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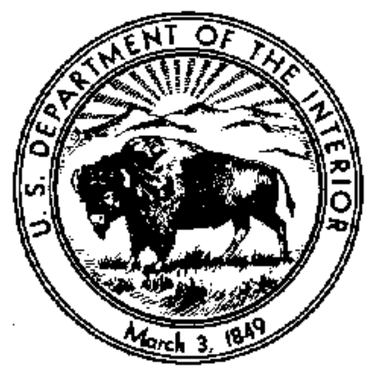
MORPHOLOGY OF THE WHITE SHRIMP *Penaeus setiferus* (Linnaeus 1758)

BY JOSEPH H. YOUNG



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CONTENTS

	Page
Introduction	1
Penaeus as comparative material	2
I. Skeletal and muscle systems	3
A. Protocephalon	3
1. Eyestalks	7
2. Antennules	17
3. Antennae	30
4. Labrum	43
B. Gnathothorax	47
1. Mandibles	60
2. Paragnatha	65
3. Maxillae	66
a. First maxillae	66
b. Second maxillae	69
4. Maxillipeds	72
a. First maxillipeds	72
b. Second maxillipeds	74
c. Third maxillipeds	81
5. Pereiopods	87
a. First pereiopods	87
b. Fifth pereiopods	94
C. Abdomen	103
1. Pleopods	115
2. Tail fan	125
II. Nervous system	132
A. Nerves of Supraesophageal ganglion and tritocerebrum	135
B. Ventral nerve cord	139
III Circulatory system	140
A. Heart and pericardium	140
B. Blood vessels of the body	140
C. Appendicular blood vessels	148
D. Venous system	149
E. Respiratory system	149
IV. Digestive system	150
A. Foregut	150
B. Midgut	154
C. Hindgut	154
V. Excretory system	155
VI. Reproductive system	155
Literature cited	160
Bibliography	162

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.

