ANATOMY OF THE EYESTALK OF THE WHITE SHRIMP, *PENAEUS SETIFERUS* (LINN. 1758)[1]

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In some of the lower Crustacea 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 the 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 neuro-hormonal 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 ten to fifteen degrees to a frontal plane at the ocular plate (fig. 1). 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 (Cochran, 1935). Had previous workers taken into ac-

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count 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. By way of uniformity, however, certain of the incorrect names are here employed.

P. setiferus, an omnivorous scavenger like many shallow water and intertidal Crustacea, is a bottom feeder. According to an unpublished observation by Charles Dawson, of the University of Texas, schools of penaeid shrimps are frequently to be 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 ommatidial cells are square in *P. setiferus* and total four per ommatidium, as determined by the study of tangential sections of the eye from which the corneal cuticle had been removed. In longitudinal section the ommatidia of *P. setiferus* are seen to be similar to those of *Astacus,* with comparatively elongate crystalline cone and short rhabdom cells (Bernhards, 1916; Ramadan, 1952). A light pink substance which is thought to give the dark-adapted shrimp eye its bright pink color in strong lights is associated with the proximal or retinal pigment of the ommatidia.

The ommatidial surface arises from a sclerotized cup, here named the *optic calathus,* or basket, to avoid confusion with the optic cup of the vertebrate embryo (fig. 1). The optic calathus rests upon the elongate stalk segment in a structural relationship permitting universal movements, although the degree of movement varies in different planes.

Two points of articulation in the dorso-ventral plane allow the optic calathus considerable horizontal movement around the distal end of its supporting stalk. These dorso-ventral 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 dorso-ventral points of articulation 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, box-like, 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. 1), it may be noted that the shrimps of the subfamily Penaeinae are said to have no distinct median tubercle on the ocular peduncle (Anderson and Lindner, 1943; Voss, 1955). 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. 1). The ocular plate is the dorsal-most region of the protocephalon, a tagma about which more will be written later.

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 fifteen or twenty degrees.

Techniques

The anatomical study of the eyestalks of *Penaeus setiferus* was made for the most part on white shrimp purchased alive from bait shrimp fishermen. The animals were fixed in Zenker's fluid, dehydrated to 70% ethyl alcohol and there stored. In spite of the 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 doing so prevents internal maceration caused by the post-mortem enzymatic activity of the hepato-pancreas. 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 muscle attachments were verified on specimens of white shrimps cleared in strong alkali and stained in picro-fuchsin. 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.

Morphological Note

For purposes of comparison the present work will have reference to the work of Berkeley (1928) on the "coon stripe" shrimp, *Pandalus danae* Stimpson 1857, to the works of Schmidt (1915) and Keim (1915) on *Astacus astacus* (Linn. 1758), to that of Welsh (1941) on *Cambarus bartoni* (Fabricius 1798) and to the work of Cochran (1935) on the blue crab, *Callinectes sapidus* Rathbun 1896. Of these animals, the white shrimp, *Penaeus setiferus,* appears to be the

