in *Penaeus*; however, a small muscle, the paragnathal muscle (fig. 39), inserts on the lateral margin of the paragnath. The paragnathal muscle moves the paragnath laterally and anteriorly against the gnathal lobe of the mandible.

Classically, the paragnatha have been interpreted as a secondary development of the mandibular segment, on grounds of their embryonic development and because of their innervation by mandibular nerves. Also, the view that they belong to the maxillae has been expressed. The idea that the paragnatha are reduced true appendages has in general been discounted, despite the presence of movable terminal lobes in the paragnatha of Tanaidacea (Crustacea). Snodgrass (1935) mentions the similarity of the insectan superlinguae to the crustacean paragnatha. This worker feels, apparently, that there is no evidence that the paragnatha are appendicular or that the superlinguae and paragnatha are homologous structures. He does indicated (Snodgrass 1952) in a study of *Cambarus*, that the paragnatha are mandibular entities. In a comparative study of arthropod nerves, Henry (1948a) assigns the paragnatha to the mandibular segment by virtue of their innervations. She invariably places the paragnathal nerves in a position posterior to those of the mandibles.

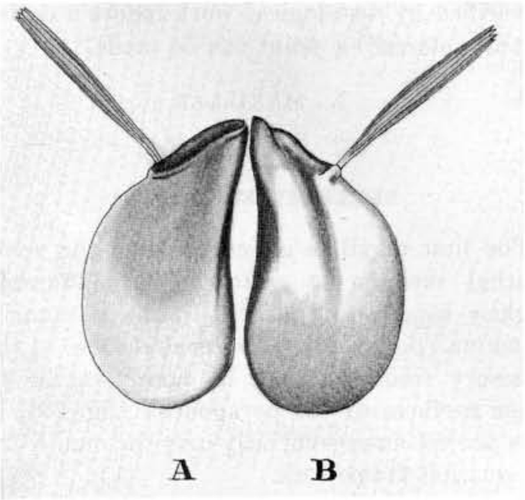

FIGURE 39.—Paragnatha. *A*. Anterior view. *B*. Posterior view.

Recently, Chaudonneret (1955, 1956), in a detailed study of the gnathal nerves of *Orconectes limosus* (Rafinesque) (=*Cambarus affinis* Say), takes issue with Henry (1948a) and advances the idea that the paragnathal nerves are in fact anterior to those of the mandibles and entirely distinct from the mandibular nerves. On other grounds, furthermore, this worker suggests that the paragnathal foramina are anterior to the mandibular foramina and holds that their relative positions with respect to the mouth are constant in the Malacostraca. In the opinion of Chaudonneret (1956), the facts make difficult the interpretation of the paragnatha as either epithelial lobes or parts of the mandibles. Instead, this investigator thinks that the paragnatha may belong to a reduced premandibular, paragnathal segment homologous to the insectan superlingual segment.

If the paragnatha are indeed premandibular and homologous to the superlinguae, an interpretation which Snodgrass (1935) seems to consider possible, certain aspects of the morphology of the insect hypopharynx will need review. Careful study of the paragnathal nerves in *Penaeus* tends to support the view of Chaudonneret (1956) that this nerve is slightly anterior to the mandibular nerve. However, the gross anatomy will have to be verified by histological work before a decision on this interesting point can be made.

3. MAXILLAE

3a. First Maxillae

SKELETAL ELEMENTS

The first maxillae articulate with the ventral gnathal skeleton at relatively large foramina slightly caudad and laterad of the paragnathal foramina (fig. 28, *A*). The medial lobes of these accessory feeding organs fit closely to the posterior surfaces of the paragnatha (fig. 30), and thus project anteroventrally over the mouth from the gnathal framework.

Although the first maxillae is true appendages, they are much modified for functional ends. The body of the first maxilla is produced into several lobes and a flagellum (figs. 29, 40). The flat medial lobes are the proximal coxopodite and the distal basipodite. The medial edges of these lobes are covered with stiff hairs or spines, those on the basipodite margin being especially strong. The spines function to hold food particles. Laterally, the coxopodite is produced into a rounded lobe from which a tuft of large, plumose, sensory setae project. Endites of the basipodite, including an anterior three-jointed flagellum, extend anterolaterally from the basipodite. Schmidt (1915) considers the endites the endopodite. Various lobes of the basipodite endites bear sensorial hairs. A single large seta projects anteriorly from the base of the flagellum.

MUSCLE ELEMENTS

The musculature of the first maxilla in *Penaeus* appears substantially similar to that of other Decapoda. Groups of muscles function to bring the spinous gnathal margins of the appendage to the midline in feeding. Other muscles open the opposing gnathal parts and make various position adjustments. *Peneaus* appears to have at least 10 muscles and muscle groups in the first maxilla, against 9 each for *Pandalus*, *Astacus*, and *Callinectes*.

COXOPODITE PROMOTOR MUSCLE OF FIRST MAXILLA

Figure 40

The first maxilla coxopodite promotor muscle (fig. 40) originates on a large sternal apodeme arising from the brachia between the first and second maxillary foramina. This apodeme penetrates the substance of the endosternite. The promotor muscle runs ventrolaterally to insert in the lateral lobe of the coxopodite. Upon contraction, the muscle turns the first maxilla forward and upward. The first maxilla coxopodite promotor muscle in *Penaeus* is homologous with the musculus promotor I maxillae of *Pandalus*, *Astacus*, and *Callinectes*. Berkeley, Schmidt, and Cochran state that the promotor muscle originates on the head apodeme, or endosternite, in the above three crustaceans, whereas in *Penaeus* the area of origin of the promotor and other lateral muscles is not directly on the endosternite.

COXOPODITE REMOTOR MUSCLE OF FIRST MAXILLA

Figure 40

Taking origin on the sternal apodeme some distance ventrad of the origin of the coxopodite promotor muscle, the first maxilla coxopodite remotor muscle (fig. 40) passes laterad to the lateral lobe of the coxopodite. Contractions of the muscle draw the first maxilla posteroventrad. The coxopodite remotor in *Penaeus* is the homolog of the musculus remotor *a* or *b* I maxillae of *Pandalus*, *Astatcus*, and *Callinectes*. In the latter three forms, two remotor muscles are described.

LATERAL COXOPODITE ADDUCTOR MUSCLE OF FIRST MAXILLA

Figure 40

The first maxilla lateral coxopodite adductor muscle (fig. 40) is a long, slender muscle originating on the laterotergal wall and running anteroventrally to a point of insertion on the medial region of the coxopodite. Contractions of the muscle raise the first maxilla and turn the gnathal lobes towards the midline. Berkeley and Schmidt maintain that the lateral coxopodite adductors in *Pandalus* and *Astacus* originate on the lateral carapace. Despite this difference, the lateral coxopodite adductors in the latter forms are homologous with those of *Penaeus*. Cochran (1935) finds in *Callinectes* a muscle termed by her the posterior adductor muscle. This muscle is a possible homolog of the lateral coxopodite adductors in *Penaeus*.

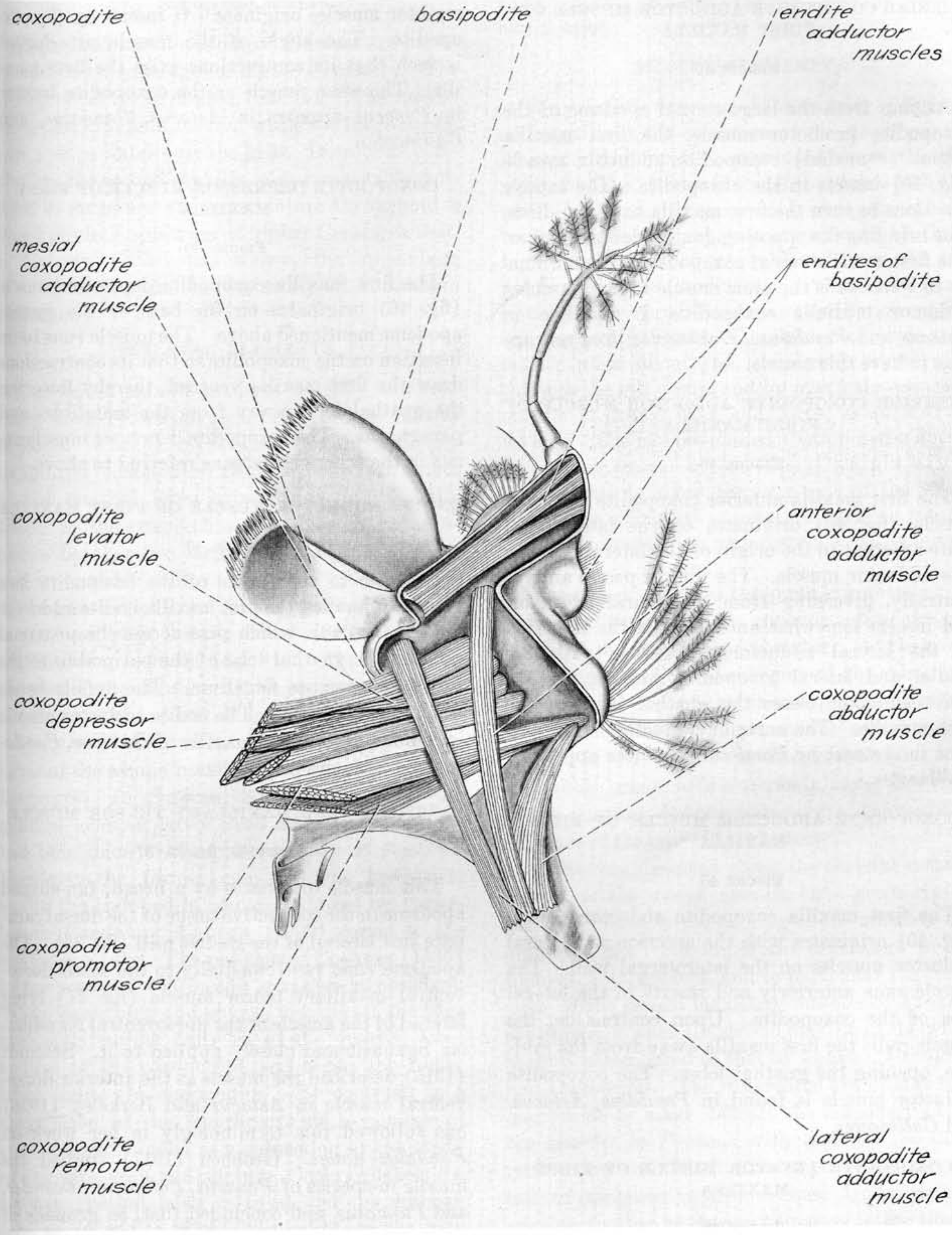

FIGURE 40.—Dorsal view of right first maxilla. Dorsal cuticle removed to show muscles.

MESIAL COXOPODITE ADDUCTOR MUSCLE OF FIRST MAXILLA

FIGURE 40

Arising from the large sternal apodeme of the coxopodite promotor muscle, the first maxilla mesial (=medial) coxopodite adductor muscle (fig. 40) inserts in the coxopodite. The muscle functions to turn the first maxilla to the midline, thus bringing the opposing gnathal lobes together. The first maxilla mesial coxopodite adductor muscle in *Penaeus* is the same muscle as the musculus adductor medialis coxopoditis I maxillae in *Astacus* and *Pandalus*. *Callinectes* does not appear to have this muscle.

ANTERIOR COXOPODITE ADDUCTOR MUSCLE OF FIRST MAXILLA

FIGURE 40

The first maxilla anterior coxopodite adductor muscle (fig. 40) originates on the laterotergal plate adjacent to the origin of the lateral coxopodite adductor muscle. The muscle passes anteroventrally, diverging from the lateral adductor, and inserts somewhat anteriorly of the insertion of the lateral adductor. Together with the medial and lateral coxopodite muscles, the anterior adductor closes the gnathal lobes of the first maxilla. The anterior adductor is not evident in *Astacus* or *Pandalus*, but does appear in *Callinectes*.

COXOPODITE ABDUCTOR MUSCLE OF FIRST MAXILLA

FIGURE 40

The first maxilla coxopodite abductor muscle (fig. 40) originates with the anterior and lateral adductor muscles on the laterotergal wall. The muscle runs anteriorly and inserts in the lateral lobe of the coxopodite. Upon contraction, the muscle pulls the first maxilla away from the midline, opening the gnathal lobes. The coxopodite abductor muscle is found in *Pandalus*, *Astacus*, and *Callinectes*.

COXOPODITE LEVATOR MUSCLE OF FIRST MAXILLA

FIGURE 40

The first maxilla coxopodite levator muscle (fig. 40) is attached to the sternal apodeme upon which the medial adductor and the promotor and remotor muscles originate. It inserts on the coxopodite. The angle of the muscle attachment is such that its contractions raise the first maxilla. The same muscle as the coxopodite levator in *Penaeus* appears in *Astacus*, *Pandalus*, and *Callinectes*.

COXOPODITE DEPRESSOR MUSCLE OF FIRST MAXILLA

FIGURE 40

The first maxilla coxopodite depressor muscle (fig. 40) originates on the base of the sternal apodeme mentioned above. The muscle runs to its insertion on the coxopodite so that its contractions draw the first maxilla ventrad, thereby lowering the gnathal lobes away from the mandibles and paragnatha. The coxopodite depressor muscle exists in the other crustaceans referred to above.

ENDITE ADDUCTOR MUSCLE OF FIRST MAXILLA

FIGURE 40

Intrinsic to the endite of the basipodite is a group of muscles, the first maxilla endite adductor muscle (fig. 40), which pass across the proximal neck of the gnathal lobe of the basipodite to the base of the endite flagellum. The muscle bends the flagellum mesad. The endite adductor muscle is common to the first maxilla of *Penaeus*, *Pandalus*, *Astacus*, and *Callinectes*.

DORSOVENTRAL MAXILLARY TENSOR MUSCLE

FIGURES 33, 34, 35, 37

This muscle originates by a broad, fan-shaped apodeme in the connective tissue of the dorsal carapace just laterad of the gastric mill (fig. 35). The apodeme runs ventromedially to the small dorsoventral maxillary tensor muscle (fig. 37) lying laterad of the muscle of the dorsoventral mandibular ligament and closely applied to it. Schmidt (1915) described the muscle as the anterior dorsoventral muscle in *Astacus* and Berkeley (1928) has followed this terminology in her work on *Pandalus danae*. Grobben (1917) studied the muscle in species of *Penaeus*, *Palaemon*, *Leander*, and *Pandalus*, and concluded that, on grounds of its innervation by nerves of the first maxilla, the muscle should be renamed the "dorsoventral maxillary tensor muscle." The name given by Grobben is adopted here.

3b. The Second Maxillae

The second maxilla is one of the most extensively modified appendages of higher Crustacea. The structure serves a double function. The medial lobes participate in feeding while the large lateral part pumps water over the gills. Despite its complexity, the second maxilla is so remarkably uniform in structure and musculature throughout a broad phyletic spectrum of higher Crustacea that, as Calman (1909) has shown, the appendage is of limited value in the study of crustacean evolution.

SKELETAL ELEMENTS

The second maxilla projects laterally and ventrally from its attachment point on the ventral skeleton. The large foramen enters a deeply sculptured coxopodite from which two small, medial gnathal lobes arises (figs. 29, *D;* 41). Distal to the coxopodite lies the complex basipodite bearing two larger, medial gnathal lobes and an anterior endite (figs. 29, *D;* 41). Spines on the gnathal lobes aid in holding food. Lateral to the basipodite lies the flat, indented scaphognathite, or gill pump (fig. 41). The folds and grooves of the scaphognathite represent areas of muscle attachment and of articulation.

Many different interpretations of the components of the second maxilla are encountered in the literature. In *Astacus*, Schmidt describes the gnathal lobes as partly coxal and partly basal, as had been done in the present study of *Penaeus*. However, the former considers the basipodite endite the endopodite, and is followed by Berkeley in *Pandalus*. Calman (1909) refers to the endite as a palp. The position of Cochran (1935) in her study of *Callinectes* is rather inconsistent. When describing the second maxilla of the blue crab, this worker calls all of the gnathal lobes endites of the coxopodite, and terms the basipodite endite the endopodite. By contrast, in a description of the mouthparts of a number of crustaceans included as a subsection of the study of the blue crab musculature, Cochran labels the median gnathal lobes as basal and the anterior lobe as an endite of the basipodite, as has been done by the present writer in *Penaeus*, even though the second maxillae of *Callinectes* and *Penaeus* are very similar. To say the least, the composition of the second maxilla needs clarification.

MUSCLE ELEMENTS

The principle function of the muscles of the second maxilla is the operation of the scaphognathite as a gill pump. As mentioned above, the gill pump lies in a narrow channel through which the water is moved that passes over the gills. If the body processes of a shrimp are reduced by chilling, and the branchiostegite is cut away, the gill pump may be observed in slow action. Two functionally interrelated but distinct oscillations of the scaphognathite occur. The more obvious is that taking place about the horizontal, lateral axis through the gill pump, and by which the scaphognathite is tipped back and forth, or rotated on its axis. The less obvious oscillation is the dorsoventral movement of the lateral margin of the scaphognathite about the long axis of the structure. The marginal undulation tends to ramify the former oscillation with respect to water pumping.

Water is drawn into the pumping chamber by a forward tipping of the anterior end of the gill pump to the floor of the chamber. At the same time the posterolateral margins of the pump are raised to the top of the chamber. The posterolateral margins of the pump are now brought ventrad at which time the anterior end rises, and the whole organ rolls anteriorly along the floor of the chamber, forcing water out of the cephalic aperture of the pumping chamber.

Conflicting opinions about the skeletal nomenclature of the second maxilla have given rise to some confusion in the naming of the muscles. In addition, small but important differences in the number, arrangement, and in particular the functions of the second maxillary muscles of *Penaeus* are apparent when the second maxilla of the white shrimp is compared to that of *Astacus*, *Pandalus*, and *Callinectes*. The differences are of sufficient magnitude to make difficult the homology of all the muscles in *Penaeus* with those in the three crustaceans mentioned without knowing the details of comparative innervations. Under pain of causing further confusion of names in the literature, the present writer renames the muscles of the second maxillae of *Penaeus* in accordance with their functions.