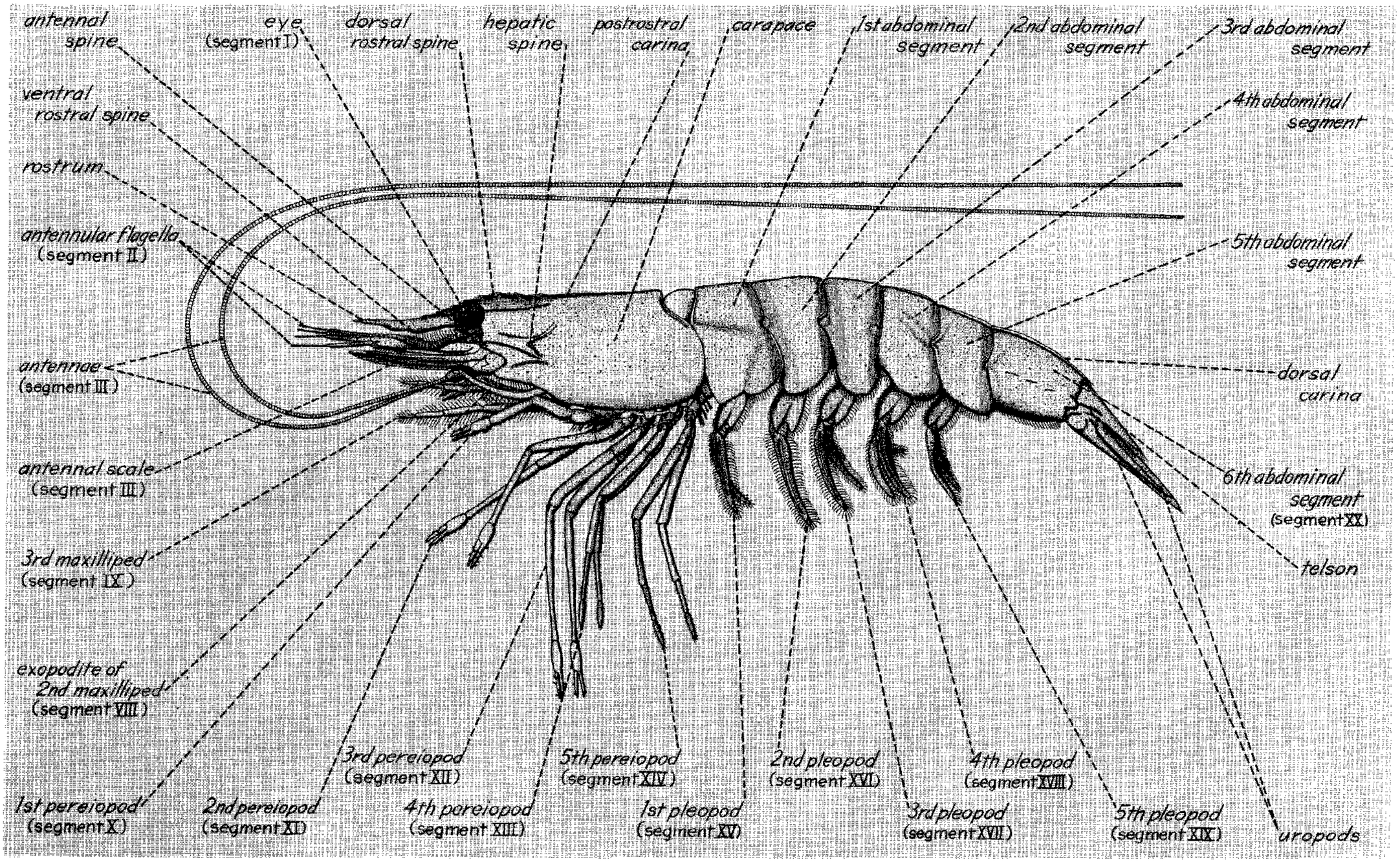

FIGURE 1.—*Penaeus setiferus*. Lateral view of adult female.

