MESIAL COXOPODITE ADDUCTOR MUSCLE OF FIRST MAXILLA

FIGURE 40

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

ANTERIOR COXOPODITE ADDUCTOR MUSCLE OF FIRST MAXILLA

FIGURE 40

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

COXOPODITE ABDUCTOR MUSCLE OF FIRST MAXILLA

FIGURE 40

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

COXOPODITE LEVATOR MUSCLE OF FIRST MAXILLA

FIGURE 40

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

COXOPODITE DEPRESSOR MUSCLE OF FIRST MAXILLA

FIGURE 40

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

ENDITE ADDUCTOR MUSCLE OF FIRST MAXILLA

FIGURE 40

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

DORSOVENTRAL MAXILLARY TENSOR MUSCLE

FIGURES 33, 34, 35, 37

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

3b. The Second Maxillae

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

SKELETAL ELEMENTS

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

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

MUSCLE ELEMENTS

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

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

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

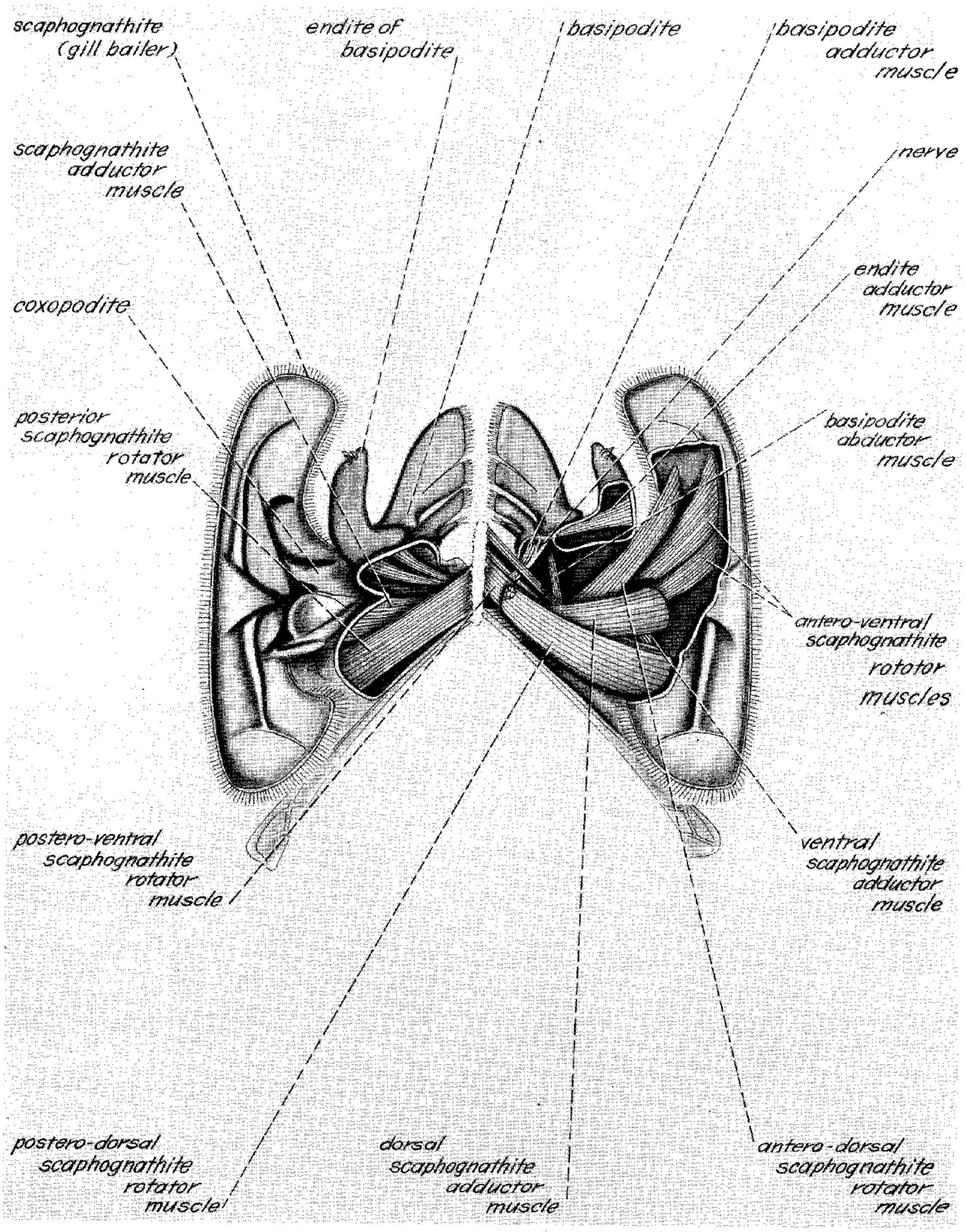

FIGURE 41.—Dorsal view of second maxilla. Left side, intact appendage. Right side, dorsal cuticle removed to show muscles.

