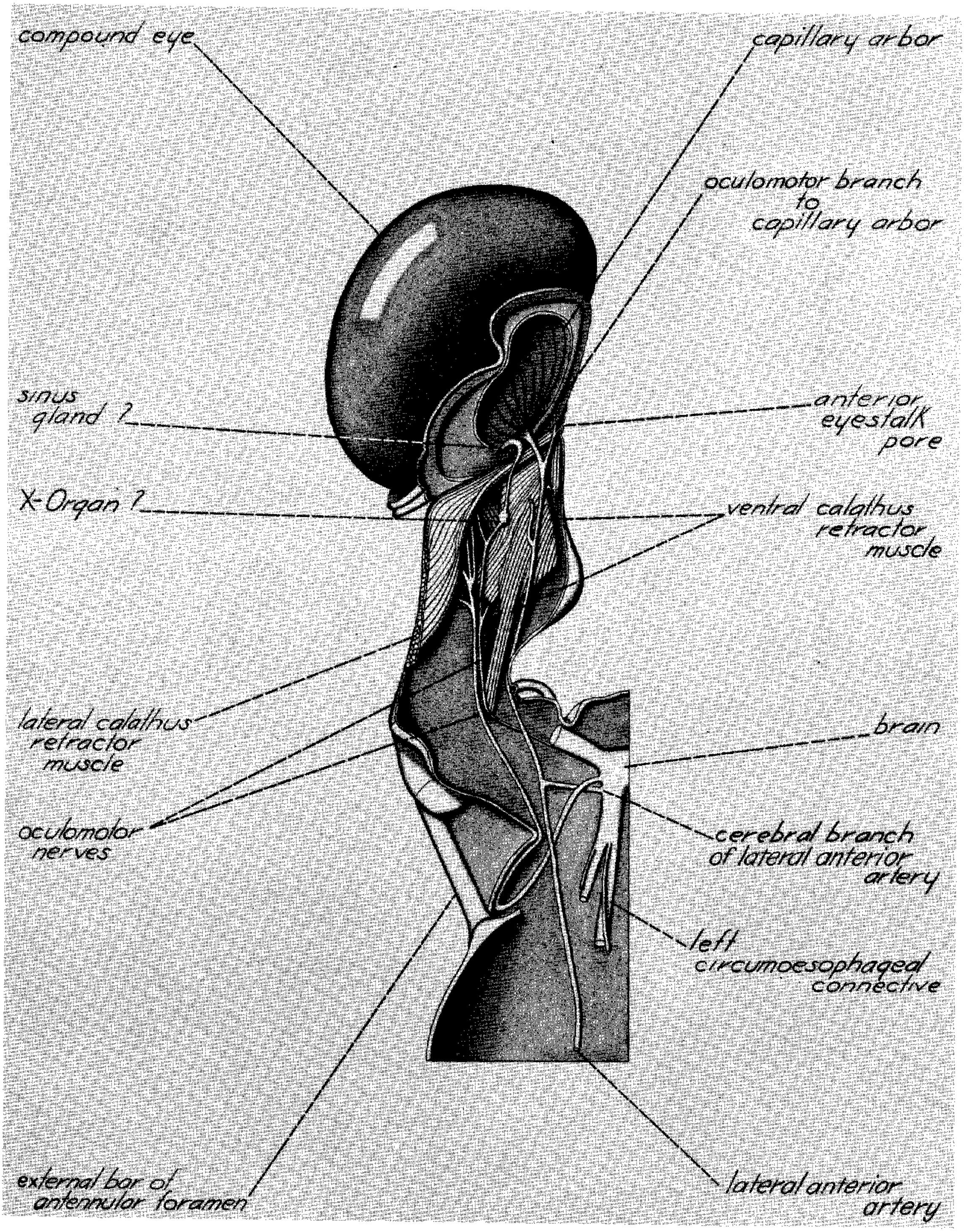

FIGURE 9.—Dorsal view of left eyestalk. Dorsal muscles and optic tract removed to show brain, branches of nerves, arterial capillary supply to distal optic ganglia, neurosecretory glands, and location of anterior eyestalk pore.

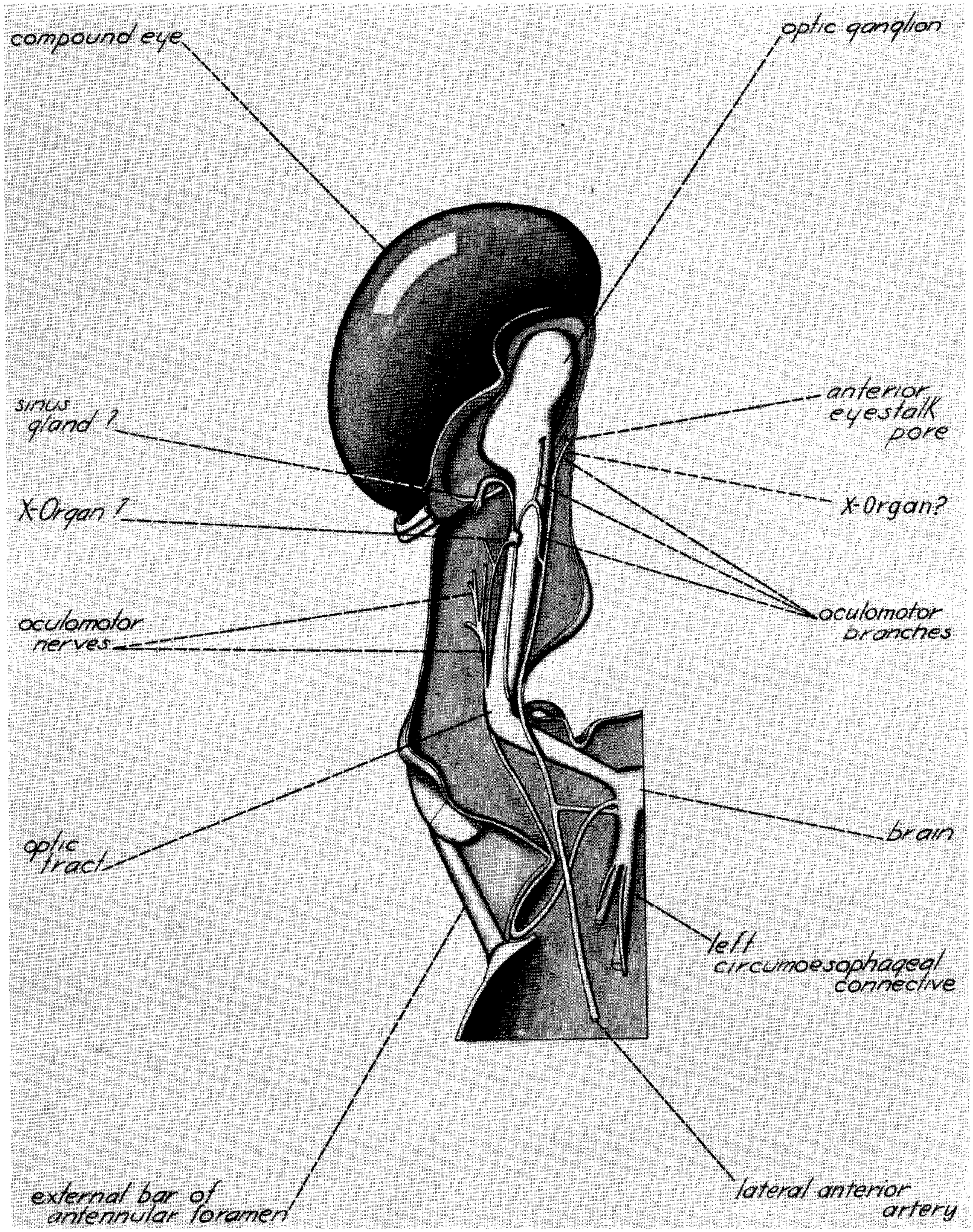

FIGURE 10.—Dorsal view of left eyestalk. Muscles removed to show optic tract, oculomotor nerves, neurosecretory glands, and branches of lateral anterior artery.