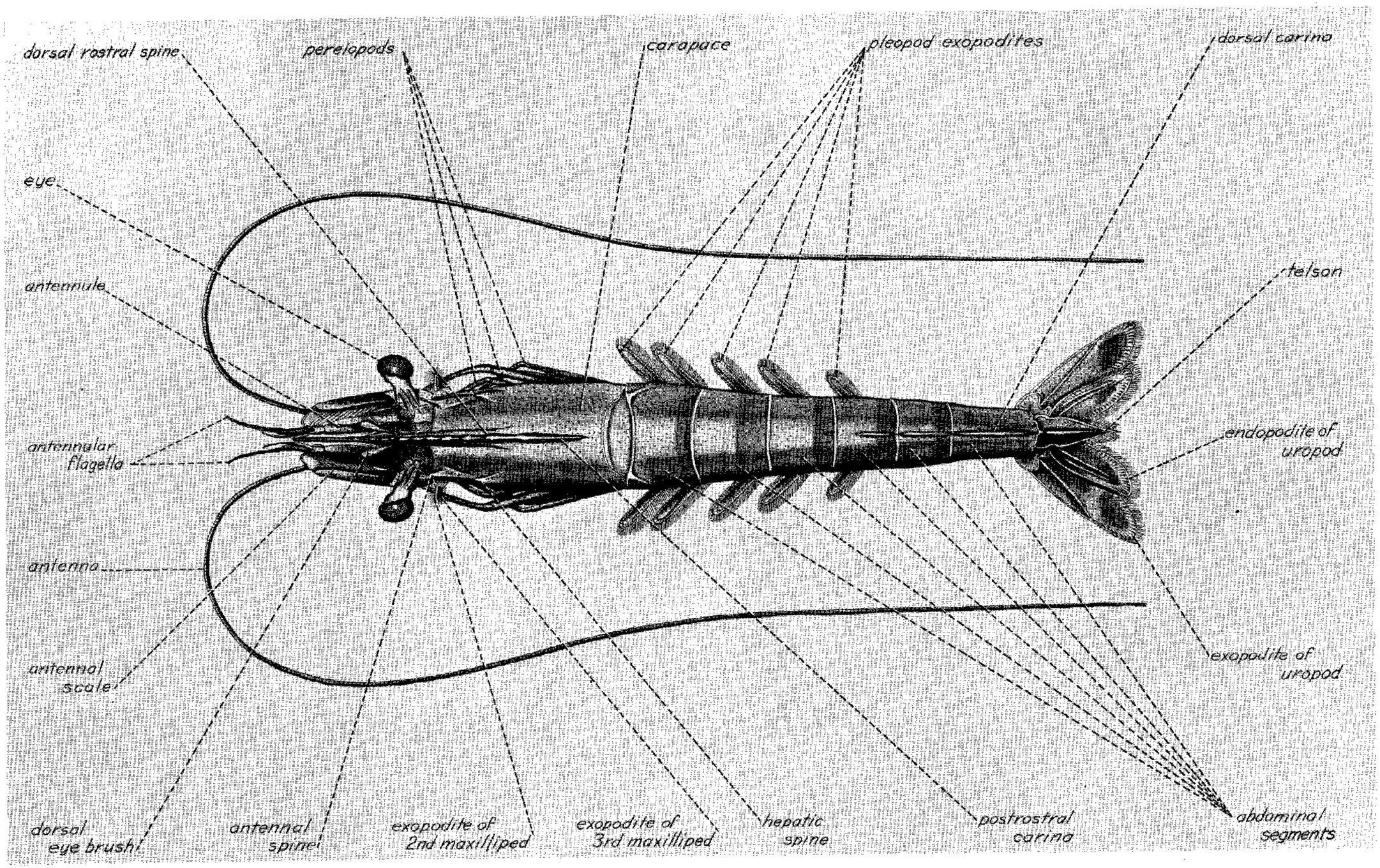

FIGURE 2.—Dorsal view of adult female.

