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THE SKELETAL MUSCULATURE OF THE BLUE  
CRAB, CALLINECTES SAPIDUS RATHBUN

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## INTRODUCTION

The need for detailed morphologic study of the muscles of crustaceans is apparent upon making a survey of the very scanty literature dealing with the myology of so diverse and important a suborder. The taxonomy and the concurrent analysis of the external anatomy of crustaceans have received a great deal of attention, and their physiologic reactions to stimuli have likewise been given a comparatively large amount of study. The internal structure and particularly the myology have been surprisingly neglected.

Huxley (1880) made a now historic contribution in his book on the crayfish, and his masterly dissections were unequalled for over a quarter of a century. Then the German school of zoology at Leipzig began a symposium on the crayfish, and the rechecking of the musculature was undertaken by Walter Schmidt, who made a most thorough and scholarly revision, in which he came upon several important points which Huxley had failed to emphasize.

The next complete myological study of a crustacean was published by Alfreda Berkeley in 1928. Her study of the shrimp *Pandalus danae* was executed in the general manner of Schmidt's treatment, so that their two papers are readily comparable.

Several papers by R. J. Daniel have since appeared dealing with the very complicated abdominal musculature of shrimps, but these papers have little bearing upon the following study, because the shrimp and the crab are structurally dissimilar in regard to their abdominal organization.

I am particularly indebted to R. E. Snodgrass, of the Bureau of Entomology and Plant Quarantine of the United States Department of Agriculture, for his invaluable assistance and advice in interpreting, describing, and figuring the muscles of the blue crab, and in comparing them with those of other arthropods.

I am likewise indebted to Prof. C. J. Pierson, of the Department of Zoology of the University of Maryland, for many suggestions, and to Dr. R. V. Truitt, of the same department, for directing my preliminary survey of other anatomical features of the blue crab.

My sincere thanks are due also to Dr. Waldo L. Schmitt, curator of the division of marine invertebrates of the United States National Museum, for donating comparative material for dissection and for making available much of the literature dealing with crustaceans.

The work on the appendages of the blue crab was done in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Maryland.

## PART I. THE MUSCLES OF THE TRUNK AND ITS APPENDAGES

## THE TRUNK

The complete fusion of the segments of head and body in the blue crab has resulted in the disappearance of those intersegmental muscles which in crustaceans like the shrimp and the crayfish give a high degree of flexibility to the movements of the body.

The crab's head and body are encased in a hard, unjointed covering, which shows no trace whatever of segmentation on its dorsal surface, although ventrally the sternal thoracic segments on which the basal leg muscles originate are well marked. Of all the extremely complex and numerous body muscles that one encounters in the shrimp and crayfish, there is but one, the attractor of the epimera, which finds a counterpart in the blue crab, where it performs the same function of holding the gill chamber in its proper relation to the carapace.

While the abdomen of the crayfish and shrimp is extremely pliable and is much used in swimming, the abdomen of the blue crab, in the male at least, is apparently progressing toward a condition of partial rigidity, as the third, fourth, and fifth segments are immovably fused in that sex. This fusion is not yet completely established, however, as the former segmentation is still partly maintained in its musculature. The female's abdomen has six distinct segments, all of which have the muscles well developed. The structure of the hard parts of the abdomen of the male is such that it can not be extended behind the body in line with the back, but at most can assume a position at right angles to the dorsal surface of the body. The abdomen in both sexes normally lies closely adpressed against the posterior region of the thorax. In this position, the dorsal part of the abdomen is underneath the body and actually ventral in position. In the text, however, it is described by the term "dorsal," applied to that part which would be uppermost in a normal crustacean abdomen extending backward behind the thorax.

1. *Musculus ventralis superficialis thoraco-abdominalis* (fig. 1 B).—This muscle arises on the outer posterior surface of the last segment of the thorax and is inserted on the anterior border of the first abdominal segment near the midline, where it helps to pull the abdomen toward the thorax. This is the only trace in the blue crab of the ventral superficial thoracic muscles, which are so prominent between the highly movable body segments in both *Astacus* and *Pandalus*.<sup>1</sup>

<sup>1</sup> In the particular discussion of the muscles, the comparisons made to homologous parts in the shrimp and crayfish refer only to the species *Pandalus danae* and *Astacus fluviatilis*.

Although this muscle is paired, as are all the other abdominal muscles, the members of the pair are so closely crowded toward the middle line that they appear as one median bundle of muscle fibers.

2-6. *Musculi ventrales superficiales abdominis* (fig. 1 B).—These muscles are arranged regularly in accordance with the original segmentation of the abdomen in the male, and the fusion of the third, fourth, and fifth abdominal somites in this sex has evidently not affected the ventral musculature at all, since the latter is similar in

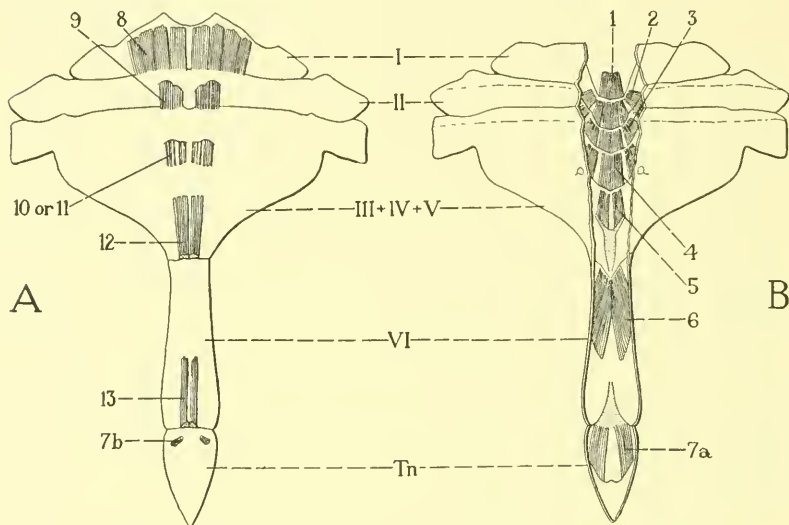


FIG. 1.—Muscles of the abdomen of the male blue crab.

A, dissection of the abdomen from the ventral side to show the dorsal muscles: 7b, small branch of musculus dilatator ani; 8-13, musculi dorsales superficiales abdominis.

B, dissection of the abdomen from the dorsal side to show the ventral muscles: 1, musculus ventralis superficialis thoraco-abdominis; 2-6, musculi ventrales superficiales abdominis; 7a, main branch of musculus dilatator ani.

I-VI, abdominal somites 1 through 6; Tn, telson.

both sexes. The muscles of the first pair (2) arise on the membrane of the anterior border of the first segment and are inserted on the heavy sclerotized ridge marking the second segment. Each muscle of the pair splits into several diverging branches, the two inner ones being practically confluent on the midline. The second (3) and third (4) pairs are similar to the first. Each muscle of the fourth (5) is definitely in a single piece, however, and its posterior attachment is made upon an arrow-shaped cartilagelike thickening of the membrane in the middle of the segment. The muscles of the fifth and last pair (6) are likewise undivided, the two muscles lying very close together

at their origin but diverging toward their insertion upon the outer walls in the middle of the sixth segment. There is no ventral muscle connecting the sixth segment with the telson in either sex. The ventral superficial muscles are much heavier in the female than in the male, owing no doubt to the fact that the "locking" device for the male's abdomen precludes the necessity for any strong contraction toward the body. The female, on the other hand, has no such locking device but must hold the abdomen bent forward under the body or curled around the egg mass, this position of the abdomen necessitating heavier muscles.

7 *a, b.* *Musculus dilatator ani* (fig. 1 A, B).—The main part of this muscle arises on a triangular cartilagelike thickening on the ventral membrane lying between the posterior border of the sixth somite and the anterior border of the telson. It is inserted ventro-medially by the side of the anal opening. The small second part arises in the same cartilagelike thickening on the ventral membrane, and is inserted on the anterior dorsal wall of the telson. By the contractions of the two muscles the anus is opened and widened, while the elasticity of the membrane around the anus opposes them.

8-13. *Musculi dorsales superficiales abdominis* (fig. 1 A).—While *Astacus* has its first superficial dorsal muscle connecting the thorax with the abdomen, this muscle does not occur either in *Pandalus* or in *Callinectes*. A very heavy U-shaped membrane connects the first abdominal segment with the thorax in *Callinectes*, and at the base of this membrane arises the first pair of dorsal superficial muscles (8), which thus corresponds to the second pair in *Astacus*. Each muscle of this pair is in several parts lying side by side. The next pair (9) arises near the middle of the second segment behind a heavy sclerotized ridge and is inserted on the anterior border of the following segment, which in the male crab represents the complete fusion of the third, fourth, and fifth abdominal somites. In the center of this fused section there is still, strange to say, a pair of definite patches of muscle tissue arising on a heavy ridge, the marks of attachment of which may be seen going through to the dorsal integument as two slight shallow depressions. This pair of muscles (numbered "10 or 11" in the figure) probably represents either the fourth or fifth pair of dorsal superficial muscles. It appears to have no function, as the hinge to its somite is entirely immovable. The adjacent pair of muscles has completely disappeared in the male. The sixth pair (12) arises some distance within the fused segment and is inserted on a cartilagelike outgrowth from the anterior border of the sixth segment. The seventh pair (13) is long and very

slender, to correspond to the shape of the male's abdomen, and is inserted on cartilagelike outgrowths emanating from the anterior border of the telson, which receives all its power of motion from this muscle, as no flexors of the telson exist in either sex. The female's dorsal superficial muscles are like those of the male, except that all six abdominal segments are distinct and hence the full complement of six pairs of muscles is present and functional. The dorsal muscles serve to extend the abdomen backward, but as this position of the abdomen is not habitual in the blue crab, occurring only at the time of mating, the muscles are very weakly developed.

14. *Musculus attractor epimeralis* (figs. 12 A, 13 B).—All that remains of this muscle, extensive in both *Astacus* and *Pandalus*, is a small patch of short muscle fibers uniting the epimeral plates and the carapace, between the metabranchial and the cardiac regions. It extends only for a short distance from the posterior angle of the first epimeral plate. It holds the gill chamber in place in the body, beneath the branchial lobe and the posterior part of the protogastric region, on which the muscle originates.