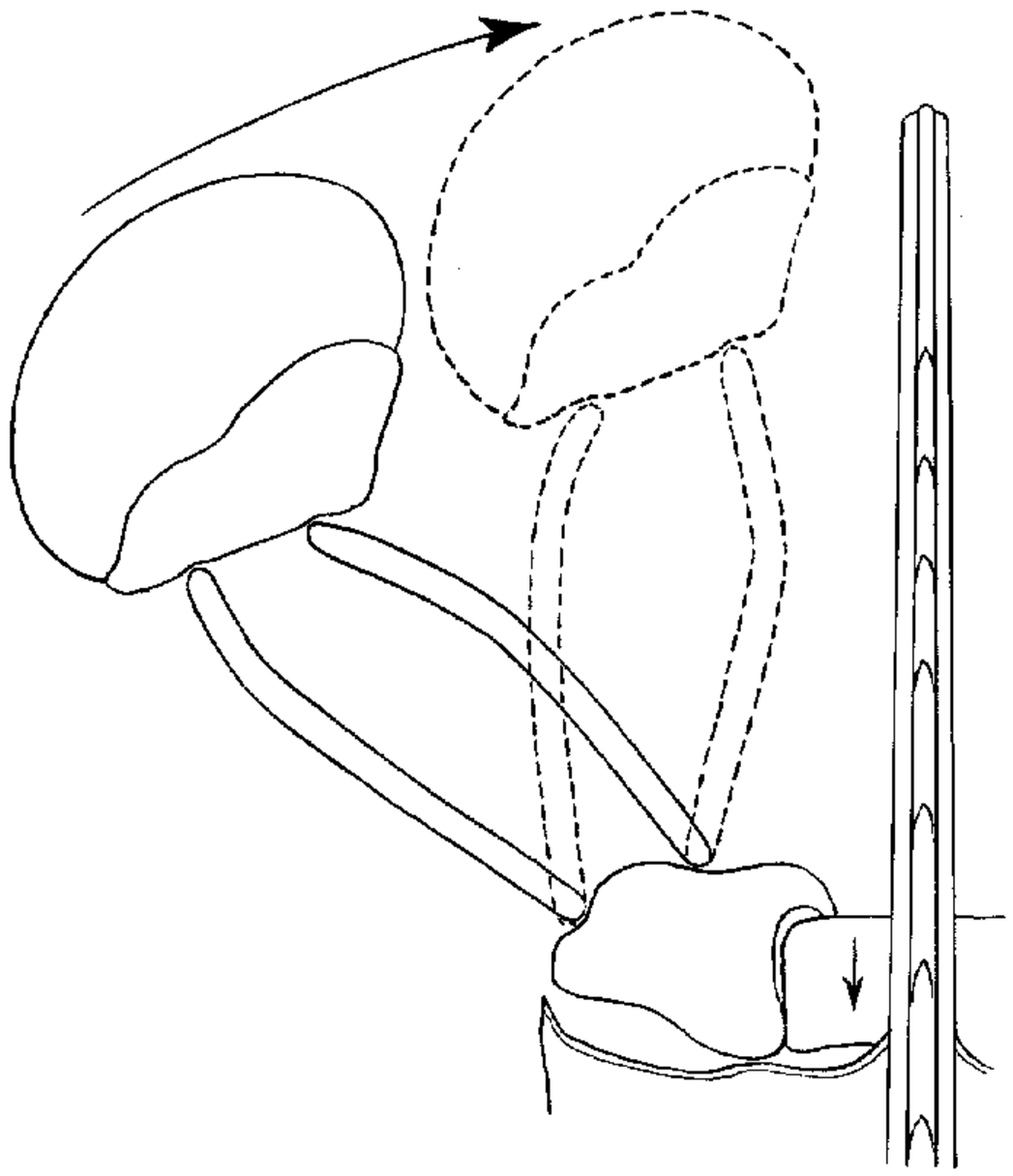

FIGURE 11.—Dorsal view of left eyestalk. Diagrammatic. The skeletal bars of the eyestalk are so arranged that the position of the ommatidial surface is maintained whatever the angle of the eyestalk with respect to the long axis of the shrimp.

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

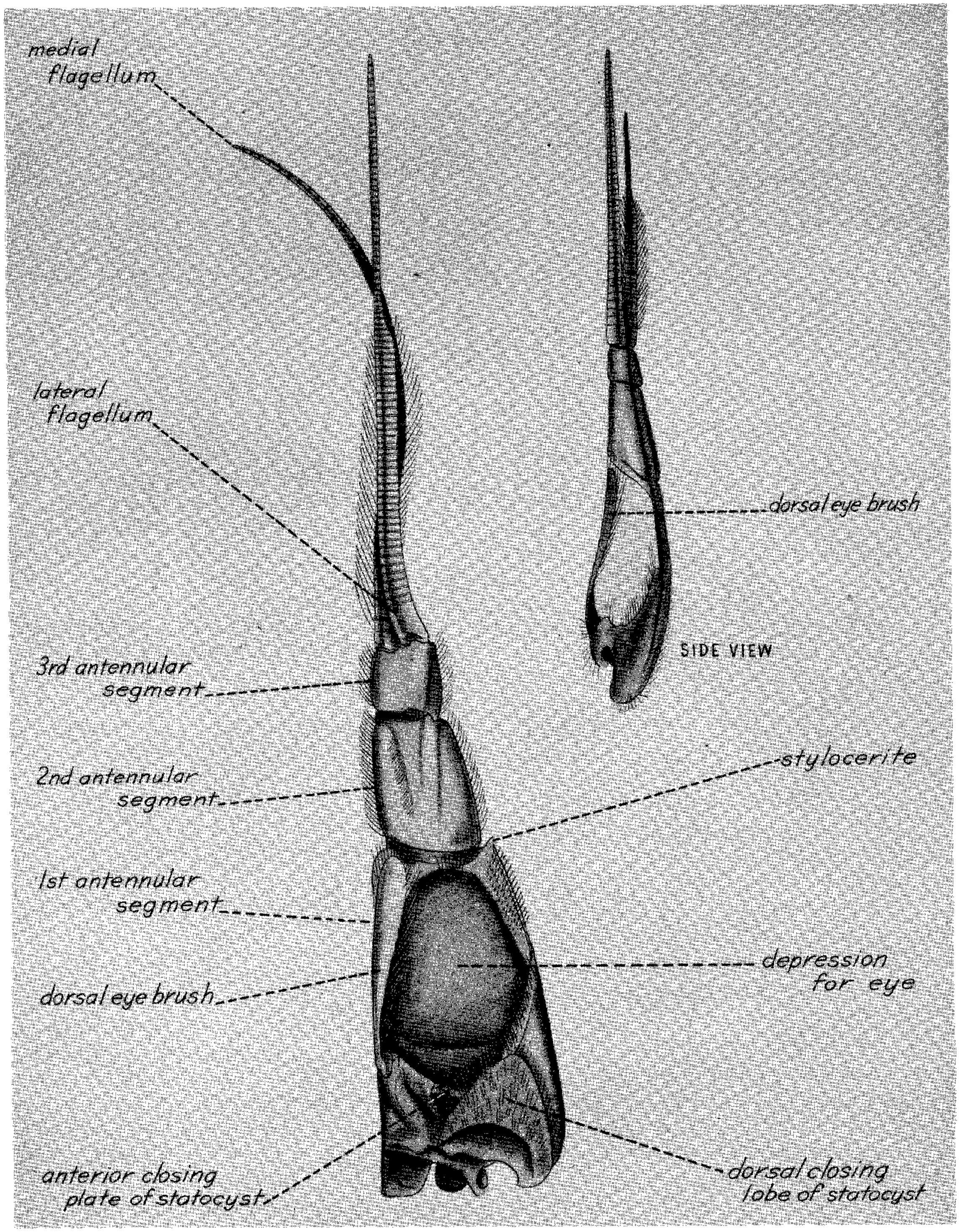

FIGURE 12.—The larger figure is a dorsal view of the right antennule, the smaller a lateral view of the right antennule.

