groove of the fifth antennal segment. Contractions of the fifth segment promotors move the fifth antennal segment anteriorly in a limited way. The homolog of these muscles in *Astacus* is very like the musculus extensor propoditis II antennae. Berkeley (1928) does not find the muscle in *Pandalus*.

FLAGELLUM EXTENSION MUSCLES

FIGURE 24

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

FLAGELLUM FLEXOR MUSCLES

FIGURE 24

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

4. LABRUM

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

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

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

No evidence is here advanced to suggest that the labrum is a reduced appendage. Indeed, this ancient "upper lip" was probably never an arthroappendage in the true sense at any time in its history. The labrum is, however, very likely paired. In support of this is the morphology of the nerves and muscles. The labral nerves are paired and arise from the clearly bilateral trito-

cerebral ganglia. Each nerve enters the sac of the labrum and innervates only those sensoria and muscles in half the labrum from the medium sagittal plane laterad. In *Penaeus* no nerve can be seen crossing the median sagittal plane. Furthermore, the embryonic labrum of many higher arthropods (Johannsen and Butt, 1941; Young 1953) develops as a paired structure, with paired coelomic sacs.

SKELETAL ELEMENTS

FIGURES 26, 27

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

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

MUSCLE ELEMENTS

EPISTOMAL STATOR MUSCLES

FIGURES 5, 6, 30, 34

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

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

LABRAL MUSCLES

FIGURE 27

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

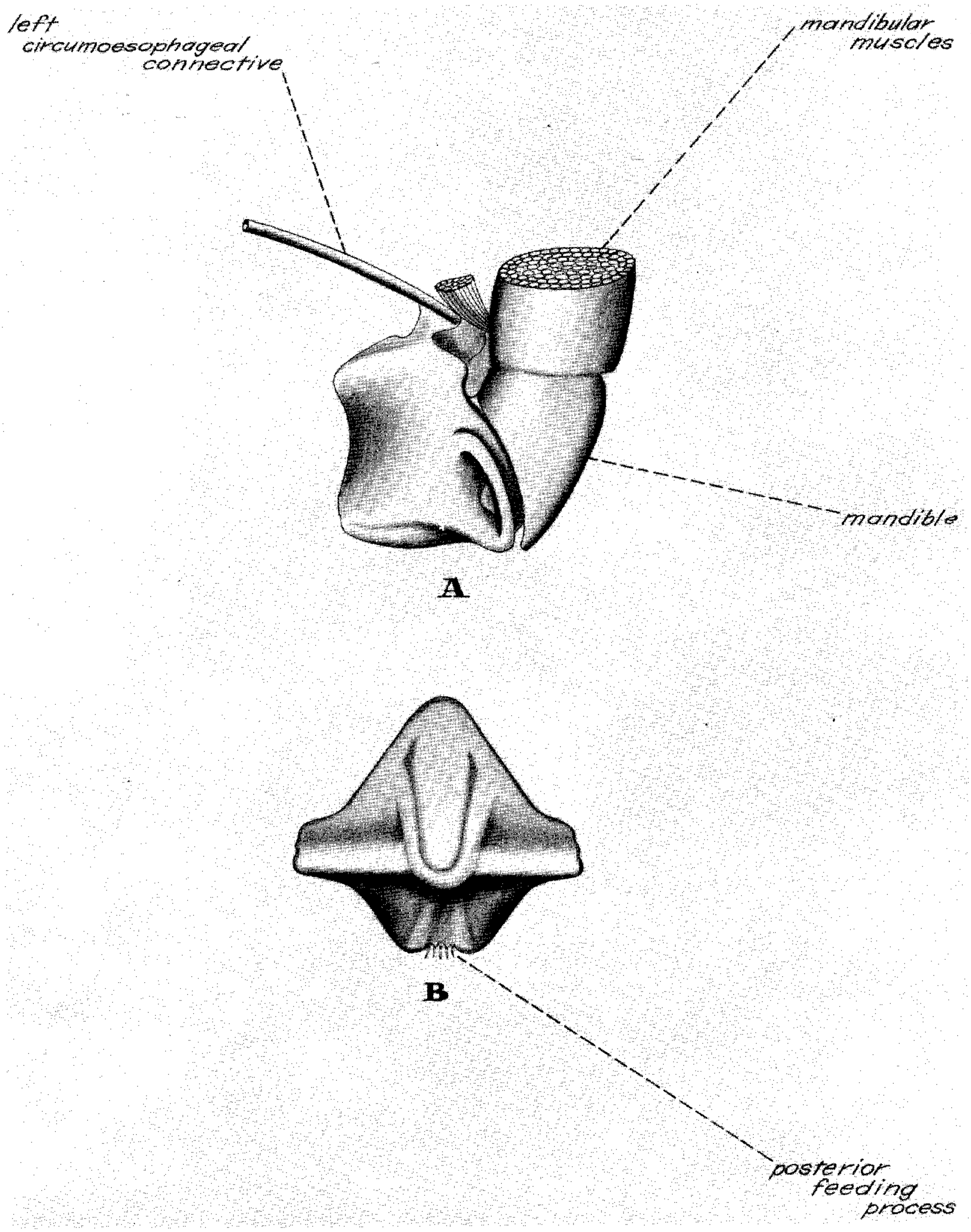

FIGURE 26.—Labrum. *A*. Lateral view of labrum from the left side showing relation of labrum to mandible. *B*. Ventral view of labrum showing posterior feeding process.

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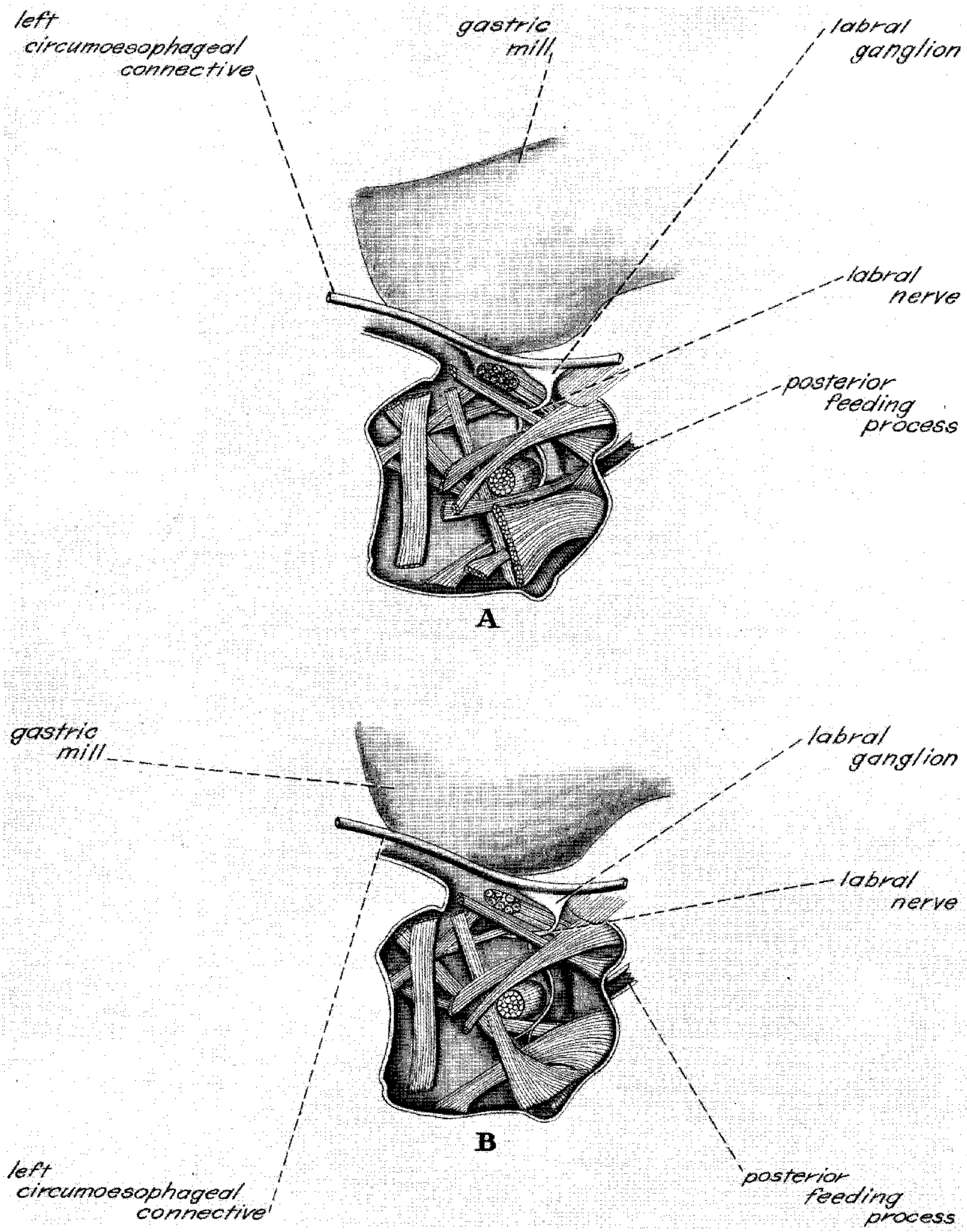