#### THE EYE

The eye of the blue crab is a highly complex organ, which presents many specializations in its structure and musculature. The shortening and broadening of the body contour have also been repeated in the changes that have taken place in the eyes. The crayfish and shrimp, both with elongate, narrow bodies, have the eyes close together on short stalks, which project forward in front of the head. The blue crab, on the other hand, has eyes which project on very long stalks at right angles to the axis of the body. The middle cylinder (*I* in fig. 2), quite distinct and having its own muscles in the crayfish and shrimp, is completely fused<sup>2</sup> to the chitinous middle ring in the blue crab, and the muscles of these parts, formerly separated, are now forced to interlace in a very constricted area. The second segment, on the contrary, is immensely elongated in the blue crab. Its proximal part contains no muscles, but only a deep groove in which lie the blood-vessels feeding the eye. Ventrally, this part of the segment is separated from the head by a thin membrane. This membrane thickens considerably toward its distal boundary, and on this membrane the adductor muscle arises, which is not the case in either the crayfish or the shrimp. The muscles arising on the distal border of the second segment, or on the heavy tendinous outgrowths from it, bear much the

<sup>2</sup> The entire fused structure will hereafter be spoken of as the middle cylinder.



same relations to one another as in the crayfish and shrimp. There are two branches to the abductor and three to the dorsal retractor, the result being that the blue crab has excellent control of its eye movements.

15. *Musculus oculi basalis anterior* (fig. 2).—This muscle arises medially on the epistome from a short, curved, movable rod, which projects first at right angles from the center of the epistome and then slopes downward and backward over the esophagus and enlarges to a buttonlike knob. From this knob the muscle runs dorsally and soon divides into two short but relatively thick branches, which find attachment side by side below the proximal edge of the chitinous middle

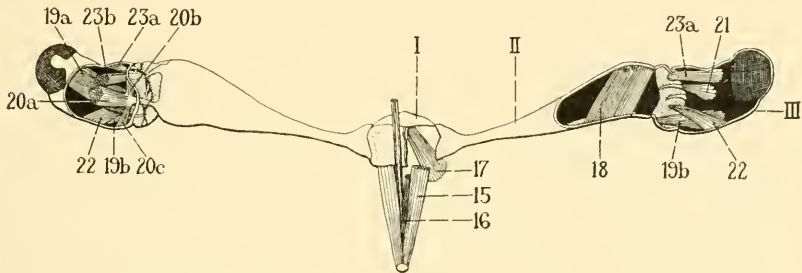


FIG. 2.—Dorsal dissection of the eye of the blue crab. On the right side the deeper muscles are exposed.

15, *musculus oculi basalis anterior*; 16, *musculus oculi basalis posterior*; 17, *musculus oculi attractor*; 18, *musculus oculi adductor*; 19a and 19b, *musculus oculi abductor*; 20a, 20b and 20c, *musculus oculi retractor dorsalis*; 21, *musculus oculi retractor ventralis*; 22, *musculus oculi retractor lateralis*; 23a and 23b, *musculus oculi retractor medialis*.

I, middle cylinder; II, second segment; III, optic cup.

cylinder which unites the optic peduncles. The distal part of each peduncle, bearing the retina, is thereby moved forward in a horizontal plane, so that the eyes are brought slightly nearer together. At the same time the second joint may be rotated slightly.

16. *Musculus oculi basalis posterior* (fig. 2).—This muscle arises on the knoblike part of the supporting rod of the preceding muscle. It runs unpaired dorsally for a short distance, closely adherent to the dorsally directed part of the preceding. Then it divides into two very fine but exceedingly strong branches which diverge slightly as they continue dorsally between the branches of the anterior basal muscle to their attachment on the frontal region of the carapace of the head, where their presence is marked usually by two small indentations.

17. *Musculus oculi attractor* (fig. 2).—This short compact muscle arises on the head carapace near its junction with the middle cylinder.

The muscles of this pair converge slightly before reaching their insertions on a T-shaped infolding of the ventral part of the middle cylinder, in front of the attachment of the anterior basal muscle. As this middle cylinder is cartilagelike and hence somewhat pliable, the attractor can assist the anterior basal muscle in depressing it and hence in bringing the solid joints attached to it nearer together. It may likewise oppose the basal muscle in rotating the second joint.

18. *Musculus oculi adductor* (fig. 2).—This heavy and powerful but short muscle arises on the thick membrane separating the ventral part of the second joint from the head. It travels forward and outward to its insertion along the anterior distal wall of the second segment not far from the base of the optic cup, which is rotated strongly by its contraction.

19 *a, b*. *Musculus oculi abductor a and b* (fig. 2).—Originating posteriorly on the heavy membrane which connects the second joint to the optic cup, the main part (*a*) of this muscle is inserted on the posterior wall of the optic cup near to the corneal surface. This is the largest and heaviest of any of the muscles lying in the cup. The second branch (*b*) originates beside the first but juts off at an angle toward the ventral surface, where it is soon inserted not far from the proximal border of the optic cup. It is much shorter than the main branch, from which it is separated near its insertion by the lateral retractor muscle. Both branches oppose the adductor by pulling the eye away from the midline and rotating it in the opposite direction.

#### THE RETRACTOR MUSCLES OF THE EYE

Like the crayfish and shrimp, the blue crab possesses four retractor muscles, all of which originate on the membrane bordering the distal edge of the second segment and are inserted on the sides of the optic cup near the cornea. They bring the cup nearer to the second segment or rotate it. The insertion of each muscle is marked externally by a characteristically different texture in the surface of the optic cup.

20 *a-c*. *Musculus oculi retractor dorsalis a, b, and c* (fig. 2).—This muscle has three branches, all of which arise from a heavy ossiclelike projection lying in the membrane and originating on the dorsal distal wall of the second segment. The main branch, the central one of the three, travels outward to its attachment on the dorsal surface of the optic cup, where its insertion is marked externally by a small area of a slightly granular texture different from the smooth surface around it. The second branch (*b*) projects forward at right angles to the first

and is attached on the front wall of the optic cup near its proximal border. The third branch (*c*) projects also at right angles but in an opposite direction to *b*, and is attached to the posterior wall of the optic cup near its proximal edge. The three branches taken together with the ossiclelike piece from which they originate form a cross, and the attachment at the extremities of the cross produces a mechanical device of great strength for moving the optic cup dorsally and for rotating it from side to side.

21. *Musculus oculi retractor ventralis* (fig. 2).—This is a relatively small and weak muscle, which arises ventrally in the membrane emanating from the distal edge of the second segment and is inserted on the ventral wall midway to the cornea. Since it runs parallel with the axis of the eye, it cannot act as a rotator. Its only function is to retract the optic cup.

22. *Musculus oculi retractor lateralis* (fig. 2).—This muscle originates in a tendinous structure in the membrane of the posterior ventral wall of the second segment, and passes diagonally backward and upward between the two parts of the abductor to its insertion on the posterior wall of the optic cup just above the insertion of the shorter branch of the abductor. It has a strong rotatory function, owing to its position diagonal to the axis of the eye.

23 *a, b. Musculus oculi retractor medialis a and b* (fig. 2).—This muscle has two branches, both of which arise from an exceedingly heavy ossiclelike projection from the anterior distal wall of the second segment. The upper branch (*a*) proceeds straight along the anterior wall of the optic cup to its attachment not far from the cornea. The lower branch (*b*) diverges slightly downward to its attachment on the anteroventral wall of the optic cup not far forward of the insertion of the ventral rotator. The medial retractor has the rotatory function in addition to being a retractor, as its diverging branches testify.

#### THE APPENDAGES

The problem of choosing names for the various muscles governing the appendages has proved to be a very puzzling one, especially in regard to those muscles governing the mandible, the maxillae, and the maxillipeds. It is often impossible in the living crab to assign to a definite one of the many complex muscles surrounding the base of each appendage a particular motion observed in that part of the appendage. In the telopodite the case is much simpler, as there are but two muscles governing each segment, and but two corresponding directions of motion. In the dissected crab, the many slender muscles con-

trolling the various basal parts of the leg are likely to break if enough tension is put upon them to show in what manner they influence the distal segments. Even the coarse and heavy muscles on tendons which do not break cannot invariably be assumed to cause the same motion in the segment of the stiffened dead tissue that they do in the pliable living organism. Thus it frequently becomes very difficult to determine whether a muscle in function is a promotor or an adductor, a remotor or an abductor. Coupled with this difficulty is the fact that the crab is so highly specialized away from the ancestral primitive condition that some of the appendages now lie in a partly reversed position, and one appendage, the mandible, is completely reversed. This makes it equally hard to give the muscles positional names according to their points of attachment, and there are, besides, so many small muscles controlling the basal segments that one soon has to resort to the expedient of giving some of them merely a number, having exhausted the available adjectives descriptive of their locations.

It is possible, however, to divide the muscles according to their place of origin, all the muscles originating on the carapace being called dorsal muscles, and those coming from the ventral surface and the sternal apodemes being referred to as ventral muscles.

Only those segments anterior to the second maxilla have both dorsal and ventral muscles. The second maxilla and the segments behind it lack dorsal muscles, but are fully equipped with ventral muscles.

The dorsal and ventral muscles are all extrinsic, meaning that they originate in the body itself beyond the boundaries of the true appendage. The intrinsic muscles are contained entirely within the appendage itself and control the distal segments of the limb and the flagellum if one be present.

As far as it has seemed possible to do it, I have followed the nomenclature adopted by Schmidt and later by Berkeley, in their respective anatomical analyses, to facilitate comparison between the three forms involved. The muscles of the blue crab do not always present perfect analogies in either position or function to those of the crayfish and the shrimp, however, and where a difference in function seems possible, the positional name may be given as first choice, with Schmidt's or Berkeley's corresponding name in synonymy. When so many muscles were found that the positional name of the one in question could not be given with the use of only one or two qualifying adjectives, the whole muscle has been referred to merely by its number. It is not well to be too arbitrary in assigning definite names to some of the more obscure muscles of the blue crab until such time as other representatives of the

order Decapoda shall have been dissected and compared carefully, muscle by muscle. It is quite possible that other genera of crabs may show up interrelationships of muscles that are quite obscure in *Callinectes*.

#### THE FIRST ANTENNA (ANTENNULE)

In the blue crab this appendage is similar to that of the shrimp and of the crayfish in regard to its high degree of flexibility. The comparatively large size of the first segment is due to the presence of a large statocyst to which no muscles are attached, these tissues being entirely sensory in function. The structure of the two flagella in the shrimp

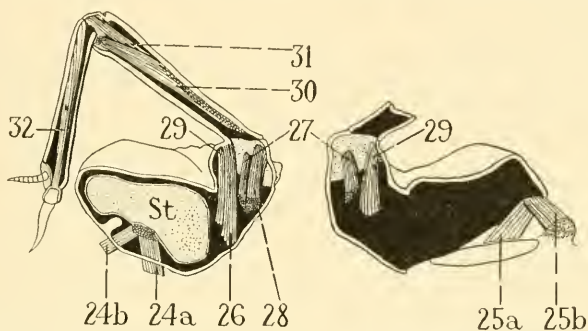


FIG. 3.—Dorsal dissection of the first antenna of the blue crab with the deeper muscles laid bare on the right side.

24a and 24b, *musculus promotor* I antennae; 25a and 25b, *musculus remotor* I antennae; 26, *musculus productor*<sub>2</sub> I antennae; 27, *musculus reductor*<sub>2</sub> I antennae; 28, *musculus adductor*<sub>2</sub> I antennae; 29, *musculus abductor*<sub>2</sub> I antennae; 30, *musculus productor*<sub>3</sub> I antennae; 31, *musculus reductor*<sub>3</sub> I antennae; 32, *musculus reductor*<sub>4</sub> I antennae.