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-

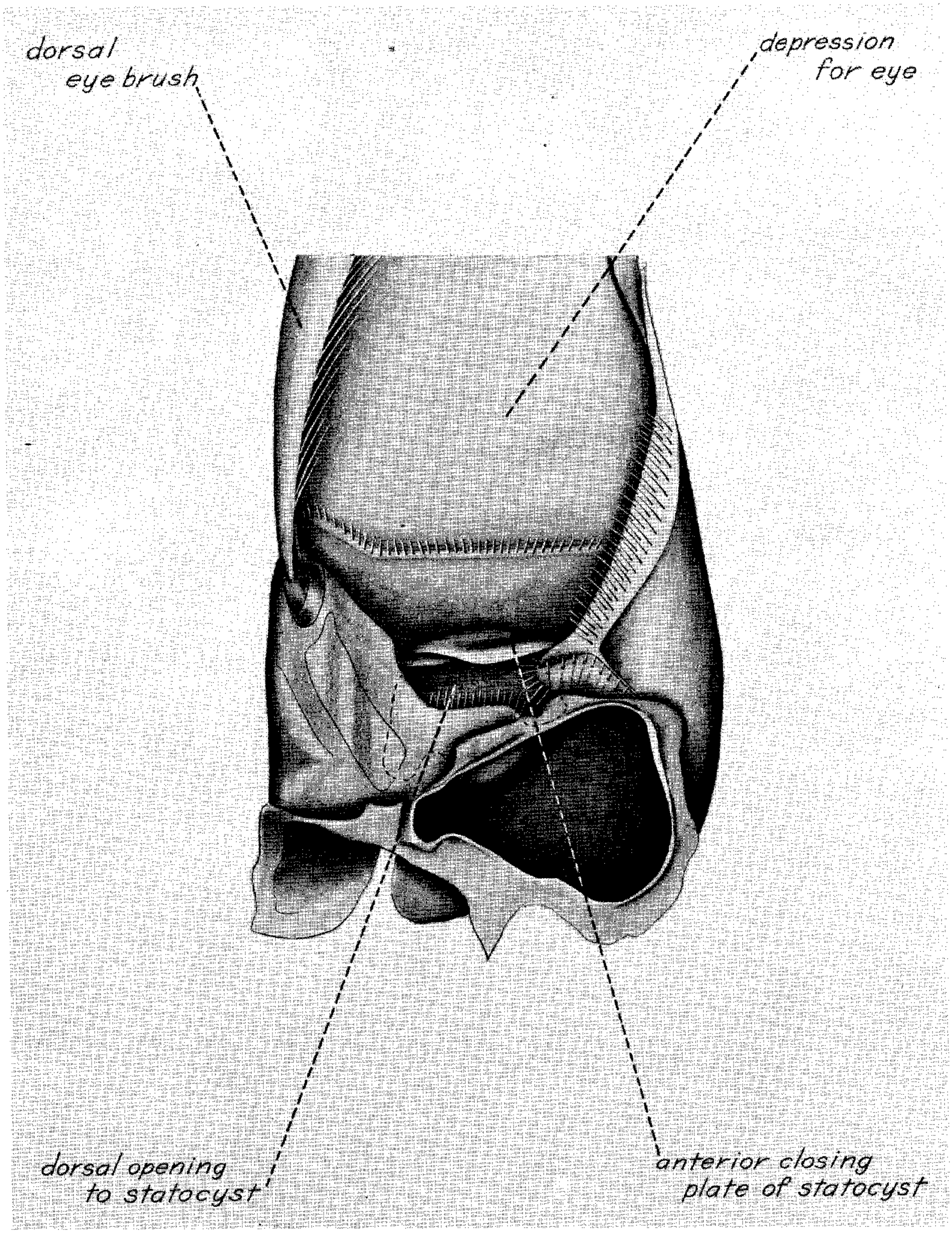

FIGURE 13.—Dorsal view of proximal region of first antennular segment, right antennule. Cleared specimen showing entrance to statocyst. Dorsal closing lobe removed.

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-

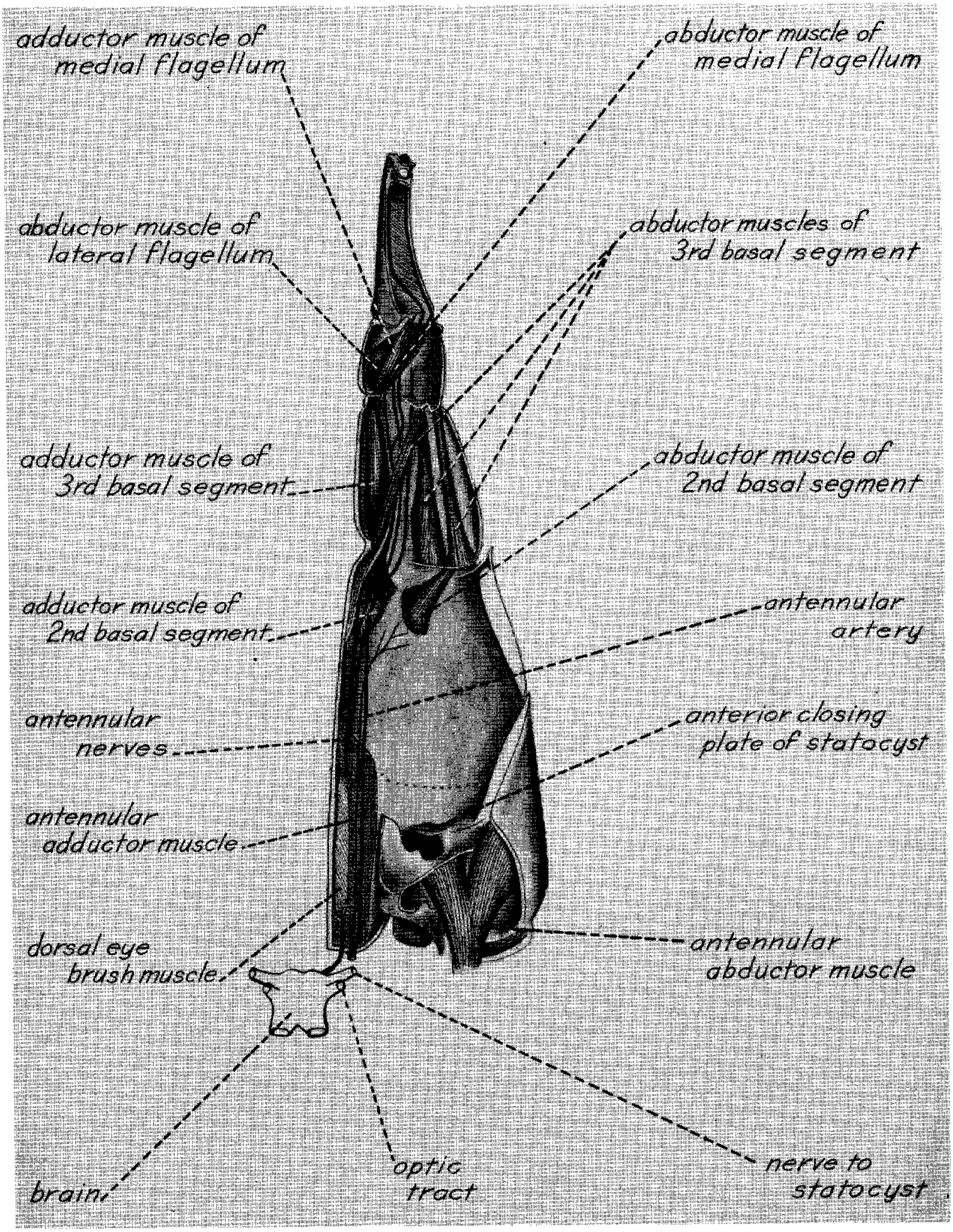

FIGURE 14.—Dorsal view of right antennule showing dorsal muscles. Dorsal cuticle removed.

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.