FIGURE 27.—Lateral views of labrum from the left side showing muscles and nerves. *A*. Cuticle removed to show superficial lateral muscles of left side. *B*. Interior muscles of labrum.

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

B. Gnathothorax

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

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

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

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

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

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

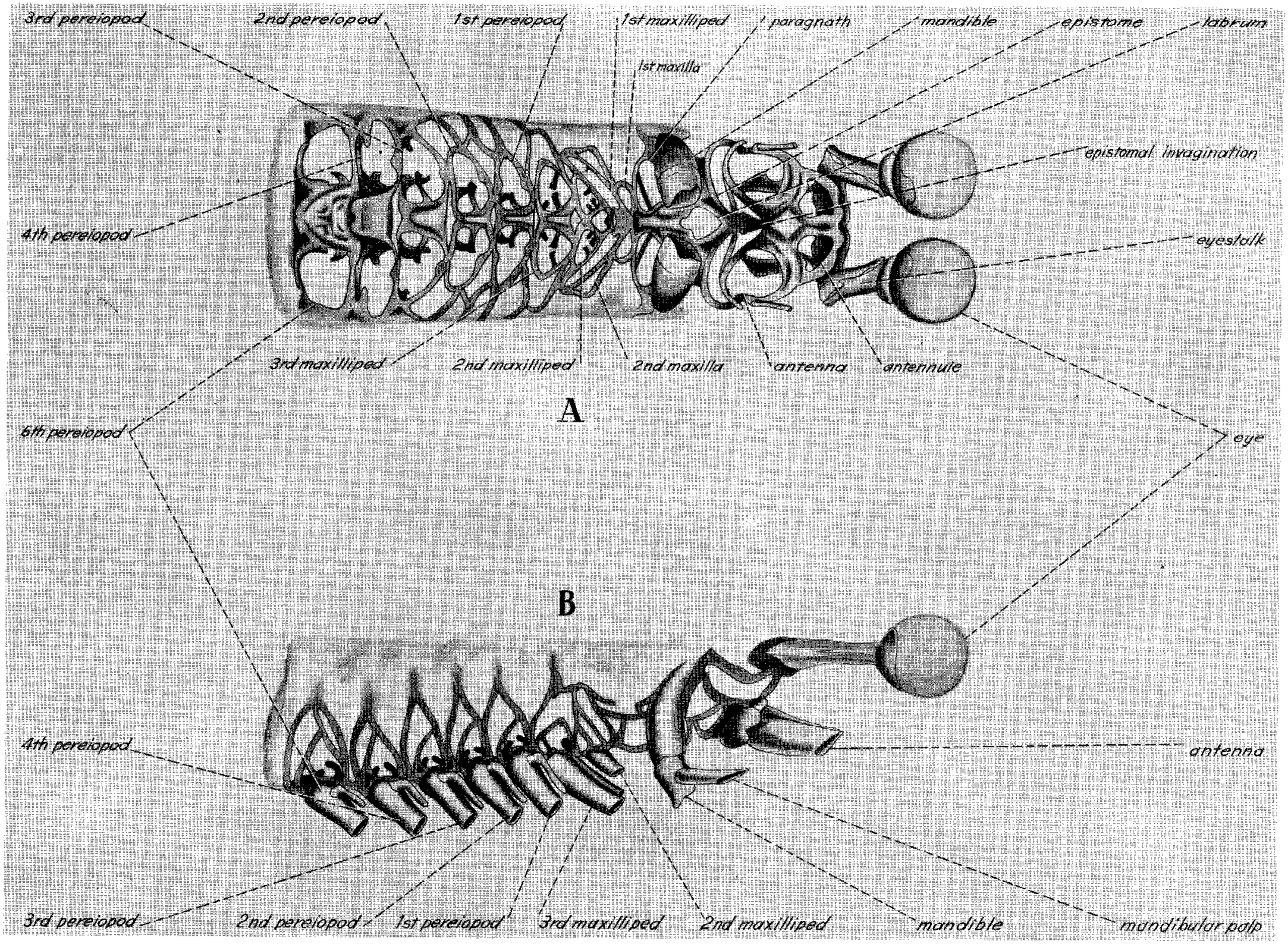

FIGURE 28.—Ventral skeleton of protocephalon and gnathothorax. *A*. Ventral view. *B*. Lateral view of right side.