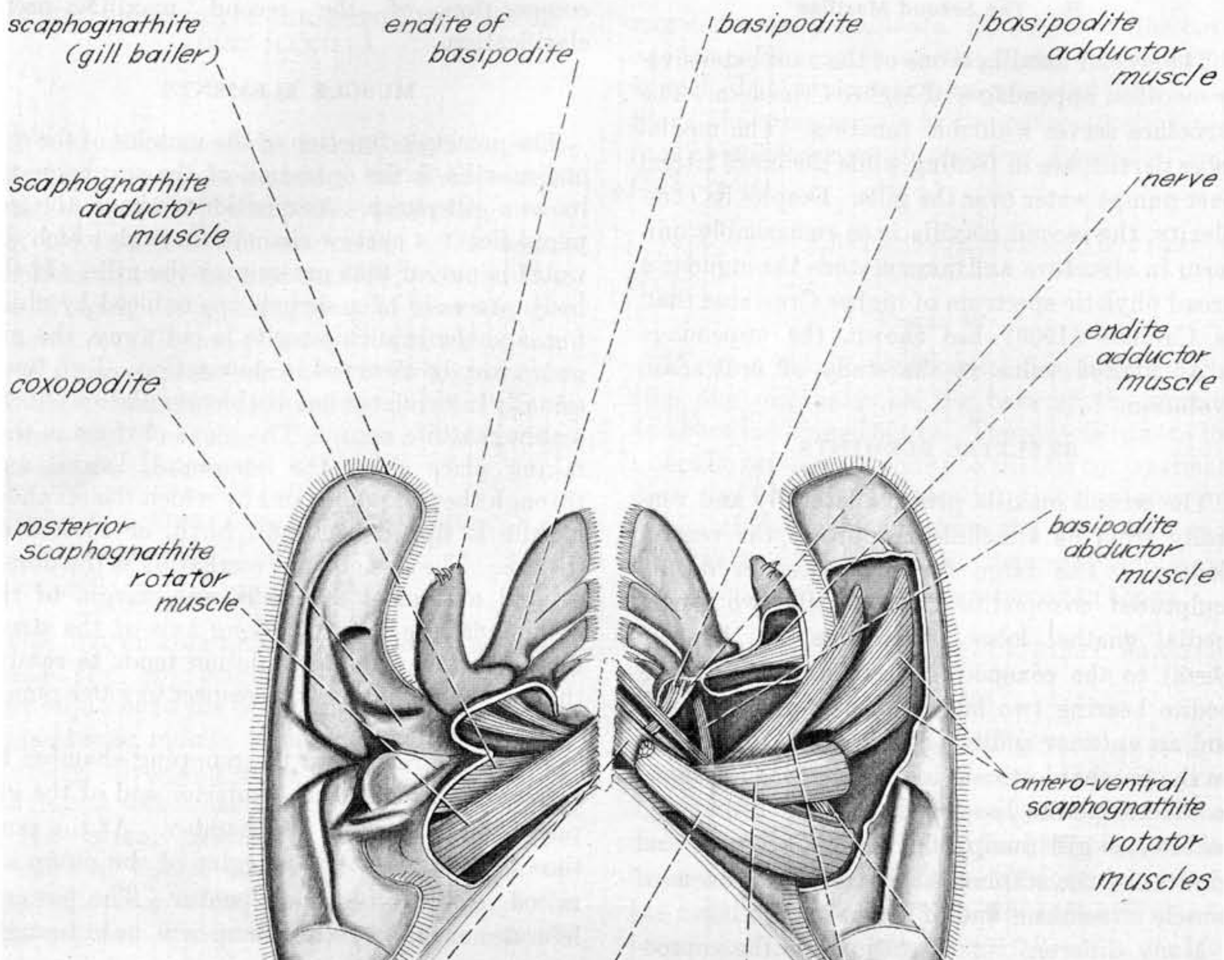

FIGURE 41.—Dorsal view of second maxilla. Left side, intact appendage. Right side, dorsal cuticle removed to show muscles.

BASIPODITE ADDUCTOR MUSCLE OF SECOND MAXILLA

FIGURE 41

This small muscle originates on the medial margin of the coxopodite and runs to the proximal region of the gnathal lobe of the basipodite. The second maxilla basipodite adductor muscle turns the basipodite lobes toward the midline. The only muscle in *Astacus* in a similar position is part of the musculus depressor II maxillae.

BASIPODITE ABDUCTOR MUSCLE OF SECOND MAXILLA

FIGURE 41

The basipodite abductor muscle runs from the posterior rim of the coxopodite to the proximal region of the basipodite gnathal lobes, laterad of the insertion of the basipodite adductor. Contractions of the basipodite abductor open the gnathal lobes. Like the basipodite adductor, the basipodite abductor may be the same muscle as part of Schmidt's musculus depressor II maxillae in *Astacus*.

ENDITE ADDUCTOR MUSCLE OF SECOND MAXILLA

FIGURE 41

The endite adductor muscles (fig. 41) arises in the proximal region of the basipodite gnathal lobes and passes laterad to insert on the lateral margin of the basipodite endite. Its contractions turn the endite mesad. The endite adductor of *Penaeus* is fully homologous with the endopodite adductor muscle of *Astacus*, *Pandalus*, and *Callinectes*.

POSTEROVENTRAL SCAPHOGNATHITE ROTATOR MUSCLE OF SECOND MAXILLA

FIGURE 41

The posteroventral scaphognathite rotator muscle, in company with several of the so-called respiratory muscles, originates on a large, sternal apodeme arising from the sternal brachia between the second maxilla and the first maxilliped. The dorsal, or distal, portion of this apodeme lies close to the dorsal end of the large sternal apodeme upon which muscles of the first maxilla are attached, but the second maxillary apodeme is not deeply embedded in the substance of the endosternite as is the first maxillary apodeme. The posteroventral scaphognathite rotator runs posterolaterally to a point of insertion on the ventral surface of the scaphognathite. This muscle brings the posterior tip of the gill pump ventrad and remotes the whole structure. The muscle is evidently the homolog of the musculus respiratorius *e* II maxillae in *Astacus* and the other forms referred to.

DORSAL SCAPHOGNATHITE ADDUCTOR MUSCLE OF SECOND MAXILLA

FIGURE 41

This muscle originates on the apodeme of the second maxilla and runs ventrolaterally to insert on the dorsal surface of the scaphognathite. The dorsal scaphognathite adductor muscle turns the posterolateral margin of the gill pump dorsad. Although far from clear, the muscle may be the same muscle as Schmidt's musculus respiratorius *b* II maxillae in *Astacus*.

POSTERODORSAL SCAPHOGNATHITE ROTATOR MUSCLE OF SECOND MAXILLA

FIGURE 41

The posterodorsal scaphognathite rotator muscle originates on the dorsal part of the sternal apodeme of the second maxilla and passes laterally to the dorsal surface of the scaphognathite. In action, the muscle aids the posteroventral rotator muscle in remoting the whole scaphognathite, but opposes the posteroventral rotator by lifting the posterior tip of the gill pump. The posterodorsal rotator in *Penaeus* is almost certainly the homolog of the musculus respiratorius *d* II maxillae of *Pandalus*, *Astacus*, and *Callinectes*.

VENTRAL SCAPHOGNATHITE ADDUCTOR MUSCLE OF SECOND MAXILLA

FIGURE 41

The ventral scaphognathite adductor muscle originates in the ventral region of the coxopodite and inserts on the scaphognathite ventrad of the insertion of the posteroventral rotator muscle. The muscle turns the lateral margin of the gill pump ventrad, in opposition to the action of the dorsal adductor.

ANTERODORSAL SCAPHOGNATHITE ROTATOR MUSCLES OF SECOND MAXILLA

FIGURE 41

The anteroventral scaphognathite rotator muscles have separate origins and may well be two different entities. The posteriormost of the two is a long muscle extending from the ventral apodeme to an area well out in the anterior region of the scaphognathite. The more anterior rotator originates in the coxopodite and passes to a broad area of insertion in the anterolateral region of the gill pump. This muscle may be the counterpart in *Penaeus* of the scaphognathite flexor muscle of *Astacus*, *Pandalus*, and *Callinectes*. The posteriormost rotator of this pair in *Penaeus* apparently is not homologous with any of the muscles in the other crustaceans referred to. These muscles bring the anterior tip of the scaphognathite dorsad and promote the whole structure.

ANTERODORSAL SCAPHOGNATHITE ROTATOR MUSCLE OF SECOND MAXILLA

FIGURE 41

The anterodorsal scaphognathite rotator muscle takes origin on the endosternal apodeme of the second maxilla and runs anteroventrally to an area of insertion mesad of the anteroventral rotator muscles. The muscle reinforces the action of the anteroventral rotators in raising the anterior tip of the scaphognathite and promoting the structure. As nearly as can be determined, the anterodorsal rotator in *Penaeus* is the musculus respiratorius *a* II maxillae in *Astacus*, *Pandalus*, and *Callinectes*.

4. MAXILLIPEDS

4a. First Maxilliped

Like the second maxilla, the first maxilliped is a highly modified appendage having a dual function. Its strong gnathal lobes and sensory flagellum participate in feeding, while its flat, lateral lobes and small arthrobranchia play a part in breathing. Superficially, the first maxilliped appears to be as widely modified from the plan of the typical appendage as is the second maxilla, but the muscles indicate otherwise. And whereas the second maxilla is a relatively stable phylogenetic entity in the Crustacea, the form of the first maxilliped is variable.

SKELETAL ELEMENTS

The skeleton of the first maxilliped is comprised of a series of lightly sclerotized lobes or plates. The appendage articulates with the ventral skeleton by a transversely elongate foramen. The foramen enters the fused coxopodite and basipodite (protopodite, fig. 42). Projecting anteroventrally from the protopodite is a set of three gnathal lobes, the large, thick distal lobe being the endite of the coxopodite (fig. 42). Together, the endites of the maxillipeds are cupped against the anterior mouthparts. Heavy spines directed mesad from the edge of the endites help to hold food. Laterad of the coxopodite endite and extending anteriorly is a slender lobe bearing on its medial surface the rudiment of the endopodite and the jointed flagellum of the exopodite. The exites of the coxopodite, lying laterally, are two large, flat sheets that close the gill pump chamber on the ventral surface. Posteriorly, a small, flattened gill may be seen. This gill is said to be an arthobranchia, but on embryological grounds it might be as easily a podobranch.

The components of the first maxilliped are interpreted in different ways by different authors. The structure called the protopodite in *Penaeus* is termed the coxopodite in *Astacus* by Schmidt. Also, Schmidt considers the coxopodite endite the basipodite, and refers to the coxopodite exites as epipodites. If, as has been discussed earlier, the coxopodite exites develop from podobranch primordia, then no objection to the term "epipodite" can be offered. In passing, we may note that the first maxilliped of *Penaeus* bears two coxopodite endites compared to one in the first maxilliped of *Pandalus*, *Astacus*, and *Callinectes*.

MUSCLE ELEMENTS

Compared to the musculature of the second maxilla, that of the first maxilliped is very light. The muscles function almost entirely in feeding, since the part played by the exites in breathing is mostly passive. Wider variation in the functions of the muscles of the first maxilliped in different crustaceans makes necessary a variety of muscle names, but most of them can be homologized. The first maxilliped of *Penaeus* has 12 muscles, against 9 for *Astacus*, 13 for *Pandalus*, and 11 in *Callinectes*.

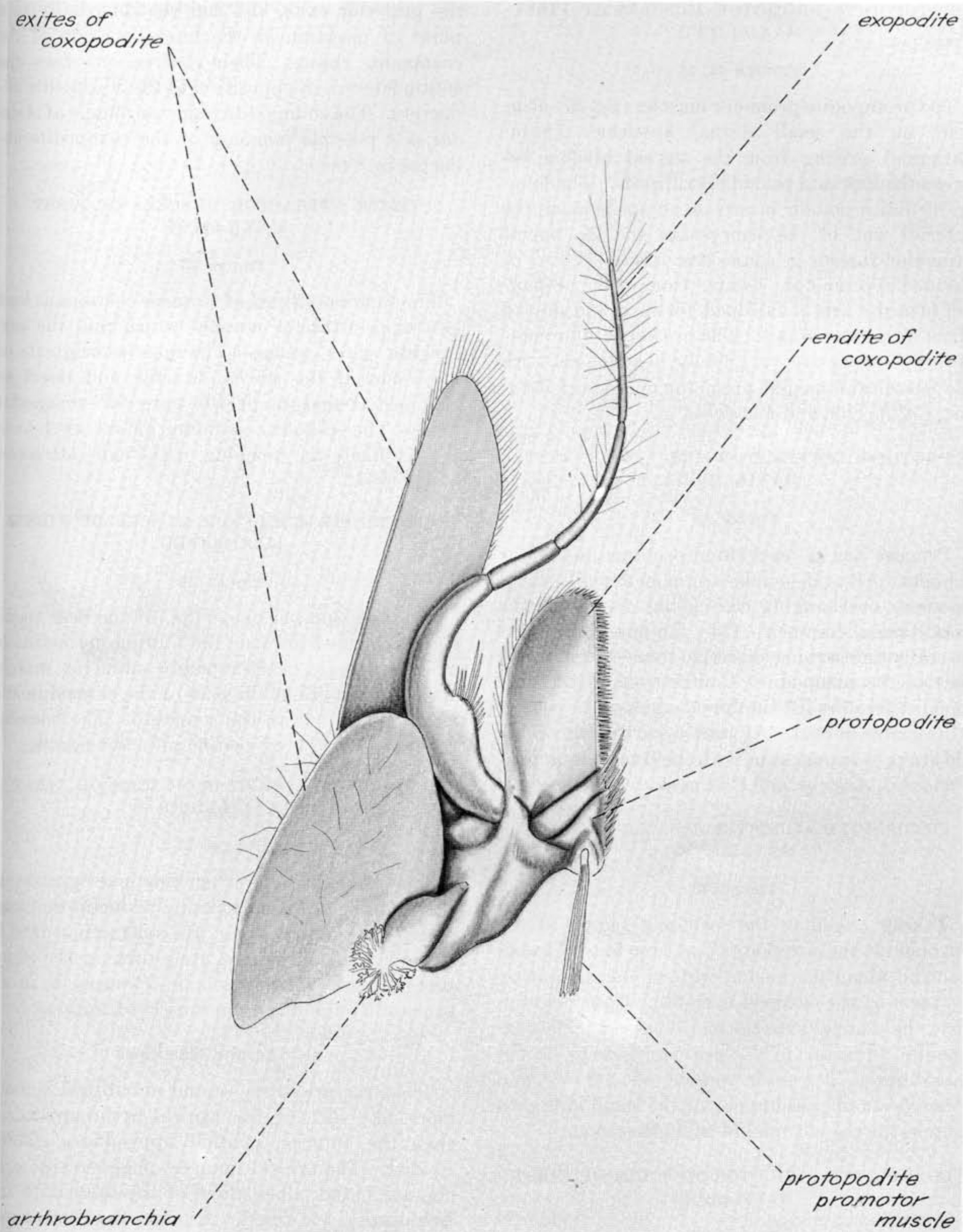

FIGURE 42.—Dorsal view of left first maxilliped.

PROTOPODITE PROMOTOR MUSCLES OF FIRST MAXILLIPED

FIGURES 42, 43

The protopodite promotor muscles (fig. 43) originate on the small sternal apodemes (paraphragms) arising from the sternal brachia between the first and second maxillipeds. The longer, medial promotor inserts on an apodeme on the anterior wall of the protopodite and the lateral promotor inserts in connective tissue ventrad of the medial promotor. Contractions of the promotors turn the first maxilliped forward and dorsad about a transverse axis. The protopodite promotors of *Penaeus* are very likely homologous with the lateral and medial promotor muscles of *Astacus*, *Callinectes*, and *Pandalus*.

PROTOPODITE LEVATOR MUSCLES OF FIRST MAXILLIPED

FIGURE 43

Penaeus has at least three protopodite levator muscles. All of them take origin on a small sternal apodeme overhanging the medial margin of the maxillipedal foramen. They fan out as they pass laterally to insert in connective tissue in the lateral part of the coxopodite. Contractions of the protopodite levators lift the dorsal edges of the coxopodite exites dorsad. At least a part of this muscle group is homologous with the levator muscle of *Pandalus*, *Astacus*, and *Callinectes*.

COXOPODITE ADDUCTOR MUSCLE OF FIRST MAXILLIPED

FIGURE 43

Taking origin in the proximal region of the coxopodite, the coxopodite adductor muscle passes ventrad along the medial wall of the coxopodite to insert on the coxopodite endite. Upon contraction, the muscle turns the endite mesad. The coxopodite adductor in *Penaeus* appears to be the maxillipedal depressor muscle of *Astacus* and *Pandalus*, and possibly one of the small unknown muscles in the coxopodite of *Callinectes*.

COXOPODITE ABDUCTOR MUSCLES OF FIRST MAXILLIPED

FIGURE 43

Two coxopodite abductor muscles exist in the first maxilliped of *Penaeus*. The muscles originate in the lateral part of the coxopodite, near the posterior exite, and run ventromedially to a point of insertion on the lateral margin of the coxopodite endite. Their contractions draw the endite laterad, in opposition to the coxopodite adductors. The endopodite reductor muscle of *Astacus* is a possible homolog of the coxopodite abductor in *Penaeus*.

EXITE ATTRACTOR MUSCLES OF FIRST MAXILLIPED

FIGURE 43

The first maxilliped of *Penaeus* contains at least two exite attractor muscles which pull the coxopodite exites caudad. The muscles originate on apodemes of the sternal brachia and insert on the medial margin of the posterior coxopodite exite. The epipodite attractor muscle in *Astacus* is very likely the homolog of the exite attractors of *Penaeus*.

EXOPODITE ADDUCTOR MUSCLE OF FIRST MAXILLIPED

FIGURE 43

The flagellum, or exopodite, of the first maxilliped is moved towards the midline by means of a short muscle, the exopodite adductor muscle, which originates at the base of the exopodite and runs distally within the structure. The homolog in *Astacus* is the exopodite adductor muscle.