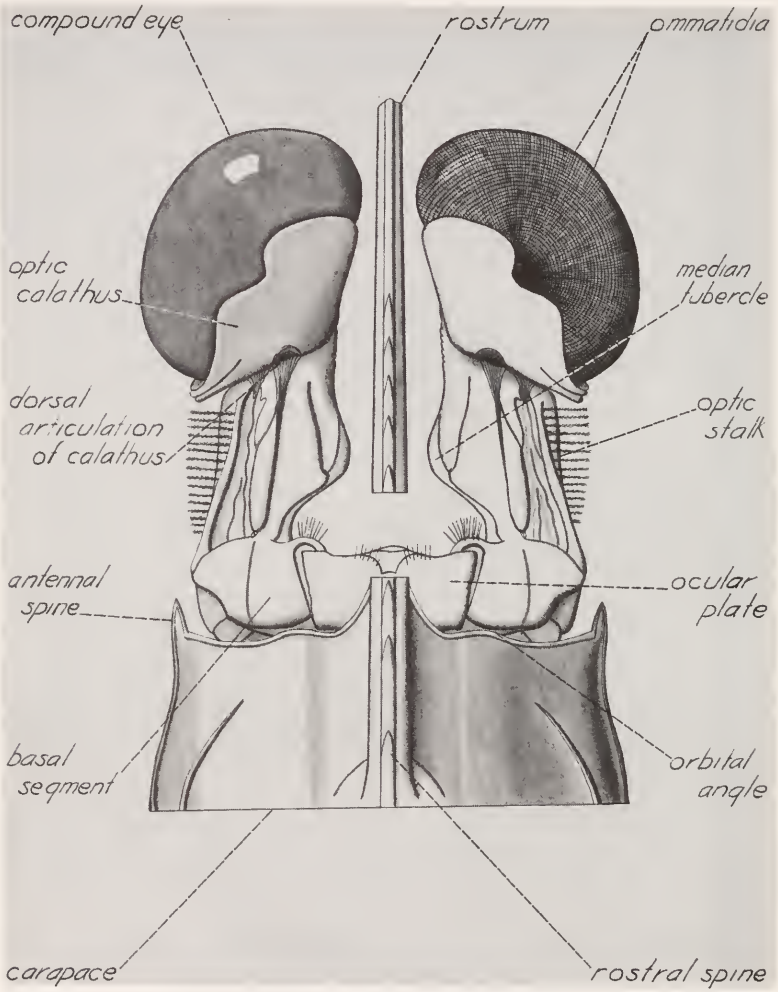

Figure 1. *Penaeus setiferus.* Dorsal view of eyestalks in anterior position. Rostrum cut away to show ocular plate.

most generalized form, the modern species most like the generalized ancestral type.

Protocephalon Muscles of 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 that morphologically

separable pre-gnathal group of segments designated by Snodgrass (1951) as the protocephalon. This simple head includes, in the order of their occurrence in the adult, the eyes, antennules, antennae, and labrum. The protocephalon is clearly distinct from the succeeding gnathal, thoracic, and abdominal tagmata, and in *Penaeus setiferus,* and other species of the genus (Grobben, 1917), is independently movable.

Not shown in any of the accompanying plates is a pair of muscles which will be included in the present discussion, the tiny *anterior protocephalon levator* muscles, which are probably the muscles designated by Grobben (1917) as the protocephalon levators in a European penaeid. These muscles are difficult to make clear, either by dissection, or by illustration, since they take origin on the carapace, upon 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 short in length. No counterpart of the anterior protocephalon levator muscles has been described for any of the species of decapod Crustacea referred to above, from which forms we must conclude that the muscles have been lost in the course of evolution.

Posterior Protocephalon Levator Muscles
(figs. 2, 3)

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 verticle transverse plate, posterior to the post-ocular region of the eyestalk base (fig. 3). 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 homologues 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