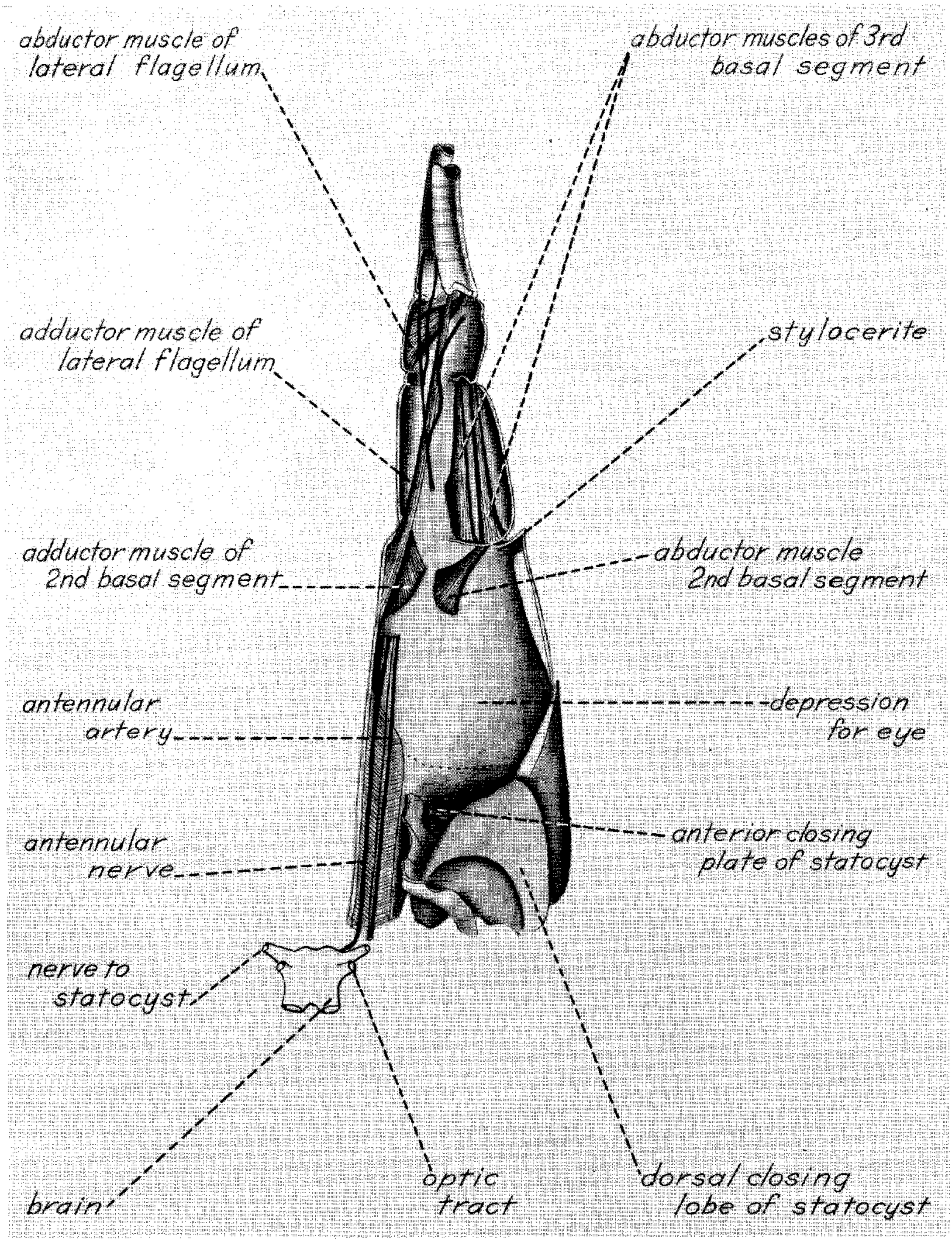

FIGURE 15.—Dorsal view of right antennule showing ventral muscles.

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-

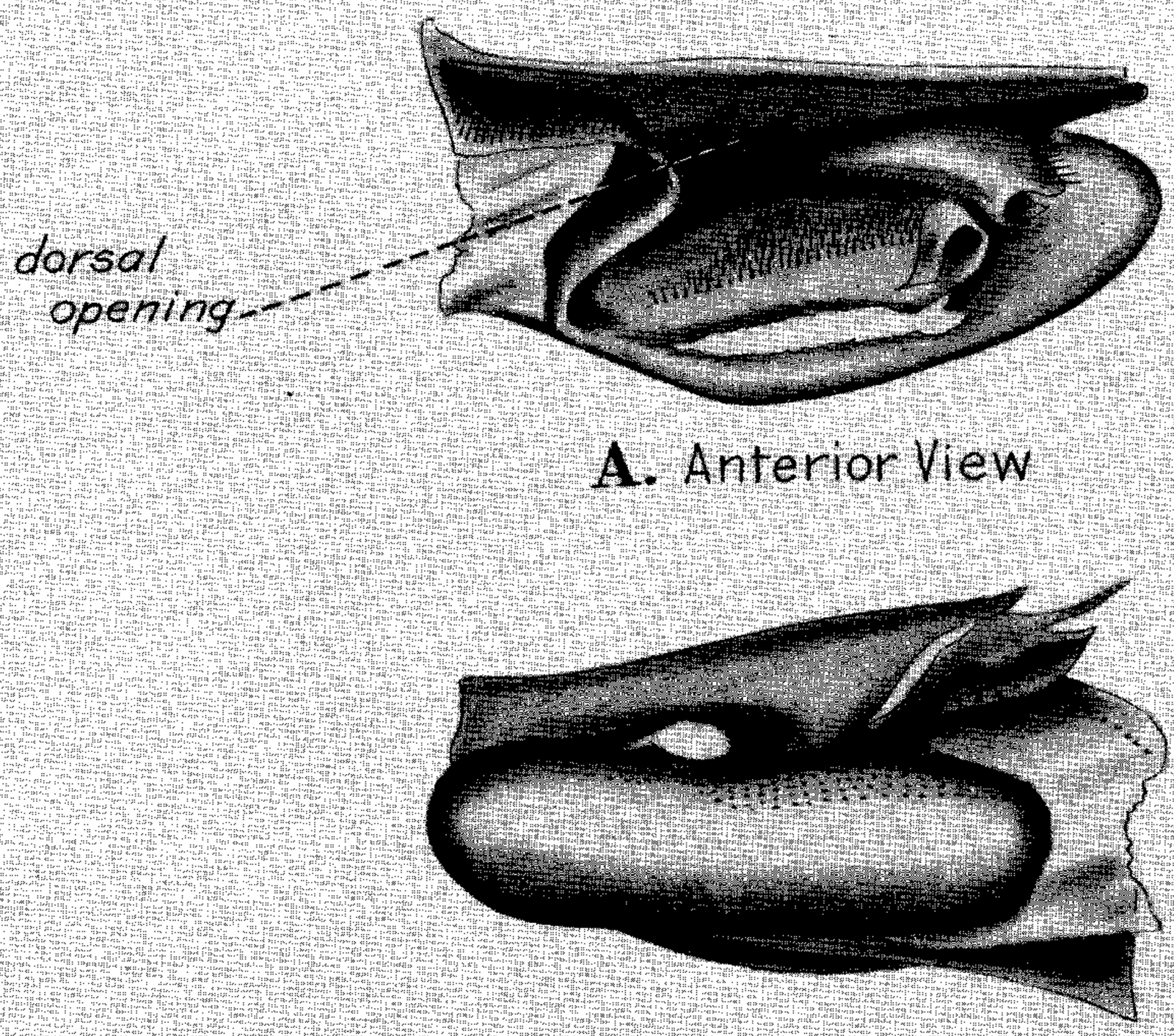

FIGURE 16.—Cleared statocyst. *A*. Anterior view. *B*. Posterior view.