EXOPODITE ABDUCTOR MUSCLE OF FIRST MAXILLIPED

FIGURE 43

The exopodite abductor muscle originates at the distal end of the exopodite adductor and runs distally in the flagellum. Its contractions tend to straighten the flagellum, thus turning the structure laterad. The muscle in *Penaeus* is in all probability the flagellum muscle of *Astacus*.

4b. Second Maxilliped

The structure of the second maxilliped is much more like that of the typical arthroappendage than the anterior gnathal appendages already treated. The typical number of appendage articles are found, albeit those of the basipodite and ischiopodite are fused. A large, flagellar exopodite is developed. A notable difference is that some of the endopodite articulations of the second maxilliped permit far more extensive movements than do the hinges of the anterior gnathal limbs.

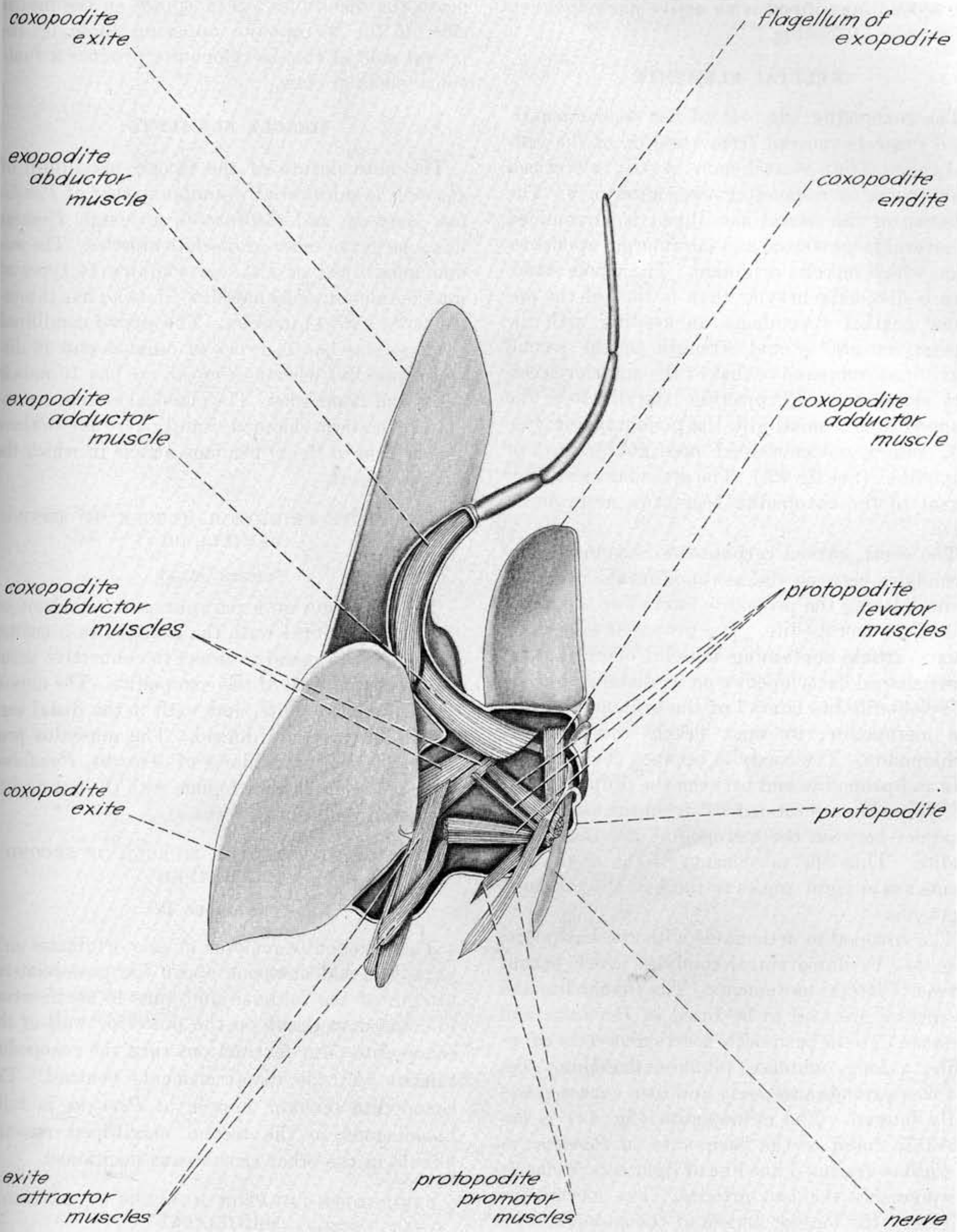

FIGURE 43.—Dorsal view of left first maxilliped, dorsal cuticle removed to show muscles.

The second maxilliped is an active participant in the process of feeding.

SKELETAL ELEMENTS

The coxopodite (fig. 44) of the second maxilliped projects ventrad from a region of the ventral skeleton thta is much more heavily sclerotized than are the corresponding areas anteriorly. The foramen of the second maxilliped is surrounded by several large sternal and laterotergal apodemes upon which muscles originate. The whole structure is distinctly heavier than is that of the anterior gnathal appendages, in keeping with the greater movability and strength of the second maxilliped compared to that of the anterior accessory mouth-parts. Projecting laterally from the coxopodite is a small gill, the podobranchia (fig. 44), and a mitten-shaped mastigobranchia, or epipodite. (See fig. 32.) The articular membrane dorsal to the coxopodite bears two arthrobranchiae.

The short, curved carpopodite is connected by dicondyles between the meropodite and the propodite placing the propodite laterad of the distal end of the meropodite. The propodite is a short, square article containing muscles operating the heart-shaped dactylopodite on its distal end. The dactylopodite lies laterad of the proximal part of the meropodite, its apex nearly touching the ischiopodite. The condyles between the carpopodite and propodite and between the propodite and dactylopodite are rotated 90° from the axis of the condyles between the meropodite and the carpopodite. Thus the movements of the distal segments are at right angles to those of the proximal segments.

The coxopodite articulates with the basipodite (fig. 44) by dorsoventral condyles which permit extensive lateral movements. The coxopodite and basipodite are said to be fused in *Pandalus* and *Astacus*. To the basipodite is articulated the exopodite, a long, annular, plumose flagellum (fig. 44) that extends anteriorly and then curves gracefully laterad. The ischiopodite (fig. 44) is immovably fused to the basipodite in *Penaeus*, as in *Callinectes*, but a fine line of light cuticle clearly distinguishes the two articles. The meropodite (fig. 44), the longest article of the endopodite, is attached to the ischiopodite so as to allow the distal segments limited movements from side to side as well as up and down. This article projects anteriorly from the ischiopodite to a position beneath the mandibles. Stiff spines on the medial side of the meropodite opposing those on the lateral side of the dactylopodite produce a functional chela or claw.

MUSCLE ELEMENTS

The musculature of the second maxilliped of *Penaeus* is substantially similar to that of *Pandalus*, *Astacus*, and *Callinectes*, although *Penaeus* has a larger number of discrete muscles. The second maxilliped of *Penaeus* contains 14 types of muscles including 23 muscles. *Astacus* has 15 muscle types with 17 muscles. The second maxilliped of *Pandalus* has 14 types of muscles and 16 discrete muscles, whereas *Callinectes* has 16 muscle types and 17 muscles. The classical muscle nomenclature has been changed slightly here as elsewhere to conform to the appendage article in which the muscles insert.

COXOPODITE PROMOTOR MUSCLE OF SECOND MAXILLIPED

FIGURES 44, 45

Taking origin on a paraphragmal apodeme on the lateral pleural wall, the coxopodite promotor muscle passes mesad to insert in connective tissue on the medial wall of the coxopodite. The muscle turns the coxopodite, and with it the distal segments, anterior and dorsad. The musculus promotor II pedis maxillaris of *Astacus*, *Pandalus*, and *Callinectes* is homologous with the coxopodite promotor muscle of *Penaeus*.

COXOPODITE REMOTOR MUSCLE OF SECOND MAXILLIPED

FIGURES 44, 45

The coxopodite remotor muscle originates on a paraphragmal apodeme above the posterolateral margin of the foramen and runs to an insertion in connective tissue on the posterior wall of the coxopodite. Its contractions turn the coxopodite caudad and the distal elements ventrad. The coxopodite remotor muscle in *Penaeus* is fully homologous to the second maxilliped remotor muscle in the other crustaceans mentioned.

BASIPODITE LEVATOR MUSCLES OF SECOND MAXILLIPED

FIGURES 44, 55

The basipodite levator muscles originate at two different points. The medial portion is attached

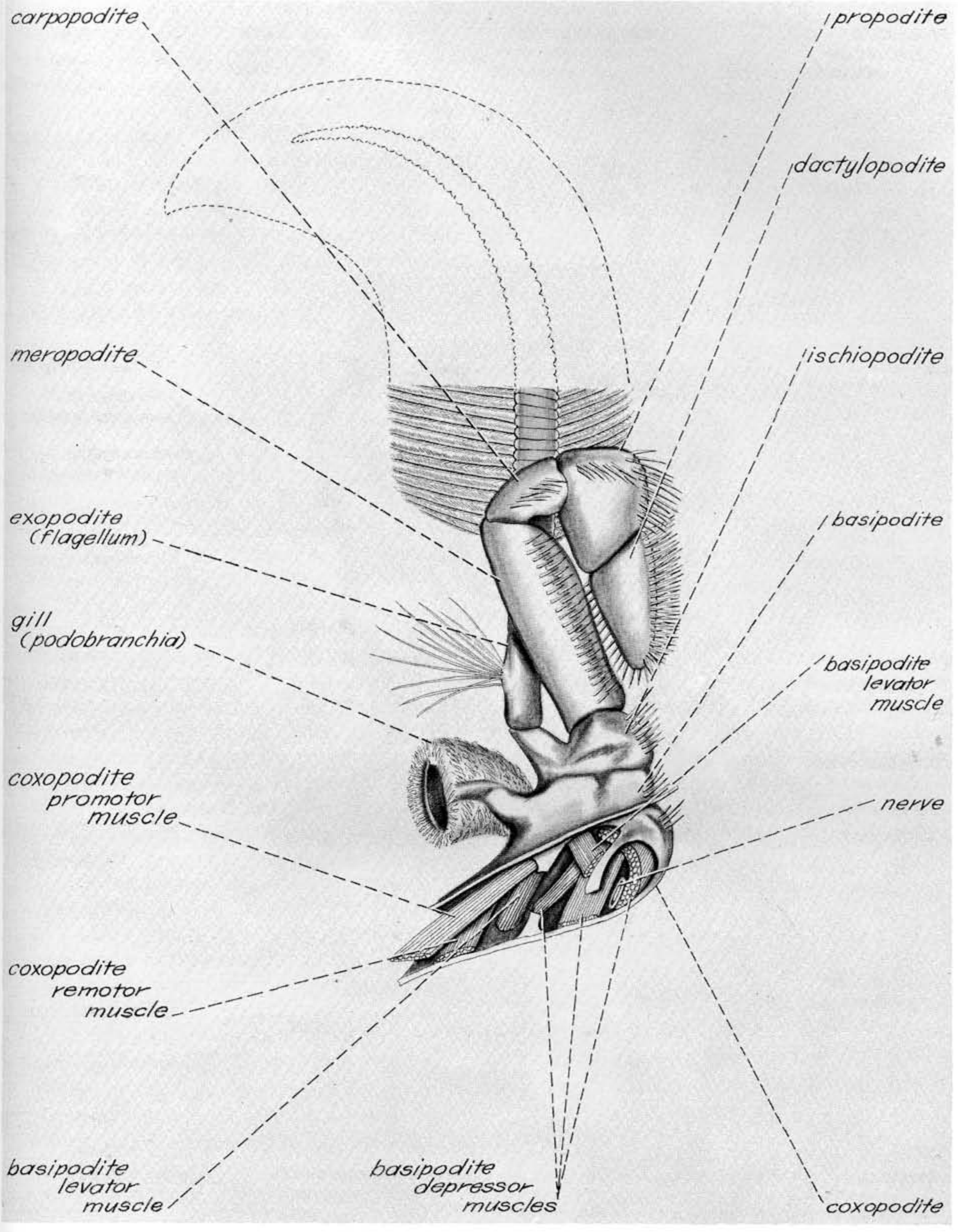

Figure 44.—Dorsal view of left second maxilliped.

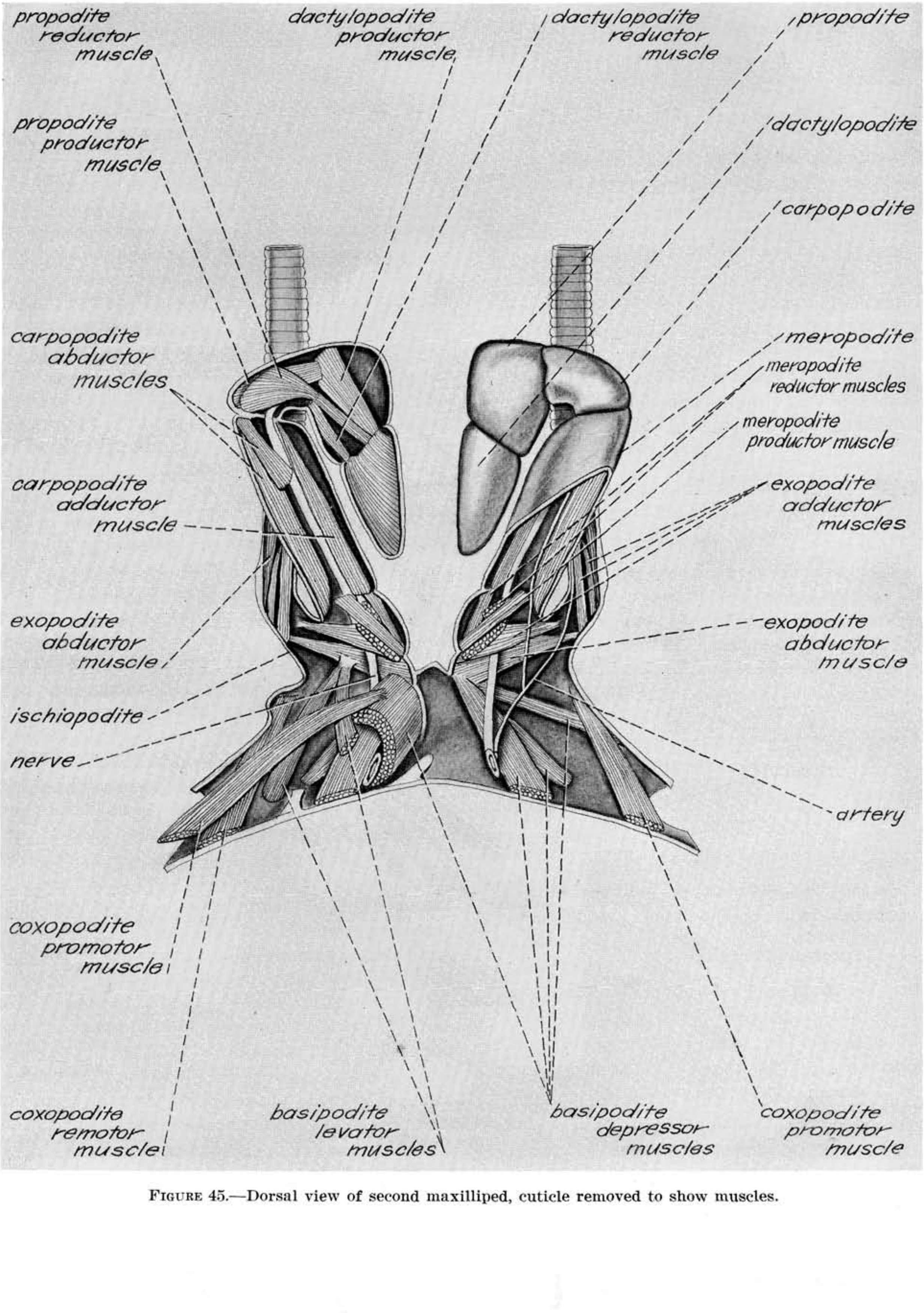

FIGURE 45.—Dorsal view of second maxilliped, cuticle removed to show muscles.

to a large sternal apodeme overhanging the anteromedial part of the foramen. The muscle runs beneath the coxopodite promotor and inserts together with the lateral basipodite levator on the anterior margin of the basipodite foramen, slightly laterad of the dorsal coxobasipodite condyle. The lateral levator muscle originates on the posterior wall of the coxopodite and runs ventrad to join the medial levator. The muscles raise the distal articles and also abduct them. The muscles are homologous with the levator muscles *a* and *b* of *Pandalus* and *Astacus*, and with the single levator in *Callinectes.*

BASIPODITE DEPRESSOR MUSCLES OF SECOND MAXILLIPED

Figures 44, 45

The second maxilliped of *Penaeus* contains four basipodite depressor muscles. The largest is the medial depressor, a short, strong, semicylindrical muscle which, in a manner of speaking, lines the medial curvature of the coxopodite. This muscle originates from the medial margin of the dorsal coxopodite foramen and inserts with the other depressors on the ventromedial margin of the coxopodite, mesad of the ventral condyle between the coxopodite and basipodite. Two other basipodite depressors arise, the larger from the posterior margin of the coxopodite foramen, the smaller from the posterior wall of the coxopodite. The fourth depressor muscle originates on the ventrolateral wall of the coxopodite, beneath the coxopodite remotor, and runs across the coxopodite to join the other basipodite depressors. The contractions of the depressor muscles turn the basipodite and thus the distal maxillipedal elements ventrad. In addition, as a consequence of their insertion mesad of the condylic axis, the depressor muscles turn the basipodite and the distal elements towards the midline.