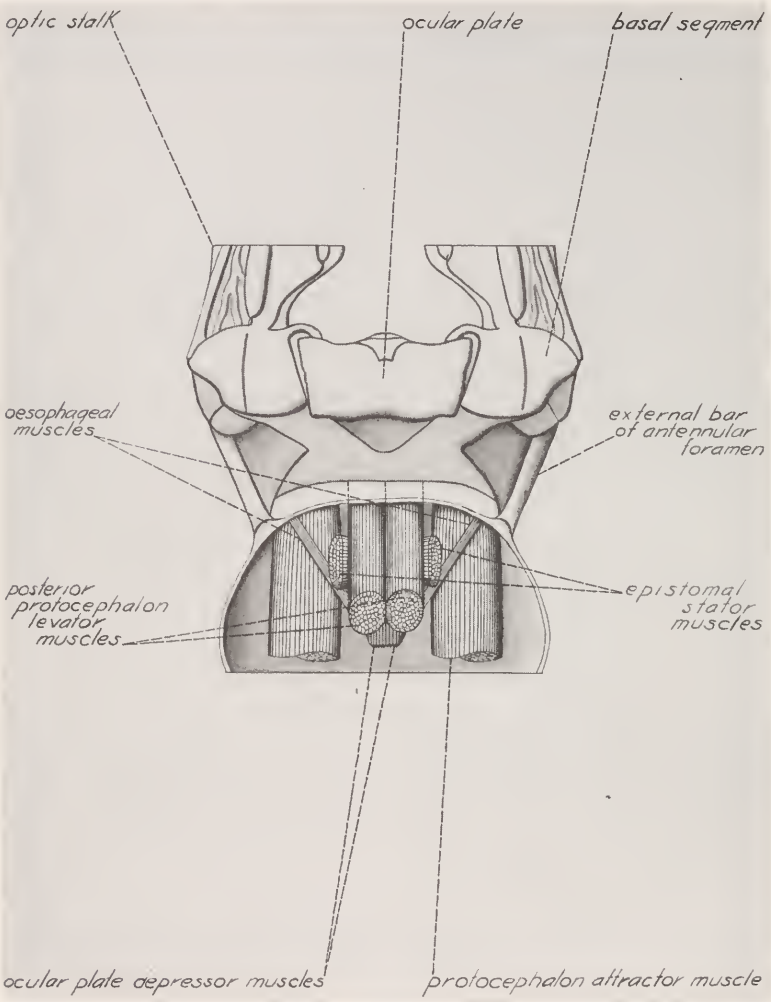

Figure 2. *Penaeus setiferus.* Dorsal view of protocephalon, carapace removed, showing muscles of postocular region.

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 below, which are more likely to be the homologues 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
(figs. 2, 3, 4)

The *ocular plate depressor muscles* originate on the posterior surface of the epistomal invagination. They run antero-dorsally, passing beneath the insertions of the posterior protocephalon levator muscles, and insert broadly on the posterior edge of the ocular plate (figs. 2, 3, 4). Upon 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 to be seen in the Brachyura.

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

Protocephalon Attractor Muscles
(figs. 2, 3, 4, 5)

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, upon 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 of cuticular material. Slightly antero-dorsal 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 ventro-lateral side of the eyestalk foramen into the thoracic hemocoel. This apodeme, like that near the antennule, broadens vertically. By virtue of apodemal position,

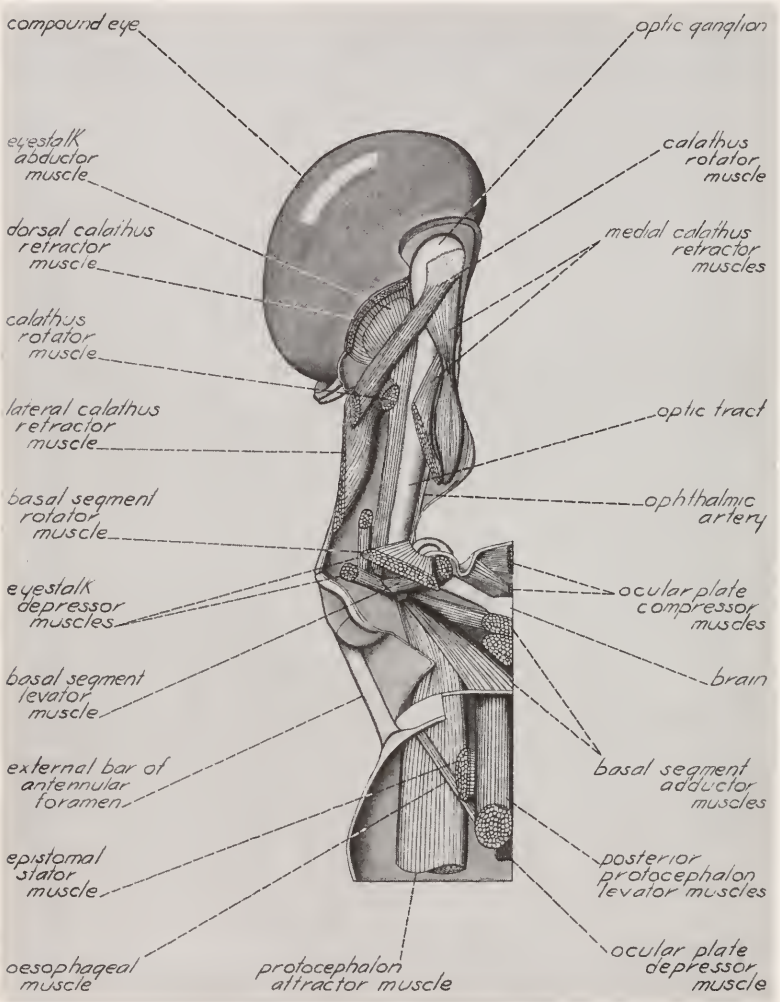

Figure 3. ***Penaeus setiferus.*** **Dorsal view of left eyestalk. Dorsal cuticle and carapace removed to show muscles.**

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. 4, 5).