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

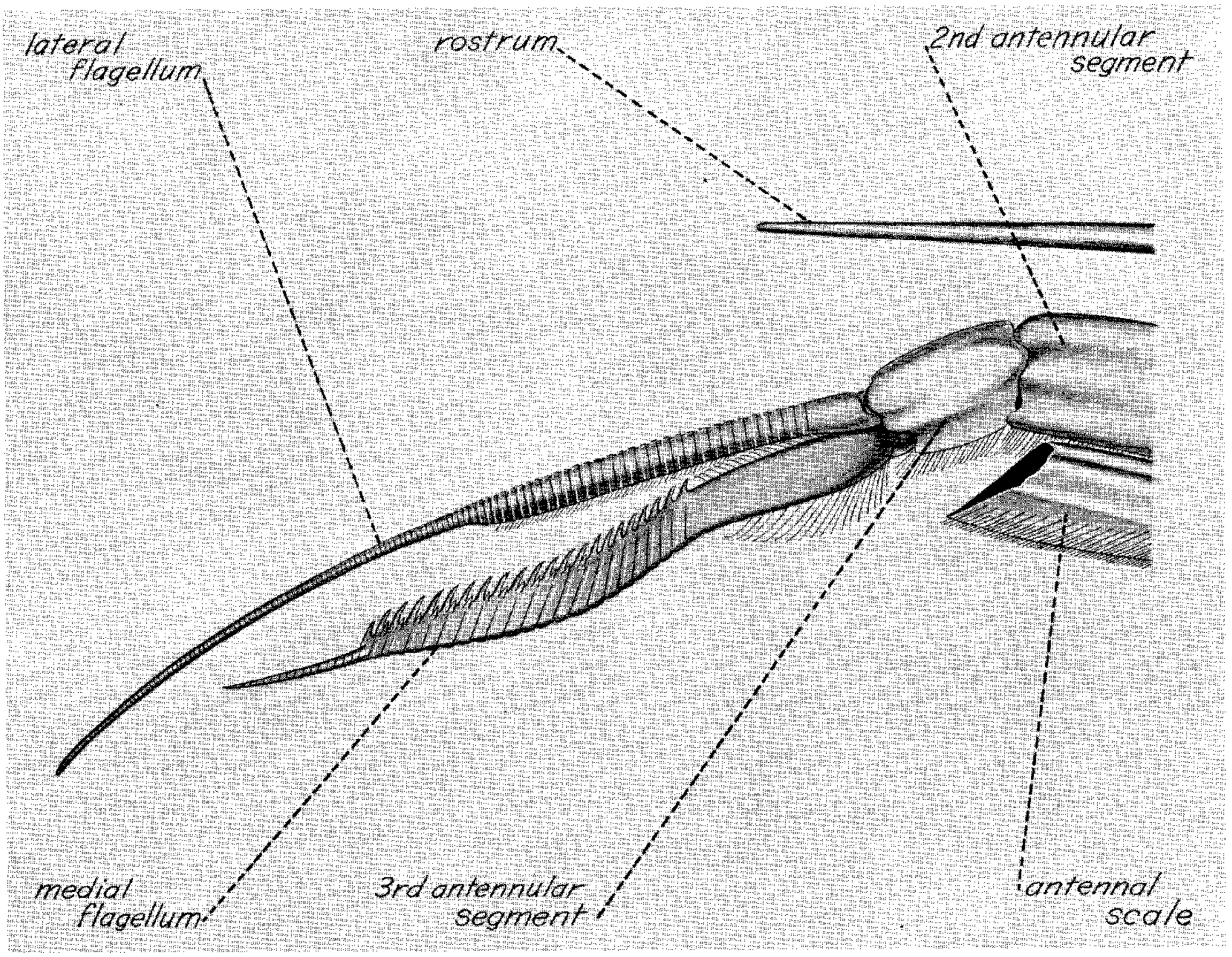

FIGURE 17.—Enlarged view of left antennular flagella showing sexual modification to medial flagellum in adult male.

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*.

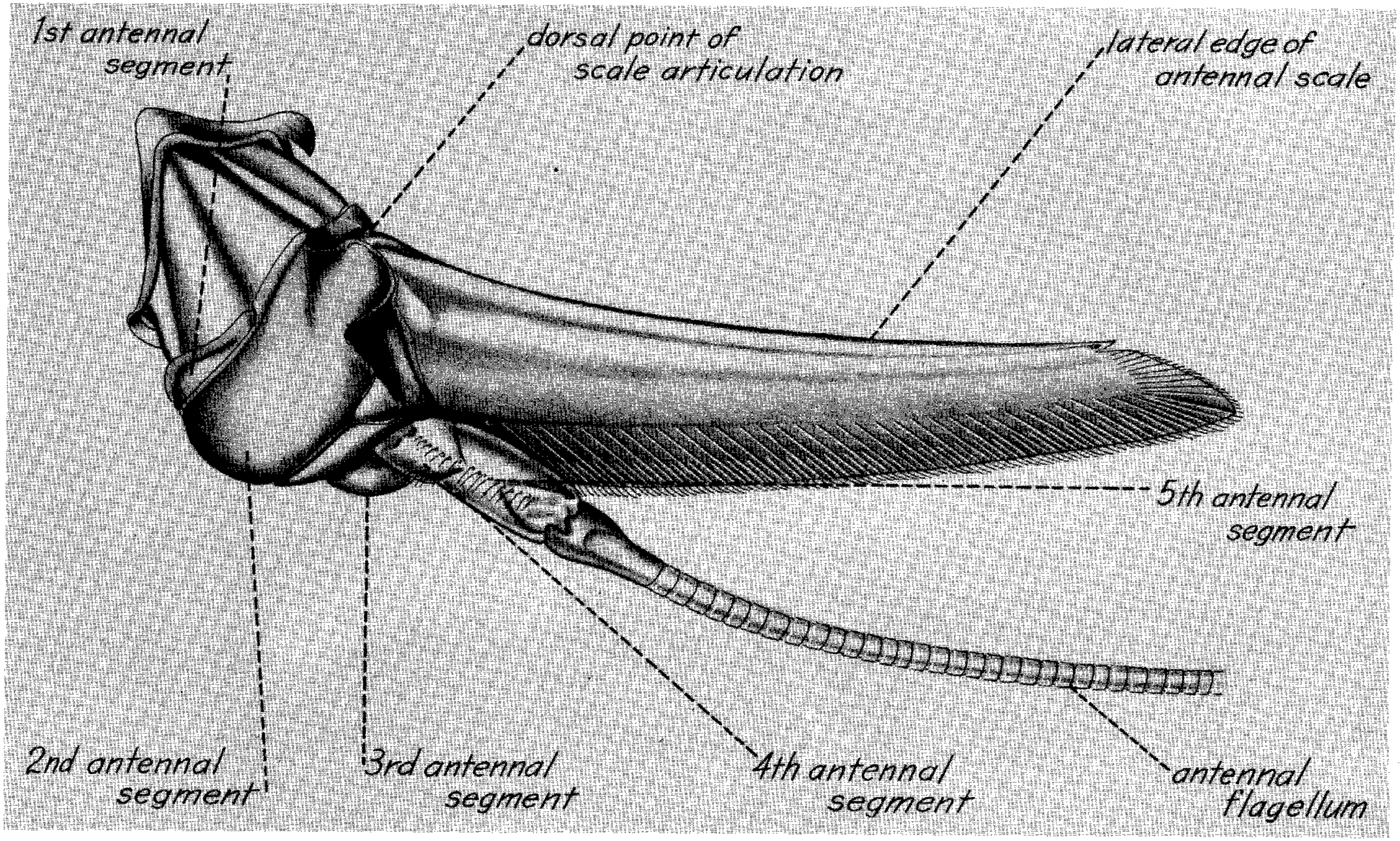

FIGURE 18.—Lateral view of right antenna.