St, statocyst.

and crayfish, as well as in the blue crab, does not give any support to Huxley's opinion that these flagella represent an endopodite and an exopodite, nor can the joint from which they arise be considered as a modified basipodite.

24 a, b. *Musculus promotor a and b I antennae* (fig. 3).—This muscle originates in two places on the posterior border of the aperture that connects the interior of the body with the interior of the antennule. Both parts are attached close together on an infolding of the membrane lying beneath the statocyst chamber in the first joint. The promotor raises the first joint, bringing it toward the midline and rotating it slightly in its socket.

25 a, b. *Musculus remotor a and b I antennae* (fig. 3).—One part of this short but heavy muscle arises on a round cartilaginous disk on

the lateral edge of the aperture connecting body and antennule. It is attached to a tendon on the outer dorsal part of the first joint. The other branch of the remotor arises on the outer anterior border of the aperture, and runs to its attachment on the opposite side of the tendon to which the first branch goes. Both remotors pull the first joint strongly downward toward the body, at the same time rotating it in its socket.

26. *Musculus productor*<sub>2</sub> *I antennae* (fig. 3).—This muscle arises dorsally on the inner proximal border of the first segment and passes forward to its attachment on the heavy basal membrane on the lateral proximal border of the second segment, on which it exerts a strong downward pull.

27. *Musculus reductor*<sub>2</sub> *I antennae* (fig. 3).—This short muscle originates on the inner posterior wall of the first segment and is inserted anteriorly on the membrane of the proximal part of the second joint. It opposes the productor<sub>2</sub> by bringing the joint upward toward the midline.

28. *Musculus adductor*<sub>2</sub> *I antennae* (fig. 3).—This is the largest of the four muscles governing the second joint of the antenna. It arises on the inner posterior wall of the first segment and is inserted anteriorly on the membrane at the inner basal part of the second segment. It thus parallels the reductor<sub>2</sub> and nearly conceals it. Like the latter, it brings the second joint upward and toward the midline. No adductor occurs in *Astacus* in any of the joints of its first antenna.

29. *Musculus abductor*<sub>2</sub> *I antennae* (fig. 3).—This muscle arises on the inner proximal border of the first segment, directly beneath the origin of the productor<sub>2</sub>, paralleling it almost to its insertion on the membrane below the outer proximal edge of the second segment. It brings the second segment strongly backward and outward.

30. *Musculus productor*<sub>3</sub> *I antennae* (fig. 3).—This muscle arises on the outer proximal part of the second joint and is attached to the cartilage emanating from the outer proximal edge of the third joint, which is pulled downward and outward by it.

31. *Musculus reductor*<sub>3</sub> *I antennae* (fig. 3).—Also arising on the outer proximal wall of the second joint, this muscle goes to its attachment on the membrane of the inner proximal border of the third joint, which it brings inward and upward in opposition to the productor<sub>3</sub>.

32. *Musculus reductor*<sub>4</sub> *I antennae* (fig. 3).—This is the only muscle lying in the third segment. It arises on the inner proximal wall and is inserted on the membrane lying between the two flagella, which are pulled sharply together by its contraction, while the elasticity

of the membrane pulls them sharply apart. Apparently there are no special muscles within the flagella themselves.

#### THE SECOND ANTENNA

In the blue crab the second antenna is so different in structure from the corresponding appendage in the crayfish and shrimp that it is not feasible to attempt to draw a parallel very closely between them. The second antenna in the crayfish, as Schmidt remarks in his masterly analysis (Schmidt, 1915, p. 205), is the most highly segmented of all the head appendages, and hence possesses the greatest ability for motion. The same complicated structure was observed by Miss Berkeley in the shrimp *Pandalus*. Both these crustaceans have a well-developed, heavily muscled exopodite, as well as an endopodite in which all the typical segments may be recognized, the flagellum being taken to represent the dactylopodite in both cases.

There is no jointed exopodite in the blue crab; the only trace of it is a hard protuberance on the outer part of the basipodite. Since a complete fusion has taken place between the basipodite and the head carapace, there are no depressor or levator muscles. The coxopodite is reduced externally to a membranous pocket lying anteriorly between the basipodite and the head carapace, in which the fusion occurs posteriorly. Arising from the basipodite, and forming the base of the endopodite, come two segments which I shall arbitrarily call the ischiopodite and the meropodite, which are provided with the typical reductor and productor muscles. Following these is a long annulated flagellum without definite muscles inside it. It is impossible to say whether the flagellum represents the division of the last three segments of the normal endopodite—carpopodite, propodite, and dactylopodite—or of the carpopodite alone, if one wishes to assume the complete loss of the other two. Because of this uncertainty, the muscles lying in the so-called meropodite and controlling the action of the flagellum are referred to as the reductor and productor of the flagellum.

33. *Musculus promotor II antennae* (fig. 4).—This muscle arises on the dorsal carapace in the protogastric region, and runs inward and forward to its attachment on a slender tendonlike structure which thickens and hardens into a sickle-shaped rod, which curves outward and forward beneath the membranous pouch lying between the basipodite and the head carapace, and finally attaches itself to this same cartilagelike membrane, which is moved forward and inward by its action.

34. *Musculus remotor II antennae* (fig. 4).—This short muscle arises partly on the head carapace where it fuses with the basipodite and partly on the upper edge of the membranous pouch below the basipodite. It passes backward to its insertion on the posterior part of the sickel-shaped rod mentioned above. The membranous pouch is pulled backward and downward by its contraction.

35. *Musculus productor ischiopoditis II antennae* (fig. 4).—This muscle arises on the proximal median portion of the basipodite and is attached to the outer proximal border of the ischiopodite, which it moves outward and downward.

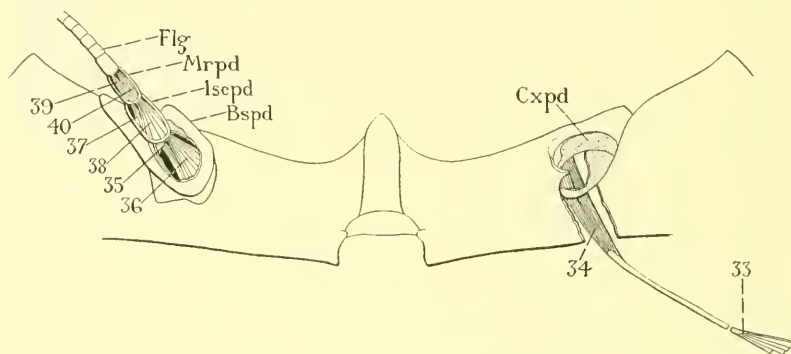


FIG. 4.—The second antenna.

33, *musculus promotor II antennae*; 34, *musculus remotor II antennae*; 35, *musculus productor ischiopoditis II antennae*; 36, *musculus reductor ischiopoditis II antennae*; 37, *musculus productor meropoditis II antennae*; 38, *musculus reductor meropoditis II antennae*; 39, *musculus productor flagellaris II antennae*; 40, *musculus reductor flagellaris II antennae*.

*Cxpd*, coxopodite; *Bspd*, basipodite; *Isepd*, ischiopodite; *Mrpd*, meropodite; *Flg*, flagellum.

36. *Musculus reductor ischiopoditis II antennae* (fig. 4).—A little heavier than the preceding, this muscle arises near it on the inner proximal wall of the basipodite, and is inserted on the inner proximal margin of the ischiopodite, which is pulled strongly inward toward the center by its action.

37. *Musculus productor meropoditis II antennae* (fig. 4).—This muscle arises on the outer proximal wall of the ischiopodite and is inserted on the outer proximal margin of the meropodite, on which it exerts an outward and downward pull.

38. *Musculus reductor meropoditis II antennae* (fig. 4).—Like the preceding in size and shape, this muscle originates on the inner proximal wall of the ischiopodite and goes to its insertion on the inner proximal edge of the meropodite, which receives a pull toward the center from it.



39. *Musculus productor flagellaris II antennae* (fig. 4).—Arising on the proximal posterior wall of the meropodite, this muscle is inserted on the base of the first annulus of the flagellum, which is pulled outward and backward by its contraction.

40. *Musculus reductor flagellaris II antennae* (fig. 4).—This muscle arises on the anterior wall of the meropodite and is inserted on the anterior part of the first ring of the flagellum, causing the latter to be brought inward and forward.

#### THE MANDIBLE

As in the crayfish, shrimp, and lobster, the mandible in the blue crab is firmly fixed at two articulations (*x* and *xx*, fig. 5) and hence cannot rotate.

The position of these articulations, however, is quite different in the blue crab from that of corresponding articulations in the crayfish and its allies, and a different mechanism for controlling the mandible is required. In the crayfish, shrimp, and lobster, one of the articulations is at the extreme upper anterior corner of the mandible, and the other is at the lower posterior corner. Therefore any muscles connecting the lower anterior corner with the skeletal part near the midline will pull the lower halves of the mandibles strongly together, functioning thus as adductors. A muscle attached to the upper posterior edge of the mandible, and running from the same central skeletal foundation, perhaps beside and even parallel to the adductors just described, will pull the mandibles just as strongly apart, performing the function of abductors. This opposition is made possible by the widely separated points of articulation of the mandible, which allow its upper and lower borders to pivot inward and outward between their hinges. This swinging motion is further intensified by such additional abductors and adductors as give sufficient power to the masticatory function of the mandible.

In the blue crab the articulations of mandible with head skeleton are both anterior, one at the upper and one at the lower corner of the mandible. Because of these anterior articulations, any muscles going from the central foundation to any available spot on the inner posterior surface of the mandible behind these forward-lying hinges are bound to open the mandible, functioning as abductors. Hence there is no anterior adductor in the blue crab, and the thin sheetlike muscle of the blue crab, which corresponds to that muscle in the crayfish, functions now as a major abductor of the mandible, and all the work of closing the mandible has to be done by the very heavy and powerful posterior and lateral adductors.