BASIPODITE ADDUCTOR MUSCLE OF SECOND MAXILLA

FIGURE 41

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

BASIPODITE ABDUCTOR MUSCLE OF SECOND MAXILLA

FIGURE 41

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

ENDITE ADDUCTOR MUSCLE OF SECOND MAXILLA

FIGURE 41

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

POSTEROVENTRAL SCAPHOGNATHITE ROTATOR MUSCLE OF SECOND MAXILLA

FIGURE 41

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

DORSAL SCAPHOGNATHITE ADDUCTOR MUSCLE OF SECOND MAXILLA

FIGURE 41

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

POSTERODORSAL SCAPHOGNATHITE ROTATOR MUSCLE OF SECOND MAXILLA

FIGURE 41

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

VENTRAL SCAPHOGNATHITE ADDUCTOR MUSCLE OF SECOND MAXILLA

FIGURE 41

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

ANTERODORSAL SCAPHOGNATHITE ROTATOR MUSCLES OF SECOND MAXILLA

FIGURE 41

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

ANTERODORSAL SCAPHOGNATHITE ROTATOR MUSCLE OF SECOND MAXILLA

FIGURE 41

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

4. MAXILLIPEDS

4a. First Maxilliped

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

SKELETAL ELEMENTS

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

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

MUSCLE ELEMENTS

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

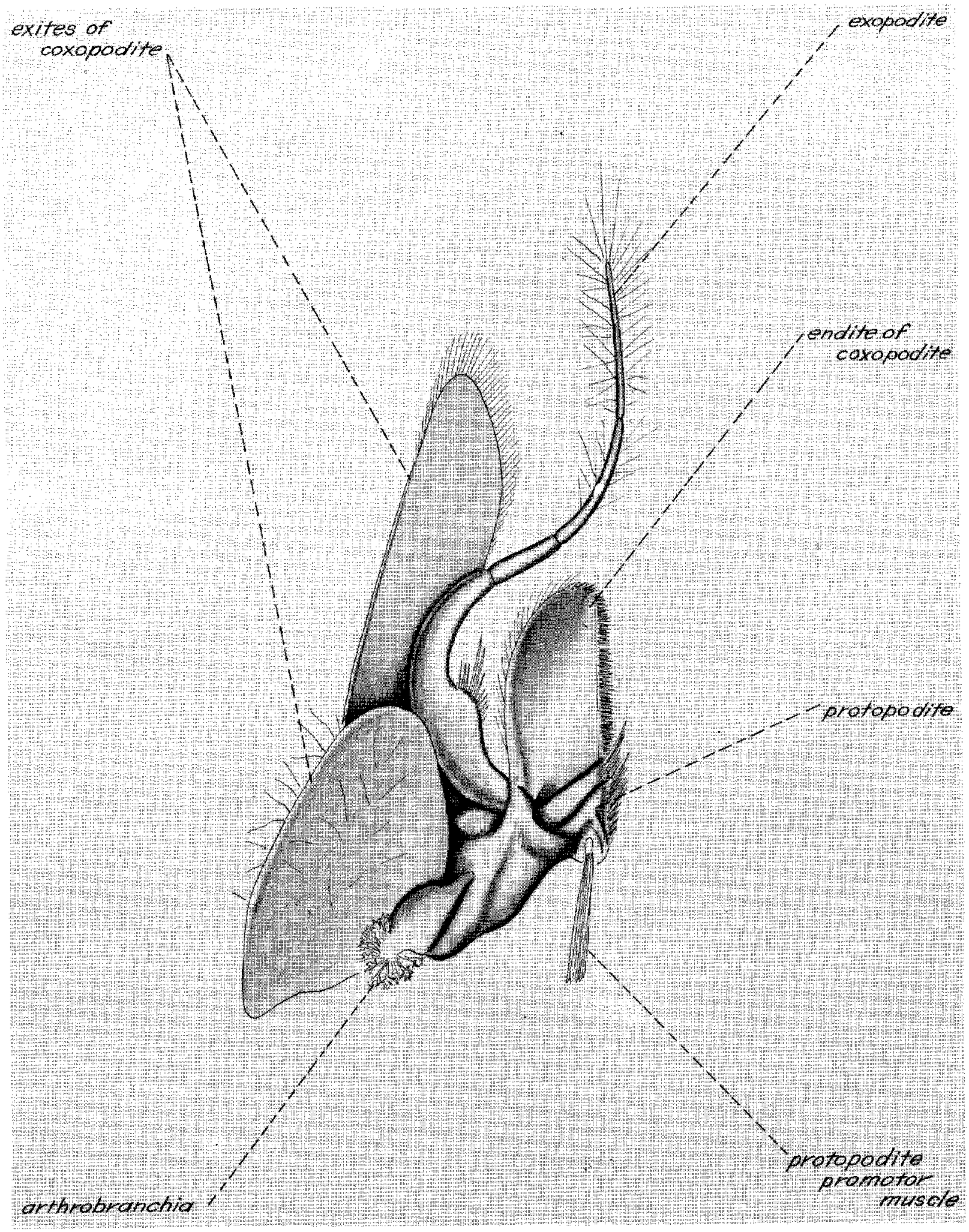

FIGURE 42.—Dorsal view of left first maxilliped.