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 same muscle has been called a protocephalon depressor by Grobben (1917). When studying a European penaeid, this worker so described the muscle in a morphological discussion of the crustacean protocephalon. The point of Grobben's discussion, that the protocephalon is movable on the gnathal tagma, is not changed by a difference in 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 not antennal, for the simple reason that they do not go to the antennae. Although it is possible that the protocephalon attractor muscles in *Penaeus brasiliensis* Latreille 1817, may be widely differnet from those in *P. setiferus,* the statement of Knowles (1953) that the two muscles lying just beneath the antero-lateral side of the carapace are antennal is probably in error. From his figures the external-most muscle is properly a depressor of the antennal scale, while the large inner muscle is the protocephalon attractor muscle.

The two antero-dorsal 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. 1), thereby swinging the eyestalks forward in a horizontal plane into the ocular depressions on the antennules. As suggested in the introduction, 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 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

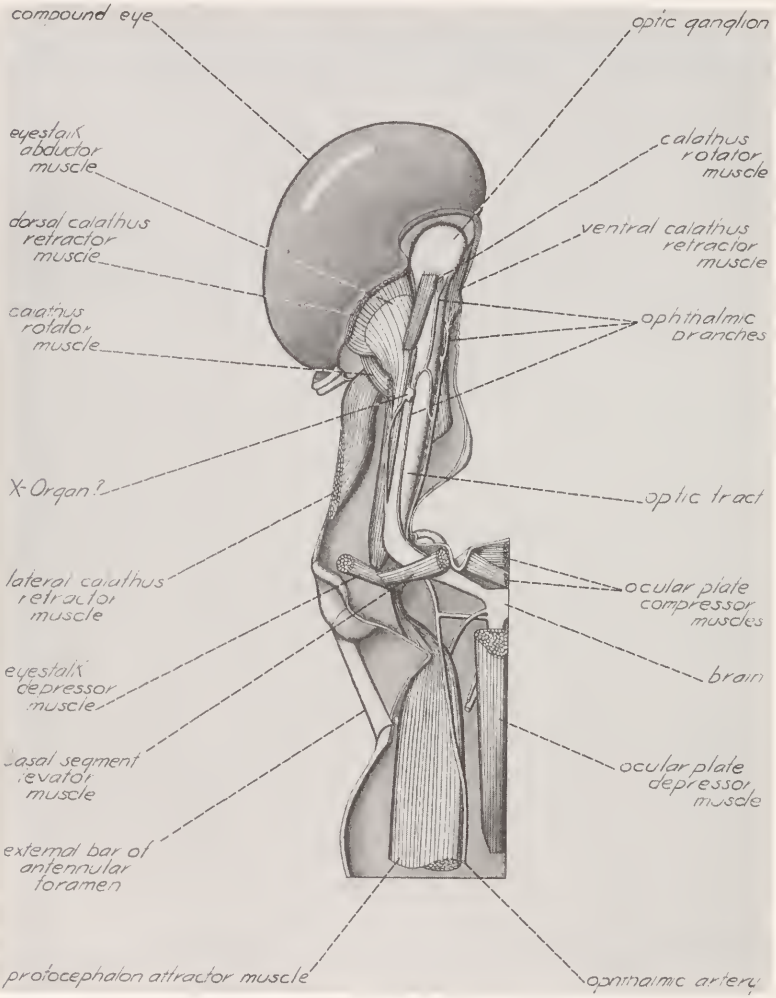

Figure 4. ***Penaeus setiferus.*** **Dorsal view of left eyestalk. Dorsal muscles removed to show branches of nerves and arteries.**

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 muscles "c" of *Pandalus* and *Astacus* on the basis of their dorso-lateral origins on the carapace and their insertions on the medio-dorsal edge of the antennal basipodite (in *Pandalus*) and coxopodite (in *Astacus*). That the depressor muscles "c" in *Pandalus* and the protocephalon levators

in *Penaeus* are homologous seems fairly certain, in spite of 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 *Penaeus* 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.

Epistomal Stator Muscles
(figs. 2, 3)

Originating on the dorsal surface of the carapace, lateral to the posterior protocephalon levator muscles, and converging on the anterior side of the epistomal invagination are a pair of small muscles which are named in the present work, the *epistomal stator muscles* (figs. 2, 3). The name derives from the fact that contractions of the muscles would appear to hold the epistomal invagination in position during the contraction of other muscles in the area. The epistomal stator muscles are homologous with the musculus oculi basalis posterior in *Pandalus* and *Astacus* and probably in *Callinectes.*

Oesophageal Muscles
(figs. 2, 3)

The last of the muscles in the anterior region of the gnathothorax to be treated is a pair of *oesophageal muscles* (figs. 2, 3) which originate on the antero-lateral surfaces of the carapace, dorsal to the protocephalon attractor muscles, and converge upon the anterior surface of the oesophagus. They function to dilate the oesophagus. Dorsal oesophageal muscles are not shown in the works of *Astacus, Pandalus,* or *Callinectes,* although Cochran (1935) figures several ventral oesophageal dilators in the latter form.