In fact, from the arrangement of the basipodite levators and depressors with respect to the basipodite condyles, the true function of the muscles may be as abductors and adductors, rather than as levators and depressors. The latter names, of course, derive from *Astacus* in which the coxopodite and basipodite of the second maxilliped are fused. On functional grounds, then, Schmidt's names are at least partially incorrect when applied to *Penaeus.* The basipodite depressor muscles of *Penaeus* are nonetheless homologous with the depressor muscles *a* and *b* in *Pandalus*, *Astacus*, and *Callinectes.*

EXOPODITE ABDUCTOR MUSCLES OF SECOND MAXILLIPED

Figure 45

Two exopodite abductor muscles exist in the second maxilliped of *Penaeus.* The medial abductor is extrinsic, originating broadly on the medial wall of the basipodite and inserting on the posterior edge of the exopodite base. The extrinsic abductor turns the exopodite laterad. Intrinsic to the exopodite is a long abductor muscle which originates by a fine tendon on the base of the exopodite and extends distally for some distance in the exopodite flagellum. Its contractions bend the flagellum laterad. The intrinsic exopodite abductor muscle in *Penaeus* is homologus with the exopodite abductor muscle of *Astacus* and *Callinectes*, and the extrinsic abductor is probably the same muscle as the flagellum abductor in *Astacus.*

EXOPODITE ADDUCTOR MUSCLES OF SECOND MAXILLIPED

Figure 45

The second maxilliped of *Penaeus* has at least three exopodite adductor muscles. The extrinsic exopodite adductor originates in a broad fan across the dorsomedial wall of the basipodite and inserts on the anterior edge of the exopodite base. When it contracts, the exopodite is turned towards the midline. Within the exopodite are two exopodite adductors which function to straighten out the exopodite flagellum, in opposition to the action of the intrinsic exopodite abductor muscle. No homolog of the extrinsic exopodite adductor muscle is evident in *Astacus* or *Callinectes.* Berkeley (1928) illustrates an extrinsic adductor of the exopodite, but does not discuss the muscle. The intrinsic exopodite adductors of *Penaeus* apparently have no homologs in the crustaceans referred to here.

MEROPODITE PRODUCTOR MUSCLE OF SECOND MAXILLIPED

Figure 45

The types and arrangement of the second maxilliped endopodite muscles are remarkably uniform in many higher Crustacea, in accordance with the evolution of this versatile accessory feeding mechanism. The meropodite productor muscle originates on the medial side of the ischiopodite, near the exopodite adductor, and inserts on a small apodeme on the dorsal surface of the meropodite. The muscle lifts the meropodite and other distal elements towards the ventral surface of the mandibles. The same muscle appears in *Pandalus*, *Astacus*, and *Callinectes*.

MEROPODITE REDUCTOR MUSCLES OF SECOND MAXILLIPED

FIGURE 45

Penaeus has two meropodite reductor muscles. The medial reductor originates on the medial wall of the ischiopodite, ventrad of the meropodite productor, and inserts on an apodeme on the ventral margin of the meropodite. Another reductor muscle originates on the anterodorsal surface of the ischiopodite and passes to the same apodeme as the medial reductor. The muscles turn the meropodite ventrad. The meropodite reductors of *Penaeus* have partial counterparts in the second maxilliped of *Astacus*, *Pandalus*, and *Callinectes*, but in the latter only one reductor has been described.

CARPOPODITE ABDUCTOR MUSCLES OF SECOND MAXILLIPED

FIGURE 45

Two carpopodite abductor muscles are found in the second maxilliped of *Penaeus*. The smaller of these originates on the dorsal side of the meropodite and inserts on the common abductor apodeme on the lateral edge of the carpopodite. The larger abductor takes origin on the lateral side of the meropodite, proximally. The muscle runs out along the lateral side of the meropodite and attaches to the abductor apodeme on the carpopodite. The two muscles turn the small carpopodite laterad. However, with respect to the gnathal surface of the dactylopodite, the carpopodite abductors cause functional adduction, in consequence of the hooked shape of the endopodite. The large carpopodite abductor muscle is the same muscle as the carpopodite abductor in *Astacus*, *Pandalus*, and *Callinectes*. The small abductor in *Penaeus* is not described in any of the foregoing crustaceans.

CARPOPODITE ADDUCTOR MUSCLE OF SECOND MAXILLIPED

FIGURE 45

The carpopodite adductor muscle runs from the proximal end of the meropodite to an adductor apodeme on the medial side of the carpopodite. The muscle is less powerful than the carpopodite abductors. The adductor turns the carpopodite mesad, but as a result of the distal hook, the gnathal surface of the dactylopodite is moved laterad. The carpopodite adductor of *Penaeus* is fully homologous with the carpopodite adductor in the other crustaceans to which reference has been made.

PROPODITE PRODUCTOR MUSCLE OF SECOND MAXILLIPED

FIGURE 45

The propodite productor muscle is a short, thick structure originating on a proximal, ventral part of the carpopodite, and running to a broad apodeme on the ventrolateral side of the propodite. Its contractions turn the propodite and dactylopodite ventrad. The propodite productors in *Penaeus* are homologous with the propodite productor in *Astacus*, *Pandalus*, and *Callinectes*.

PROPODITE REDUCTOR MUSCLE OF SECOND MAXILLIPED

FIGURE 45

The propodite reductor muscle occupies the dorsal part of the carpopodite in the shape of a fan. The broad portion originates in the proximal region of the carpopodite. The muscle becomes narrow as it inserts on a little apodeme on the dorsal side of the propodite. The muscle turns the propodite and dactylopodite dorsad, about the horizontal axis through the condyles. The propodite reductor muscle of *Penaeus* is represented in the second maxilliped of the three crustaceans to which frequent reference has been made.

DACTYLOPODITE PRODUCTOR MUSCLE OF SECOND MAXILLIPED

FIGURE 45

The dactylopodite productor muscle is a small, fan-shaped muscle that originates proximally in the propodite and inserts on the ventral margin of the dactylopodite. It serves to straighten the dactylopodite and turn the distal article ventrad, in opposition to the dactylopodite reductor. The same muscle as the dactylopodite productor in *Penaeus* is found in *Pandalus*, *Astacus*, and *Callinectes*.

DACTYLOPODITE REDUCTOR MUSCLE OF SECOND MAXILLIPED

FIGURE 45

Attached between the proximal part of the propodite and the dorsal edge of the dactylopodite is the small dactylopodite reductor muscle. Its function is to turn the dactylopodite dorsad, opposing the action of the productor. The muscle is homologous with the dactylopodite reductor of *Pandalus*, *Astacus*, and *Callinectes*.

4c. Third Maxilliped

The third maxilliped is the first accessory feeding appendage which lacks the jawlike characteristics of the anterior gnathal limbs. Far more than any of the other appendages, the third maxillipeds function to grasp large food particles passed up by the chelate legs and hold them next to the mouthparts for further reduction in size and for swallowing. Structurally, the third maxilliped is closely similar to the pereiopods.

SKELETAL ELEMENTS

The body hemocoel is confluent with that of the third maxilliped by means of a ventral skeletal foramen whose fringes are strongly sclerotized and from which phragmal apodemes project over the opening. The sternal plate between the foramina is wider at this point than that between the anterior mouthpart foramina. The heavily sclerotized coxopodite articulates with the ventral skeleton by a dorsal, laterotergal condyle and a ventral sternal condyle, the typical situation in the white shrimp limb. The axis through the condyles is about 45° from the vertical, with respect to the transverse plane. Since the distal elements are anterior, movements about these coxopodite condyles raise and lower the appendage, as well as promote and remote it. The basipodite articulates with the coxopodite by typical dicondylic connections, the axis of the condyles being horizontal. Thus the basipodite accounts for most of the depression and levation of the distal elements, an arrangement that is common to the third maxilliped and all of the walking legs. A large, tapering, annulated exopodite articulates with the basipodite laterally.

The ischiopodite is fused to the basipodite immovably, although the line of demarcation is clear. The ischiopodite is the longest article of the third maxilliped. The meropodite is connected to the distal end of the ischiopodite by two condyles whose axis permits both flexion of the distal articles towards the midline and reduction of the distal elements. The movements at this joint are extensive. Due to the bending at this joint the shrimp is able to grasp food with the third maxilliped. The carpopodite articulates with the distal end of the meropodite by two condyles. The axis of these dicondyles is vertical, permitting the carpopodite to flex on the meropodite.

The axis through the condyles of the joint between the carpopodite and the propodite is also vertical allowing the propodite to be flexed upon the carpopodite. The small dactylopodite is similarly articulated with the propodite.

The distal elements, beginning with the ischiopodite, bear rows of stout spines on their medial sides for holding food particles. The exopodite has long, plumose setae. The third maxilliped has a branchial arrangement similar to that of the first three walking legs. From the pleural plate arises a pleurobranchia. Two arthrobranchiae project from the dorsal articular membrane, and a bilobed mastigobranchia arises from the coxopodite.

MUSCLE ELEMENTS

The musculature of the third maxilliped of *Penaeus* is typical of that seen in the walking legs. Some variation, however, is evident when the third maxilliped of different crustaceans is compared, especially in the musculature of the exopodite and the distal articles of the endopodite. In *Penaeus*, most of the basipodite and coxopodite muscles originate on the laterotergal, pleural plates rather than on phragmal elements as in the anterior gnathal appendages. Pleural origins of these muscles are typical of all the posterior appendages, thoracic and abdominal alike.

The third maxilliped of *Penaeus* is operated by twenty muscles comprising 12 functional types. That of *Astacus* contains 17 muscles, including 14 types. The third maxilliped of *Pandalus* is somewhat modified, containing 13 muscles of 9 functional types, whereas the same appendage in

Callinectes has 16 muscles grouped into 15 muscle types.

COXOPODITE PROMOTER MUSCLE OF THIRD MAXILLIPED

FIGURES 46, 47, 48

The coxopodite promotor muscle is a strong, lozenge-shaped muscle (fig. 47, *B*) originating on the pleural plate along the anterodorsal margin of the muscle. The insertion is on the anterior margin of the coxopodite (fig. 46). The promotor turns the coxopodite forward and, since the distal parts extend directly anterior, the latter are raised against the other mouthparts. The promotor muscles of *Pandalus*, *Astacus*, and *Callinectes* are the counterparts of the coxopodite promotors in *Penaeus*.

COXOPODITE REMOTOR MUSCLES OF THIRD MAXILLIPED

FIGURES 46, 47

The third maxilliped of *Penaeus* contains two coxopodite remotor muscles. They are much more powerful than the coxopodite promotor muscles which they oppose. The remotors originate on the the laterotergal plate dorsad (fig. 47) and insert on the posterior margin of the coxopodite. They turn the coxopodite caudad and thus the distal elements ventrad as well as laterally. The larger, lateral coxopodite remotor of *Penaeus* is fully homologous with the remotors in the three crustaceans to which we have referred.

BASIPODITE LEVATOR MUSCLES OF THIRD MAXILLIPED

FIGURES 46, 47

The two basipodite levator muscles that have been found in *Penaeus* have different origins. The short, stout lateral levator takes origin on the anterolateral margin of the coxopodite and inserts on the anterior margin of the basipodite. The larger basipodite levator lies internal to the smaller muscle. The origin of the former is on the laterotergal plate and its insertion on the anterior rim of the coxopodite. The levators pull the anterior side of the basipodite upward and with it the distal maxillipedal elements. Three levators of the third maxilliped are described in *Pandalus*, *Astacus*, and *Callinectes*. Part of this group is very likely homologous with the levator pair in *Penaeus*.

BASIPODITE DEPRESSOR MUSCLES OF THIRD MAXILLIPED

FIGURES 46, 47, 48

Considerable variation from the pattern of the depressor musculature of *Penaeus* is seen in the third maxillipeds of *Astacus*, *Pandalus*, and *Callinectes*. Schmidt and Berkeley describe two depressors of the third maxillipeds of *Astacus* and *Pandalus*, whereas Cochran shows one depressor in *Callinectes*. By contrast, *Penaeus* has at least four basipodite depressor muscles in the third maxilliped, just as in the second maxilliped.

The lateral basipodite depressor takes origin on the posterolateral margin of the coxopodite (fig. 47) and inserts, together with the other depressors, on the large apodeme on the posterior rim of the basipodite. Interior to the lateral basipodite depressor is a long, two-part depressor muscle (fig. 47, *B*) originating on the laterotergal plate mesad of the coxopodite remotor muscle. This depressor joins the short lateral depressor on the basipodite depressor apodeme. Immediately mesad of the long depressor lies a small, flat basipodite depressor muscle (figs. 46; 47, *A*) which originates on a medial apodeme of the maxillipedal foramen and inserts on the basipodite apodeme. The most internal basipodite depressor muscle (figs. 46, 48) is a semicylindrical structure originating on medial phragmal apodemes and inserting on the posteromedial edge of the basipodite.

The total action of the basipodite depressor muscles is relatively powerful. By their contractions the basipodite and distal elements of the third maxilliped are turned ventrad. The homologies of these muscles with those of *Astacus*, *Pandalus*, and *Callinectes* are not entirely clear. The depressor muscle *a* of *Astacus* and *Pandalus* is the same muscle as the innermost, medial basipodite depressor muscle in *Penaeus*. Undoubtedly, the depressor muscles a_1 and *b* in *Astacus*, and a_1, a_2 and *b* in *Pandalus* have counterparts in the third maxilliped of *Penaeus*, but their exact relationships are difficult to determine.

EXPODITE ABDUCTOR MUSCLES OF THIRD MAXILLIPED

FIGURES 46, 47

Similar to the arrangement in the second maxilliped, the third maxilliped exopodite of *Penaeus* is moved by 2 exopodite abductor muscles, 1 ex-

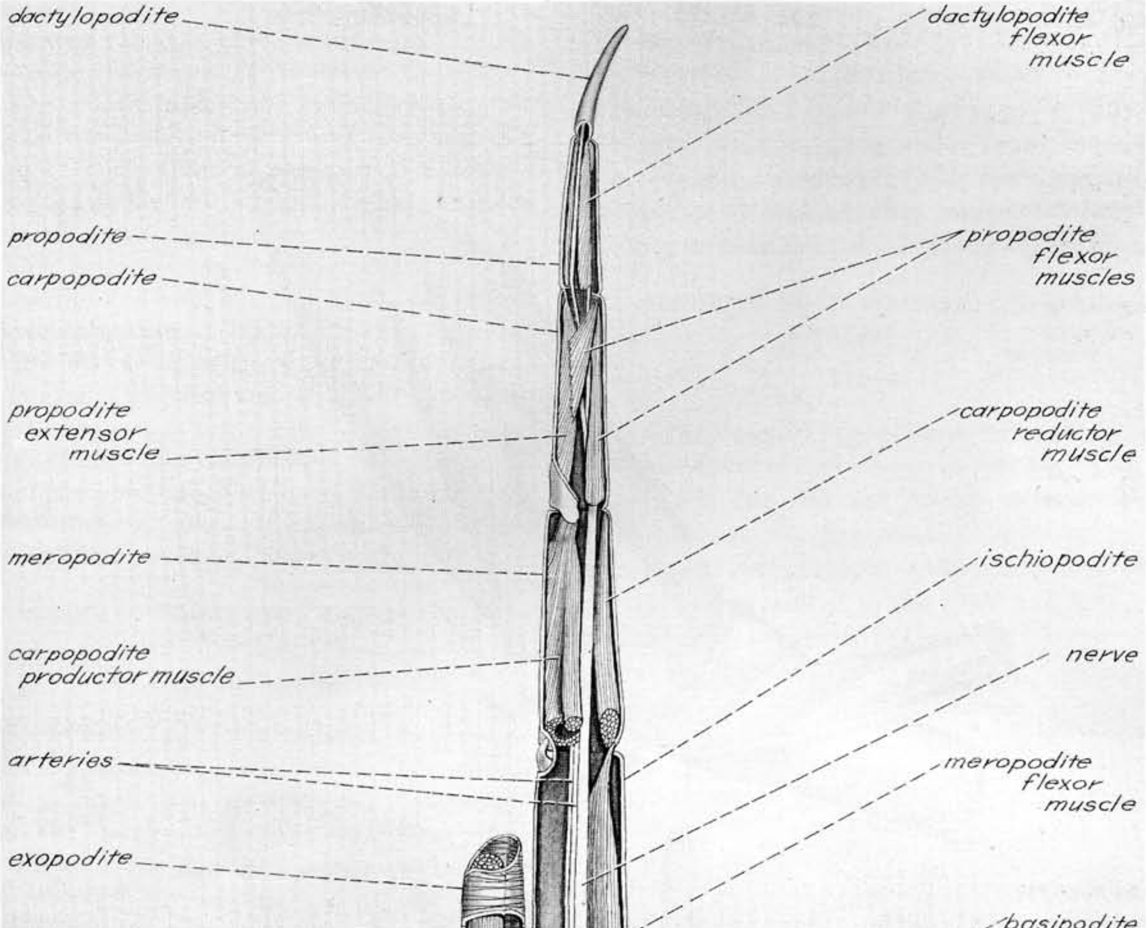

FIGURE 46.—Dorsal view of left third maxilliped, dorsal cuticle removed to show muscles.