PROTOPODITE PROMOTOR MUSCLES OF FIRST MAXILLIPED

FIGURES 42, 43

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

PROTOPODITE LEVATOR MUSCLES OF FIRST MAXILLIPED

FIGURE 43

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

COXOPODITE ADDUCTOR MUSCLE OF FIRST MAXILLIPED

FIGURE 43

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

COXOPODITE ABDUCTOR MUSCLES OF FIRST MAXILLIPED

FIGURE 43

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

EXITE ATTRACTOR MUSCLES OF FIRST MAXILLIPED

FIGURE 43

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

EXOPODITE ADDUCTOR MUSCLE OF FIRST MAXILLIPED

FIGURE 43

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

EXOPODITE ABDUCTOR MUSCLE OF FIRST MAXILLIPED

FIGURE 43

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

4b. Second Maxilliped

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

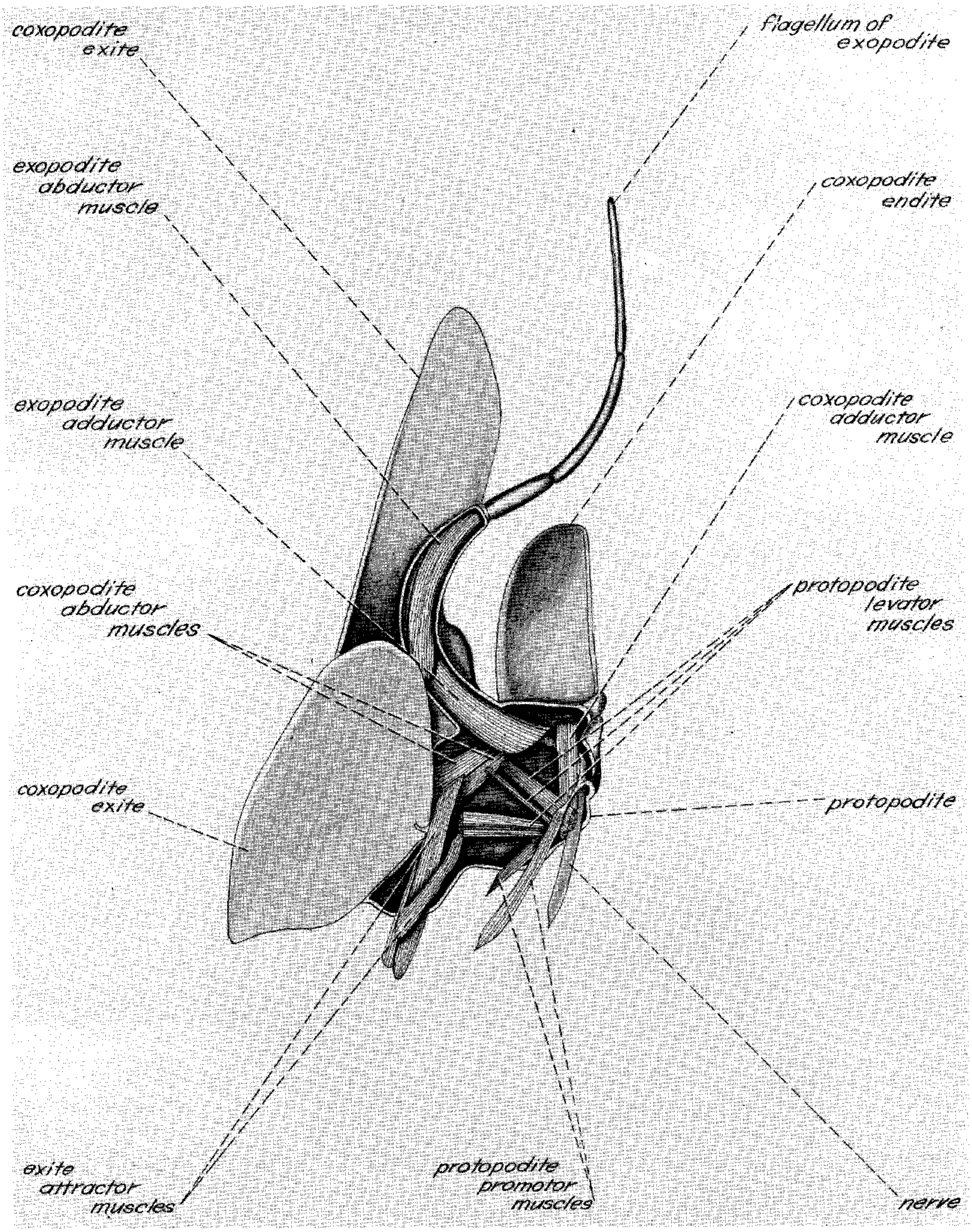

FIGURE 43.—Dorsal view of left first maxilliped, dorsal cuticle removed to show muscles.

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

SKELETAL ELEMENTS

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

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

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

MUSCLE ELEMENTS

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

COXOPODITE PROMOTOR MUSCLE OF SECOND MAXILLIPED

FIGURES 44, 45

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

COXOPODITE REMOTOR MUSCLE OF SECOND MAXILLIPED

FIGURES 44, 45

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

BASIPODITE LEVATOR MUSCLES OF SECOND MAXILLIPED

FIGURES 44, 55

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

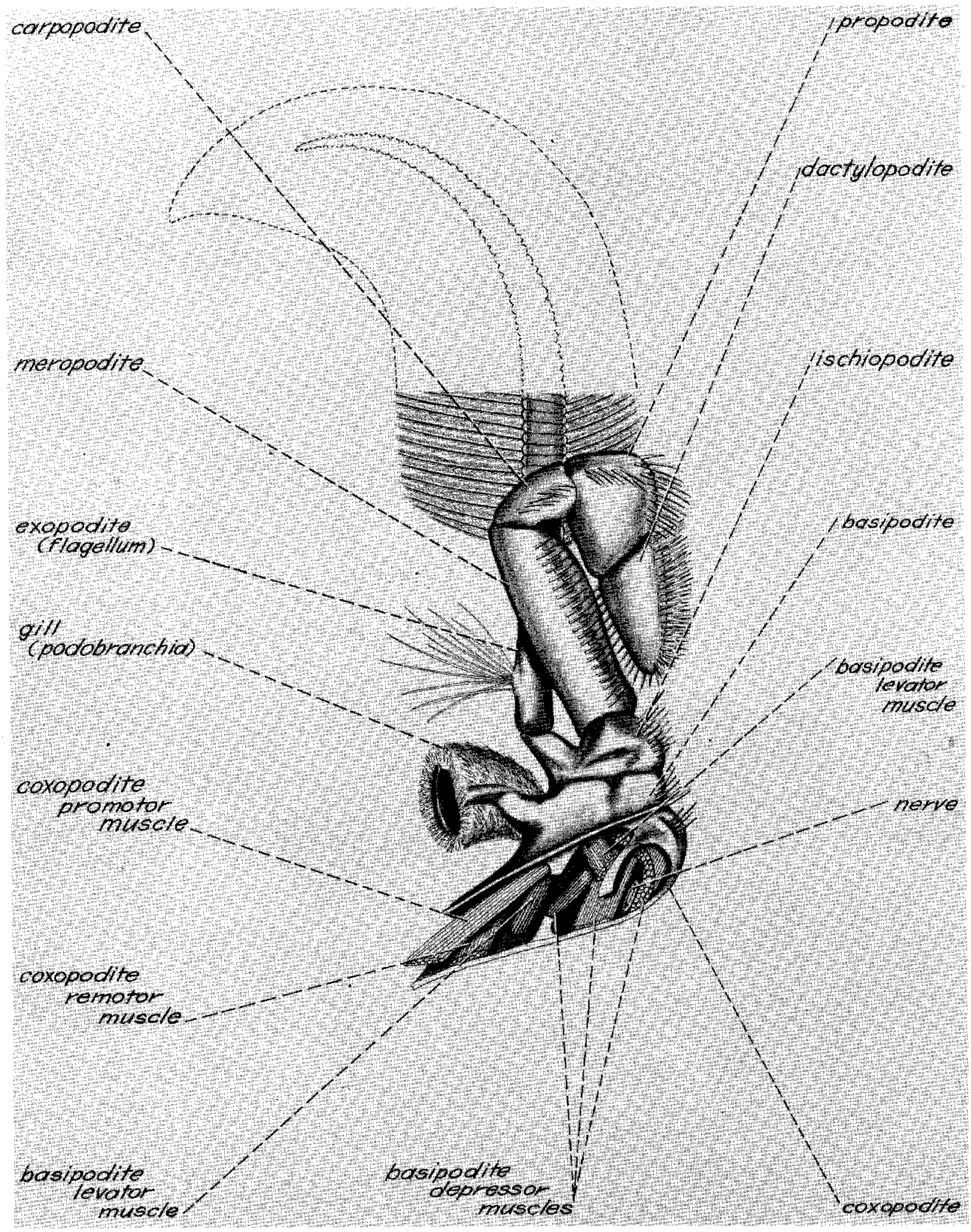

FIGURE 44.—Dorsal view of left second maxilliped.