Ocular Plate Muscles

Arising in the ocular plate or post-ocular 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
(figs. 3, 4)

Attached about the shallow antero-dorsal groove of the ocular plate is a group of muscles which runs to the lateral wall of the ocular lobe (figs. 3, 4), 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
(fig. 3)

The *anterior basal segment adductor muscle* originates on the ocular plate dorsal to the brain and attaches to connective tissue and apodemal

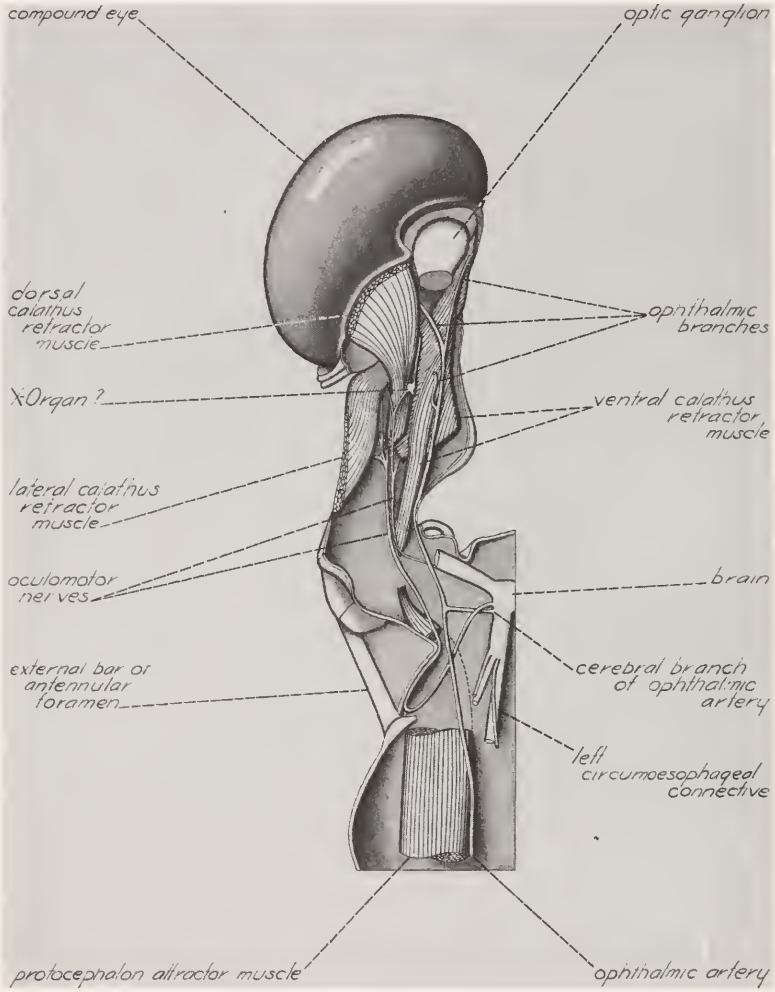

Figure 5. *Penaeus setiferus.* Dorsal view of left eyestalk. Dorsal muscles and optic tract removed to show ventral muscles and branches of nerves and arteries.

material in the ventral part of the basal segment (fig. 3). Contractions of the muscle turn the basal segment toward the ocular plate in a horizontal plane.

Posterior Basal Segment Adductor Muscle
(fig. 3)

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 post-ocular region (fig. 3). 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 the situation 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 homologues 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
(fig. 3)

The *basal segment levator muscle* originates at the antero-dorsal corner of the ocular plate and runs ventrally to the connective tissue and apodemal cuticle on the ventral surface of the basal segment (fig. 3). 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 if in their lifelike, lateral positions.

Basal Segment Rotator Muscle
(fig. 3)

The *basal segment rotator muscle* is a short, broad structure originating on the antero-dorsal edge of the basal segment and inserting on the antero-ventral 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 Muscle
(fig. 3)

Two very small muscles, the *eyestalk depressor muscles,* one slightly lateral to the other (fig. 3), function to draw the eyestalk ventrally. After a review of the literature, the present writer concludes that neither of these muscles, the basal segment rotator or the eyestalk depressor muscle, has been previously described.