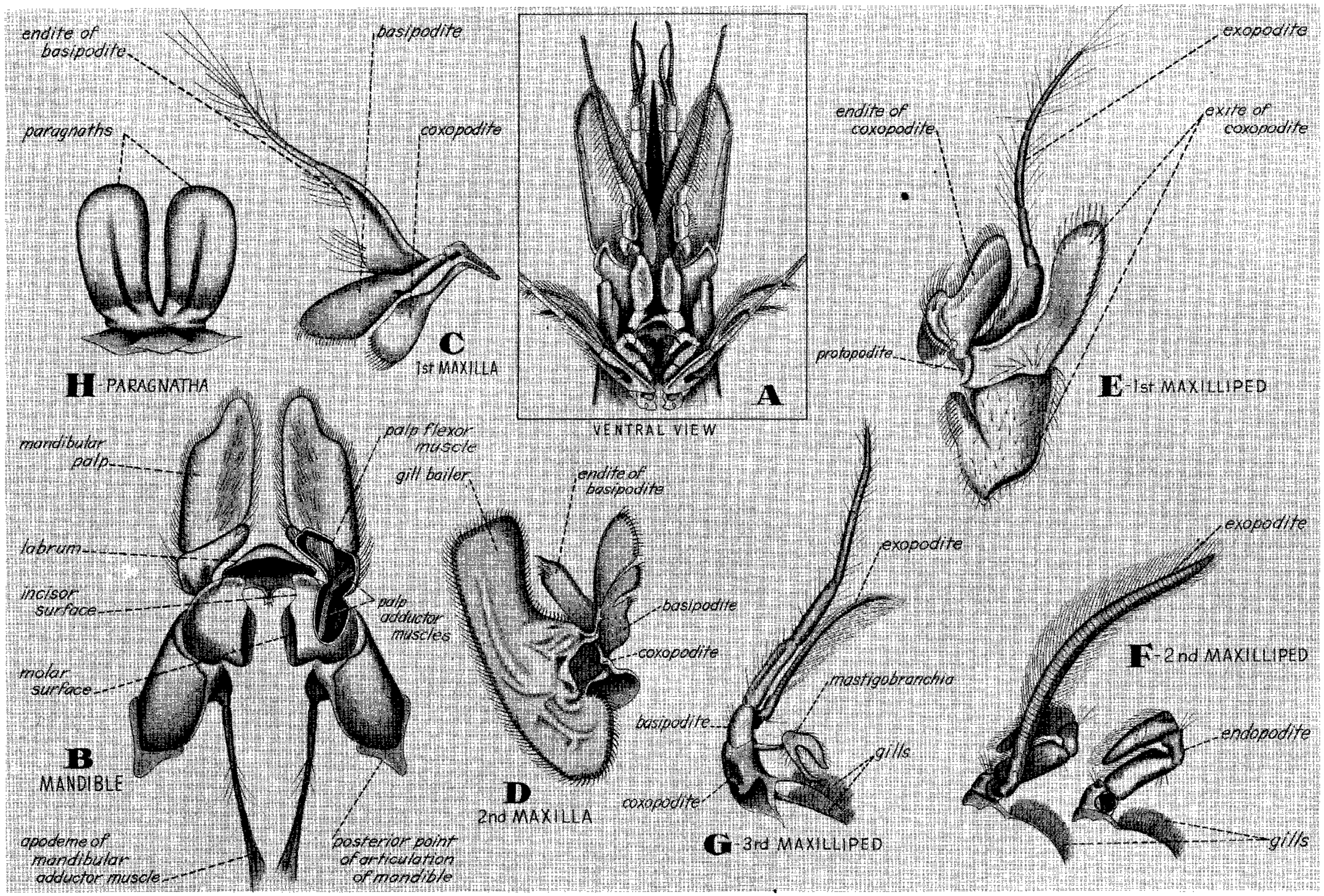

FIGURE 29.—Mouthparts.

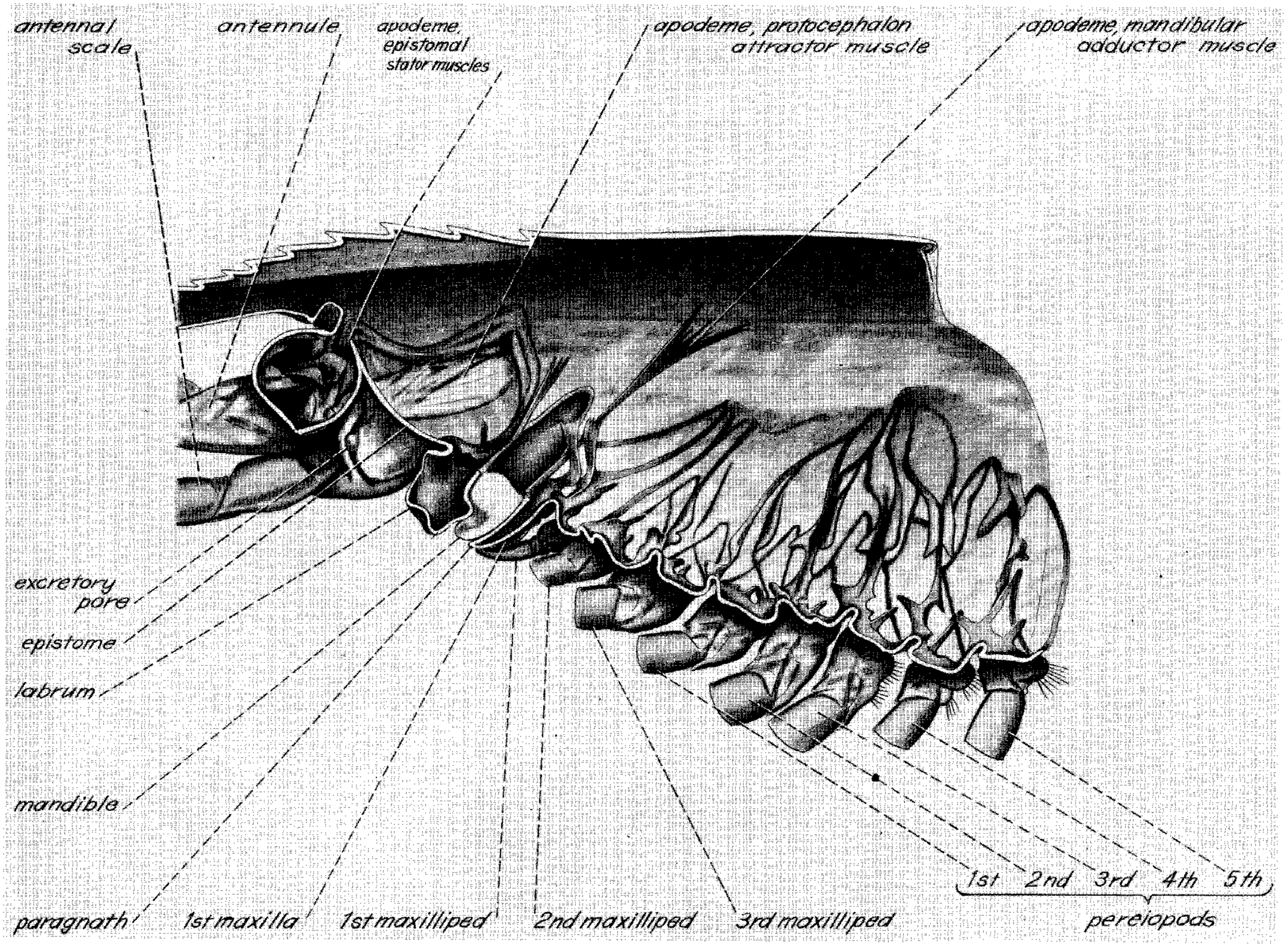

FIGURE 30.—Internal view of right half of protocephalon and gnathothorax.