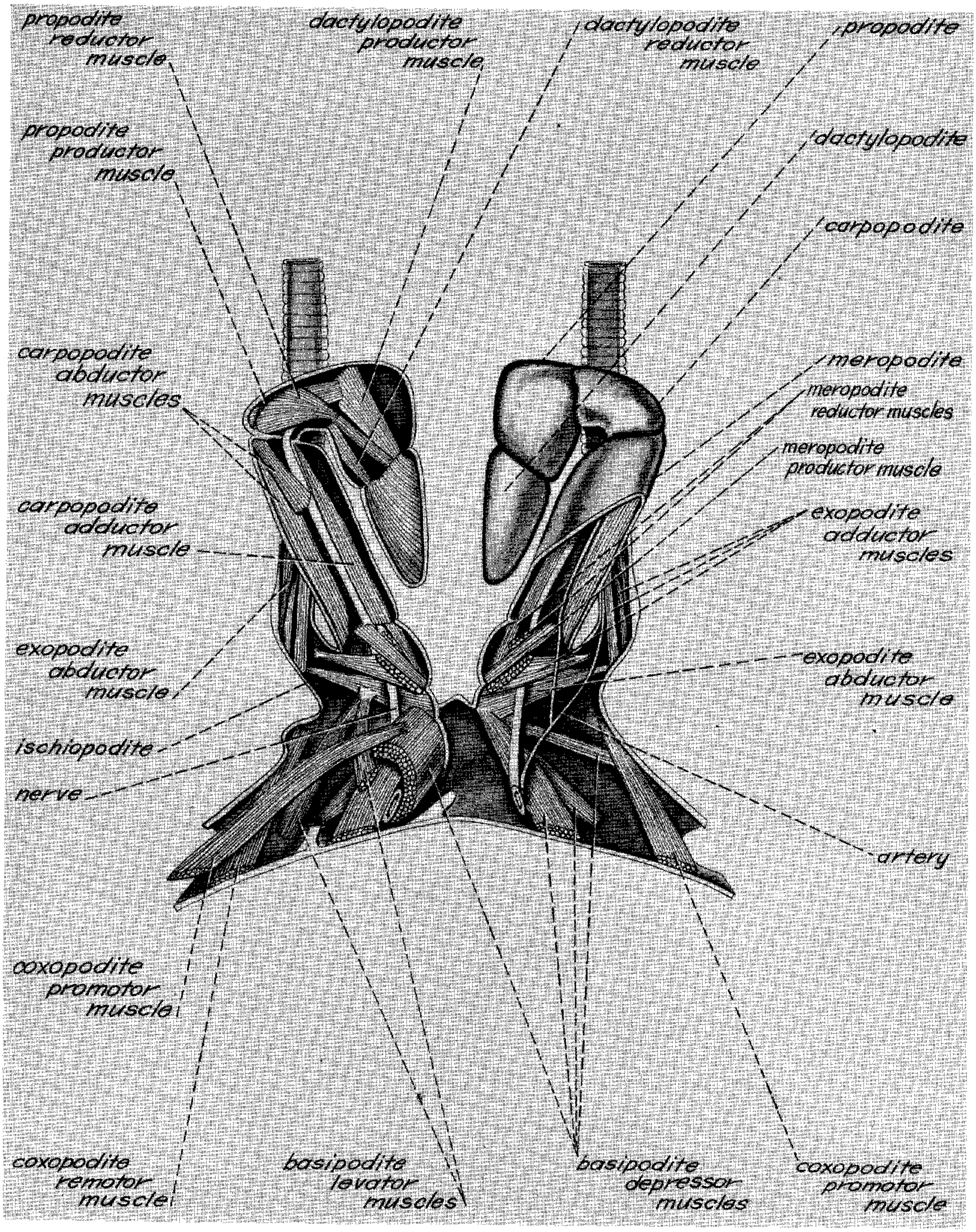

FIGURE 45.—Dorsal view of second maxilliped, cuticle removed to show muscles.

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

BASIPODITE DEPRESSOR MUSCLES OF SECOND MAXILLIPED

FIGURES 44, 45

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

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

EXOPODITE ABDUCTOR MUSCLES OF SECOND MAXILLIPED

FIGURE 45

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

EXOPODITE ADDUCTOR MUSCLES OF SECOND MAXILLIPED

FIGURE 45

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

MEROPODITE PRODUCTOR MUSCLE OF SECOND MAXILLIPED

FIGURE 45

The types and arrangement of the second maxilliped endopodite muscles are remarkably uniform in many higher Crustacea, in accordance

with the evolution of this versatile accessory feeding mechanism. The meropodite productor muscle originates on the medial side of the ischiopodite, near the exopodite adductor, and inserts on a small apodeme on the dorsal surface of the meropodite. The muscle lifts the meropodite and other distal elements towards the ventral surface of the mandibles. The same muscle appears in *Pandalus*, *Astacus*, and *Callinectes*.

MEROPODITE REDUCTOR MUSCLES OF SECOND MAXILLIPED

FIGURE 45

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

CARPOPODITE ABDUCTOR MUSCLES OF SECOND MAXILLIPED

FIGURE 45

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

CARPOPODITE ADDUCTOR MUSCLE OF SECOND MAXILLIPED

FIGURE 45

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

PROPODITE PRODUCTOR MUSCLE OF SECOND MAXILLIPED

FIGURE 45

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

PROPODITE REDUCTOR MUSCLE OF SECOND MAXILLIPED

FIGURE 45

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

DACTYLOPODITE PRODUCTOR MUSCLE OF SECOND MAXILLIPED

FIGURE 45

The dactylopodite productor muscle is a small, fan-shaped muscle that originates proximally in the propodite and inserts on the ventral margin of the dactylopodite. It serves to straighten the

dactylopodite and turn the distal article ventrad, in opposition to the dactylopodite reductor. The same muscle as the dactylopodite productor in *Penaeus* is found in *Pandalus*, *Astacus*, and *Callinectes*.

DACTYLOPODITE REDUCTOR MUSCLE OF SECOND MAXILLIPED

FIGURE 45

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

4c. Third Maxilliped

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

SKELETAL ELEMENTS

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

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

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

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

MUSCLE ELEMENTS

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

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

Callinectes has 16 muscles grouped into 15 muscle types.