Eyestalk Muscles

Eyestalk Abductor Muscle
(fig. 3)

All of the muscles of the eyestalk and optic calathus are associated with retraction and rotation of the optic calathus on the eyestalk, except for the long *eyestalk abductor muscle* (fig. 3). 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 setiferus* 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 setiferus* which retract the optic calathus appear to be clearly represented by the retractor muscles of the eyes of *Astacus, Cambarus, Pandalus,* and *Callinectes.* Phylogenetically, the situation in *Penaeus setiferus* 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
(figs. 3, 4, 5)

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
(figs. 3, 4, 5, 6)

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. 6). 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
(fig. 6)

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

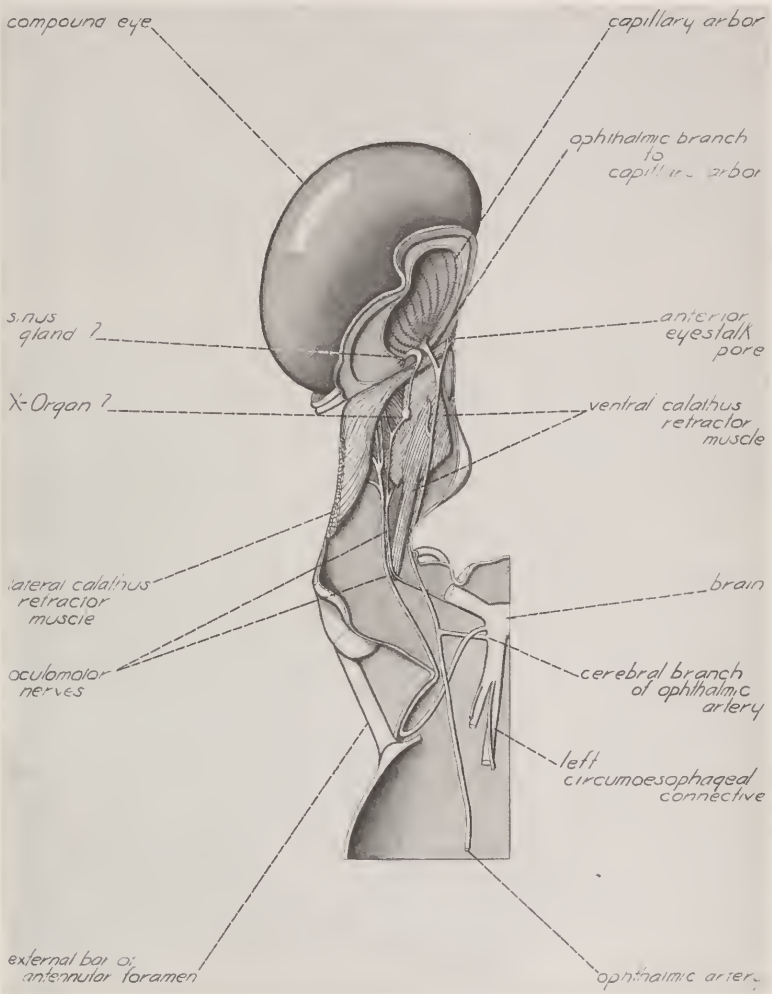

Figure 6. *Penaeus setiferus.* Dorsal view of left eyestalk. Dorsal muscles and optic tract removed to show brain, branches of nerves, arterial capillary supply to distal optic ganglia, neurosecretory glands, and location of anterior eyestalk pore.

origins (fig. 6). The muscle is inserted over a wide area on the ventral edge of the calathus.

Medial Calathus Retractor Muscle
(fig. 3)

The *medial calathus retractor muscle* orignates on two points in

the region of the median tubercle, and actually is comprised of two muscles (fig. 3). The larger muscle originates in the median tubercle and inserts in connective tissue dorsal to the distal optic ganglionic mass. The smaller muscle originates dorsal to the larger muscle, crosses over the optic tract beneath the larger muscle and inserts on a ventro-medial 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
(figs. 3, 4)

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 originate and insert in the heavy connective tissue underlying the thick cuticle of the calathus.