In this appendage a division of the extrinsic muscles into those with dorsal origin and those with ventral origin is first clearly apparent. There is as a matter of fact only one ventral muscle, the greater abductor (41, fig. 5 A, C), and this might be referred to as *musculus ventralis mesalis*, the mesal ventral muscle of the mandible, if positional names were adopted. There are three dorsal muscles of the

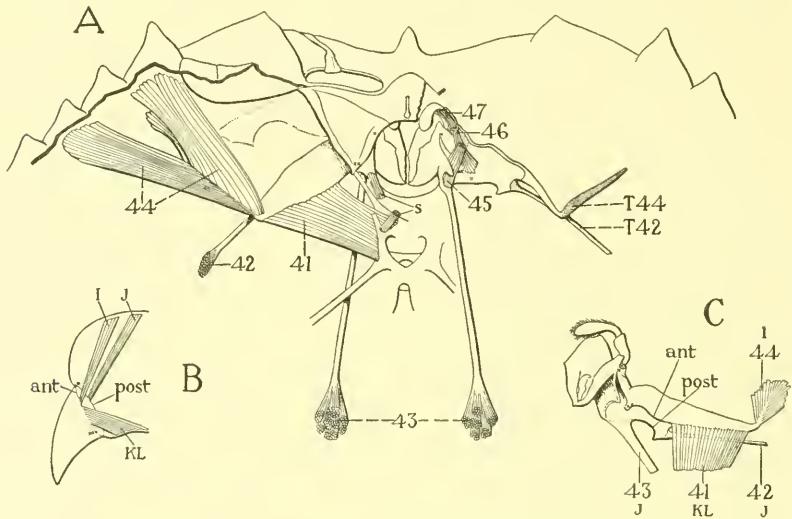


FIG. 5.—The mandible.

A, dorsal view of the mandible in place.

B, analysis of the mandible as an appendage.

C, mesal view of the mandible.

41, *musculus abductor maior mandibulae*; 42, *musculus abductor minor mandibulae*; 43, *musculus adductor posterior mandibulae*; 44, *musculus adductor lateralis mandibulae*; 45, *musculus extensor palpi mandibulae*; 46, *musculus flexor a palpi mandibulae*; 47, *musculus flexor b palpi mandibulae*.

*x-x-x*, hinges of the mandible; *T42*, tendon of *musculus abductor minor mandibulae*; *T44*, tendon of *musculus adductor lateralis mandibulae*; *S*, cut ends of two stomach muscles; *I*, the dorsal promotor; *J*, the dorsal remotor; *KL*, the ventral promotor and ventral remotor combined; *Ant*, anterior border of the mandible; *Post*, posterior border of the mandible.

mandible, a posterior outer (42), a posterior inner (43), and a third one (44), in function a lateral adductor, which is very puzzling to name as to position, since it attaches itself to the now outer posterior angle of the mandible, which has reversed itself in the blue crab from its primitive anterior position.

It has been repeatedly stated that the blue crab is a highly specialized creature, which departs in certain noticeable ways from the more generalized morphological aspects of many other crustacean types. Hence

many of the blue crab's appendages might be expected to show a variation from the usual structure, and this expectation is fulfilled when the mandible is examined and compared specifically to that of the crayfish and shrimp. Because of its two anterior articulations, to which reference has already been made, the mandible of the blue crab lies in a partly reversed position; as a matter of fact, its true anterior border now is its upper posterior border when the crab occupies a normal attitude, and its true posterior surface is now entirely ventral in position.

The primitive appendage, as shown by R. E. Snodgrass in his "Evolution of the Insect Head and the Organs of Feeding,"<sup>3</sup> has essentially

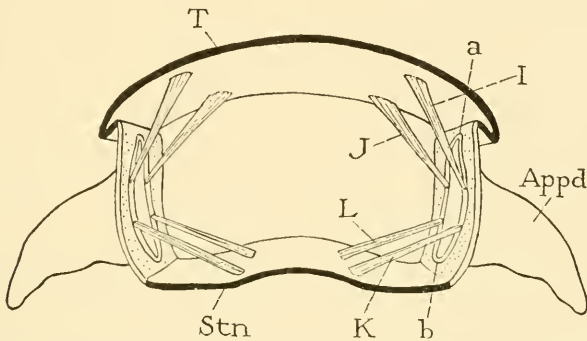


FIG. 6.—Diagram of the theoretical elementary musculature of the segmental appendages (after Snodgrass).

*a-b*, primitive dorsoventral axis of the appendage.

*I*, dorsal promotor muscle; *J*, dorsal remotor; *K*, ventral promotor; *L*, ventral remotor; *T*, tergum; *Stn*, sternum; *Appd*, appendage. (After R. E. Snodgrass, "The Thoracic Mechanism of a Grasshopper and its Antecedents," Smithsonian Misc. Coll., vol. 82, no. 2, p. 10, 1929.)

four muscles to control the movements of its basal part, two of which originate in the dorsal region of the body, and two on the ventral region (see fig. 6). The dorsal muscle, which is inserted on the anterior upper border of the rim of the appendage, is called the dorsal promotor (*I*), and the corresponding muscle inserted on the posterior upper border is the dorsal remotor (*J*). The muscle inserted on the anterior lower rim of the appendage is the ventral promotor (*K*), and the corresponding muscle with a posterior lower insertion is the ventral remotor (*L*).

An attempt has been made (fig. 5 B) to analyze the extrinsic muscles of the mandible in the blue crab to see just how they conform to the simple ancestral type. It was found that the dorsal muscle numbered

<sup>3</sup> Smithsonian Rep. 1931, p. 465, fig. 14, 1932.

44, functioning as the lateral adductor, corresponds to the primitive muscle *I* with insertion on the upper anterior rim of the appendage. The two remaining dorsal muscles, the minor abductor (42) and the posterior adductor (43) together represent the muscle *J*, since both originate dorsally and are inserted on the posterior (now ventral!) rim of the appendage. In the same way the muscle numbered 41, acting as the major abductor, represents a combination of the ventrally-rising primitive muscles *K* and *L*, since 41 is the only muscle of the appendage having a ventral origin.

41. *Musculus abductor maior mandibulae* (fig. 5 A, C).—Appearing as a broad sheetlike muscle, this muscle originates in two places on the head apodeme, and runs outward to its insertion along the posterior part of the mandible, which it helps to open.

42. *Musculus abductor minor mandibulae* (fig. 5 A, C).—This muscle arises laterally on the dorsal head carapace on the inner part of the epibranchial region and is inserted by a very slender but strong tendon on the lower outer part of the mandible, which is opened by it.

43. *Musculus adductor posterior mandibulae* (fig. 5 A, C).—This very strong muscle arises on the urogastric region of the carapace in several heavy muscle bundles, which shortly fuse together into a long and extremely heavy tendon that passes forward and downward to its attachment on the mandible at the point of its lower articulation with the head skeleton. It brings the mandible strongly toward the midline.

44. *Musculus adductor lateralis mandibulae* (fig. 5 A, C).—This extremely heavy muscle arises on the head carapace partly at the base of the first spine and partly at the base of the third spine, the parts uniting on a heavy tendon attaching them to the outer posterior end of the mandible, which they bring strongly toward the midline.

45. *Musculus extensor palpi mandibulae* (fig. 5 A).—This muscle arises on the inner surface of the mandible near the base of the tendon of the posterior adductor muscle. It is inserted on the heavy membrane connecting the palp and the mandible, and its contraction straightens the palp and brings it away from the center, opposing flexor *a* in its action. There is no extensor for the distal segment of the palp.

46. *Musculus flexor a palpi mandibulae* (fig. 5 A).—This short but stout muscle arises on the outer part of the mandible and travels forward and slightly inward to its attachment on the posterior proximal border of the first segment of the palp. Its function is to lower the palp, thereby bringing it toward the median plane.

47. *Musculus flexor b palpi mandibulae* (fig. 5 A).—This muscle fills the whole of the first segment of the palp. It arises in the membrane proximal to this first segment, and is inserted on the proximal joint of the last (second) segment. It lowers this last segment, thus bringing it toward the center.

#### THE FIRST MAXILLA

The first maxilla in the blue crab, as in the crayfish and shrimp, is flattened, and while it normally lies close to the outer anterior surface of the mandible, it has a considerable degree of freedom of motion. This is due to the fact that its basal part is really in two pieces, the posterior half rather loosely attached to the lower distal margin of the anterior half, and the two halves working together somewhat like the blades in a pair of scissors. The anterior half has been called the basipodite by Huxley, Schmidt, Berkeley, and some other investigators, but since there are no muscles between it and the posterior half, and since the body muscles go to both of them equally, it appears that the structure is in reality a coxopodite, semi-divided and provided with hinges to give necessary pliability. Borrodaile also considers that both parts belong to the coxopodite. It appears that the true basipodite is completely fused with and indistinguishable from the inner border of the coxopodite, as the endopodite arises from this region.

Three dorsal muscles run to the first maxilla, although it is impossible to separate them at their origin because of their extremely attenuate form. They separate distinctly into three strands as they pass behind the mandible to their respective points of insertion on the first maxilla. The first of these (fig. 7, 51) is the anterior inner, which may be called *musculus dorsalis anterior mesalis* and whose functional name is the anterior adductor of the coxopodite. The next (52) is a posterior inner, *musculus dorsalis posterior mesalis*, which acts as a posterior adductor to the coxopodite. There is but one outer dorsal muscle, which may be referred to as *musculus dorsalis externalis* and which functions as an abductor of the coxopodite.

The ventral muscles may be classed as follows:

54. Upper inner: *Musculus ventralis superior mesalis* (levator).
55. Lower inner: *Musculus ventralis inferior mesalis* (depressor).
48. Anterior outer: *Muculus ventralis anterior externalis* (promotor).
49. Posterior outer: *Musculus ventralis posterior externalis* (remotor a).
50. Median outer: *Musculus ventralis medialis externalis* (remotor b).

The only intrinsic muscle in this appendage is 56, the adductor of the endopodite.

48. *Musculus promotor I maxillae* (fig. 7).—This muscle arises on the head apodeme and runs forward and outward to its dorsal insertion in the extreme lateral part of the coxopodite beneath a disklike ossification near the inner hinge of the coxopodite. This muscle moves the coxopodite forward and upward.

49-50. *Musculus remotor I maxillae a and b* (fig. 7).—The shorter branch of the remotor (49) arises on the ventral part of the head

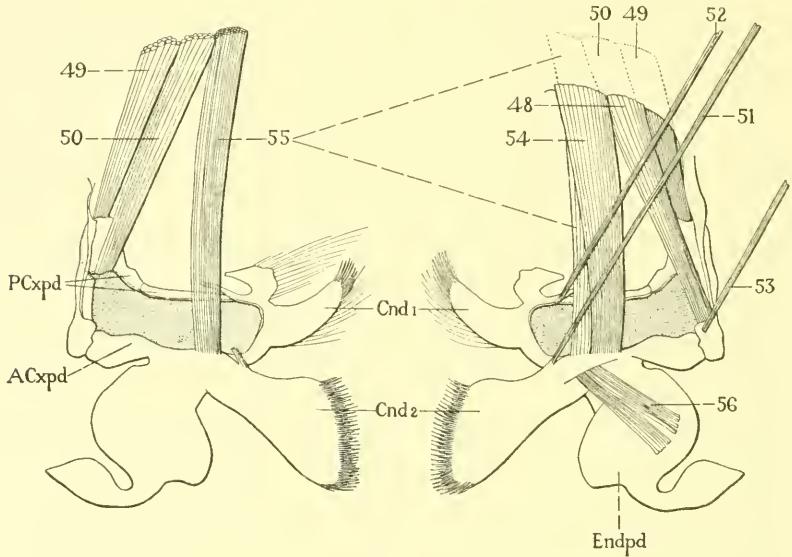


FIG. 7.—The first maxilla.