COXOPODITE PROMOTER MUSCLE OF THIRD MAXILLIPED

FIGURES 46, 47, 48

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

COXOPODITE REMOTOR MUSCLES OF THIRD MAXILLIPED

FIGURES 46, 47

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

BASIPODITE LEVATOR MUSCLES OF THIRD MAXILLIPED

FIGURES 46, 47

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

BASIPODITE DEPRESSOR MUSCLES OF THIRD MAXILLIPED

FIGURES 46, 47, 48

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

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

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

EXPODITE ABDUCTOR MUSCLES OF THIRD MAXILLIPED

FIGURES 46, 47

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

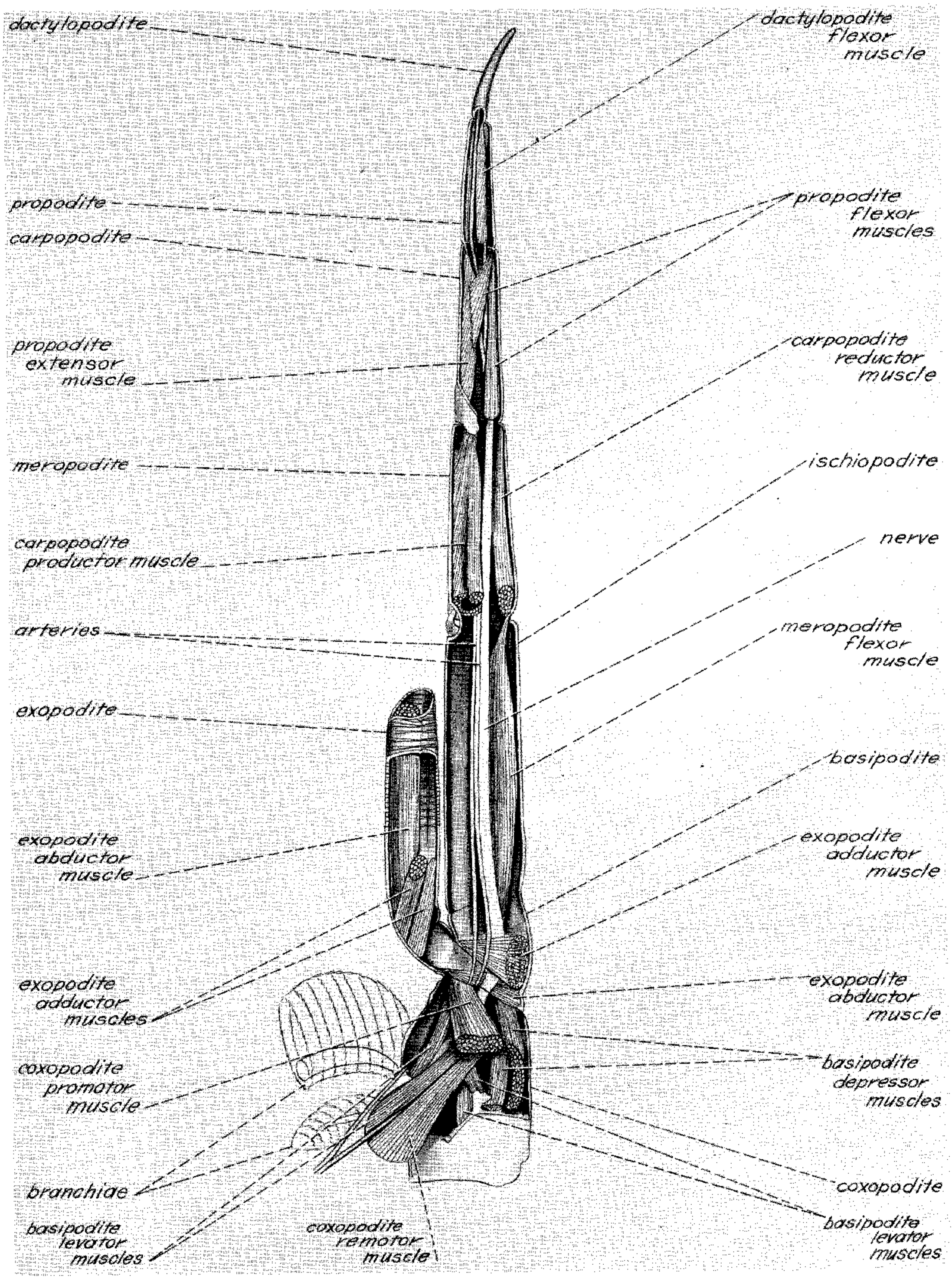

FIGURE 46.—Dorsal view of left third maxilliped, dorsal cuticle removed to show muscles.