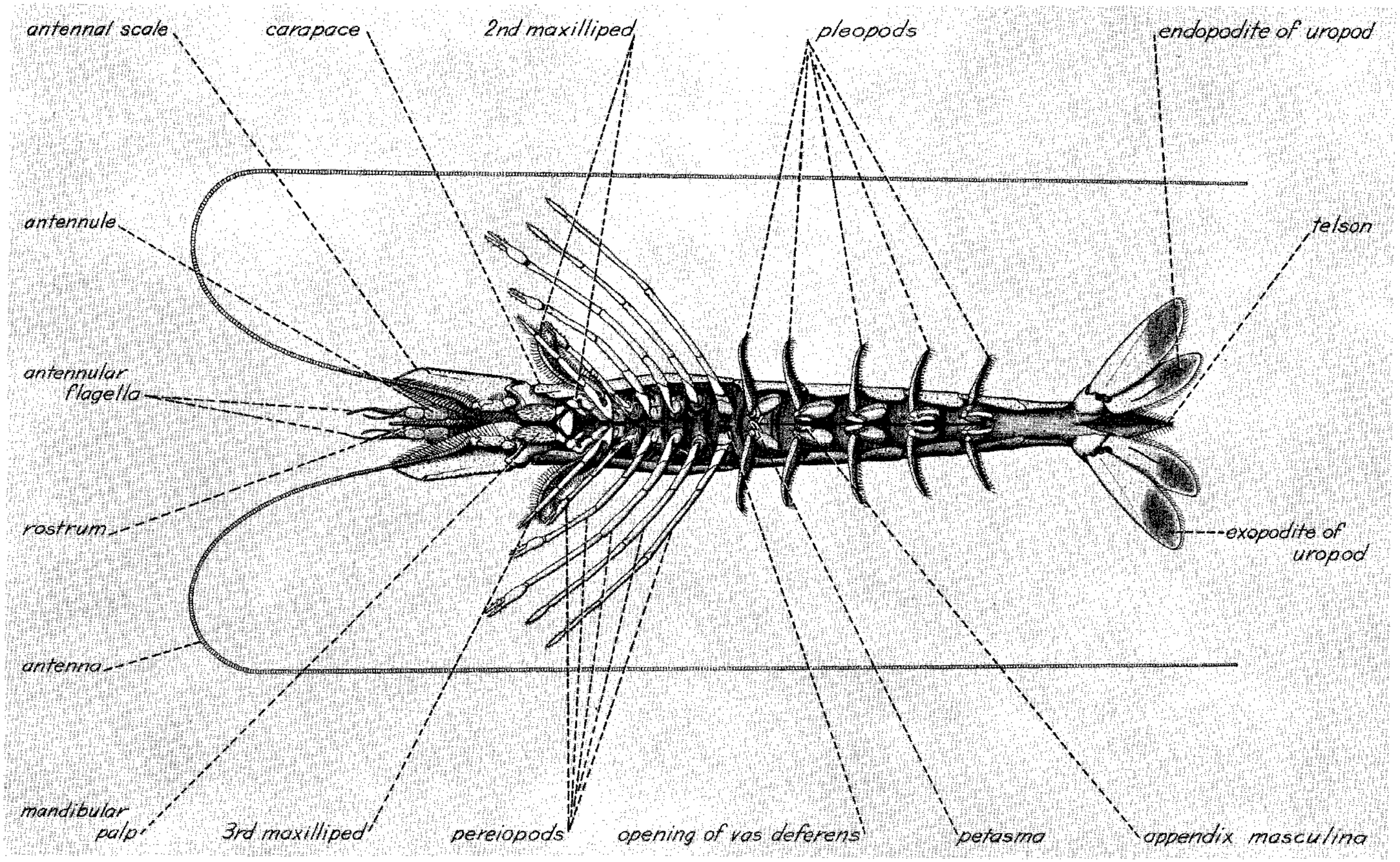

FIGURE 3.—Ventral view of young male.