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-

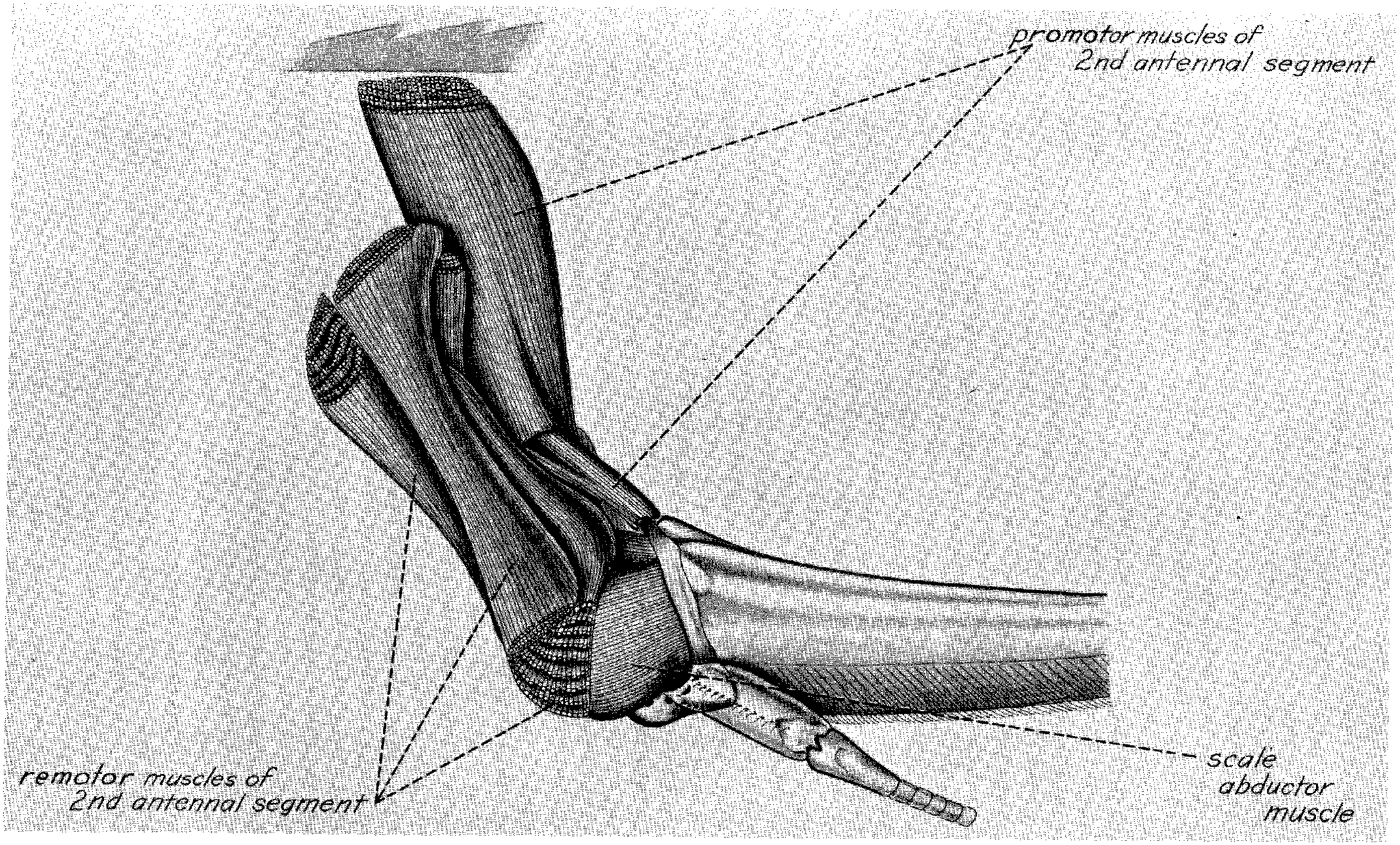

FIGURE 19.—Lateral view of right antenna, carapace and cuticle removed to show muscles.

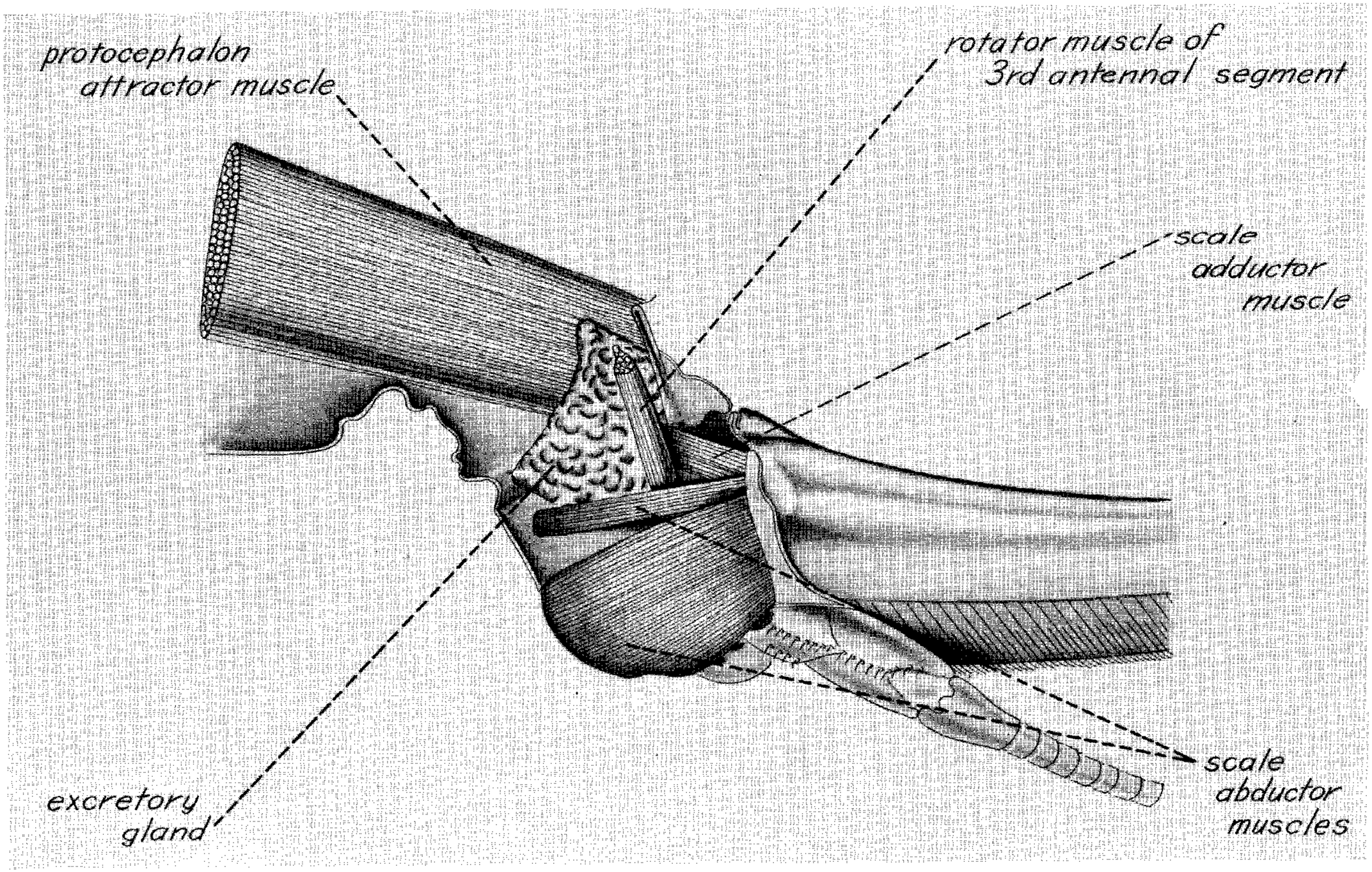

FIGURE 20.—Lateral view of right antenna. Lateral muscles removed to show excretory gland.

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

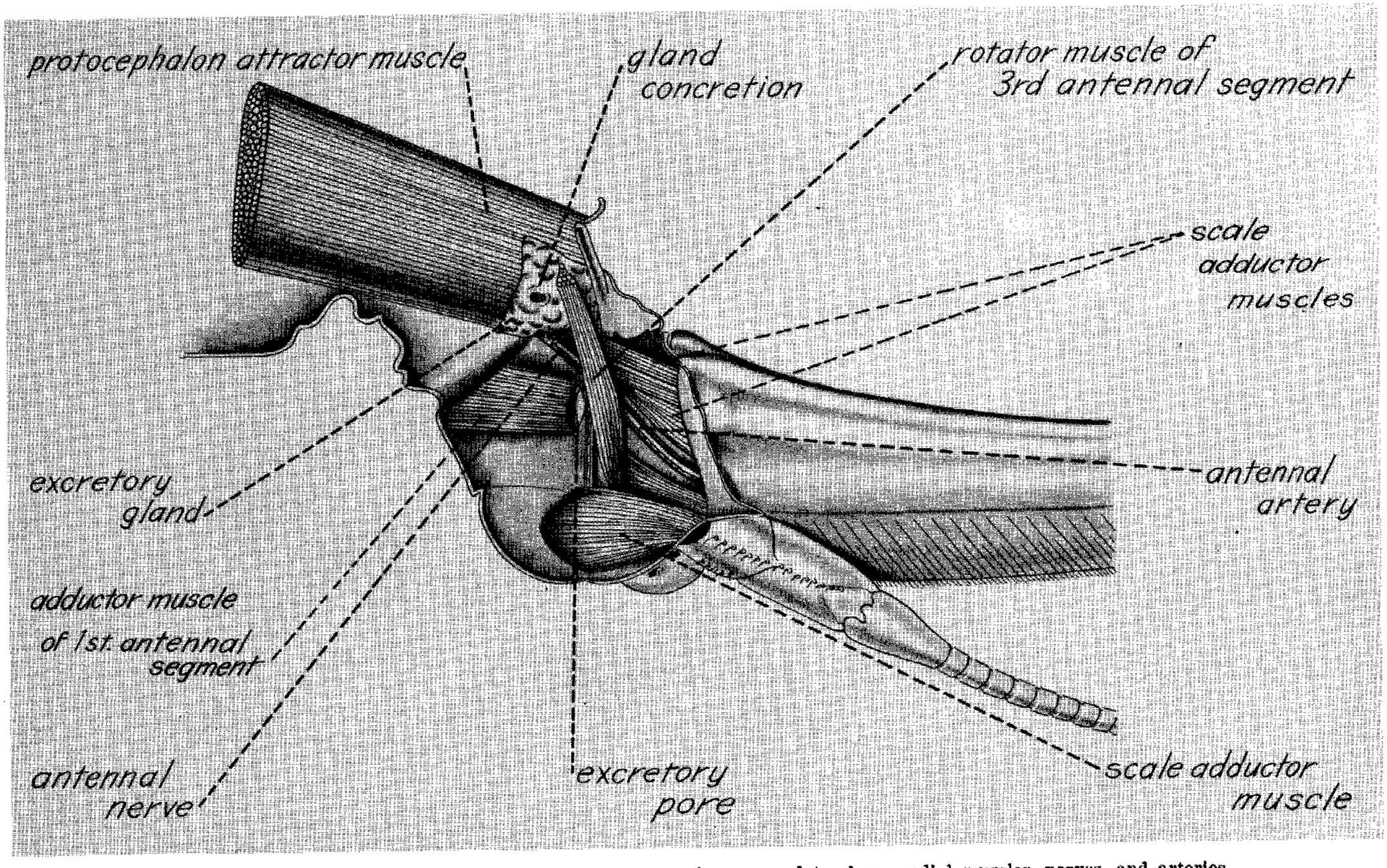

FIGURE 21.—Lateral view of right antenna. Lateral muscles removed to show medial muscles, nerves, and arteries. Part of excretory gland removed to show gland concretion.