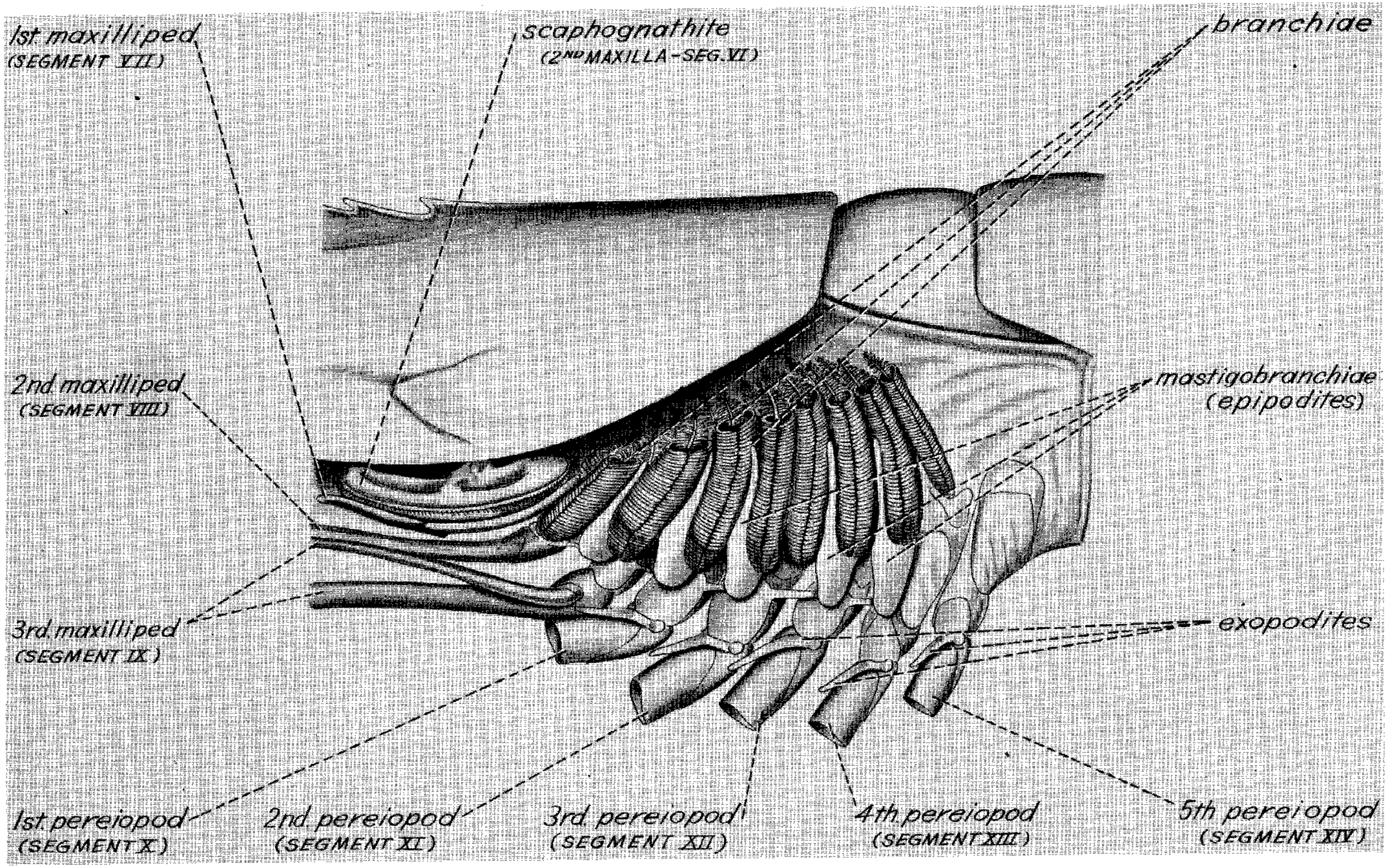

FIGURE 31.—Lateral view of left side of thorax, carapace cut away to show gill chamber, gills, and mastigobranchiae.

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

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

Gills

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

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

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

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

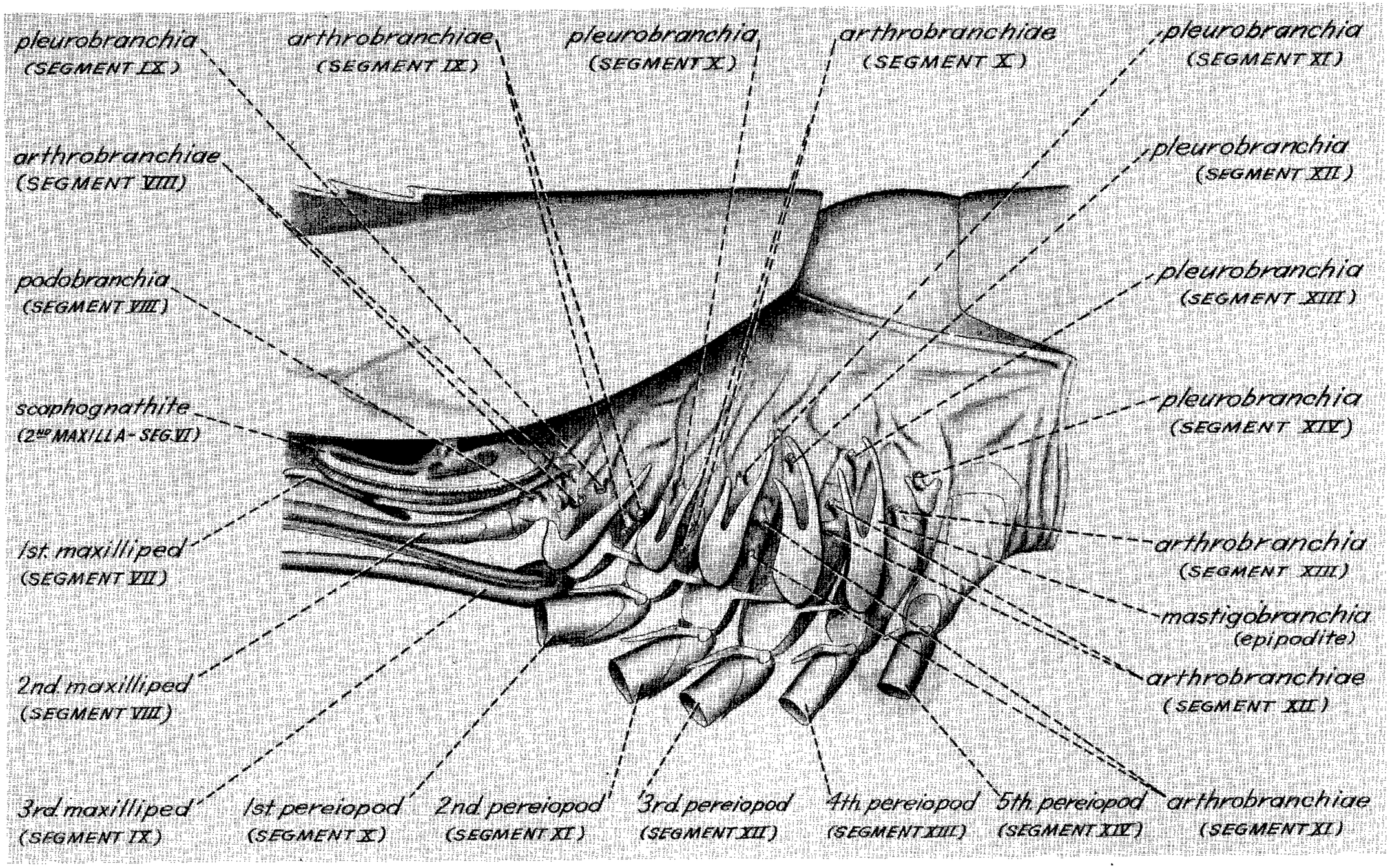

FIGURE 32.—Lateral view of left side of thorax, carapace, and gills removed to show mastigobranchiae and gill attachments.