48, *musculus promotor I maxillae*; 49-50, *musculus remotor I maxillae*; 51, *musculus adductor anterior I maxillae*; 52, *musculus adductor posterior I maxillae*; 53, *musculus abductor coxopoditis I maxillae*; 54, *musculus levator I maxillae*; 55, *musculus depressor I maxillae*; 56, *musculus adductor endopoditis I maxillae*.

*ACxpd*, anterior part of the coxopodite; *PCxpd*, posterior part of the coxopodite; *Cnd<sub>1</sub>* and *Cnd<sub>2</sub>*, first and second endites of the coxopodite; *Endpd*, endopodite.

apodeme external to the origin of the main branch, traveling parallel to the latter to its insertion on the posterior dorsal angle of the basal rim of the coxopodite beneath and slightly median to the insertion of the promotor. Lying directly below the promotor, the longer branch of the remotor (50) arises on the ventral surface of the head apodeme somewhat posterior to the origin of the promotor. It is inserted ventrally in the anterior dorsal angle of the basal rim of the coxopodite at a point considerably posterior to the insertion of the promotor and near the union of the coxopodite with the ringlike outgrowth which

encircles it and holds it near to the mandible. Both remotor muscles oppose the promotor by lowering the coxopodite.

51. *Musculus adductor anterior coxopoditis I maxillae* (fig. 7).—This exceedingly long and slender muscle arises on the epibranchial region of the head carapace and is inserted without a tendon on the anterior margin of the base of the coxopodite near its mesal end. It brings the free end of the coxopodite toward the mouth.

52. *Musculus adductor posterior coxopoditis I maxillae* (fig. 7).—This very slender, long muscle originates on the head carapace with the preceding and is indistinguishable from it at first; it travels forward, inward and ventrally to its insertion on the posterior margin of the base of the coxopodite, which it pulls forward and inward.

53. *Musculus abductor coxopoditis I maxillae* (fig. 7).—Arising on the head carapace at the origin of the preceding two and at first indistinguishable from them, this muscle, likewise very slender, is attached dorsally to the extreme outer border of the coxopodite on the same disk-shaped ossification that gives attachment to the promotor. It opposes the adductor in pulling the coxopodite away from the midline.

54. *Musculus levator I maxillae* (fig. 7).—This muscle arises on the anterior part of the head apodeme, just median to the promotor, traveling forward to the dorsal median proximal border of the inner half of the coxopodite, which it raises.

55. *Musculus depressor I maxillae* (fig. 7).—Arising on the ventral surface of the head apodeme under and slightly posterior to the origin of the levator, this muscle continues forward directly under the levator to its insertion on the ventral proximal border of the inner half of the coxopodite, which it pulls downward.

56. *Musculus adductor endopoditis I maxillae* (fig. 7).—This muscle arises on the inner proximal border of the inner half of the coxopodite and branches into a fanlike formation at its manifold insertion in the central part of the endopodite, which it brings toward the center of the body. The basipodite is no longer distinguishable as such in this appendage, and its position is postulated only by the presence of the endopodite, which when present always arises from the basipodite.

#### THE SECOND MAXILLA

Although this appendage has the most complex system of muscles of any in the blue crab, yet its muscles correspond more closely to those in *Astacus* and in *Pandalus* than do the muscles of its other appendages. The muscles leading to the parts bordering the mouth are

relatively slender and weak, so that the appendage evidently does not assist greatly in the process of food-taking. Its true function is shown in the great development and complexity of the muscles controlling the scaphognathite, which cause the currents of water to pass continually over the gills. These muscles are attached to a very thick swelling, continuous at its outer end with the skeletal ridge running across the membrane covering the gill chamber. Its inner course borders the juncture of scaphognathite and coxopodite in a crooked and irregular swelling, which finally comes to an end as a cuplike thickening that bounds the outer proximal borders of endopodite and basipodite. This cup gives origin on its inner side to the adductor muscle of the endopodite and on its outer side to the flexor of the scaphognathite. No tendons are found in any muscles of the second maxilla. There is no levator muscle in this appendage in *Callinectes*, *Astacus*, or *Pandalus*.

The coxopodite bears two mesal bilobed endites, the anterior of which has been assigned to the basipodite by Brooks and many later writers. There is no distinguishable basipodite present as such in either of the two maxillae in the blue crab, but in both maxillae the coxopodite is so irregularly shaped that its appearance does not suggest superficially that it is in reality all one structure. As in the first maxilla, the position of the basipodite in the second maxilla is to be inferred only by the position of the endopodite. This region is so irregularly convoluted and infolded to give sufficient room for insertion to the complex and numerous respiratory muscles that the original boundaries between coxopodite, basipodite, scaphognathite, and endopodite are completely obliterated in the blue crab. In describing the muscles of the second maxilla, no further reference will be made to a basipodite.

As all the dorsal muscles are missing in this as in all the following segments, the naming of the ventral muscles remaining might appear to be an easy task, but such is not the case. The myological plan of the second maxilla is greatly complicated by the presence of no less than seven respiratory muscles, some of which are extrinsic, some intrinsic. As a matter of fact, the only muscle which permits of an easily descriptive positional name is 60, an anterior inner ventral muscle, *musculus ventralis mesalis*, which functions as an adductor of the coxopodite. The remaining extrinsic ventral muscles (fig. 8) are 57, promotor; 58, remotor; 59, depressor; and 63 through 66, the anterior respiratory muscles.

The remaining respiratory muscles (67 through 69), are intrinsic, as are likewise the adductor of the endopodite (61), and the flexor of the scaphognathite (62).



57. *Musculus promotor II maxillae* (fig. 8).—This long, cylindrical muscle originates on the dorsal surface of the endopleurite of the last head segment, which segment coalesces with the first two thoracic segments. It runs straight forward to its insertion on the skeletal ridge that borders the proximal part of the coxopodite. It brings the coxopodite backward and upward, at the same time causing a similar movement in the attached anterior part of the scaphognathite.

58. *Musculus remotor II maxillae* (fig. 8).—Almost hidden by the respiratory muscles, the remotor arises on the dorsal surface of the endosternite of the same segment just in front of the apodemal fora-

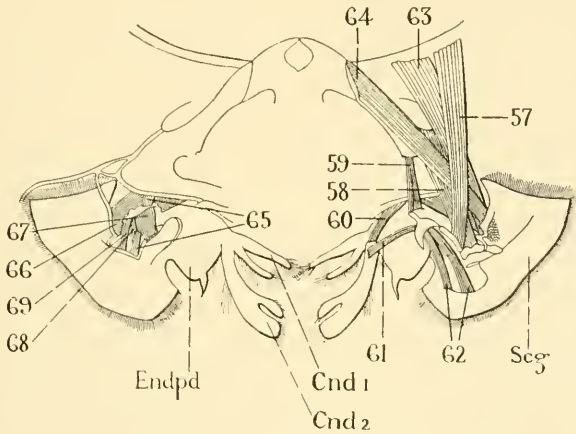


FIG. 8.—The second maxilla.

57, *musculus promotor II maxillae*; 58, *musculus remotor II maxillae*; 59, *musculus depressor II maxillae*; 60, *musculus adductor coxopoditis II maxillae*; 61, *musculus adductor endopoditis II maxillae*; 62, *musculus flexor scaphognathitis II maxillae*; 63-69, *musculi respiratorii II maxillae*.

*Cnd*<sub>1</sub> and *Cnd*<sub>2</sub>, first and second endites of the coxopodite; *Endpd*, endopodite; *Scg*, scaphognathite.

men, and passes forward and outward between respiratory muscles one and two to its insertion on the thickened edge of the coxopodite slightly lateral to and below that of the promotor. It brings the coxopodite upward and somewhat toward the center.

59. *Musculus depressor II maxillae* (fig. 8).—This is the smallest and weakest muscle in the entire appendage. It arises ventrally on the endosternite, appearing as two very thin branches which travel forward through the coxopodite to their insertion on its proximal border. It causes the coxopodite to move downward and inward. In *Astacus* this muscle also has two branches.

60. *Musculus adductor coxopoditis II maxillae* (fig. 8).—This relatively short and slender but strong muscle arises on the inner anterior

corner of the endosternite, running inward and forward to its insertion on the inner proximal border of the coxopodite. It pulls the coxopodite strongly backward and thus toward the center.

61. *Musculus adductor endopoditis II maxillae* (fig. 8).—This slender threadlike muscle arises on the inner proximal part of the coxopodite, passing laterally to its insertion on the cuplike swelling at the lateral outer border of the endopodite. It causes the endopodite to be bent somewhat toward the inner region.

62. *Musculus flexor scaphognathitis II maxillae* (fig. 8).—This muscle originates in the cuplike thickening that borders the outer part of coxopodite and endopodite, and runs outward with pronounced ramification through the scaphognathite to its attachment on the cartilaginous fold which parallels the outer border of the scaphognathite. This segment is bent by means of the flexor muscle. In *Pandalus* there is an additional superior flexor muscle which is unbranched.

63-69. *Musculi respiratorii II maxillae* (fig. 8).—Arising on the dorsal surface of the endopleurite just mesal to the origin of the promotor, the first of these muscles, *musculus respiratorius primus* (63), goes forward and outward beneath the promotor to its insertion on the lateral part of the skeletal swelling between coxopodite and scaphognathite. This and the remaining respiratory muscles induce a strong undulating motion in the scaphognathite, thus forcing the water that is drawn into the gill chamber to flow forward. The second muscle, *musculus respiratorius secundus* (64), heavy and powerful like the first, arises mediodorsally on the head apodeme, runs outward and forward, and passes above the first and below the promotor to reach its insertion just over the first. The third, *musculus respiratorius tertius* (65), is a small and slender muscle completely hidden until the more dorsal muscles are removed. It originates on the thickened skeletal ridge on the anterior part of the head apodeme, and runs forward and slightly outward to its insertion on the skeletal swelling of the scaphognathite just below the insertion of the remotor. The fourth, *musculus respiratorius quartus* (66), is an exceedingly heavy but short muscle arising under the third on the same skeletal ridge of the head apodeme, running outward to its insertion on the scaphognathite, between two angles of the skeletal swelling marking its proximal border. The fifth, *musculus respiratorius quintus* (67), is a small, powerful muscle arising on an infolding of the apodemal membrane behind the fourth, then passing forward and slightly inward to its insertion on the skeletal swelling just beneath the insertion of the promotor. The sixth muscle, *musculus respiratorius sextus* (68), arises on the same infolding just lateral to the fifth, and proceeds straight forward

to its insertion on the swelling, directly below the insertion of the third. The seventh muscle, *musculus respiratorius septimus* (69), like the sixth, is short and slender, arising laterally to it on the infolding and being inserted on the swelling midway between the insertions of the fourth and the sixth.