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

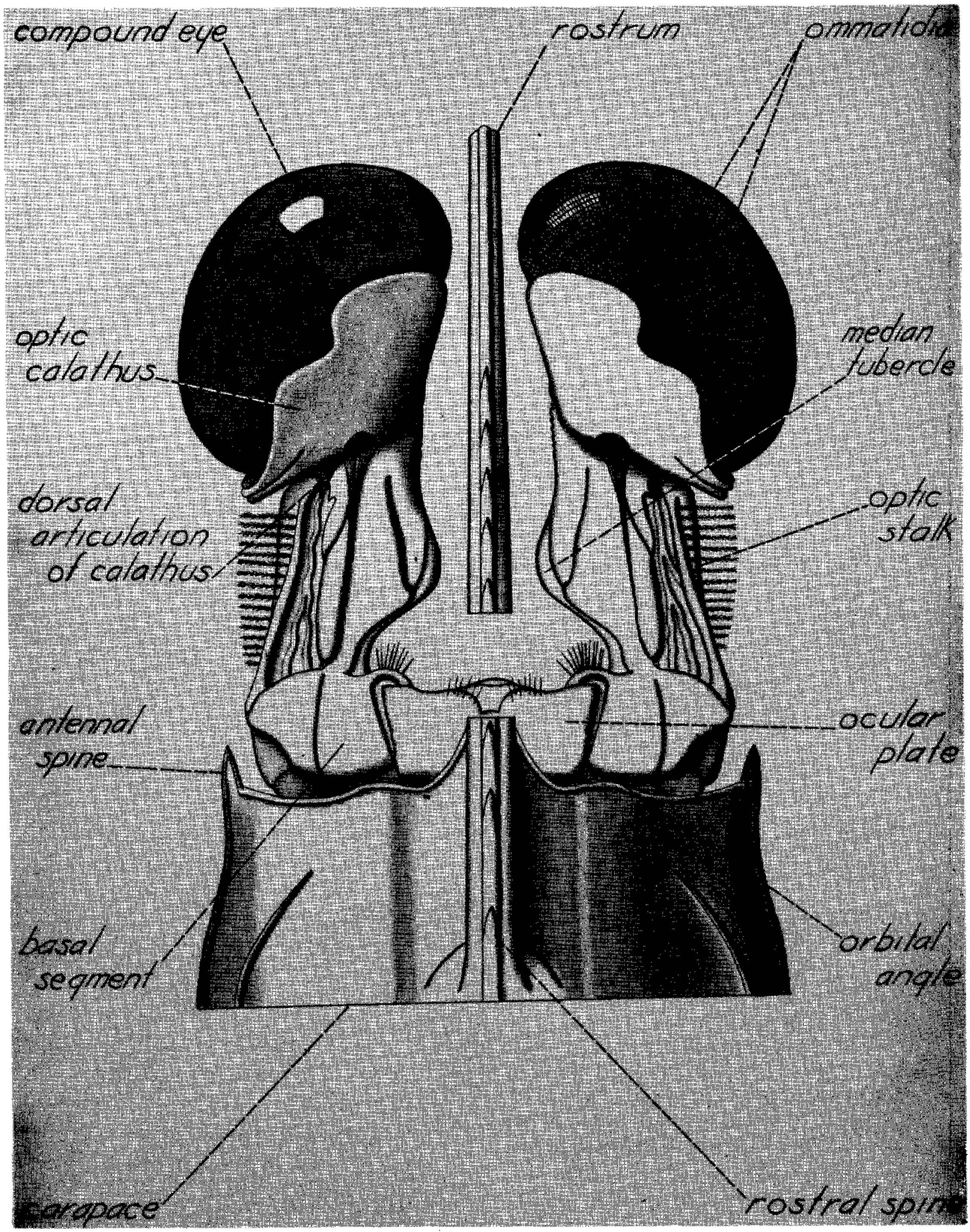

FIGURE 4.—Dorsal view of eyestalks in anterior position. Rostrum cut away to show ocular plate.

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 no 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