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

MUSCLE ELEMENTS

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

SUPERFICIAL LATERAL THORACIC MUSCLES

FIGURE 33

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

VENTRAL MUSCLES

SUPERFICIAL VENTRAL THORACIC MUSCLES

FIGURE 36

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

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

ANTERIOR THORACIC MUSCLES

FIGURES 33 TO 36

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

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

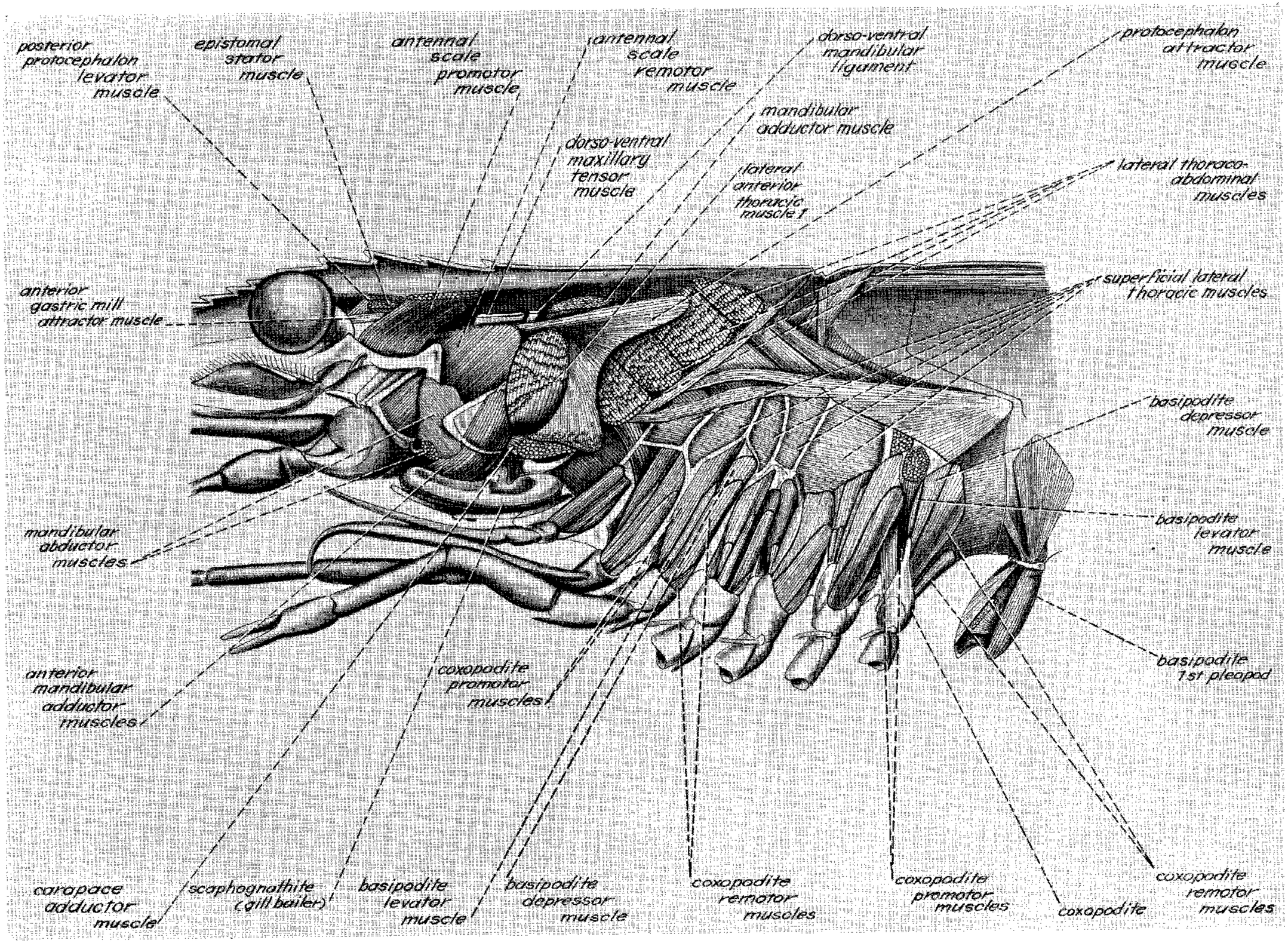

Figure 33.—Lateral view of left side of protocephalon and gnathothorax showing muscle origins. Carapace and left body wall removed.

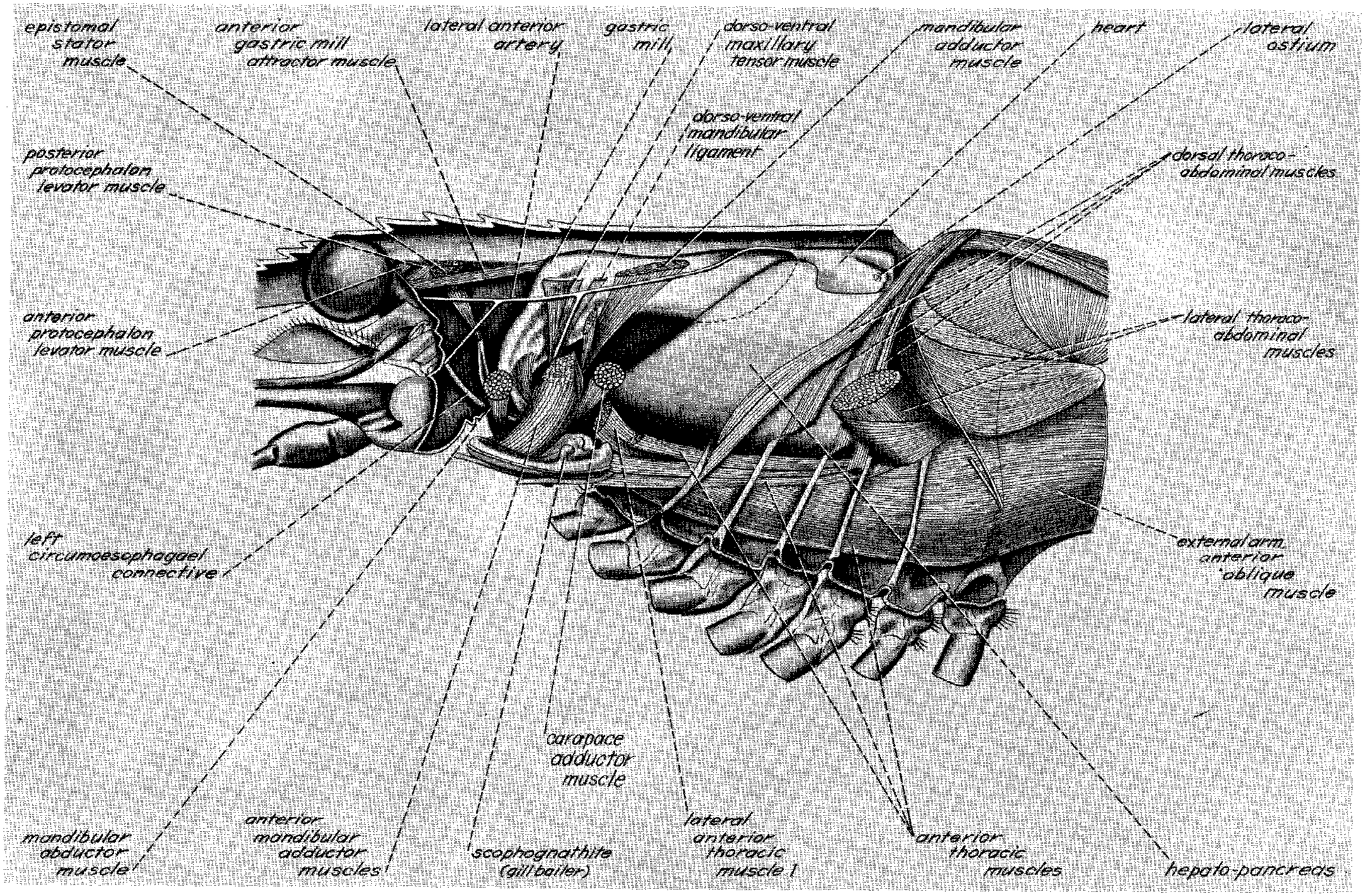

FIGURE 34.—Lateral view of left side of gnathothorax: Lateral muscles removed to show medial muscles and internal organs.