Eyestalk Vascular Supply
(figs. 4, 5, 6, 7)

Blood is pumped to the eyestalk in the vessel described by Huxley (1906) as the *ophthalmic artery*. From the anterior end of the heart, the ophthalmic artery runs forward dorsal to the gastric region, turns ventrally and laterally through dorso-lateral muscle origins to the protocephalon attractor muscle, with which muscle it enters the eyestalk, giving off a large branch to the brain in passing. Once in the eyestalk, the artery runs medially along the optic tract and divides into several branches at the distal end of the eyestalk. The most proximal branch bifurcates on the dorsal surface of the optic tract (figs. 4, 7), sending a short vessel to and apparently through a small gland on the optic tract here designated as the X-Organ described by Hanström (1948) and about which more will be said below. A small part of the arterial branch to the gland continues proximally along the dorsal surface of the optic tract and has not been traced beyond the connective tissue of the basal segment. The larger part of the proximal ophthalmic branch runs distally into the distal optic ganglionic mass (figs. 4, 7).

Distally, the ophthalmic artery divides into two large branches, one of which (figs. 5, 6) carries blood into a highly-branched, dendritic structure embedded deeply among the optic ganglion cells (fig. 6). The organ has been named the *capillary arbor,* since it appears to distribute blood to ganglionic cells. Nothing similar has been found in the literature of the arthropod eye.

The other, and most-distal ophthalmic branch, repeatedly divides to form a vascular plexus on the medial surface of the eyestalk, just beneath a heretofore undescribed pore to the exterior (figs. 6, 7).

The pore is designated as the *anterior eyestalk pore.* Its function is unknown.

Circulation to the eyestalk of *Penaeus setiferus,* like that to some of the other appendages, is made up of a closed afferent system which is subdivided into capillaries in muscles, ganglia, and other organs. Venous returns of the blood to the heart is carried out in an open system, by means of sinuses in to the hemocoel. To what extent the closed-arterial, open-venous blood vascular system is representative of the Crustacea must wait upon further study (Calman, 1909).

Eyestalk Nerves
(figs. 5, 6, 7)

By far the largest nervous element in the eyestalk of *Penaeus setiferus* is the optic tract, a part of the brain, which rises from the anterolateral region of the brain, runs distally in the eyestalk, increasing in diameter, and enters the calathus. Within the calathus the optic tract enlarges to incorporate the various distal optic ganglia and makes contact with the nerves from the ommatidia (figs. 6, 7). If the distal optic ganglionic mass is pulled away from the dioptric elements of the eye, the tearing is confined to natural lines of weakness representing a deep concavity. Lining the concavity so produced will be found the capillary arbor described above (fig. 6).

Along the lateral side of the optic tract, and embedded in the perineurium in the proximal region of the optic tract, is a small nerve which branches out of the perineurium distal to the basal segment. This nerve puts out several tiny branches to muscles and then enters a glandlike structure for which the name *X-Organ* (Hanström, 1948) is proposed (fig. 7). From the X-Organ a nerve continues along the optic tract distally to enter another, and larger, glandlike organ here termed the *sinus gland* (fig. 7). The sinus gland lies against and sends branches into the optic ganglionic mass at the distal end of the optic tract. It should be emphasized that the identification of the X-Organ and the sinus gland is made on doubtful grounds, since no supporting histological or experimental evidence is presented.

On the other hand, certain anatomical information lends support to the identification of the above-mentioned glandlike structures as the X-Organ and sinus gland. The support is to be found in the literature of neurosecretory experiments. The illustrations in some works of this literature are, to say the least, circumscribed (Passano, 1953), and useless to the morphologist. However, Welsh (1941) has taken pains to illustrate clearly his experiments on retinal pigment migration in *Cambarus bartoni.* From his figures, indicating careful anatomical work on the nerves of the eyestalk of *C. bartoni,* the locations and innervations of the X-Organ and the sinus gland appear to be similar to the glandlike structures in *Penaeus setiferus.*