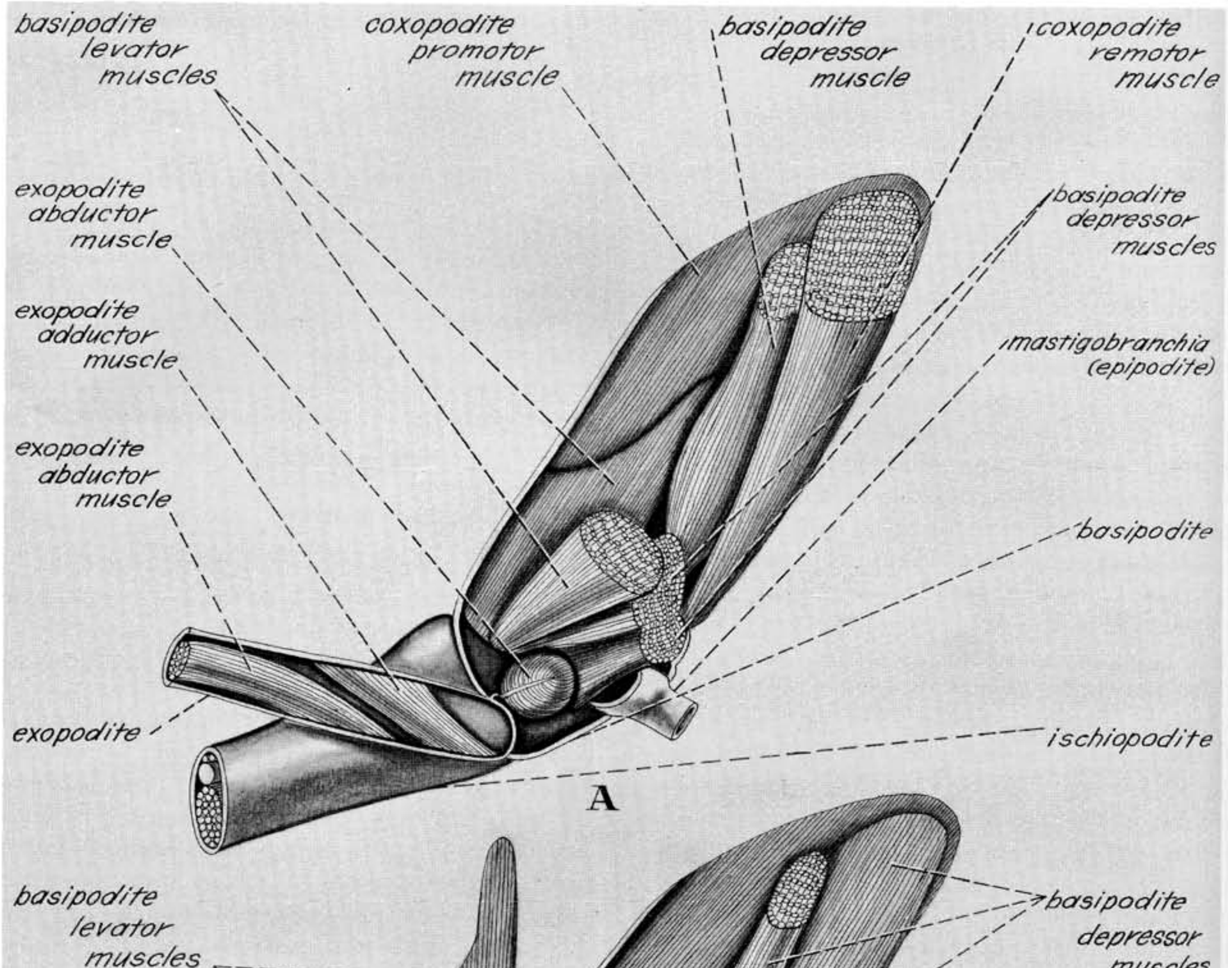

FIGURE 47.—Lateral view of leg base of left third maxilliped. Cuticle removed to show muscles. *A*. Superficial lateral and exopodite muscles. *B*. Lateral muscles, exopodite removed.

trinsic and 1 intrinsic to the structure. The wedge-shaped extrinsic abductor (figs. 46; 47, *B*) originates on the ventromedial wall of the basipodite. The muscle tapers to a point, laterally, inserting on the posterior margin of the exopodite foramen. Contractions of the exopodite abductor turn the exopodite laterad. Intrinsic to the flagellar exopodite is a long abductor muscle (fig. 46) which originates in the proximal region of the exopodite and runs distally along the lateral side of the flagellum. Its contractions increase the lateral curvature of the flagellum, thus turning it laterad. The extrinsic exopodite abductor muscle of *Penaeus* is represented under the same name in *Astacus* and *Callinectes.* The exopodite of *Pandalus* is extremely reduced. The intrinsic exopodite abductor probably appears as the exopodite flagellum muscle in *Astacus* and *Callinectes.*

EXPODITE ADDUCTOR MUSCLES OF THIRD MAXILLIPED

FIGURES 46; 47, *B*

Two exopodite adductor muscles in *Penaeus* turn the exopodite flagellum mesad. The conical extrinsic adductor originates on the dorsomedial wall of the basipodite, dorsad of the extrinsic exopodite abductor muscle (fig. 46), and inserts on the anterior rim of the exopodite foramen. The intrinsic exopodite adductor is comprised of a pair of small muscles originating on the posterolateral side of the flagellum base and attaching a short distance distally on the medial and dorsal wall of the flagellum. The extrinsic adductor has a counterpart in *Callinectes*, but not in *Astacus.* The little intrinsic adductor muscle in *Penaeus* possibly may be the exopodite flagellum abductor muscle of *Astacus* and *Callinectes*, although this is doubtful.

MEROPODITE FLEXOR MUSCLE OF THIRD MAXILLIPED

FIGURES 46, 47

The meropodite flexor muscle is a long, spindle-shaped muscle arising in the basipodite and passing distally along the lateral wall of the ischiopodite to an apodemal insertion on the proximal end of the meropodite. The apodeme of insertion is located ventromedially. When the meropodite flexor contracts, the meropodite and distal articles of the endopodite are turned sharply mesad and, due to the arrangement of the condyles, ventrad. The ischiopodite-meropodite junction is the major functional joint in the third maxilliped. The meropodite flexor muscle of *Penaeus* is fully homologous with the meropodite flexor muscle of *Astacus* and *Callinectes.* The third maxilliped endopodite of *Pandalus* has lost parts by fusion, making difficult the homologies of its muscles.

CARPOPODITE PRODUCTOR MUSCLE OF THIRD MAXILLIPED

FIGURE 46

The carpopodite productor muscle takes origin over an extensive area along the lateral side of the meropodite (fig. 46) and inserts on an apodeme of the carpopodite. Its contractions straighten the carpopodite with respect to the meropodite. The muscle is represented in the third maxilliped of *Astacus* and apparently in *Pandalus.* The productor muscle is referred to as an extensor by Cochran in *Callinectes* due to a difference in condylic orientation.

CARPOPODITE REDUCTOR MUSCLE OF THIRD MAXILLIPED

FIGURE 46

Opposing the action of the carpopodite productor muscle is the carpopodite reductor muscle. This muscle originates in the proximal region of the meropodite and passes distally along the medial side of the meropodite to insert on a ventromedial apodeme of the carpopodite. Upon contraction, the muscle turns the carpopodite and the distal articles ventrad. The carpopodite reductor muscle of *Penaeus* is the same muscle in *Astacus*, *Pandalus*, and *Callinectes*, although in the latter Cochran describes it as a flexor.

PROPODITE EXTENSOR MUSCLE OF THIRD MAXILLIPED

FIGURE 46

Originating for some length along the lateral margin of the carpopodite, the propodite extensor muscle inserts on a laterally located apodeme of the propodite. The muscle extends the propodite and dactylopodite directly anterior to the carpopodite. The same muscle is found in all the crustaceans to which reference has been made.

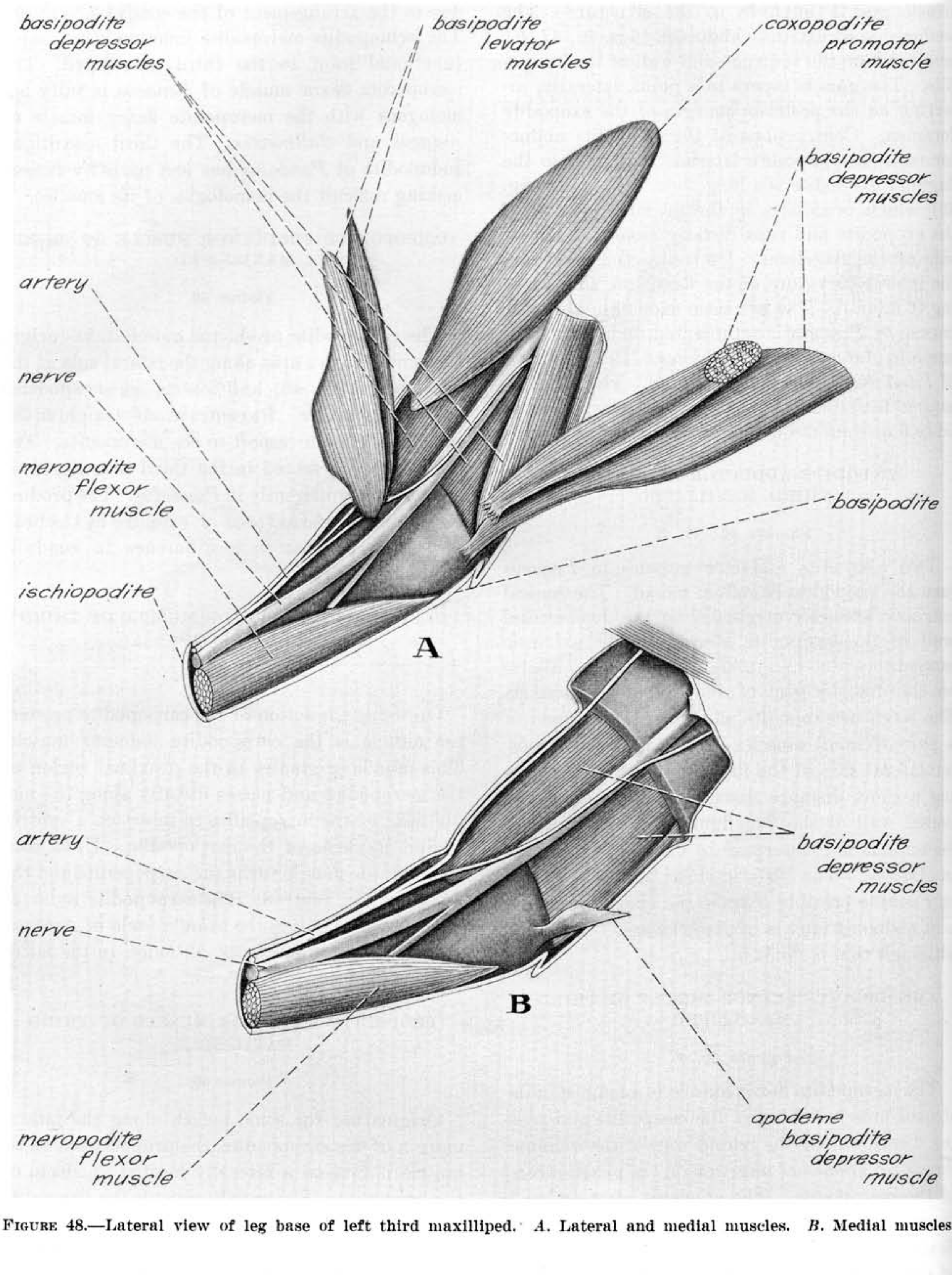

FIGURE 48.—Lateral view of leg base of left third maxilliped. *A*. Lateral and medial muscles. *B*. Medial muscles.

PROPODITE FLEXOR MUSCLES OF THIRD MAXILLIPED

FIGURE 46

The third maxilliped of *Penaeus* is unique by comparison with the same appendage of *Pandalus*, *Astacus*, and *Callinectes* in having two propodite flexor muscles. The larger originates in the carpopodite proximally and passes distally on the lateral side of the article to its insertion on an apodeme of the propodite. The smaller propodite flexor is a little triangular muscle (fig. 46) which has a common insertion with the larger flexor. The flexor muscles turn the propodite mesad on the carpopodite. The larger propodite flexor muscle is found in all the crustaceans referred to.

DACTYLOPODITE FLEXOR MUSCLE OF THIRD MAXILLIPED

FIGURE 46

The dactylopodite flexor muscle arises in the proximal portion of the propodite and is attached to an apodeme of the dactylopodite. The muscle turns the dactylopodite toward the midline. Dactylopodite flexors appear in the third maxilliped of *Astacus* and *Callinectes*. The distal articles are fused in *Pandalus* and the muscles thus lost. The third maxilliped of *Penaeus* has no dactylopodite extensor muscle, a structure described in *Astacus* and *Callinectes*.

5. PEREIOPODS

In the Crustacea Decapoda the last five pairs of thoracic appendages are usually referred to as walking legs, or pereiopods. Although their length, size, and functional modifications are variable in the group, the walking legs are all fundamentally alike in structure. Exopodites, usually small, are either present or absent. The large protopodite-endopodite is almost always composed of the typical seven appendage articles, although fusion of the basipodite with the ischiopodite has occurred in some groups. Some or all of the pereiopods may be chelate. Incidentally, Dougherty (Steinberg and Dougherty, 1957) objects to the spelling of the word "pereiopod" and offers good reasons for dropping the *i* in American usage. The common and perhaps incorrect spelling is used in the present work.

In *Penaeus*, the pereiopods are all relatively long and slender as befits a lightly sclerotized form whose body weight on the walking legs is not great. The first three pereiopods bear small chelae with sharp cutting edges. The last two walking legs are subchelate. Small exopodites are found on all five pairs of pereiopods. The joint between the basipodite and ischiopodite is movable in the walking legs of *Penaeus*. The coxopodite and basipodite comprise the protopodite to which an endopodite with the typical five articles is attached. Associated with the pereiopods are branchiae. With the third maxillipeds, the first, second, and third pereiopods have a bilobed mastigobranchia (epipodite) arising from the coxopodites, 2 arthrobranchiae on the dorsal articular membrane, and 1 pleurobranchia on the laterotergal plate. The mastigobranchia and one arthrobranchia is missing on the fourth pereiopod and the fifth pereiopod has only a pleurobranch.

Due to pronounced serial similarity of parts in the walking legs, only the first and fifth pereiopods will be considered in detail here.

5a. First Pereiopod

The first pereiopod is considered as an example of a chelate limb. It is ordinarily treated as the first walking leg. Whereas in the Reptantia the first pereiopods are modified into huge chelate chelipeds, those of the Penaeidae, while chelate, are similar in size to the remaining four pairs of walking legs. In point of fact, the first pereiopod of *Penaeus* is not a functional walking leg. That is to say, none of the body weight is supported on the appendage. The first pereiopods are carried horizontally, directed anteriorly, ventrad of the third maxillipeds, and function to pass food particles to the latter.

SKELETAL ELEMENTS

The strongly sclerotized coxopodite articulates with the ventral skeleton by dorsoventral dicondyles. The axis through the condyles is such that when the coxopodite swings forward it also approaches the midline. The rearward motion, on the other hand, turns the coxopodites away from the midline. The angular attitude of the dicondylic axis of the first pereiopod is thus raised laterally with respect to the frontal plane and rostrad with respect to the transverse plane. Proceeding caudad, the angular attitude of the axis through the coxopodite condyles rises laterally with respect to the frontal plane in conjunction with the shift dorsad of the dorsal condyle and the increased width between the ventral sternal condyles. To the coxopodite is attached the strong, curving tube of the basipodite. The axis of the condyles between the coxopodite and basipodite is rotated 90° from the axis of the condyles connecting the coxopodite and the ventral skeleton. Primarily by means of the basipodite, the distal elements of the pereiopod are raised and lowered. A sharp process projects distally from the distomedial portion of the basipodite. A small, fingerlike exopodite bearing long setae projects laterad from the basipodite.

The ischiopodite is hinged to the basipodite to permit limited reduction of this article, and also some rotation of the distal elements due to the oblique angle of the condyles. Like the basipodite, the ischiopodite bears a sharp spine medially. The meropodite, one of the longer articles of the first pereiopod, articulates with the distal end of the ischiopodite, allowing some flexion and extension, together with a little reduction, of the distal segments. The most movable joint in the first walking leg is that connecting the meropodite and the carpopodite. The axis of the joint is horizontal, and the carpopodite is thereby capable of deep flexion on the meropodite. An antennal cleaning brush composed of comb-like setae resides in a distomedial depression of the carpopodite.

The chela is freely movable on the carpopodite. The propodite component is made up of a base element and a distal process (fig. 49). The dactylopodite articulates with the distal part of the base of the propodite, opposing the distal propodite process. Extremely fine calcareous teeth on the inner margins of the propodite process and dactylopodite enhance the cutting ability of the chela. Chemosensory pits from which project chemoreceptor tufts of fine setae are distributed in rows about the propodite process and dactylopodite surface.

MUSCLE ELEMENTS

The musculature of the first pereiopod is closely similar to that of the third maxilliped and the remaining walking legs. It is also similar to the pereiopod musculature of other decapods. The first pereiopod of *Penaeus* contains at least 21 discrete muscles arranged in 14 functional muscle types. *Astacus* has 19 muscles of 13 types, and *Callinectes* has 20 muscles functioning in 11 ways. The third pereiopod of *Pandalus* contains 16 muscles of 13 types.

COXOPODITE PROMOTOR MUSCLES OF FIRST PEREIOPOD

FIGS. 49, 50, 51

The first pereiopod of *Penaeus* possesses at least two coxopodite promotor muscles. They originate by broad regions along the anterodorsal margin of the pleural plate belonging to the segment and insert on the anterior rim of the coxopodite. Their contractions turn the coxopodite forward. The coxopodite promotors of *Penaeus* are represented in *Astacus*, *Pandalus*, and *Callinectes*.

COXOPODITE REMOTOR MUSCLE OF FIRST PEREIOPOD

FIGS. 49, 50, 51

The strong, spatulate coxopodite remotor muscle originates on the posterodorsal part of the laterotergal plate and attaches to a small apodeme on the posterior margin of the coxopodite foramen. The muscle turns the coxopodite rearward and in so doing brings the distal elements of the pereiopod ventrad, in opposition to the coxopodite promotors. The movement is evidently weaker than that of promotion, since the single remotor is much smaller than the promotor muscles. The homologies of the coxopodite remotor muscle of *Penaeus* with the remotor muscle of *Callinectes* are fairly obvious. *Astacus*, however, has three remotors. Which of these is homologous with the coxopodite remotor of *Penaeus* is not certain.

BASIPODITE LEVATOR MUSCLES OF FIRST PEREIOPOD

FIGURES 49, 50, 51

A characteristic of pereiopod musculature is the great weight and strength of the basipodite musculature, affording powerful levation and depression of that article and with it the distal elements of the leg. The situation in the Decapoda is reminiscent of the trochanteral musculature of the insects, except that the levators and depressors of the latter originate within the coxa, rather than on the pleural wall. Functionally, the basipodite depressors are the major support of the body between the walking legs.

The first walking leg of *Penaeus* has 4 basipodite levator muscles, of which 3 originate within the coxopodite and 1 dorsally on the pleural wall.