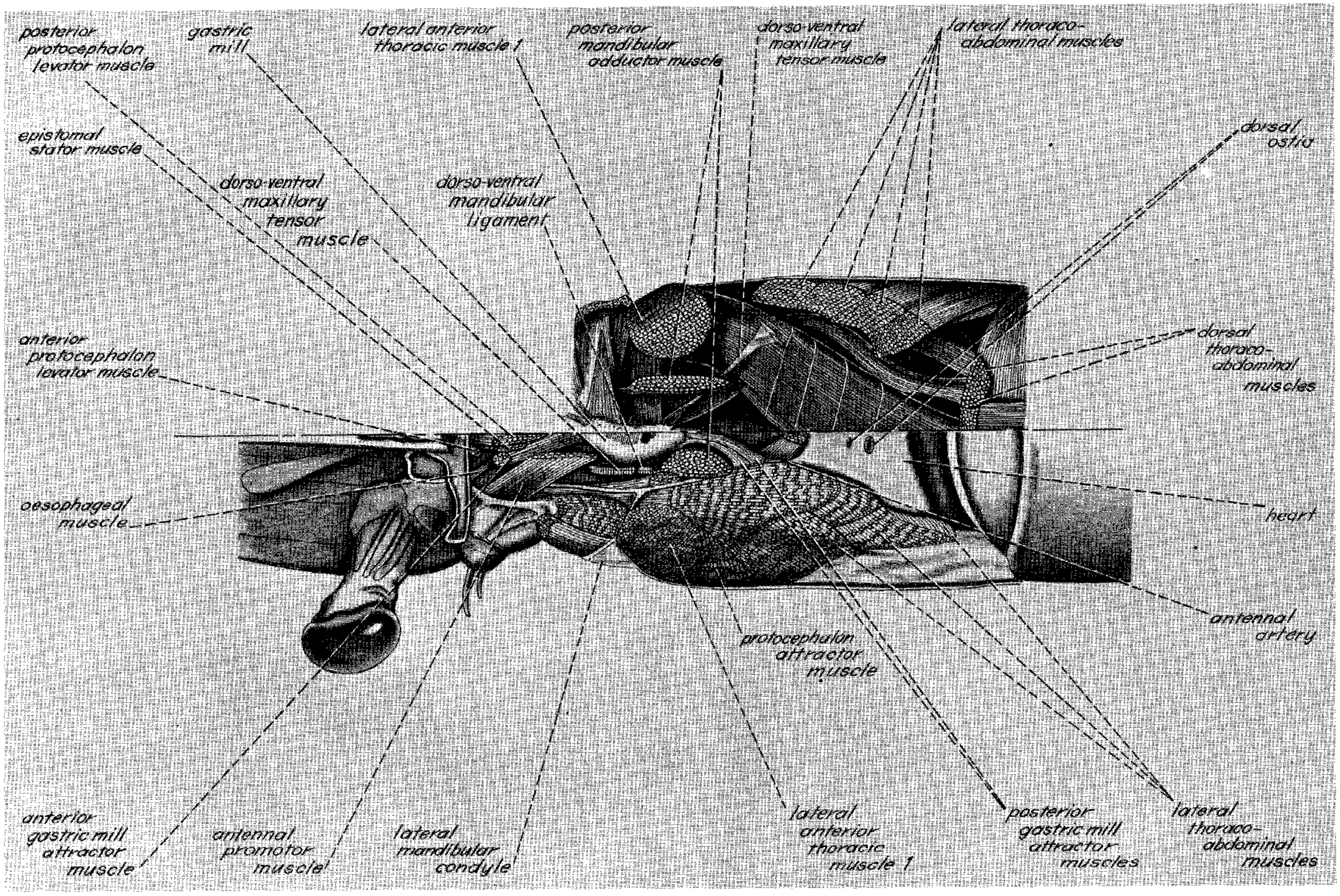

FIGURE 35.—Dorsal views of protocephalon and gnathothorax. Lower section, dorsal muscles. Upper section ventral muscles.

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

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

VENTRAL HEAD LIGAMENTS

FIGURES 37, 38

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

CARAPACE ADDUCTOR MUSCLE

FIGURES 33, 34, 37, 38

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

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

DORSAL MUSCLES

DORSAL THORACOABDOMINAL MUSCLES

FIGURES 34, 35

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

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

LATERAL THORACOABDOMINAL MUSCLES

FIGURES 34, 35

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

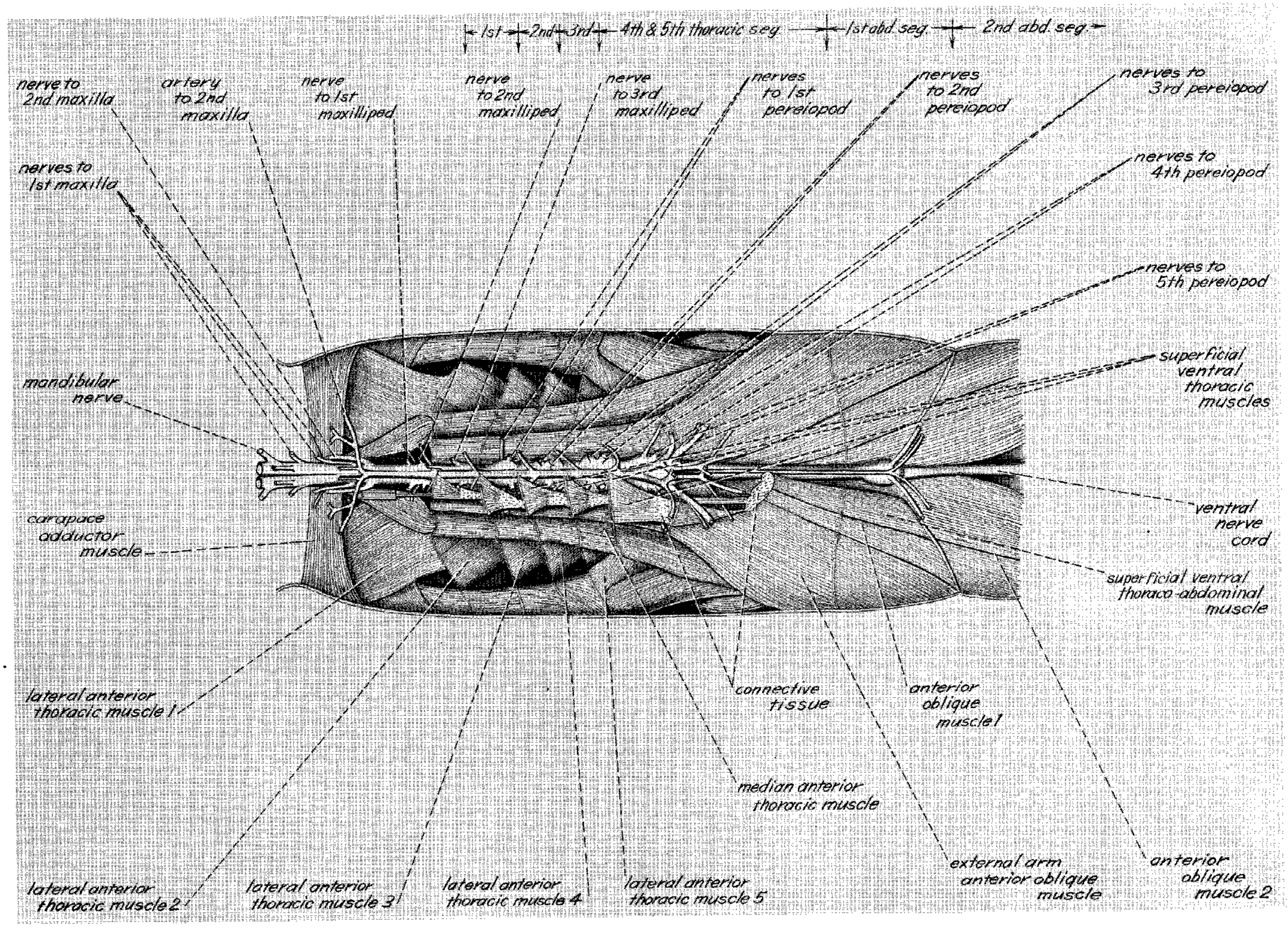

Figure 36.—Ventral view of gnathothorax showing muscles, nerves, and blood vessels.