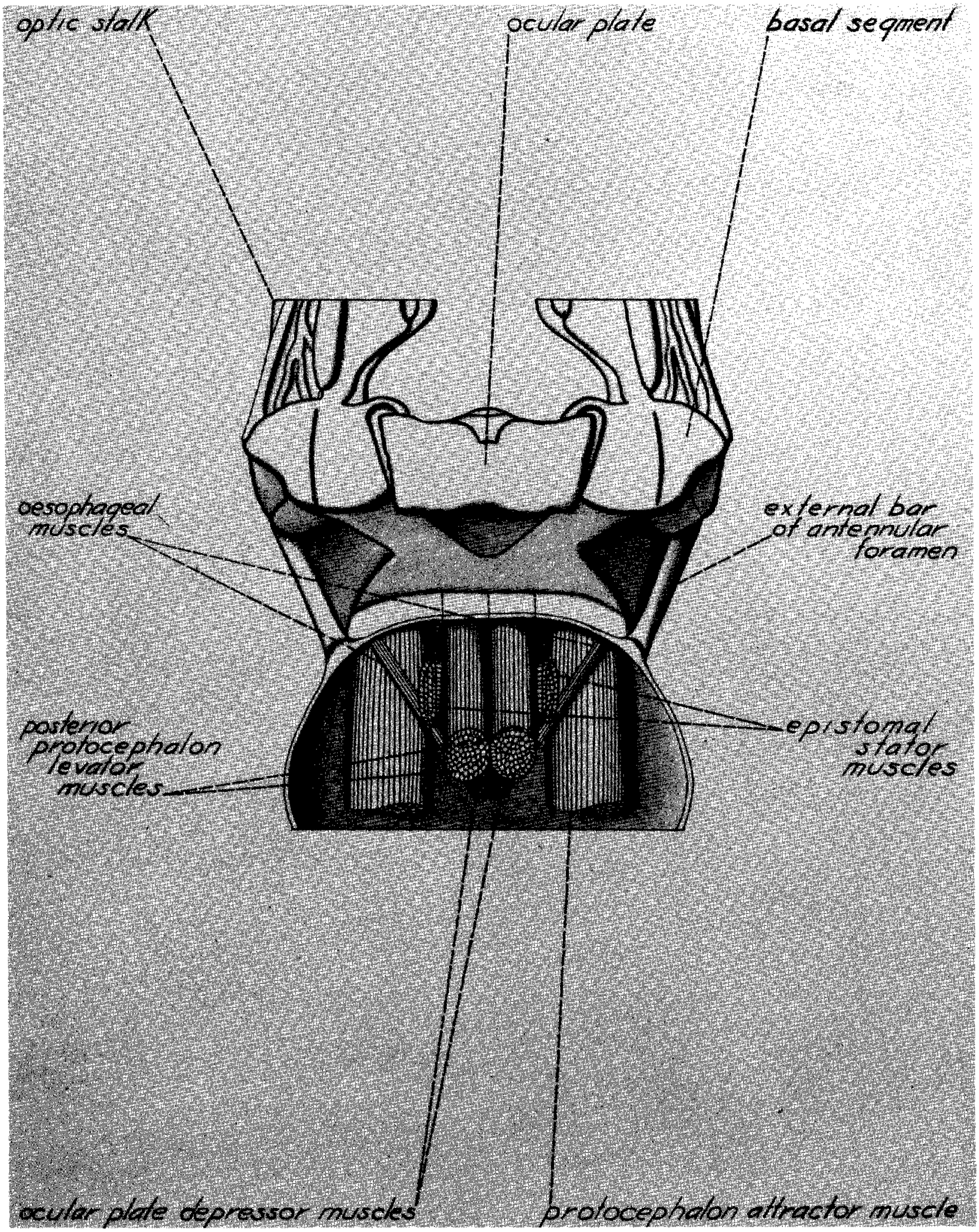

FIGURE 5.—Dorsal view of protocephalon, carapace removed, to show muscles of postocular region.

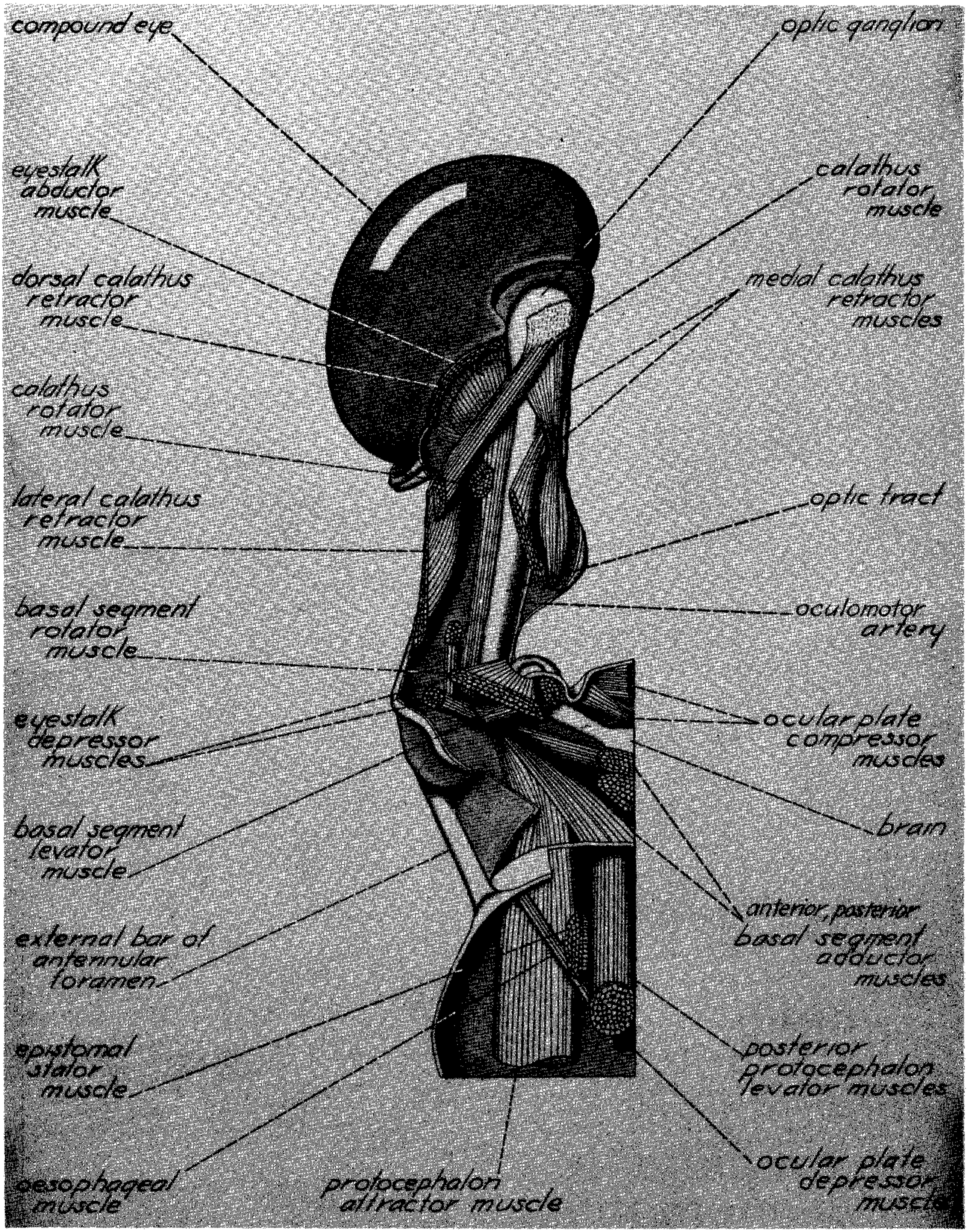

Figure 6.—Dorsal view of left eyestalk. Dorsal cuticle and carapace removed to show muscles.