#### THE FIRST MAXILLIPED

The resemblance of this appendage to the maxillae rather than to the typical thoracic appendage has already been commented upon by several authors. The endopodite is weakly developed and devoid of muscles in the blue crab, but as its basal part is partly fused to the exopodite, it naturally partakes of the motion of the exopodite caused by the adductor muscle of the latter. The exopodite is relatively heavily muscled. The muscle extending through the flagellum originates entirely within the proximal segment of the flagellum, which is considerably enlarged. This origin is similar to that found in *Astacus*. In *Pandalus* the origin of this muscle is in the basal lobe of the first segment of the exopodite. The extremely poor development of the abductor of the flagellum in *Pandalus* appears to throw the whole task of moving the flagellum upon the flagellar muscle itself, which therefore needs the wider attachment space. In *Astacus* and *Callinectes*, where the abductor of the flagellum is relatively very large, the flagellar muscle is rather slender and weak.

Of the extrinsic muscles in the first maxilliped of the blue crab, it is possible to name positively only the promotor and the attractor of the epipodite. The small anomalous muscles which take the place of reductor, levator, and depressor have been referred to by number only, as their true function is as yet obscure. Further dissection of other representative decapods may subsequently reveal some species in which the functions of the corresponding muscles will be more apparent, and it may be possible in this way to assign names by analogy to these which it is now inadvisable to attempt to name arbitrarily.

As in both maxillae, the basipodite of the first maxilliped is no longer traceable as a distinct segment, being either eliminated completely or indistinguishably fused with the coxopodite. Its normal position if it were present may be ascertained in relation to the origins of endopodite and exopodite. In that case it would have lain between the second endite of the coxopodite and the epipodite.

70. *Musculus promotor medialis I pedis maxillaris* (fig. 9).—This strong but slender muscle arises on the inner anterior border of the paraphragm between the first and second thoracic segments near the

midline of the body. It passes forward and slightly outward to its tendinous insertion on the tough membrane composing the dorsal surface of the coxopodite. It causes the coxopodite, and with it to some extent the inner part of the whole appendage, to be brought upward and inward.

71. *Musculus promotor lateralis I pedis maxillaris* (fig. 9).—This muscle is hidden partly beneath the first of the attractors of the epipodite and partly by the fused lamellae of the first and second thoracic paraphragms, on the outer ventral surface of which it arises. It runs

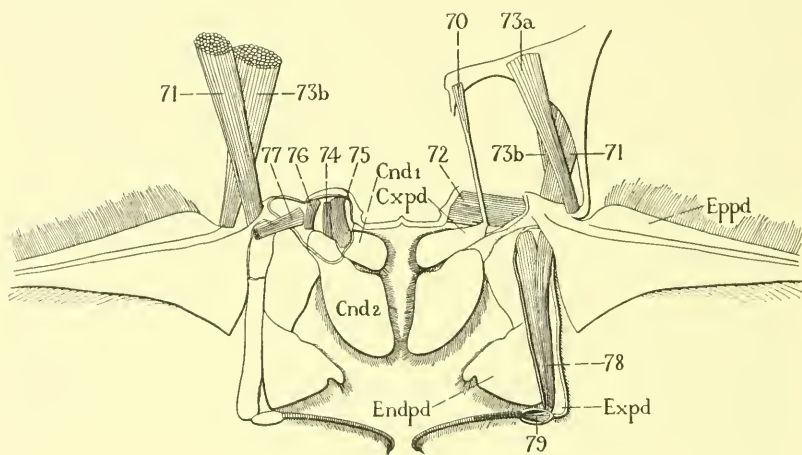


FIG. 9.—The first maxilliped.

70, *musculus promotor medialis I pedis maxillaris*; 71, *musculus promotor lateralis I pedis maxillaris*; 72, unnamed muscle; 73a-b, *musculus attractor epipoditis I pedis maxillaris*; 74, unnamed muscle; 75, unnamed muscle; 76, unnamed muscle; 77, *musculus adductor exopoditis I pedis maxillaris*; 78, *musculus abductor flagelli exopoditis I pedis maxillaris*; 79, *musculus flagellaris exopoditis I pedis maxillaris*.

Cnd<sub>1</sub> and Cnd<sub>2</sub>, first and second endites of the coxopodite; Cxpd, coxopodite; Endpd, endopodite; Eppd, epipodite; Expd, exopodite.

forward and slightly inward to its attachment on the lateral border of the coxopodite just at the point of origin of the epipodite. It helps to raise the appendage but otherwise opposes the median promotor by exerting an outward pull.

72. (Fig. 9).—This powerful but short muscle originates on the endosternite, passing outward beneath the median promotor to its insertion on the extreme outer ventral borders of the coxopodite without a tendon. It is not feasible to attempt to name this muscle functionally, as no definite movement of the appendage can be assigned solely to it. It appears to lie in approximately the same position as does the levator muscle in *Astacus*.

73 *a, b. Musculus attractor epipoditis a and b I pedis maxillaris* (fig. 9).—One branch of this muscle arises on the dorsal portion of the paraphragm between the first and second thoracic segments, lying directly below the first respiratory muscle of the second maxilla. It passes outward and forward to its insertion on the outer dorsal proximal border of the epipodite, which it raises strongly, at the same time causing it to move backward and inward. The second branch, larger and more powerful than the first, passes under the first on its forward and outward path to its insertion beneath it on the ventral proximal border of the epipodite, which it brings strongly backward and downward.

74. (Fig. 9).—This short muscle arises deeply within a cuplike membrane beside the inner epistomal rim and is inserted at the base of the first endite on the coxopodite. It is impracticable to give a functional name to this muscle, although it undoubtedly controls the coxopodite in some way. It might perform the duties of a levator, but this can not be ascertained directly.

75. (Fig. 9).—This short but thick muscle arises on the mesal edge of the same cuplike membrane as does the preceding muscle, and is inserted deeply within the first endite of the coxopodite. It is not possible to name it as to function, although it presumably causes whatever motion the first endite is capable of making. Its position is somewhat similar to that of the depressor in *Pandalus* and *Astacus*.

76. (Fig. 9).—This short but heavy muscle arises on the lateral edge of the same cuplike membrane which gives origin to the two preceding muscles and is inserted beside and lateral to 74, where the first and second endites come together. Again a functional name is not forthcoming as no positive motion can be assigned to this particular muscle.

77. *Musculus adductor exopoditis I pedis maxillaris* (fig. 9).—This muscle originates on the posterior surface of the coxopodite just lateral to the insertion of 76, and runs laterally to its insertion on the outer anterior proximal border of the exopodite just above the origin of 78. It brings the exopodite, and with it the partly fused endopodite, away from the epipodite and toward the center. Berkeley mentions a well-developed *abductor exopoditis* in *Pandalus*, not present in the blue crab. The endopodite of the blue crab has no muscles of its own.

78. *Musculus abductor flagelli exopoditis I pedis maxillaris* (fig. 9).—Arising in two places on the inner ventral proximal wall of the exopodite, this powerful muscle unites and passes to its insertion on the inner proximal edge of the enlarged first segment of the flagellum. It causes a strong upward and outward movement in the flagellum.

79. *Musculus flagellaris exopoditis I pedis maxillaris* (fig. 9).—Originating in the proximal segment of the enlarged first joint of the flagellum, this muscle runs outward through the various segments nearly to the tip of the flagellum, giving off small fibers in each segment which attach themselves to the wall, thus giving a high degree of pliability to the flagellum.

#### THE SECOND MAXILLIPED

In this appendage the first true hinges between the segments appear, just as they do in both *Astacus* and *Pandalus*. In section, the ischiopodite is found to be fused with the basipodite. The exopodite is merely an annulated flagellum as in *Pandalus*. The promotor appears to be inserted by a tendon, as are some of the muscles at the distal segments of the endopodite. A long, flat epipodite and two podobranchiae are present, with a slender attractor muscle to control the epipodite. In *Astacus* there are two podobranchiae and no epipodite; in *Pandalus*, a single podobranchia and an epipodite are present.

80. *Musculus promotor II pedis maxillaris* (fig. 10).—This muscle arises usually in two parts on the inner median edge of the paraphragm between the first and second thoracic segments in a very broad attachment. The muscle fibers rapidly converge into a single thin tendon, which is attached to the extreme inner edge of the coxopodite. It causes the entire endopodite to move inward and upward.

81. *Musculus remotor II pedis maxillaris* (fig. 10).—This muscle arises on a more lateral part of the two paraphragms next to the gill-chamber, and proceeds forward and inward to its insertion on the outer posterior border of the coxopodite. It lowers the outer part of the coxopodite, bringing it distinctly outward and backward.

82. *Musculus levator II pedis maxillaris* (fig. 10).—This muscle arises as a heavy and massive muscle on the inner lateral edge of the paraphragm between the first and second thoracic segments, and passes without diminution in size to its insertion on the dorsal proximal membranous portion of the basi-ischiopodite. There is but one levator in *Callinectes*; both *Astacus* and *Pandalus* have two.

83 a, b. *Musculus depressor a and b II pedis maxillaris* (fig. 10).—The main branch of the depressor arises on the inner edge of the paraphragm between the first and second thoracic segments midway between the origins of promotor and levator. It parallels these two muscles to its insertion on the inner posterior border of the coxopodite. It gives a strong inward and downward pull to the coxopodite and hence to the whole of the endopodite. The small depressor *b* arises

near the junction of the coxopodite with the paraphragm and is inserted just ventral to the main branch. It assists in lowering the coxopodite.

84. *Musculus attractor epipoditis II pedis maxillaris* (fig. 10).—Arising laterally on the meeting point of the body wall and the coxopo-

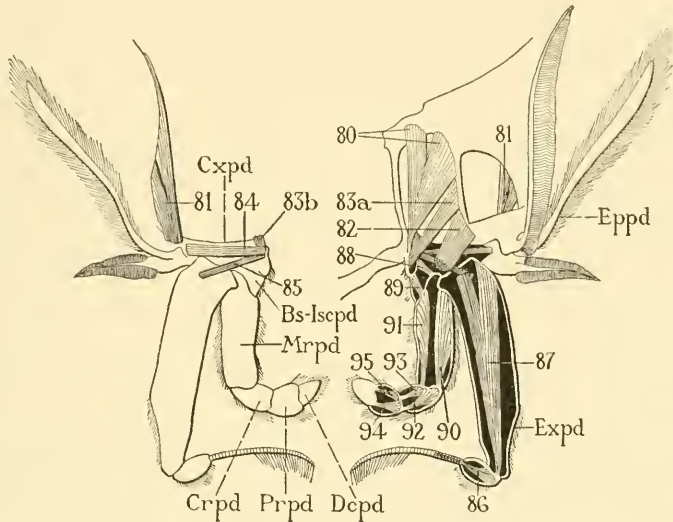


FIG. 10.—The second maxilliped.