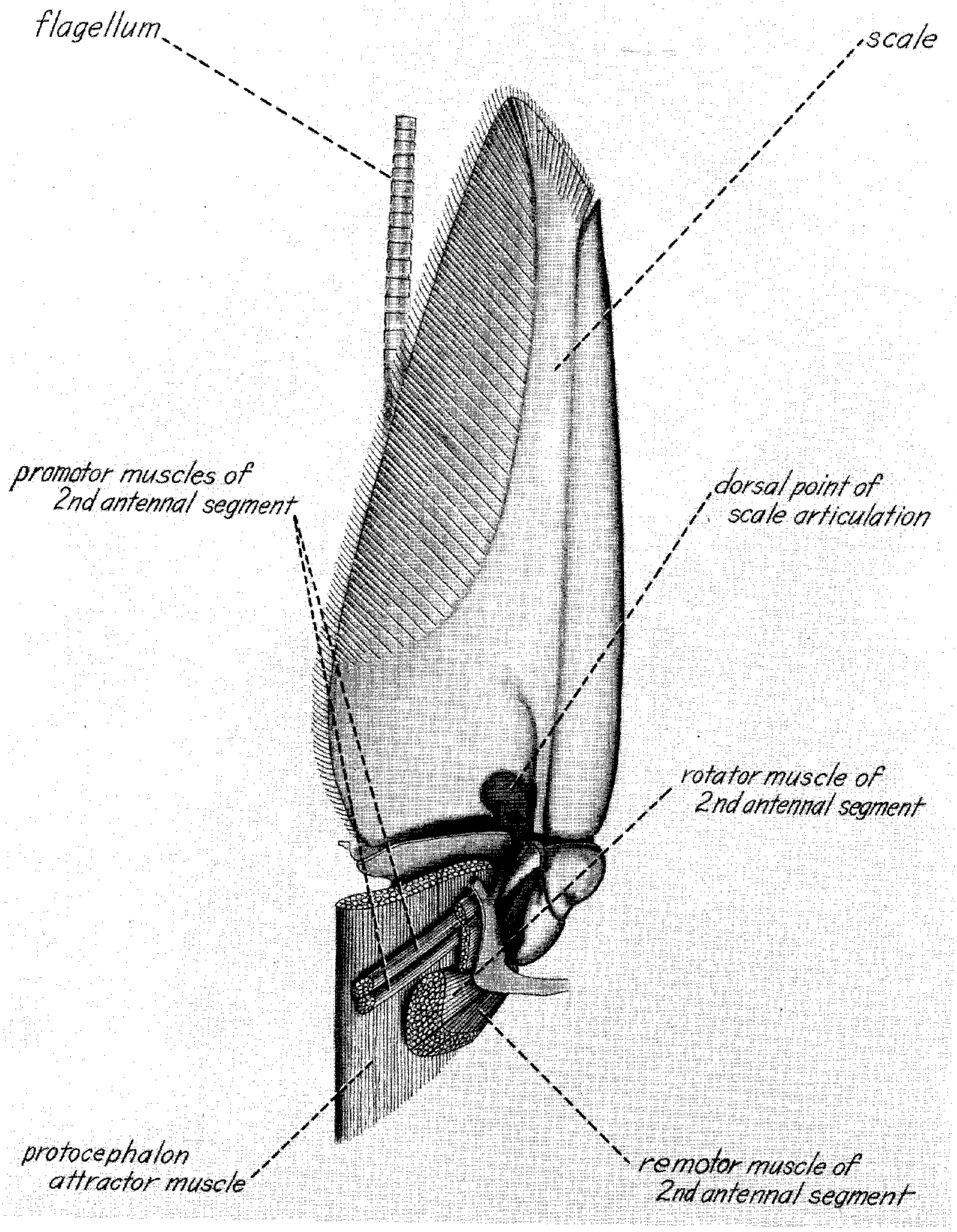

FIGURE 22.—Dorsal view of right antenna showing antennal scale and protopodite muscles. Carapace removed.

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-

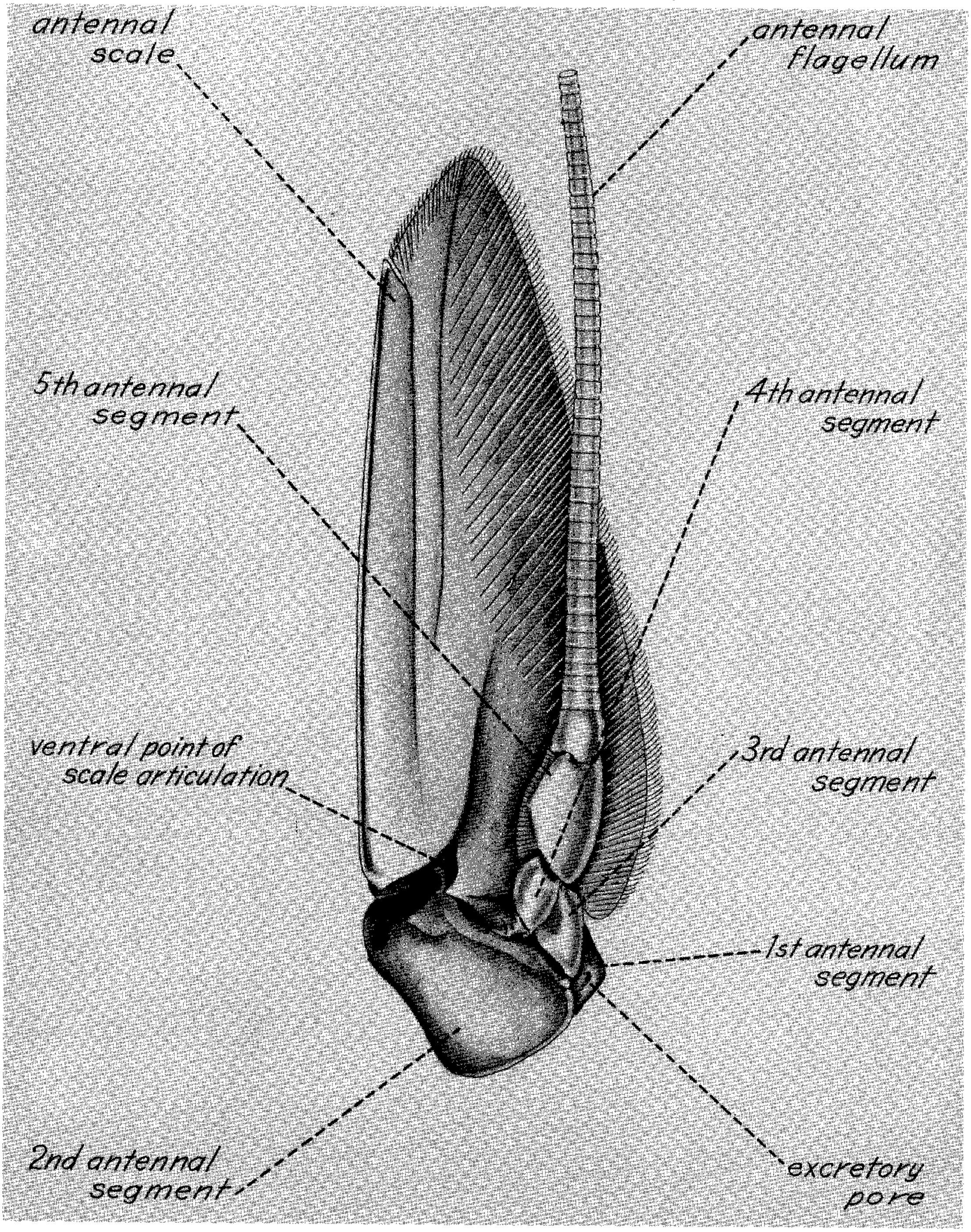

FIGURE 23.—Ventral view of right antenna showing skeletal elements.