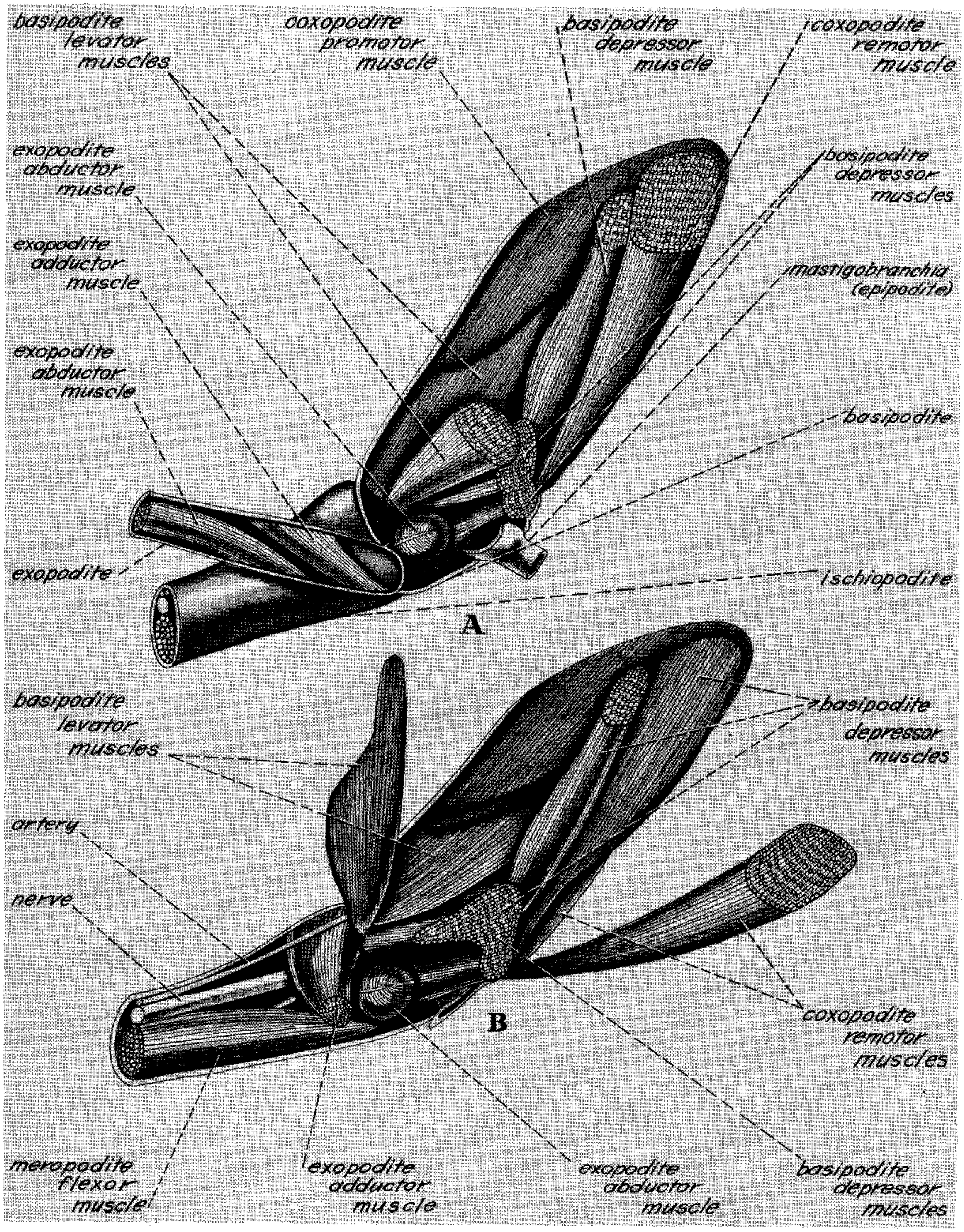

FIGURE 47.—Lateral view of leg base of left third maxilliped. Cuticle removed to show muscles. *A*. Superficial lateral and exopodite muscles. *B*. Lateral muscles, exopodite removed.

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

EXPODITE ADDUCTOR MUSCLES OF THIRD MAXILLIPED

FIGURES 46; 47, *B*

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

MEROPODITE FLEXOR MUSCLE OF THIRD MAXILLIPED

FIGURES 46, 47

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

CARPOPODITE PRODUCTOR MUSCLE OF THIRD MAXILLIPED

FIGURE 46

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

CARPOPODITE REDUCTOR MUSCLE OF THIRD MAXILLIPED

FIGURE 46

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

PROPODITE EXTENSOR MUSCLE OF THIRD MAXILLIPED

FIGURE 46

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

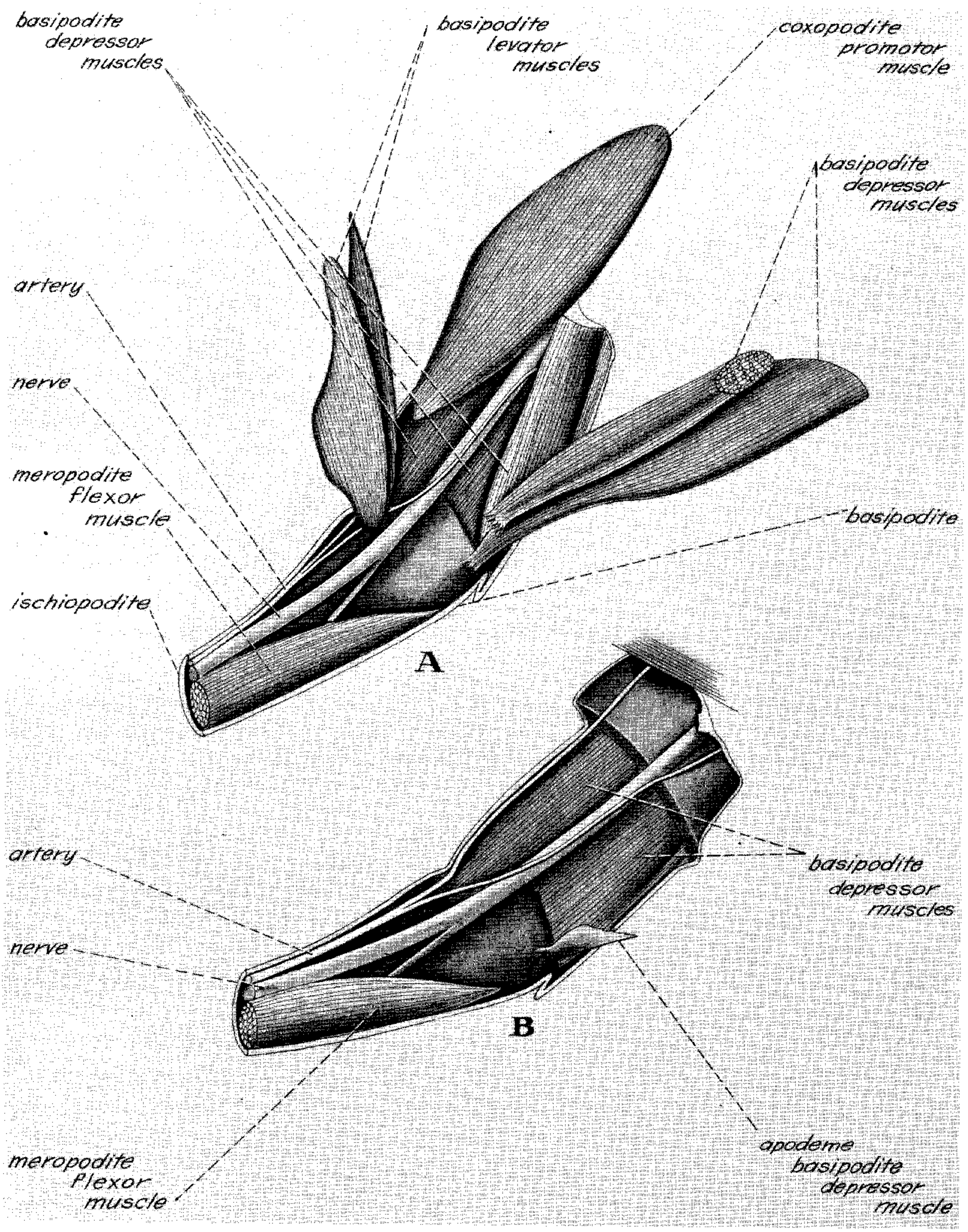

FIGURE 48.—Lateral view of leg base of left third maxilliped. *A*. Lateral and medial muscles. *B*. Medial muscles.

PROPODITE FLEXOR MUSCLES OF THIRD MAXILLIPED

FIGURE 46

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

DACTYLOPODITE FLEXOR MUSCLE OF THIRD MAXILLIPED

FIGURE 46

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

5. PEREIOPODS

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

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

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

5a. First Pereiopod

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

SKELETAL ELEMENTS

The strongly sclerotized coxopodite articulates with the ventral skeleton by dorsoventral dicondyles. The axis through the condyles is such that when the coxopodite swings forward it also approaches the midline. The rearward motion, on the other hand, turns the coxopodites away from the midline. The angular attitude of the dicondylic axis of the first pereiopod is thus raised laterally with respect to the frontal plane and rostrad with respect to the transverse plane. Proceeding caudad, the angular attitude of the axis through the coxopodite condyles rises laterally with respect to the frontal plane in conjunction with the shift dorsad of the dorsal condyle and the increased width between the ventral sternal

condyles. To the coxopodite is attached the strong, curving tube of the basipodite. The axis of the condyles between the coxopodite and basipodite is rotated 90° from the axis of the condyles connecting the coxopodite and the ventral skeleton. Primarily by means of the basipodite, the distal elements of the pereiopod are raised and lowered. A sharp process projects distally from the distomedial portion of the basipodite. A small, fingerlike exopodite bearing long setae projects laterad from the basipodite.