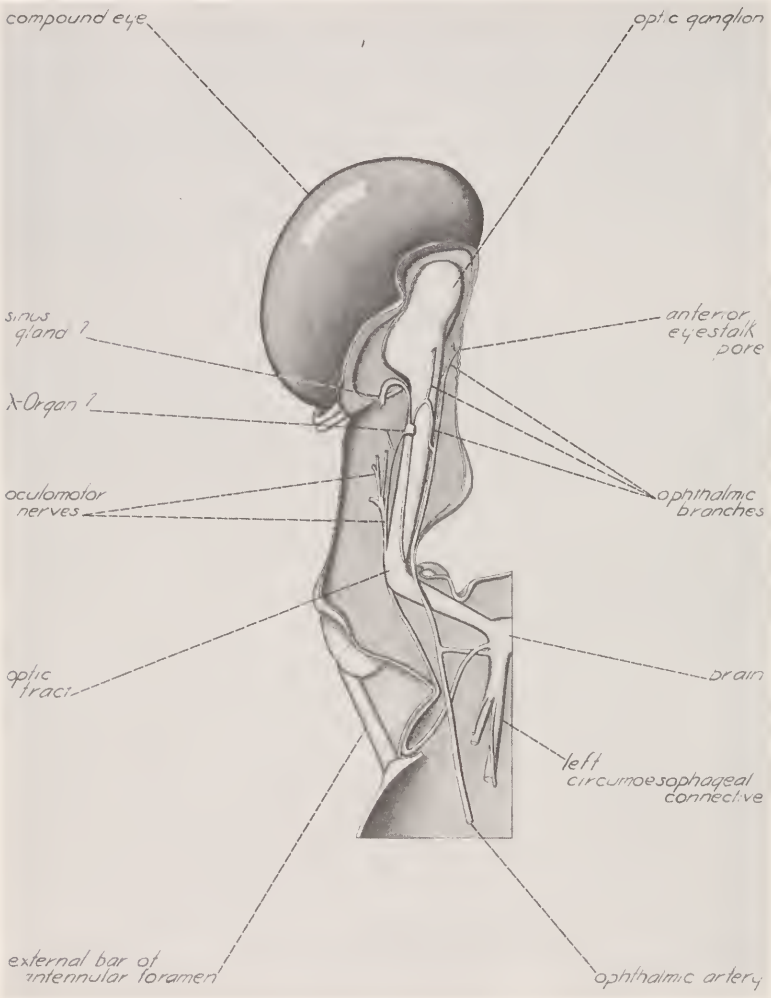

Figure 7. *Penaeus setiferus.* Dorsal view of left eyestalk. Muscles removed to show optic tract, oculomotor nerves, neurosecretory glands, and branches of ophthalmic artery.

Keim (1915) in his account of the nerves in *Astacus* does not illustrate the structures.

The eyestalk nerve to be considered last in the present account originates on the lateral side of the brain, slightly posterior to the optic tract, and, beginning ventrally describes an almost complete loop around the protocephalon attractor muscles (figs. 5, 6, 7). The nerve

procedes to the dorso-lateral region of the muscle, between the muscle and the outer epidermis. From the latter position, the nerve turns sharply anterior and runs into the eyestalk, giving off branches to various of the muscles. The nerve in *Penaeus* is the same as the eye muscle nerve, or *oculomotor nerve* described by Keim (1915) in *Astacus.*

Regrettably, very little can be said of homologies between the eyestalk nerves of the various Crustacea, since so little information exists on the subject. Certainly, the optic tracts and the oculomotor nerves in *Penaeus, Astacus,* and *Cambarus* are homologous structures. Further anatomical information on the nerves will have to be provided before the compartive morphology of the Crustacea Decapoda will be in any way a satisfactory story.

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Summary and Conclusions

1. The eyestalks of the white shrimp, *Penaeus setiferus,* are discussed briefly in connection with its natural history.

2. The earlier observation that the ommatidia are square in *Astacus* is also true in *Penaeus setiferus* as borne out by a study of longitudinal and cross sections of the eye.

3. The name, optic cup, for the sclerotized hemisphere containing the dioptric elements of the stalked crustacean eye is changed to optic calathus, or basket, to end confusion with the optic cup of the vertebrate embryo.

4. The eyestalk of *Penaeus setiferus* is compared to that of *Pandalus danae, Astacus astacus, Cambarus bartoni,* and *Callinectes sapidus.*

5. Seventeen muscles associated with the eyestalk of the white shrimp are discussed and figured. Several of them have not been previously described.

6. The vascular supply of the eyestalk is treated, including an undescribed circulatory structure, the capillary arbor.

7. A previously unknown pore, the anterior eyestalk pore, on the anterior or leading edge of the eyestalk segment is described.

8. The neural elements of the eyestalk are considered, including possible identifications of the neurosecretory glands, the X-Organ and sinus gland.

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