80, *musculus promotor II pedis maxillaris*; 81, *musculus remotor II pedis maxillaris*; 82, *musculus levator II pedis maxillaris*; 83a-b, *musculus depressor a-b II pedis maxillaris*; 84, *musculus attractor epipoditis II pedis maxillaris*; 85, *musculus abductor exopoditis II pedis maxillaris*; 86, *musculus flagellaris exopoditis II pedis maxillaris*; 87, *musculus abductor flagelli exopoditis II pedis maxillaris*; 88, *musculus productor meropoditis II pedis maxillaris*; 89, *musculus reductor meropoditis II pedis maxillaris*; 90, *musculus abductor carpopoditis II pedis maxillaris*; 91, *musculus adductor carpopoditis II pedis maxillaris*; 92, *musculus productor propoditis II pedis maxillaris*; 93, *musculus reductor propoditis II pedis maxillaris*; 94, *musculus productor dactylopoditis II pedis maxillaris*; 95, *musculus reductor dactylopoditis II pedis maxillaris*.  
*Bs-Iscpd*, basi-ischiopodite; *Cp*, carpopodite; *Cxp*, coxopodite; *Dcp*, dactylopodite; *Eppd*, epipodite; *Expd*, exopodite; *Mrpd*, meropodite; *Prp*, propodite.

dite, this slender muscle travels laterally to its insertion on the proximal border of the epipodite, which it moves slightly inward.

85. *Musculus abductor exopoditis II pedis maxillaris* (fig. 10).—This muscle arises ventrally in the outer side of the coxopodite and proceeds laterally to its attachment on the median ventral proximal part of the exopodite. It causes the exopodite to move outward and forward.

86. *Musculus flagellaris exopoditis II pedis maxillaris* (fig. 10).—This muscle arises on the proximal border of the enlarged first ring of the flagellum and runs nearly to the tip, giving off short fibers at every annulation. As a consequence the flagellum has a considerable degree of mobility.

87. *Musculus abductor flagelli exopoditis II pedis maxillaris* (fig. 10).—This muscle arises in two parts on the proximal dorsal side of the basal segment of the exopodite, fuses and runs to its insertion on the first ring of the flagellum, to which it imparts a strong outward motion.

88. *Musculus productor meropoditis II pedis maxillaris* (fig. 10).—This muscle arises on the ventral lateral border of the basi-ischiopodite and is inserted on the inner ventral proximal edge of the meropodite. The muscle is short but powerful. It moves the meropodite forward.

89. *Musculus reductor meropoditis II pedis maxillaris* (fig. 10).—More slender than 88 but likewise short, this muscle rises on the dorsal proximal border of the basi-ischiopodite and is inserted on the lateral proximal border of the meropodite. It tends to pull the meropodite backward.

90. *Musculus abductor carpopoditis II pedis maxillaris* (fig. 10).—This muscle originates in many bundles of fibers near the inner proximal border of the meropodite and is inserted on the proximal inner edge of the carpopodite. It moves the carpopodite upward and outward.

91. *Musculus adductor carpopoditis II pedis maxillaris* (fig. 10).—About the same size as the preceding, this muscle arises in a bundle of fibers on the inner surface of the meropodite and is inserted on the proximal inner edge of the carpopodite which it moves downward and inward.

92. *Musculus productor propoditis II pedis maxillaris* (fig. 10).—Arising on the outer proximal wall of the carpopodite, this muscle narrows rapidly to its tendinous insertion on the outer proximal edge of the propodite, which it moves strongly forward.

93. *Musculus reductor propoditis II pedis maxillaris* (fig. 10).—This relatively small muscle arises on the inner proximal part of the carpopodite and is inserted by a tendon on the inner proximal border of the propodite which it bends backward, and hence toward the mouth.

94. *Musculus productor dactylopoditis II pedis maxillaris* (fig. 10).—Arising on the outer proximal part of the propodite, this muscle is inserted by a short tendon on the outer proximal border of the dactylopodite, which it moves forward.

95. *Musculus reductor dactylopoditis II pedis maxillaris* (fig. 10).—Like the preceding in size and shape, this muscle arises on the inner



proximal part of the propodite and passes quickly to its tendinous insertion on the inner proximal edge of the dactylopodite, which is brought inward and backward.

#### THE THIRD MAXILLIPED

This appendage in the blue crab, as in the crayfish, retains its function of a true mouthpart, and is essentially similar to the second maxilliped in structure. In the shrimp, on the other hand, the third maxilliped no longer assists in the taking of food, but is pediform and has completely lost its exopodite, while its endopodite has fewer segments, a characteristic condition in the *Caridea*. The endopodite in the blue crab is bent inward in its natural position; in fact, it can not be straightened perfectly, owing to the shape of the segments and the uniformly weak development of all the extensors except the one controlling the dactylopodite.

The coxopodite and the basipodite of the third maxilliped of the blue crab appear to be represented by a single segment, the protopodite. Brooks (1882) has labeled as "basipodite" the narrowed proximal part of the ischiopodite, which externally appears to be set off from the main part of the segment by a suture. An examination of the musculature of this segment, however, shows no evidence that it is composed of two elements. Furthermore, the exopodite does not originate upon this proximal region of the ischiopodite, which it would naturally do if a true basipodite were involved here.

96. *Musculus promotor III pedis maxillaris* (fig. 11).—This muscle arises mostly on the dorsal side of the endosternite of the third thoracic segment, and partly on the ventral (now anterior) side of the paraphragm, which is very narrow here. It is a powerful and wide muscle, narrowing and thickening as it goes forward to its insertion on a heavy tendinous ligament of the dorsal proximal inner corner of the protopodite, which is moved inward and forward by it.

97. *Musculus remotor III pedis maxillaris* (fig. 11).—Arising laterally on the endosternite, this strong muscle is inserted by a tendon on the lateral proximal edge of the protopodite. It opposes the promotor effectively, although it is somewhat less developed.

98 *a-c*. *Musculus levator a, b, and c III pedis maxillaris* (fig. 11).—This muscle is much smaller than the preceding. Its main branch (*a*) arises on the endosternite beneath the promotor and is inserted near the center of the posterior wall of the protopodite. The shortest branch (*b*) originates near the main branch on the endosternite, and joins the main branch before its insertion on the protopodite.

Another branch (*c*) arises in the extreme lateral border of the propodite not far from the insertion of the remotor and passes inward to its insertion anterior to that of the main branch on the posterior wall of the propodite. The levators move the basipodite outward and forward.

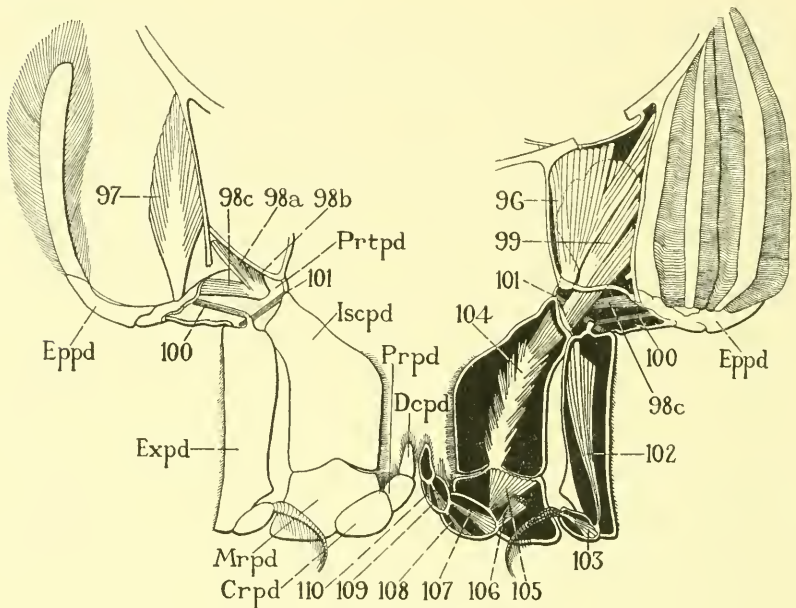


FIG. 11.—The third maxilliped.

96, musculus promotor III pedis maxillaris; 97, musculus remotor III pedis maxillaris; 98*a-c*, musculus levator *a-c* III pedis maxillaris; 99, musculus depressor III pedis maxillaris; 100, musculus adductor exopoditis III pedis maxillaris; 101, musculus abductor exopoditis III pedis maxillaris; 102, musculus abductor flagelli III pedis maxillaris; 103, musculus flagellaris exopoditis III pedis maxillaris; 104, musculus flexor meropoditis III pedis maxillaris; 105, musculus extensor meropoditis III pedis maxillaris; 106, musculus flexor carpopoditis III pedis maxillaris; 107, musculus flexor propoditis III pedis maxillaris; 108, musculus extensor propoditis III pedis maxillaris; 109, musculus flexor dactylopoditis III pedis maxillaris; 110, musculus extensor dactylopoditis III pedis maxillaris.

*Crpd*, carpopodite; *Dcpd*, dactylopodite; *Eppd*, epipodite; *Expd*, exopodite; *Iscpd*, ischiopodite; *Mrpd*, meropodite; *Prpd*, propodite; *Prtpd*, protopodite.

99. *Musculus depressor III pedis maxillaris* (fig. 11).—This is a very heavy muscle which originates over a relatively broad area on the epimeral plate beneath and beside the promotor, as well as the dorsal side of the endopleurite. Its many branches run forward and inward to join before the insertion of the muscle on the ventral median distal part of the propodite. It opposes the levators.

100. *Musculus adductor exopoditis III pedis maxillaris* (fig. 11).—This slender but strong muscle originates in the extreme distal anterior part of the protopodite and runs inward to its insertion on a short, hard projection of the inner proximal border of the exopodite, which is pulled strongly toward the midline by the contraction of the muscle. The crayfish does not appear to have this muscle.

101. *Musculus abductor exopoditis III pedis maxillaris* (fig. 11).—This is a short, loosely-knit muscle arising ventrally on the median border of the protopodite and running obliquely outward and forward to its insertion on the heavy membrane attached to the ventral proximal wall of the exopodite. It moves the exopodite away from the center and slightly outward.

102. *Musculus abductor flagelli III pedis maxillaris* (fig. 11).—This strong muscle originates in two places on the proximal part of the exopodite. The two sections soon unite, and the muscle is inserted by a tendon on the outer proximal edge of the greatly enlarged first segment of the flagellum, which is moved strongly upward and outward by its action.

103. *Musculus flagellaris exopoditis III pedis maxillaris* (fig. 11).—Originating on the proximal wall of the enlarged first segment of the flagellum, this muscle goes almost to the tip of the flagellum, giving off fibers to each annulus, and thus insuring freedom of motion to the flagellum.

104. *Musculus flexor meropoditis III pedis maxillaris* (fig. 11).—This muscle arises in numerous groups of fibers on both dorsal and ventral walls of the ischiopodite. These fibers all join a tendon before their final insertion on the inner proximal edge of the meropodite, which is strongly pulled down by their action. There is apparently no extensor muscle, the tension of the joint itself being sufficient to bring the meropodite back into position after its contraction by the flexor.