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

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

MUSCLE ELEMENTS

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

COXOPODITE PROMOTOR MUSCLES OF FIRST PEREIOPOD

FIGS. 49, 50, 51

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

COXOPODITE REMOTOR MUSCLE OF FIRST PEREIOPOD

FIGS. 49, 50, 51

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

BASIPODITE LEVATOR MUSCLES OF FIRST PEREIOPOD

FIGURES 49, 50, 51

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

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

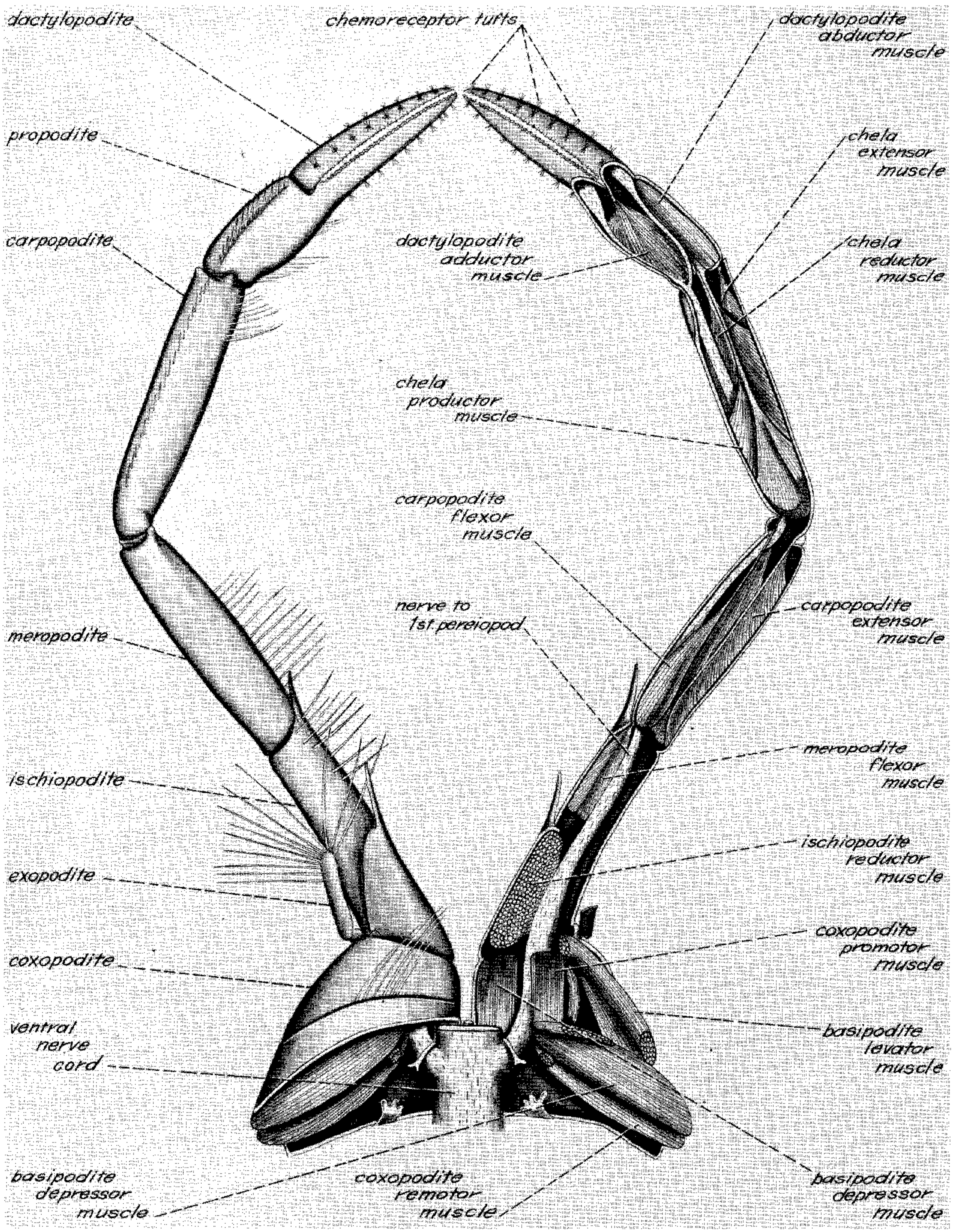

Figure 49.—Dorsal view of first pereiopod. Left side, intact appendage. Right side, dorsal cuticle removed to show muscles.