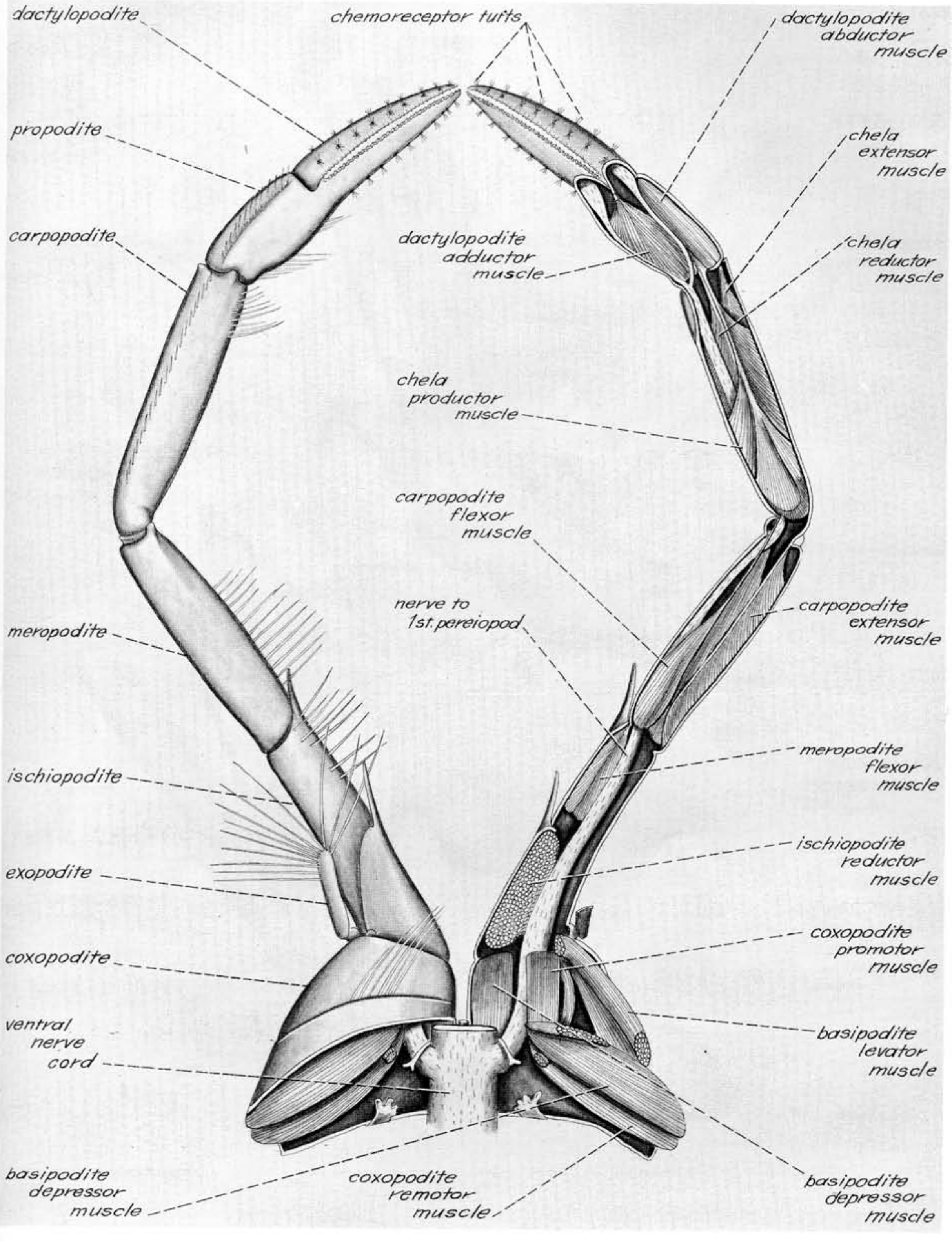

FIGURE 49.—Dorsal view of first pereiopod. Left side, intact appendage. Right side, dorsal cuticle removed to show muscles.

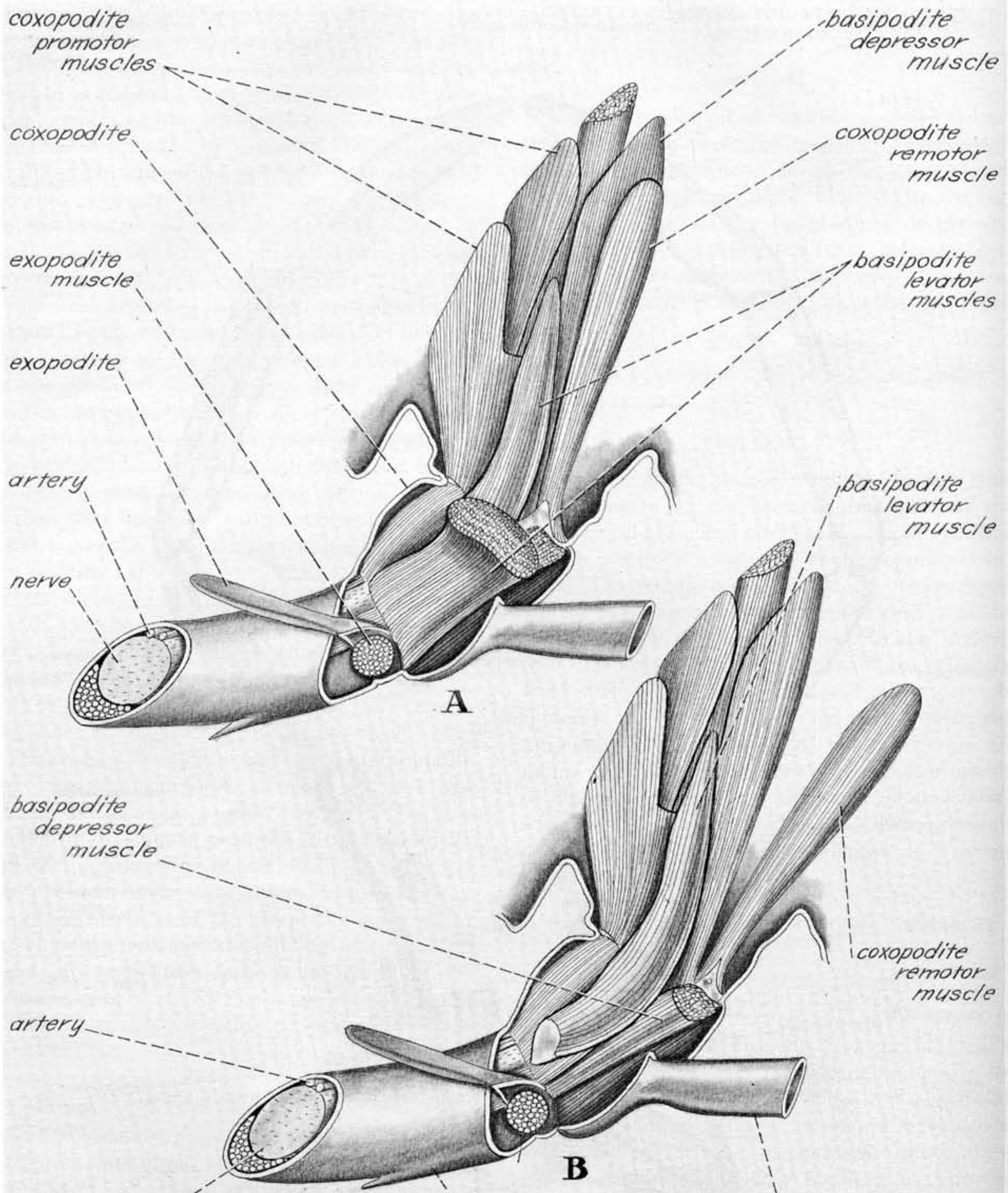

FIGURE 50.—Lateral view of leg base of left first pereiopod. *A.* Superficial lateral muscles. *B.* Some lateral muscles removed to show deeper muscles.

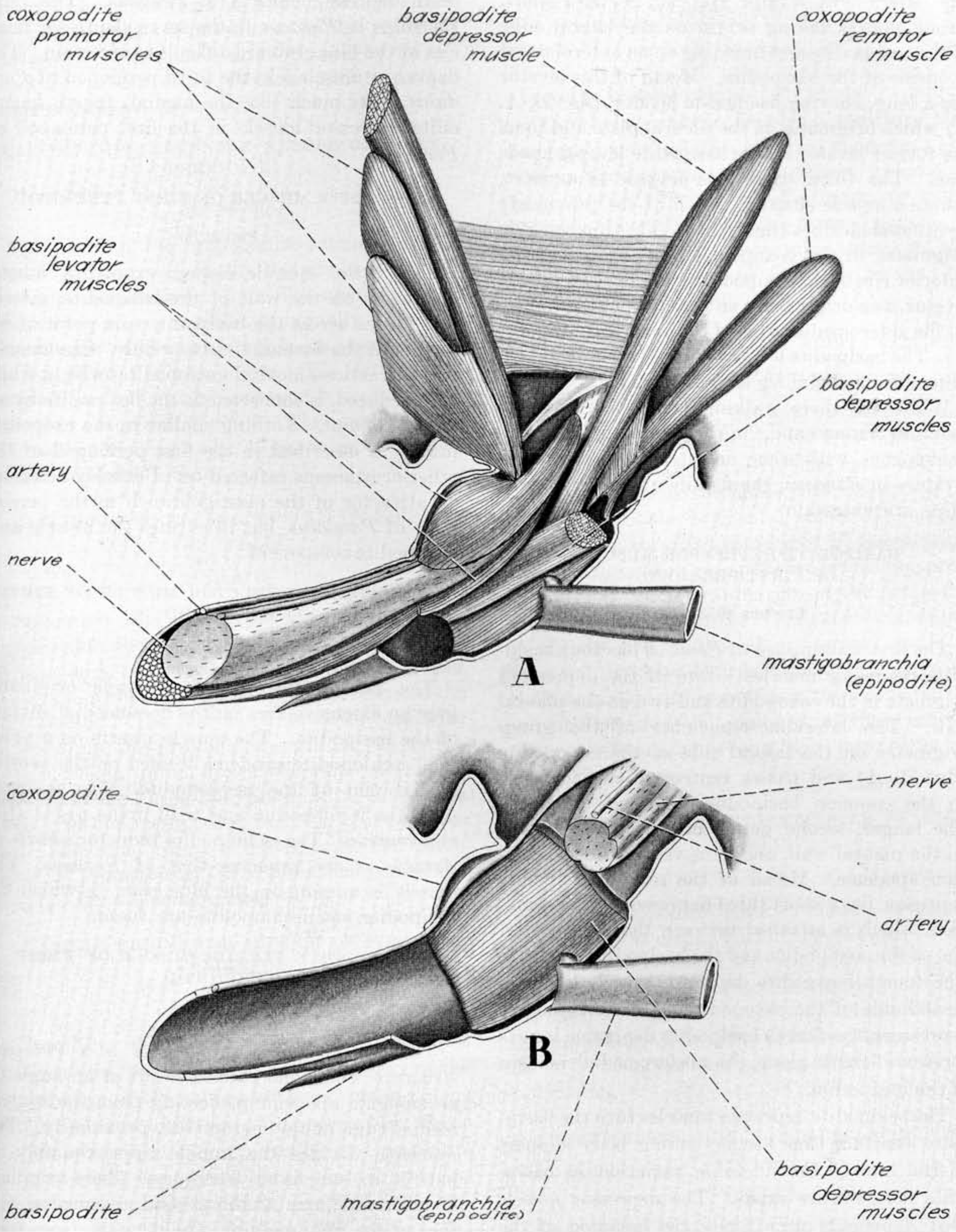

FIGURE 51.—Lateral view of leg base of left first pereiopod. *A*. Lateral and medial muscles. *B*. Medial muscles.

The lateralmost levator (fig. 50, *A*) is a short, strong muscle taking origin on the lateral edge of the coxopodite and inserting on an anterolateral apodeme of the basipodite. Mesad of this levator lies a long, curving basipodite levator (fig. 50, *A*, *B*) which originates on the pleural plate and joins the former levator on the basipodite levator apodeme. The third basipodite levator is a short, rounded muscle situated mesad of the previously mentioned levators (fig. 50, *A*). The third levator originates in the coxopodite and inserts on the anterior rim of the basipodite. The medial, fourth levator, also originating on the coxopodite, inserts on the anteromedial edge of the basipodite (fig. 51, *A*). The basipodite levator muscles turn the basipodite and the distal leg article dorsad.

While the three walking leg levator muscles found in *Astacus* and *Callinectes* are undoubtedly homologous with some or all of the basipodite levators in *Penaeus*, the details of their relationships are uncertain.

BASIPODITE DEPRESSOR MUSCLES OF FIRST PEREIOPOD

FIGURES 49, 50, 51

The first walking leg of *Penaeus* has four basipodite depressor muscles. Two of the depressors originate in the coxopodite and two on the pleural wall. The lateralmost member of the group originates on the lateral side of the coxopodite (fig. 51, *A*) and passes ventromedially to insert on the common basipodite depressor apodeme. The longer, second depressor originates dorsad, on the pleural wall, and runs ventrad to the common apodeme. Mesad of the second basipodite depressor lies a short third depressor of the basipodite which is attached between the dorsomedial rim of the coxopodite and the basipodite apodeme. The fourth basipodite depressor muscle lines the medial side of the coxopodite. Unlike the other depressors, the fourth basipodite depressor inserts for some length along the posteromedial margin of the basipodite.

The basipodite depressor muscles turn the basipodite ventrad, thus accomplishing body support on the limbs. Considerable variation in basipodite musculature exists. The depressor muscle *a* of *Astacus* is very likely the homolog of the long, second basipodite depressor of *Penaeus*, whereas the depressor muscle *b* of *Astacus* is probably homologous to the lateral, first basipodite depressor muscle in *Penaeus*. The relationships in *Penaeus* to the seven depressor muscles of the blue crab are difficult to ascertain. The depressor muscle *b* in the third pereiopod of *Pandalus* looks much like the medial, fourth basipodite depressor muscle in the first pereiopod of *Penaeus*.

EXOPODITE MUSCLE OF FIRST PEREIOPOD

FIGURE 50

The little, spindle-shaped exopodite muscle originates on the wall of the basipodite, mesad, and passes across the basipodite to a point of insertion at the base of the exopodite. Presumably its contractions move the exopodite, which, while very reduced, is connected to the basipodite by an articular joint. Nothing similar to the exopodite muscle is described in the first pereiopod of the other crustaceans referred to. Berkeley describes an attractor of the mastigobranch in the pereiopods of *Pandalus*, but illustrates the muscle as a coxopodite component.

ISCHIOPODITE REDUCTOR MUSCLE OF FIRST PEREIOPOD

FIGURE 49

The ischiopodite reductor muscle originates over an extensive area on the dorsomedial surface of the basipodite. The muscle inserts on a proximal ischiopodite apodeme located on the ventromedial rim of the ischiopodite. The reductor pulls the ischiopodite and with it the distal articles ventrad. The ischiopodite reductor muscle of *Astacus* is the same as that of *Penaeus*. The muscle is missing in the blue crab, in which the basipodite and ischiopodite are fused.

MEROPODITE FLEXOR MUSCLE OF FIRST PEREIOPOD

FIGURE 49

The meropodite flexor muscle is a two-part structure whose short fibers insert at an angle on an elongate apodeme projecting from the ventromedial edge of the meropodite, proximally. The apodeme divides the muscle approximately in half on its long axis. The muscle fibers originate about a wide area of the ventral and medial surface of the ischiopodite. Their contractions turn the meropodite mesad and to a lesser extent ventrally. The meropodite flexor muscle apparently is subdivided into two parts in *Astacus*, in which

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.

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.

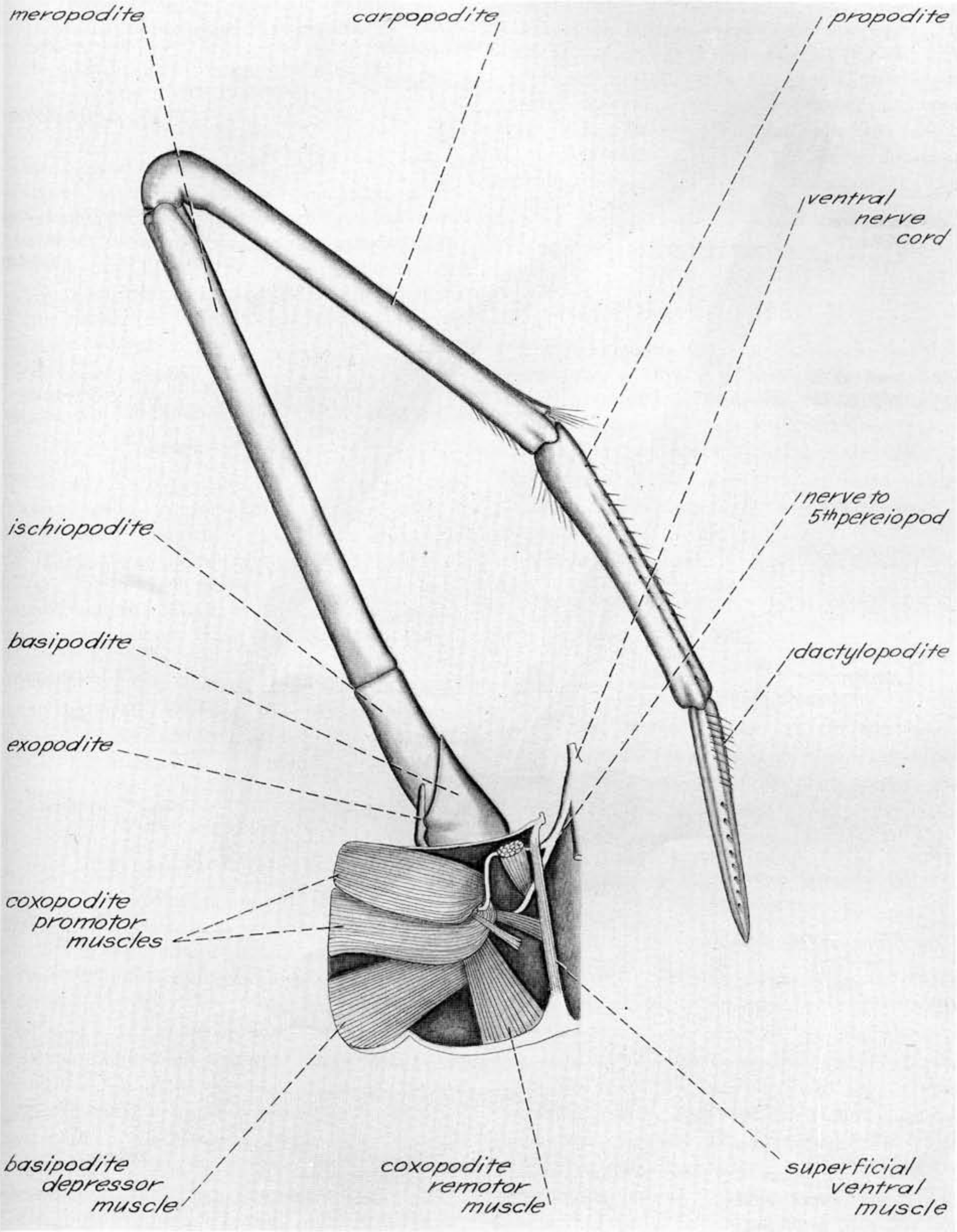

FIGURE 52.—Dorsal view of left fifth pereiopod showing protopodite muscles.