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

APPENDAGES OF THE GNATHOTHORAX

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

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

1. MANDIBLES

SKELETAL ELEMENTS

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

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

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

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

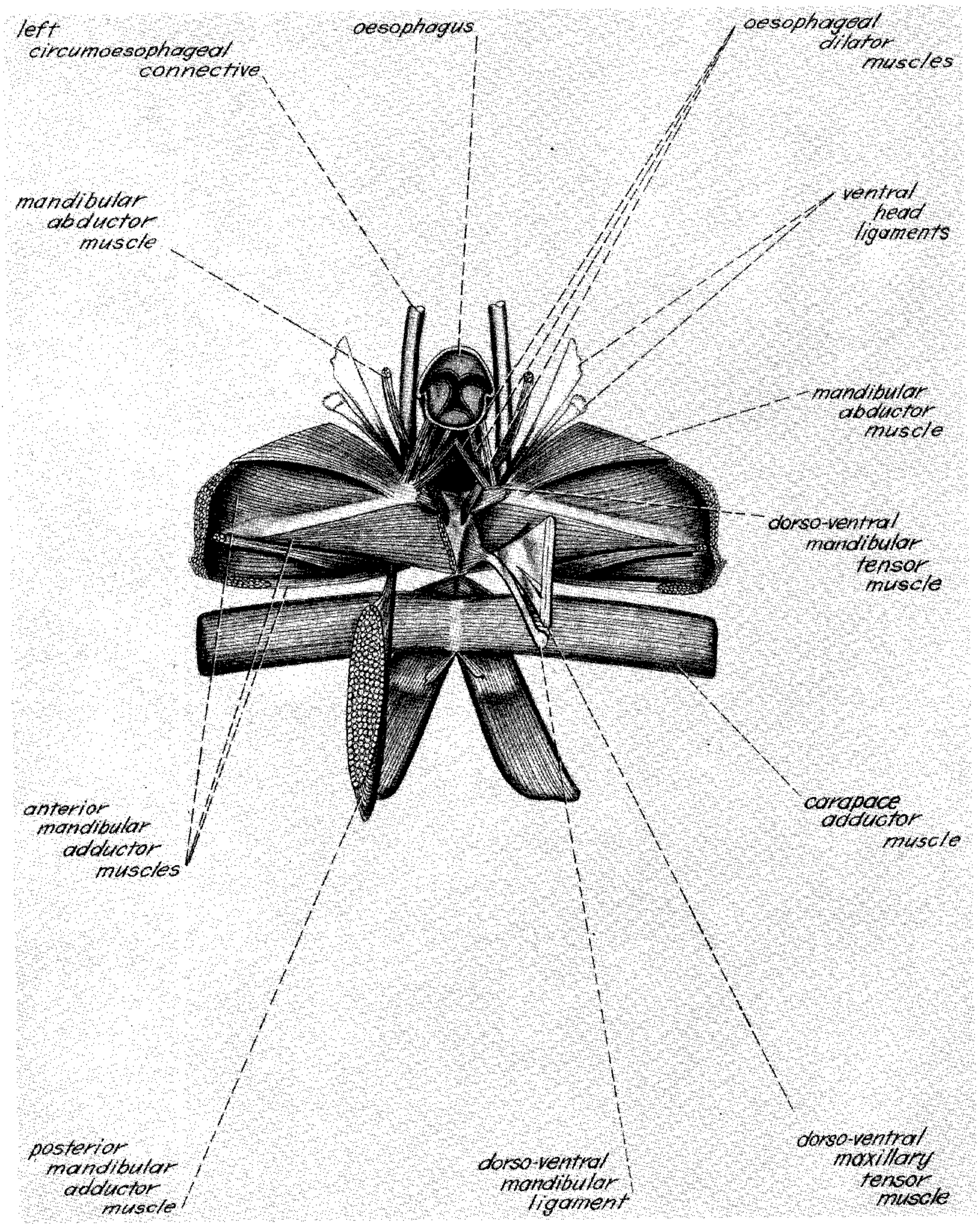

FIGURE 37.—Dorsal view of mandibular musculature.

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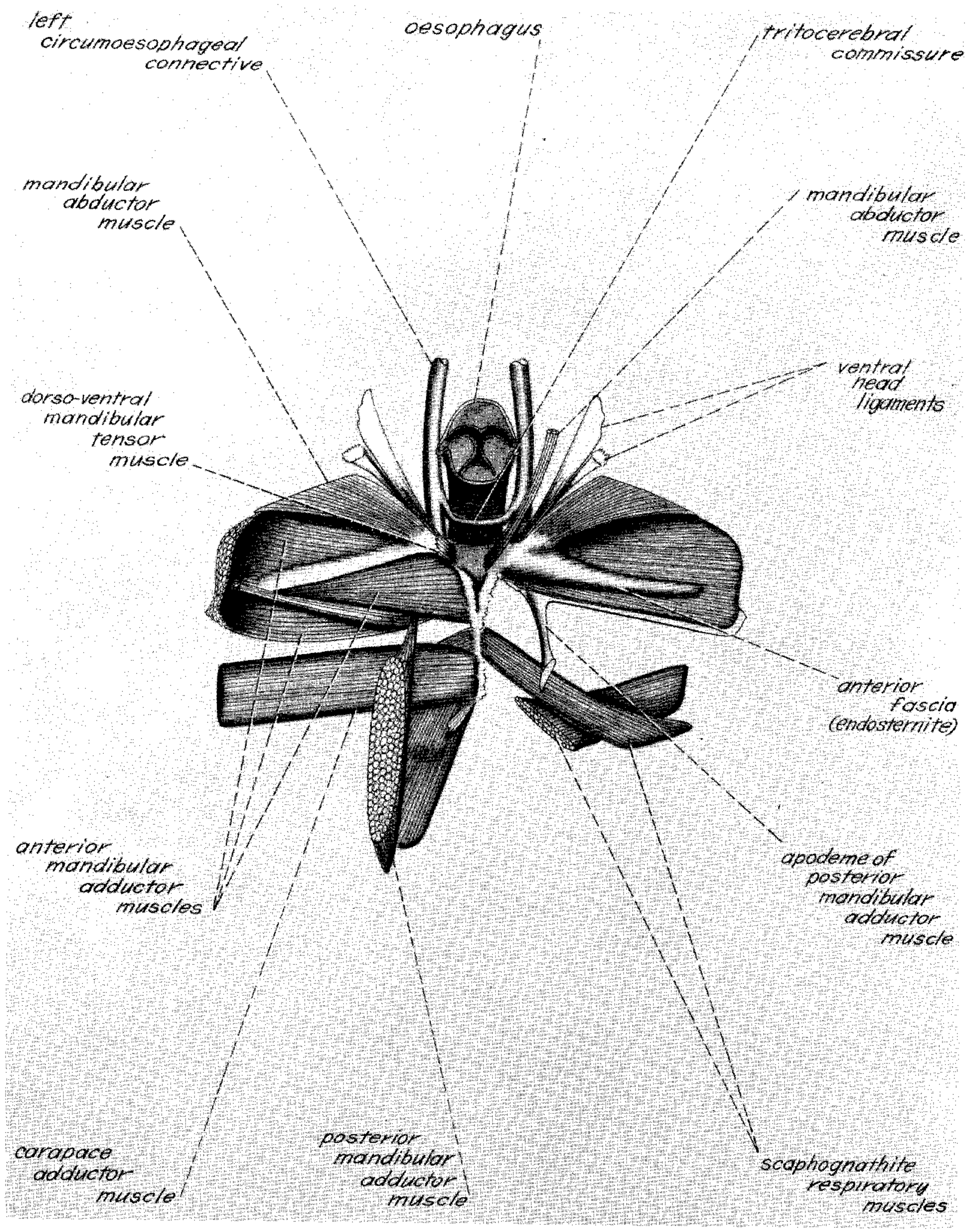

FIGURE 38.—Dorsal view of mandibular musculature, dorsal-most muscles removed.

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

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

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

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

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

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

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

MUSCLE ELEMENTS

MANDIBULAR ABDUCTOR MUSCLES

FIGURES 33, 37, 38

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

The large and important mandibular abductors originate in connective tissue on the laterotergal plates (fig. 33) and run posteromedially to insertion areas on the mandibular endoskeleton (figs. 37, 38). Their contractions serve to open the

gnathal elements of the mandibles. These two mandibular abductor muscles are fully homologous with the major and minor mandibular abductor muscles in *Astacus* and with the mandibular abductor muscle in *Pandalus*. Presumably the homology holds for the major and minor mandibular abductors of *Callinectes*.

DORSOVENTRAL MANDIBULAR TENSOR MUSCLE

FIGURE 37

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

ANTERIOR MANDIBULAR ADDUCTOR MUSCLES

FIGURES 33, 34, 37, 38

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

DORSOVENTRAL MANDIBULAR LIGAMENT

FIGURES 33, 34, 35, 37

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

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

POSTERIOR MANDIBULAR ADDUCTOR MUSCLE

FIGURES 30, 33, 34, 35, 37, 38

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

MANDIBULAR PALP FLEXOR MUSCLE

FIGURE 29

The muscles operating the mandibular palp are situated either in the gnathal lobe of the mandible or in the basal segment of the palp. The distal lobe of the palp contains no muscles. The mandibular palp flexor muscle (fig. 29) originates in the proximal region of the basal palp segment near the foramen between the gnathal lobe and the palp base. The muscle runs distally, becoming broad and flat, and inserts on the posteroventrad margin of the distal palp lobe. In action, the mandibular palp flexor turns the distal lobe ventrad. An ap-

parently similar muscle in the palp of *Astacus* is called by Schmidt (1915) a palp flexor also. Berkeley (1928) describes both a palp flexor and a palp extensor in the body of the mandible of *Pandalus*.