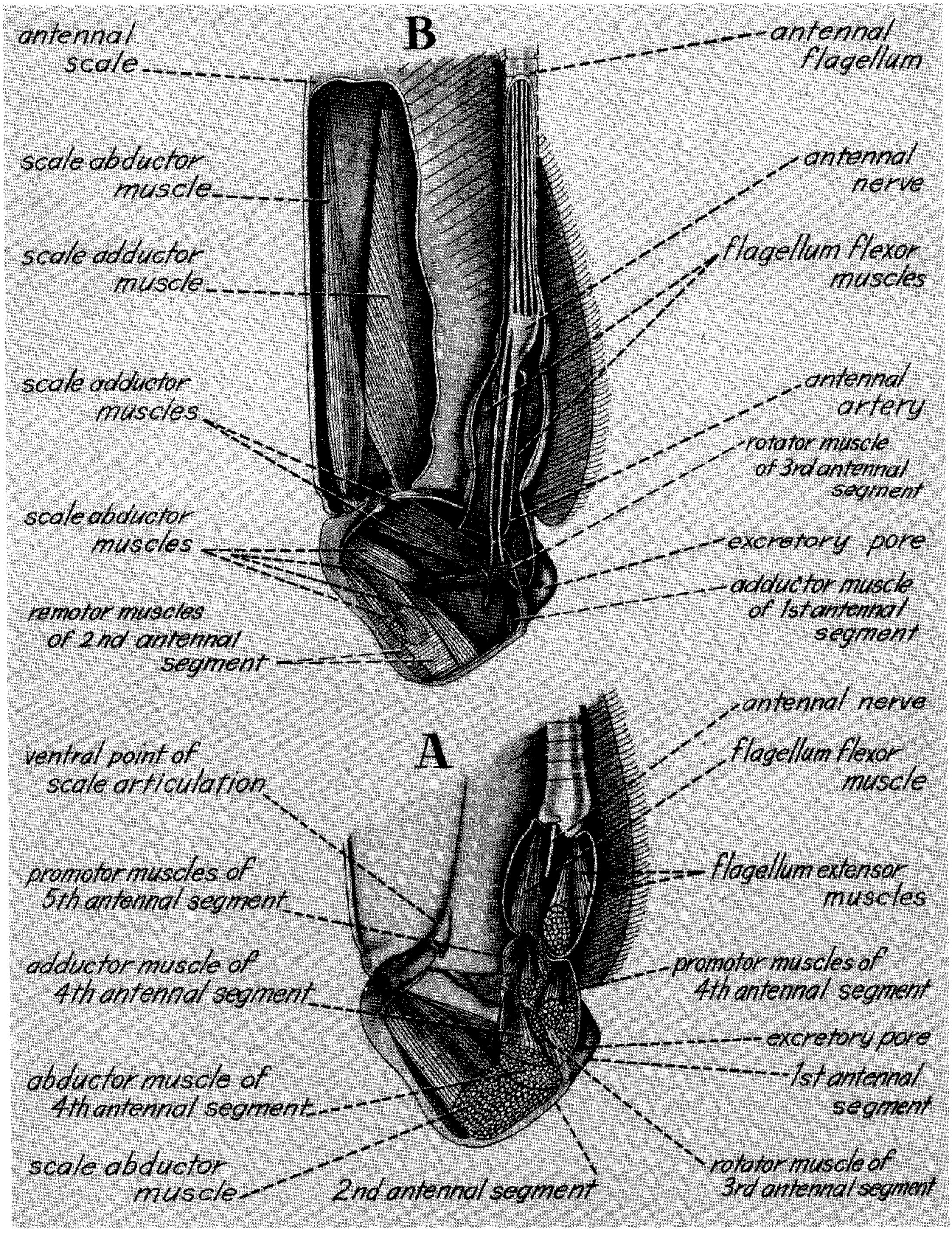

FIGURE 24.—Ventral view of right antenna showing ventral muscles, nerves, and blood vessels. Ventral cuticle removed. *A*. Superficial ventral elements. *B*. Dorsal elements.

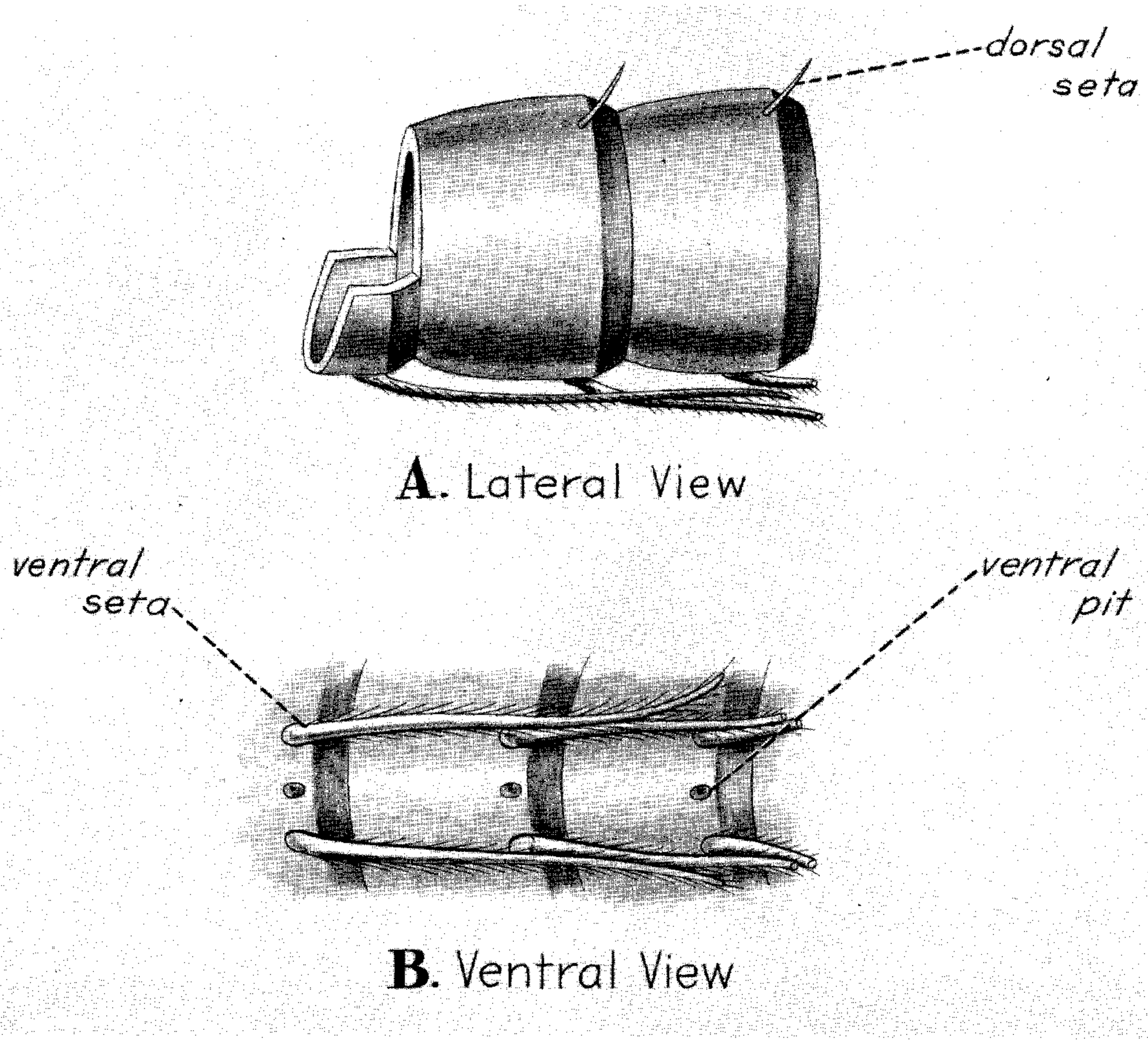

FIGURE 25.—Enlargement of proximal segments of antennal flagellum showing sensory structures.

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