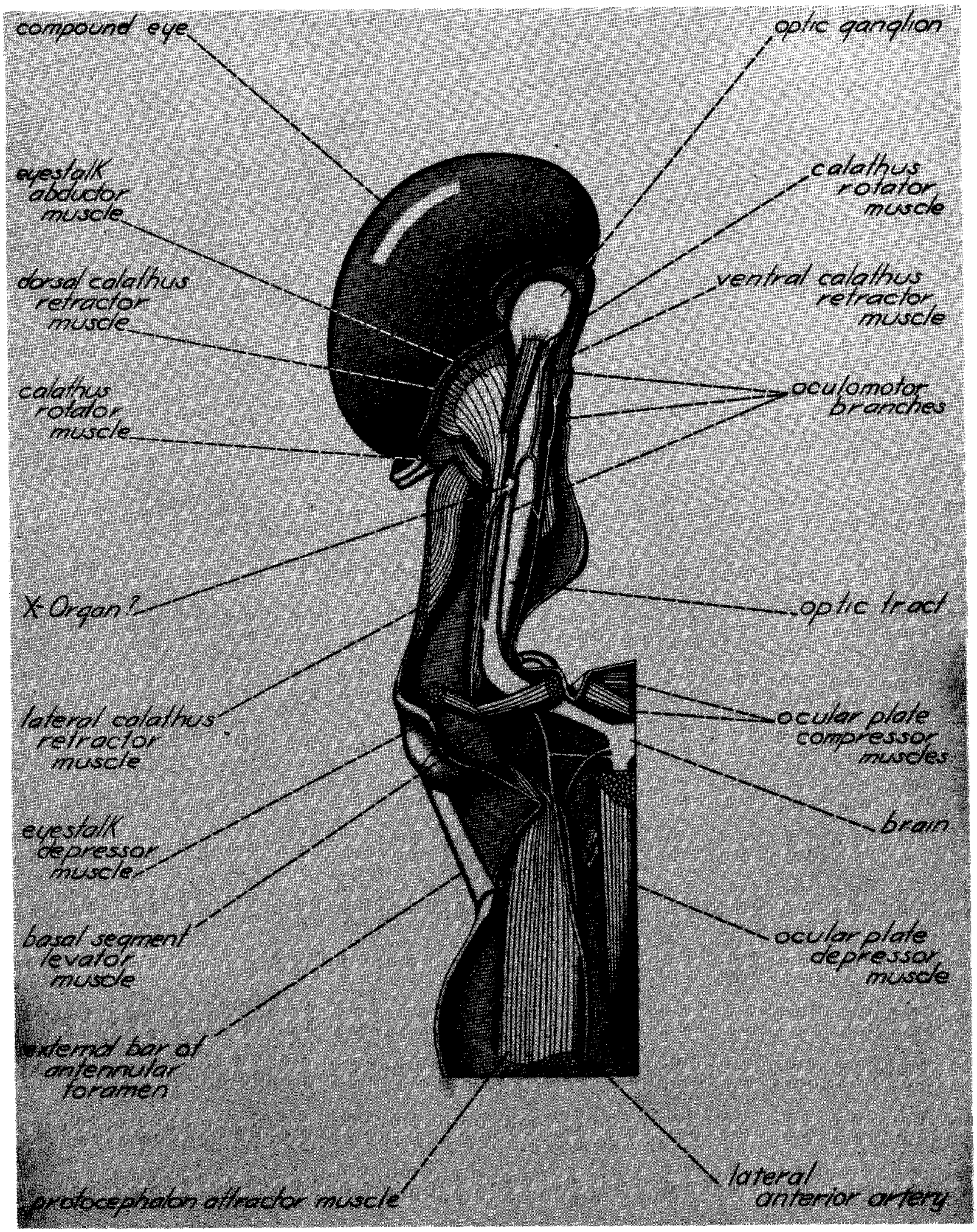

Figure 7.—Dorsal view of left eyestalk. Dorsal muscles removed to show branches of nerves and arteries.