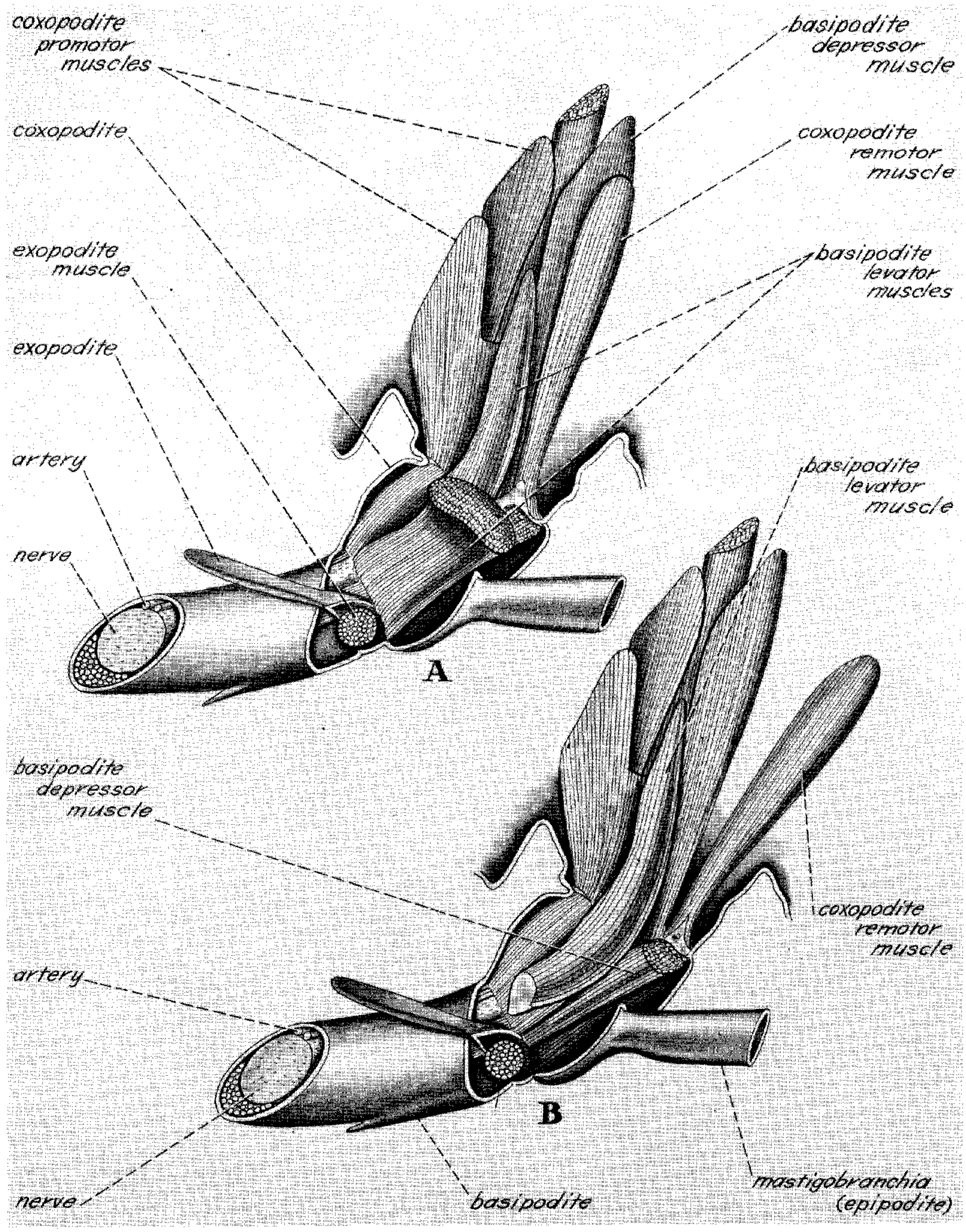

FIGURE 50.—Lateral view of leg base of left first pereiopod. *A*. Superficial lateral muscles. *B*. Some lateral muscles removed to show deeper muscles.

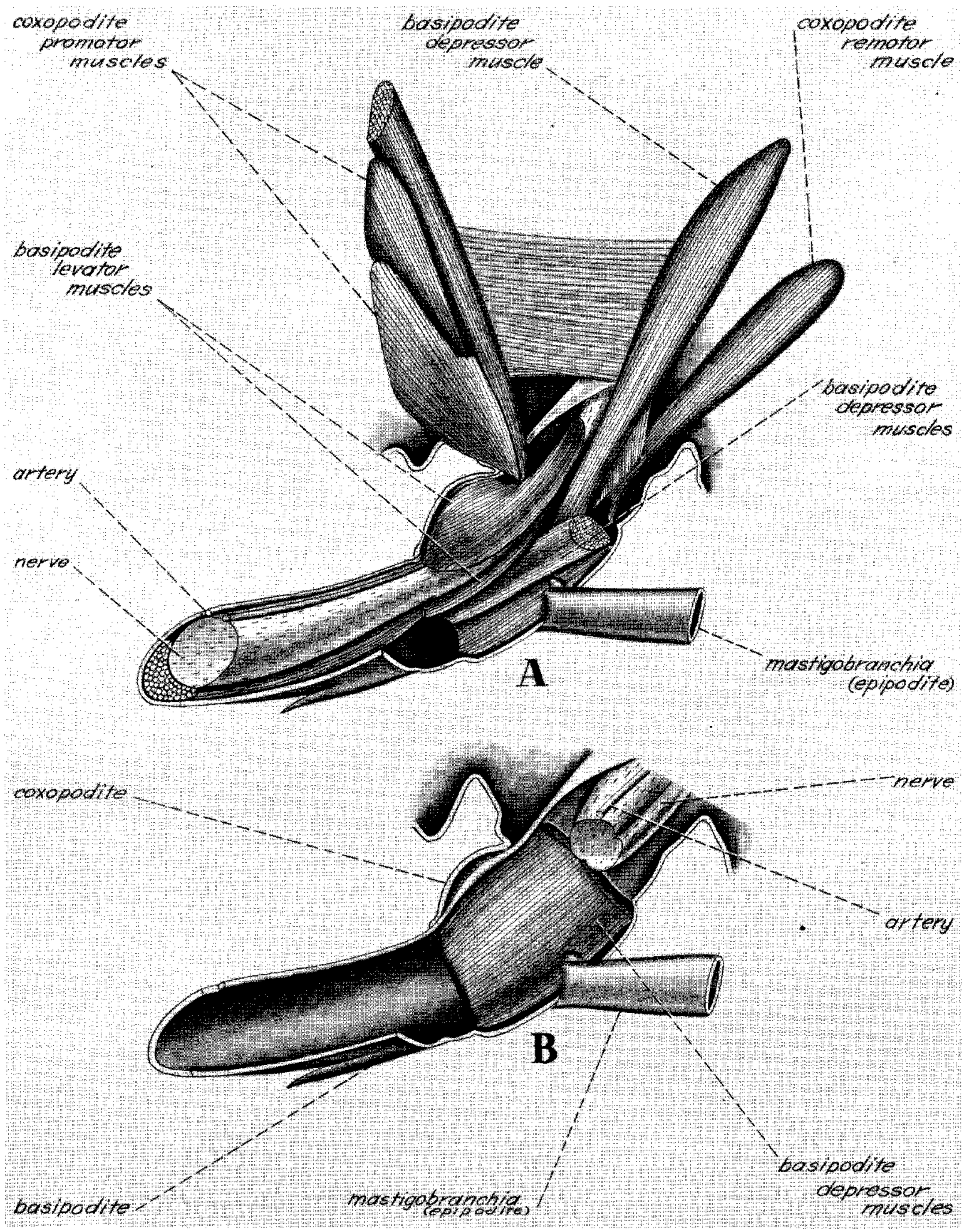

FIGURE 51.—Lateral view of leg base of left first pereiopod. *A*. Lateral and medial muscles. *B*. Medial muscles.

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

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

BASIPODITE DEPRESSOR MUSCLES OF FIRST PEREIOPOD

FIGURES 49, 50, 51

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

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

EXOPODITE MUSCLE OF FIRST PEREIOPOD

FIGURE 50

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

ISCHIOPODITE REDUCTOR MUSCLE OF FIRST PEREIOPOD

FIGURE 49

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

MEROPODITE FLEXOR MUSCLE OF FIRST PEREIOPOD

FIGURE 49

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