MANDIBULAR PALP ADDUCTOR MUSCLES

FIGURE 29

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

2. PARAGNATHA

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

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

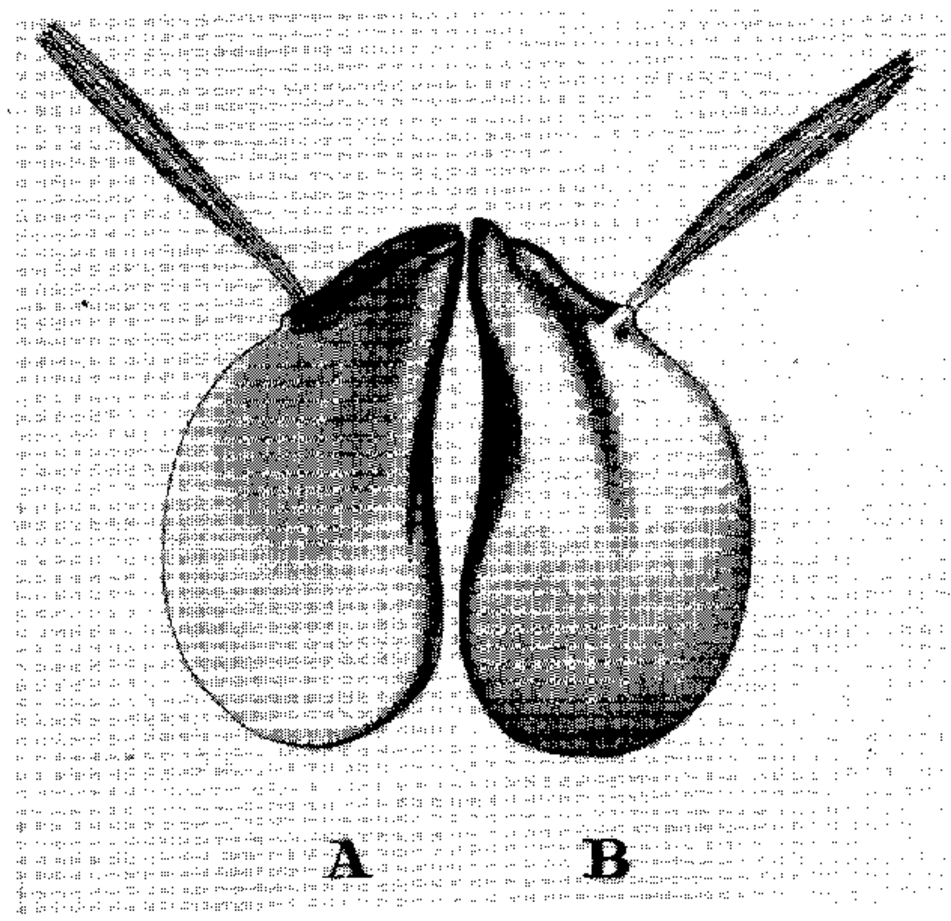

FIGURE 39.—Paragnatha. *A*. Anterior view. *B*. Posterior view.

mandibular entities. In a comparative study of arthropod nerves, Henry (1948a) assigns the paragnatha to the mandibular segment by virtue of their innervations. She invariably places the paragnathal nerves in a position posterior to those of the mandibles.

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

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

be verified by histological work before a decision on this interesting point can be made.

3. MAXILLAE

3a. First Maxillae

SKELETAL ELEMENTS

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

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

MUSCLE ELEMENTS

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

COXOPODITE PROMOTOR MUSCLE OF FIRST MAXILLA

FIGURE 40

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

COXOPODITE REMOTOR MUSCLE OF FIRST MAXILLA

FIGURE 40

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

LATERAL COXOPODITE ADDUCTOR MUSCLE OF FIRST MAXILLA

FIGURE 40

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

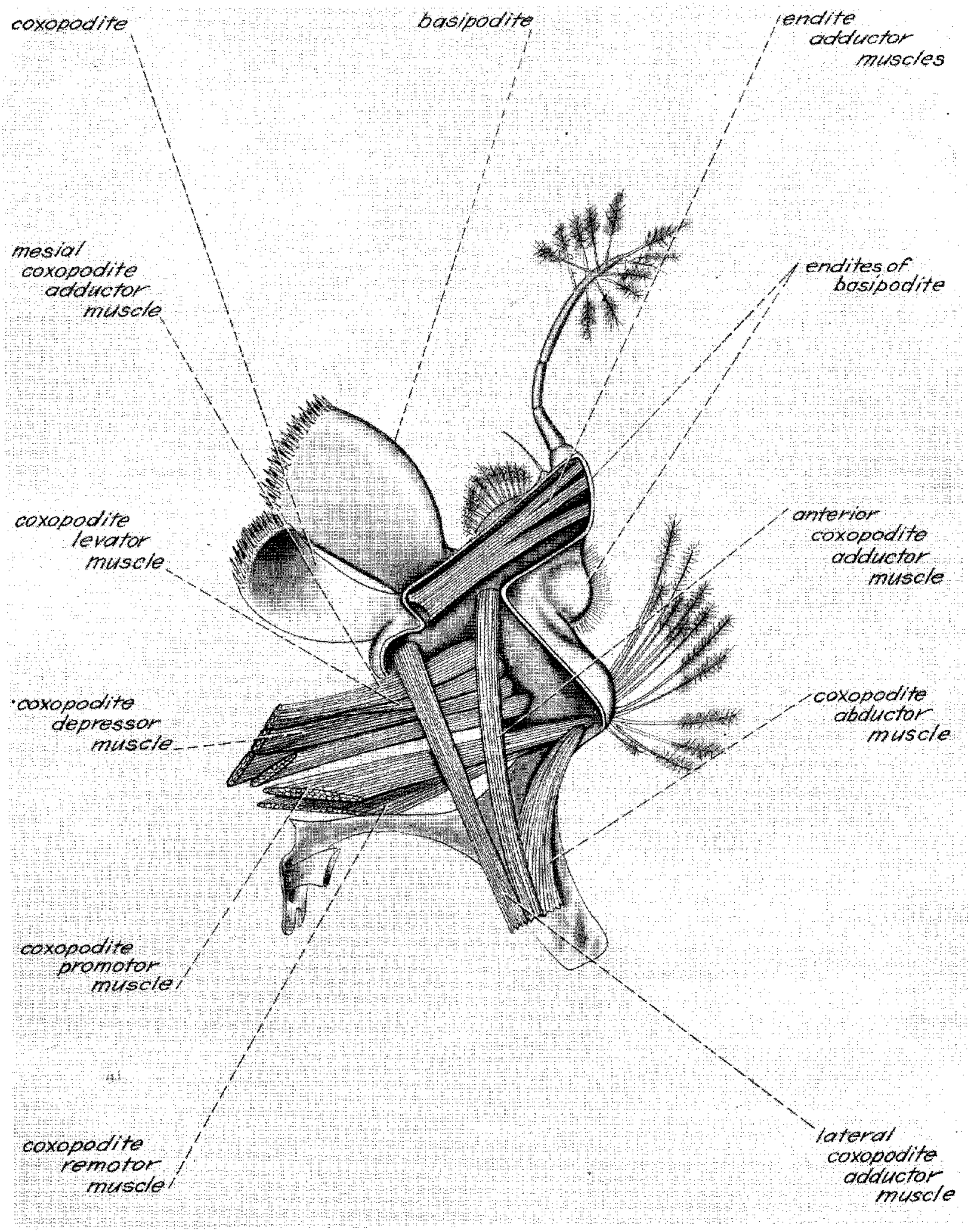

FIGURE 40.—Dorsal view of right first maxilla. Dorsal cuticle removed to show muscles.