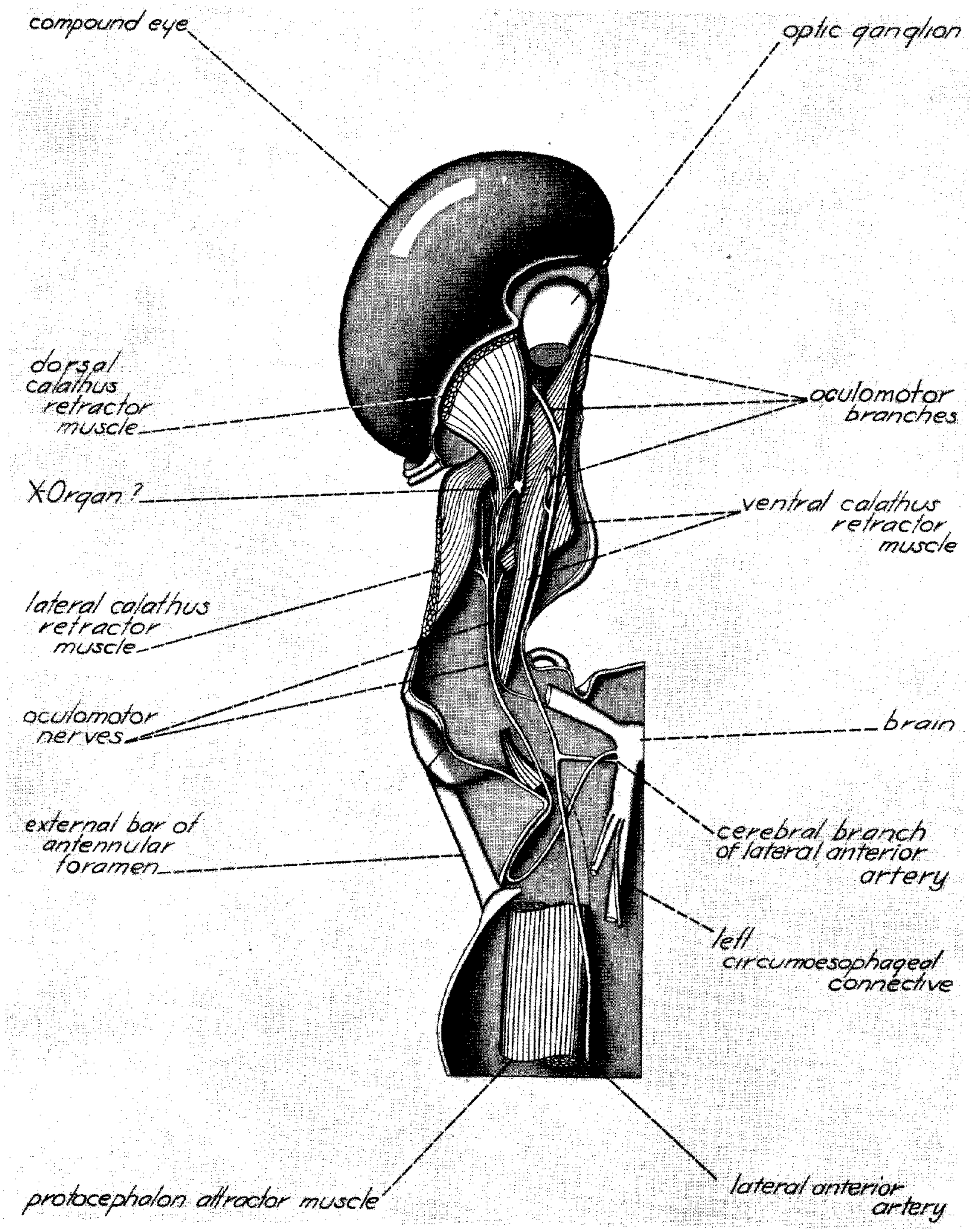

FIGURE 8.—Dorsal view of left eyestalk. Dorsal muscles and optic tract removed to show ventral muscles and branches of nerves and arteries.

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-