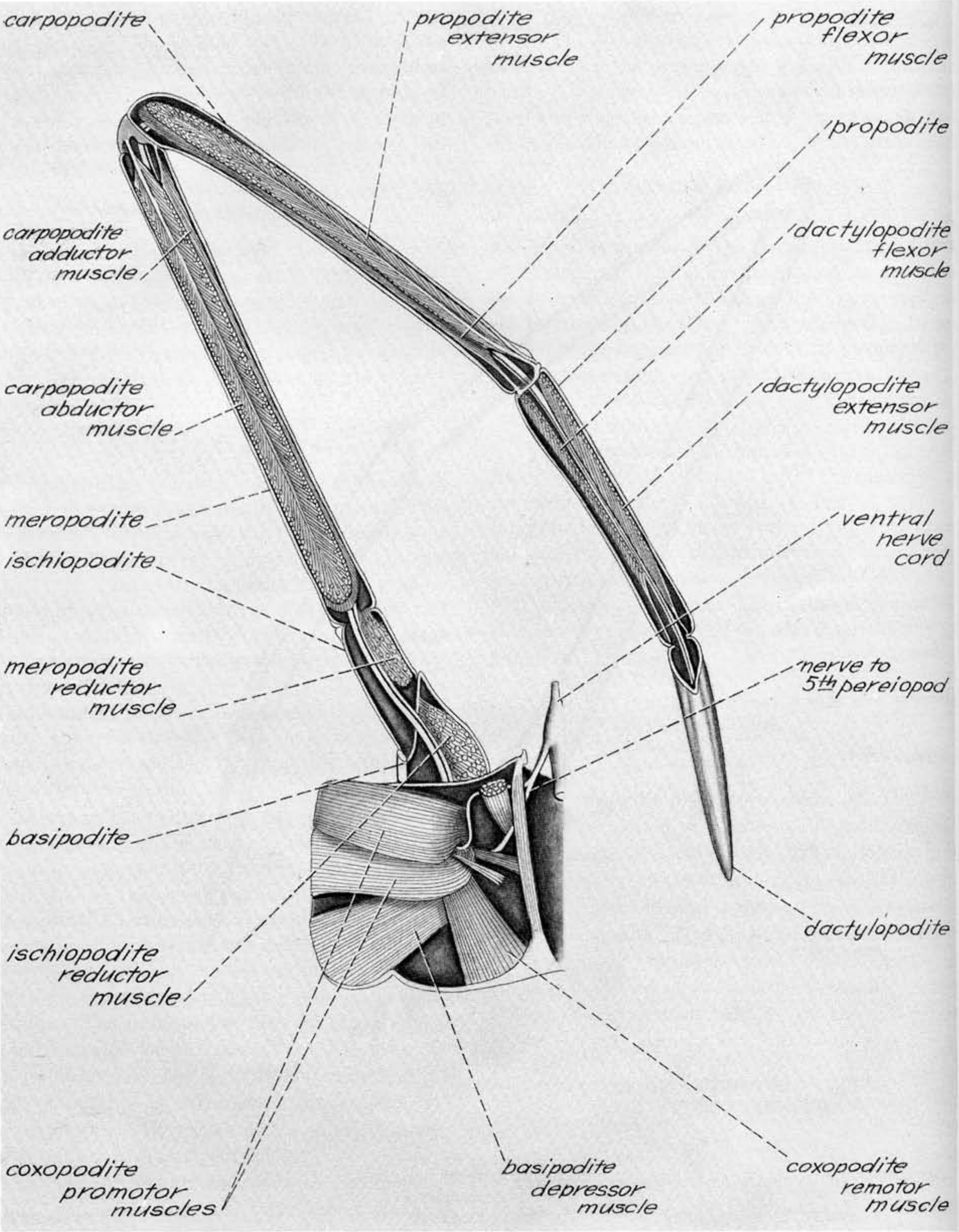

FIGURE 53.—Dorsal view of left fifth pereiopod. Dorsal cuticle removed to show muscles of protopodite and endopodite.

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.

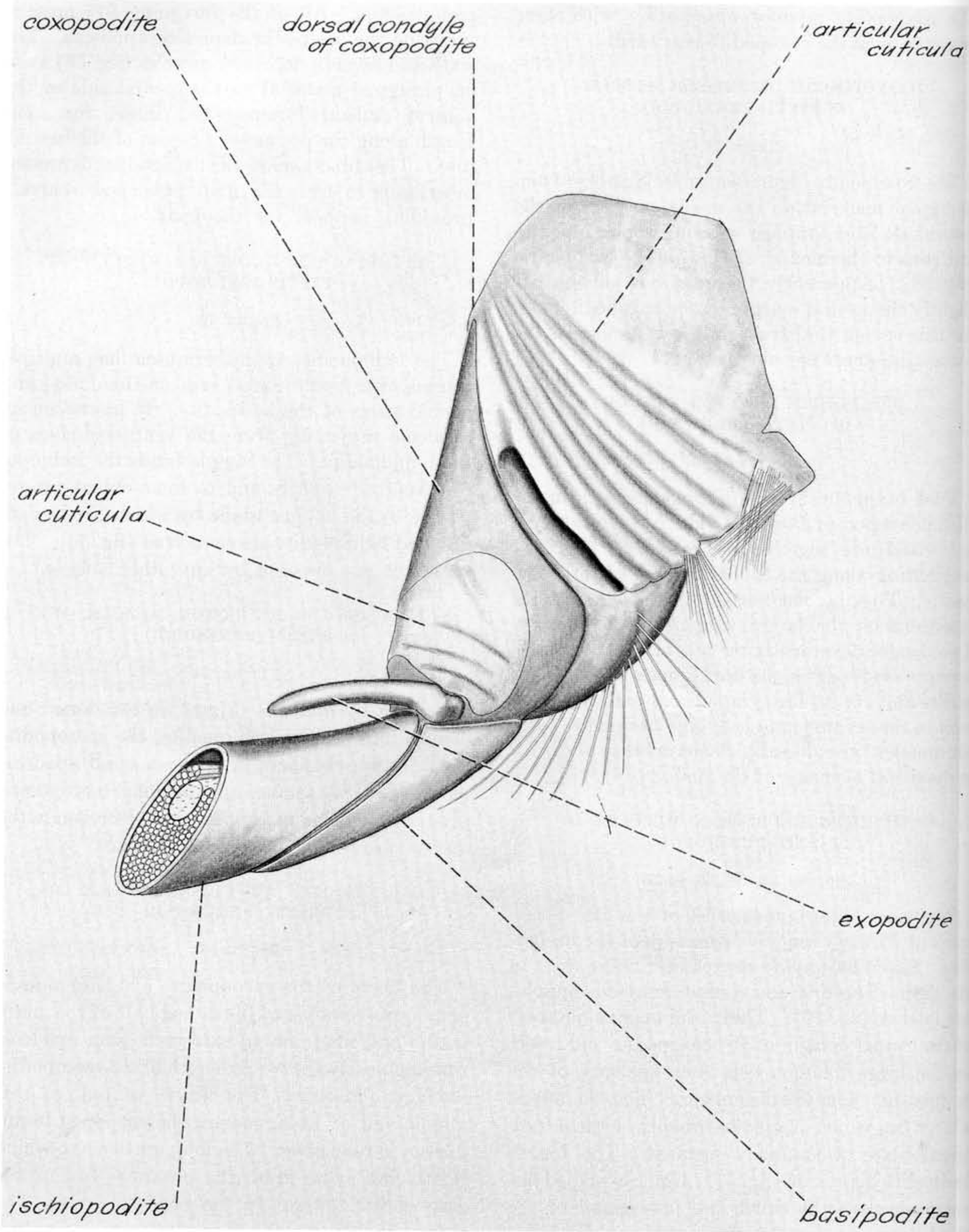

FIGURE 54.—Lateral view of leg base of left fifth pereiopod.

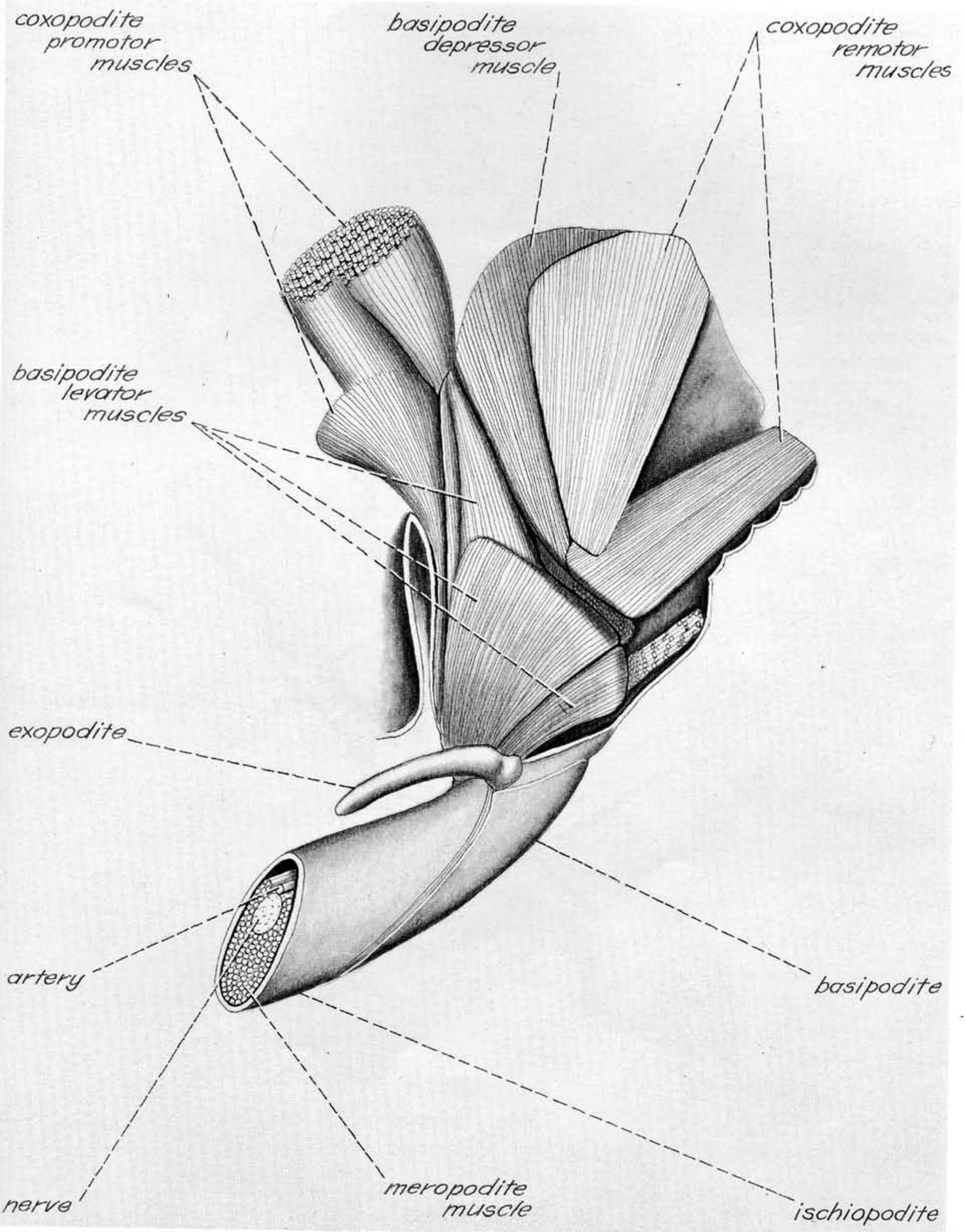

FIGURE 55.—Lateral view of leg base of left fifth pereiopod. Lateral cuticle removed to show superficial lateral muscles.

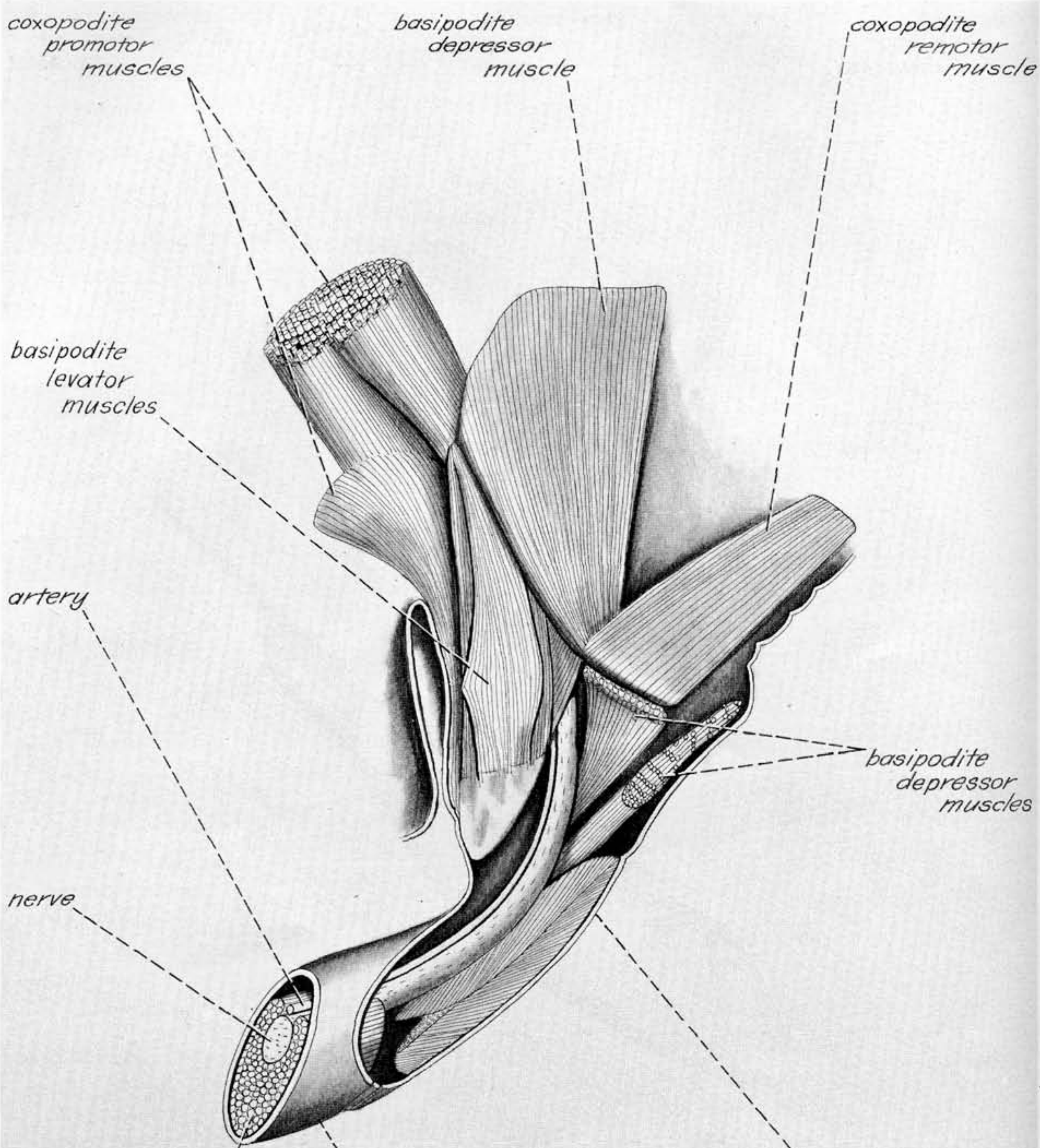

FIGURE 56.—Lateral view of leg base of left fifth pereiopod. Some superficial lateral muscles removed.

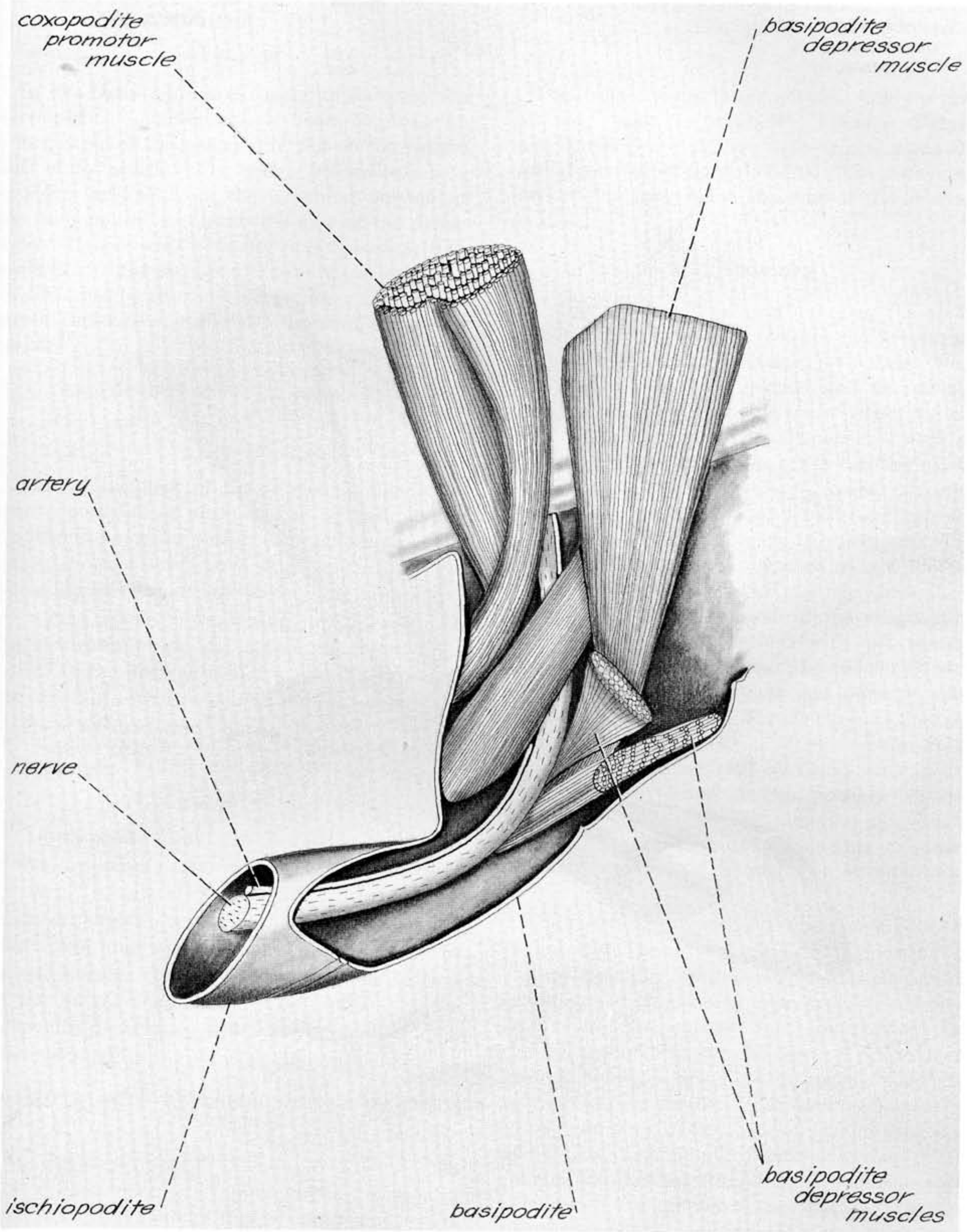

FIGURE 57.—Lateral view of leg base of left fifth pereiopod. Lateral muscles removed to show medial muscles.

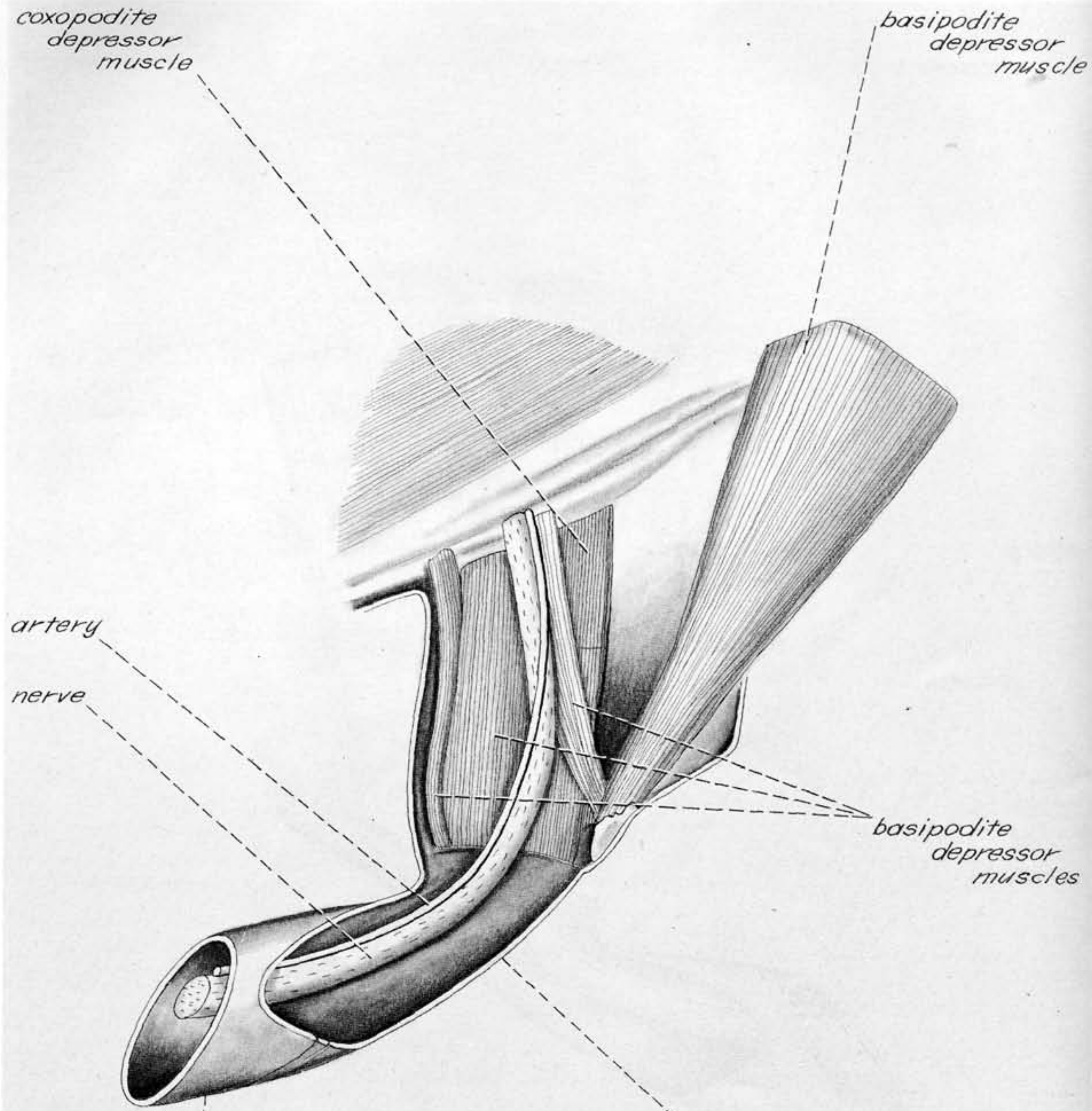

FIGURE 58.—Lateral view of leg base of left fifth pereiopod. Medial muscles.

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).

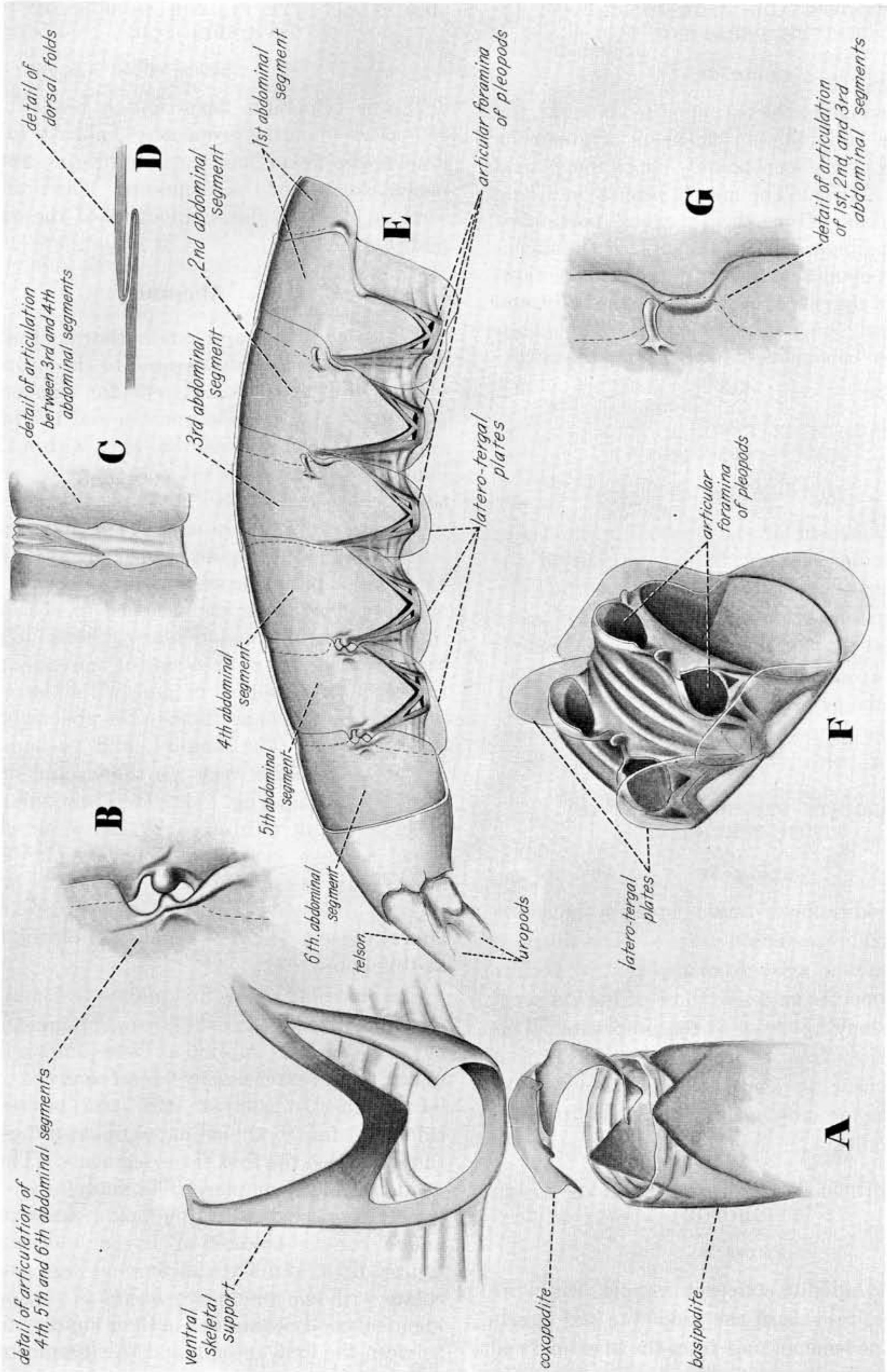

FIGURE 59.—Details of abdominal skeletal elements.

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-

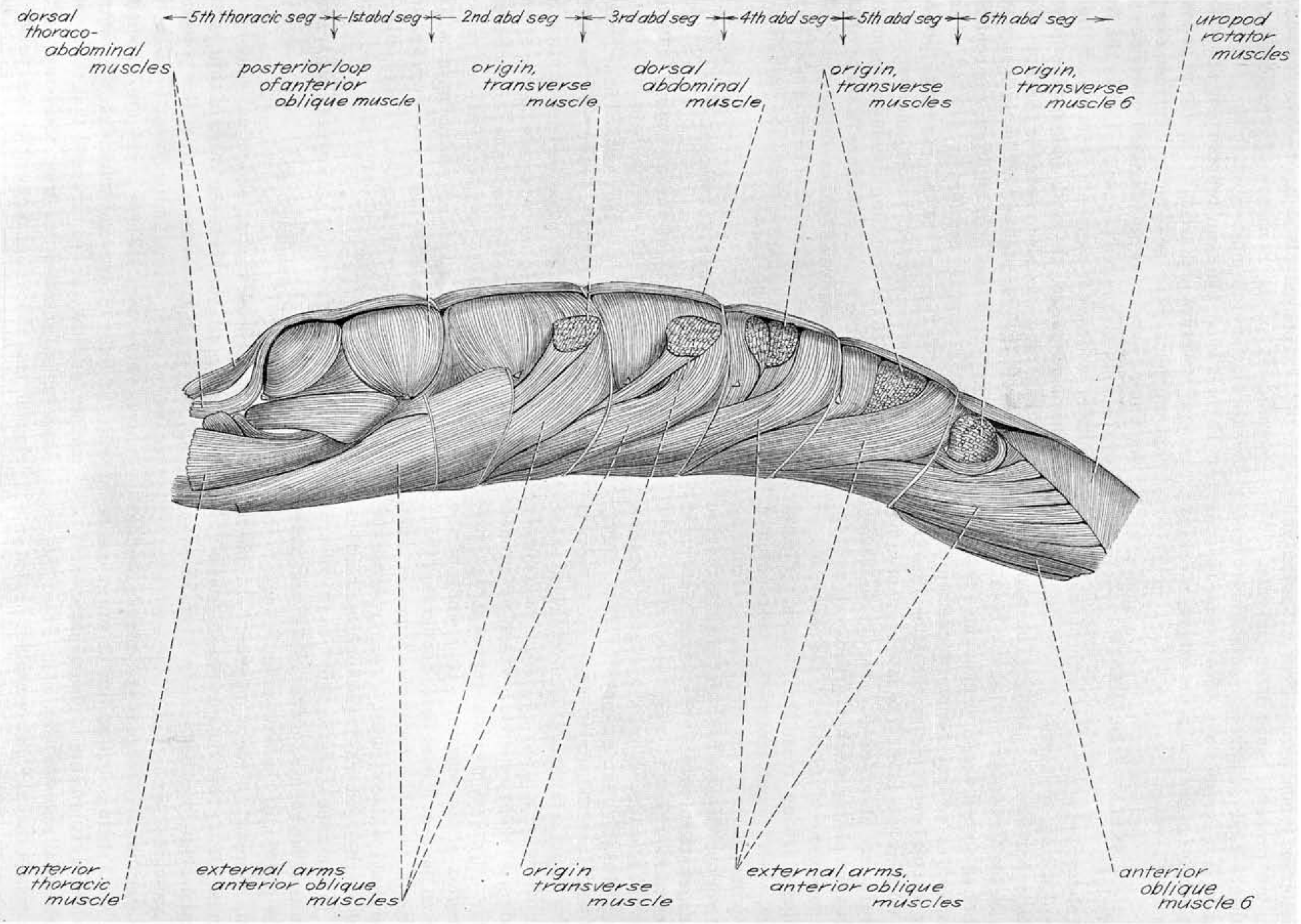

FIGURE 60.—Lateral view of left side of abdomen showing superficial abdominal muscles.

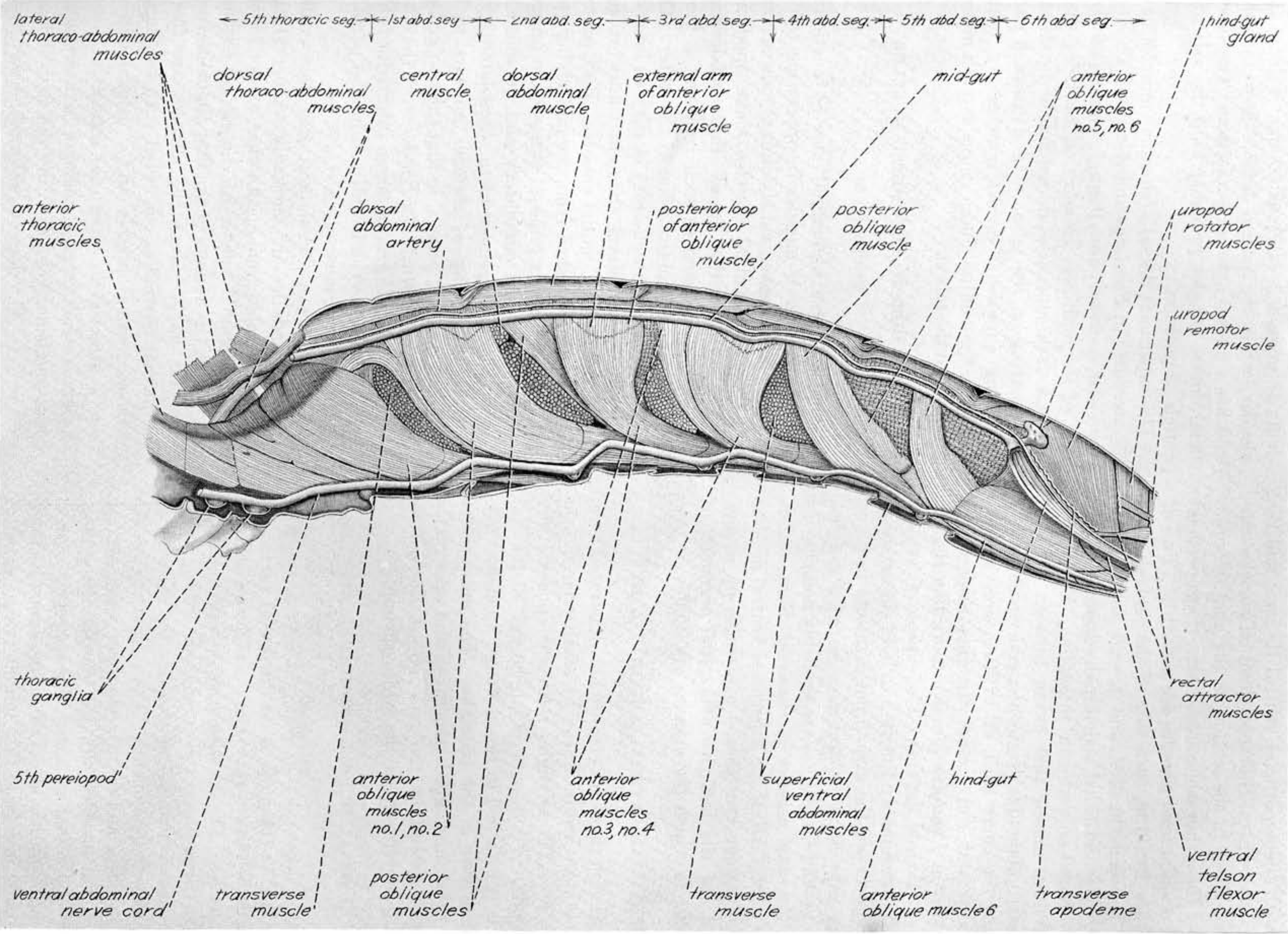

FIGURE 61.—Median sagittal cut through abdomen showing medial muscles.