105. *Musculus extensor carpopoditis III pedis maxillaris* (fig. 11).—This very slender and weak muscle originates midway on the walls of the meropodite and is inserted on the outer proximal edge of the carpopodite, which it pulls upward rather weakly.

106. *Musculus flexor carpopoditis III pedis maxillaris* (fig. 11).—As might be expected from the condition in the preceding segment, this muscle, which causes the bending toward the center, is very well developed. It originates widely on the proximal margin of the meropodite and narrows to its tendinous insertion on the inner proximal margin of the carpopodite.

107. *Musculus flexor propoditis III pedis maxillaris* (fig. 11).—This muscle is similar to the flexor in the preceding segment in size

and function. It originates on the outer walls of the carpopodite, narrowing to an insertion on the outer proximal edge of the propodite.

108. *Musculus extensor propoditis III pedis maxillaris* (fig. 11).—Originating on the inner proximal walls of the carpopodite and inserted by a tendon on the inner proximal corner of the propodite, this muscle is like the corresponding one in the preceding segment in form and function.

109. *Musculus flexor dactylopoditis III pedis maxillaris* (fig. 11).—This muscle originates on the outer proximal border of the propodite and is inserted by a tendon on the outer proximal edge of the dactylopodite. Relative to the size of its opposing extensor, it is better developed than any other flexor in this endopodite, and apparently can exert a strong outward pull upon the dactylopodite.

110. *Musculus extensor dactylopoditis III pedis maxillaris* (fig. 11).—Originating on the inner proximal margin of the propodite, this muscle is inserted on the inner proximal edge of the dactylopodite, which is brought strongly downward by it. In this segment the extensor and the flexor are nearly the same in size and apparent strength.

#### THE PEREIOPODS

The five pairs of pereio-pods, or true legs, occur upon the last five of the eight thoracic segments. The promotor, the remotor, and the levator muscles of each pereio-pod are extrinsic in the origin of all their parts. The depressor of the telopodite, however, is both extrinsic and intrinsic in origin, for the larger and heavier branches originate in the body wall or some of its apodemes, while there are usually two or more branches originating proximally on the anterior and posterior walls of the coxopodite.

The functions of the different pairs of legs become evident upon examining their distal segments. On the first pair of legs, the dactylo-podite arises on the anterior (preaxial) border of the propodite nearly at the middle; the unhampered tip of the propodite curves and tapers to a point, while the dactylo-podite curves in a way to oppose it effectively, the two forming a powerful pinching claw, the chela, which is rendered still more effective by the horny teeth that have developed on the opposable surfaces. The claw is held out in front of the carapace, and may swing widely forward and sidewise in a horizontal plane, and less widely in a perpendicular plane, both movements serving as the means to repulse an enemy or to seize and tear up food. The extension of the leg forward has caused it to assume a position half-turned from the normal one, and now the true anterior (preaxial) surface of the first pereio-pod is uppermost.

The second, third, and fourth pereopods resemble one another rather closely, as they are nearly the same in size and perform the same kinds of motions, being adapted for walking. In these, the dactylopedite arises on the distal part of the propodite, tapering rapidly and becoming much flattened. The tip is pointed and sharp, and on these tips the crab is able to walk. The overhang of the carapace allows little upward motion to these legs, and so they have retained the normal position of hanging downward beneath the body. The anterior surface of these legs is preaxial, as is usually the case in arthropods.

The fifth and last pereopod is the swimming leg, and projects backward and upward behind the carapace when the crab is swimming. Its basal muscles are very powerful, especially the remotor, which is relatively weak in the preceding pereopods. The terminal segment is very thin and flat like the blade of a paddle, ovoid in shape, and propels the crab sidewise very swiftly. Like the first pereopod, the fifth is also a half-turn away from its normal position, but in a direction opposite to that of the first, so that its anterior (preaxial) face is now downward, and its postaxial face uppermost.

Since the muscles of the segments distal to the basipodite are essentially similar in all the pereopods, those of the third pereopod have been chosen to be described in detail, while the corresponding muscles of the other legs may be referred to the third as a model, taking into consideration the fact that the first and fifth legs are not identical with it in position. The basal muscles are sufficiently different in each leg to merit a full description.

A cross-section of the body at the level of the anterior part of the fourth and of the sixth thoracic segments shows the relations of some of the muscles of the first and third legs to their respective surroundings. (See fig. 13.)

The promotor of the fifth pereopod deserves notice because of the peculiar disposition of its anterior branch. This projects forward through the thorax into the fourth thoracic segment, surrounded by a membrane, on the posterior surface of which its own fibers originate, and on the anterior surface of which about a dozen branches of muscles pertaining to the legs of the fourth, fifth, sixth, and seventh segments also take their origin.

Another feature of the endoskeletal structure must here be explained. An intermediate endopleurite exists in the center of each of the basal chambers occupied by the fourth, fifth, sixth, and seventh segments. This endopleurite is fastened to the membrane covering the

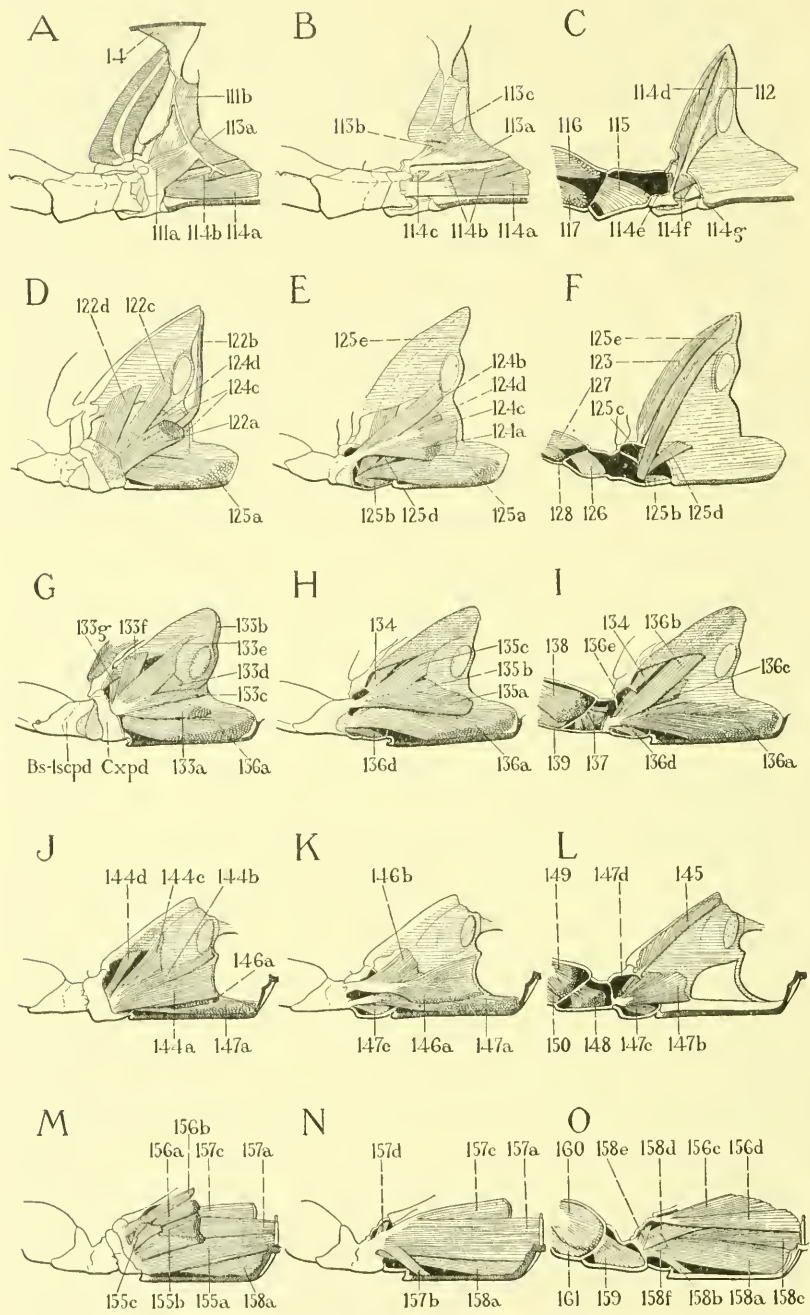


FIG. 12. (For legend see next page.)

anterior projection of the promotor of the fifth pereopod, and gives additional room for attachment to the numerous branches of muscles governing the movements of the leg base.

#### THE FIRST PEREIOPOD

*111 a, b. Musculus promotor a and b* (figs. 12 A, 13 B).—The anterior branch (*a*) originates upon a narrow, curved apodeme which comes inward and forward from the floor of the gill chamber and attaches itself laterally by a process to the sternum and medially to the endosternite between the third and fourth thoracic segments. The muscle passes outward and downward to its attachment on a heavy membrane coming from the preaxial proximal border of the coxopodite. The posterior branch (*b*) originates on the anterior border of the intermediate endopleurite of this segment and ends upon a heavy tendon attached to the anterior border of the coxopodite and directly behind the attachment of branch *a*. These two parts give a strong forward pull to the basal part of the leg.

*112. Musculus remotor* (fig. 12 C). This is the only unbranched muscle controlling the leg base. It takes origin partly on the lateral surface of the membrane enclosing the anterior promotor of the fifth pereopod behind *113 c* and partly on the anterior part of the endopleurite separating the fifth and sixth thoracic segments. It is inserted

FIG. 12.—The pereiopods.

A, B, C, the first pereopod.

*14*, musculus attractor epimeralis; *111a-b*, musculus promotor *a-b*; *112*, musculus remotor; *113a-c*, musculus levator *a-c*; *114a-g*, musculus depressor *a-g*; *115*, musculus reductor meropoditis; *116*, musculus abductor carpopoditis; *117*, musculus adductor carpopoditis.

D, E, F, the second pereopod.

*122a-d*, musculus promotor *a-d*; *123*, musculus remotor; *124a-d*, musculus levator *a-d*; *125a-e*, musculus depressor *a-e*; *126*, musculus reductor meropoditis; *127*, musculus abductor carpopoditis; *128*, musculus adductor carpopoditis.

G, H, I, the third pereopod.

*133a-g*, musculus promotor *a-g*; *134*, musculus remotor; *135a-c*, musculus levator *a-c*; *136a-e*, musculus depressor *a-e*; *137*, musculus reductor meropoditis; *138*, musculus abductor carpopoditis; *139*, musculus adductor carpopoditis.

*Bs-Ischpd*, basi-ischiopodite; *Cxpd*, coxopodite.

J, K, L, the fourth pereopod.

*144a-d*, musculus promotor *a-d*; *145*, musculus remotor; *146a-b*, musculus levator *a-b*; *147a-d*, musculus depressor *a-d*; *148*, musculus reductor meropoditis; *149*, musculus abductor carpopoditis; *150*, musculus adductor carpopoditis.

M, N, O, the fifth pereopod.

*155a-c*, musculus promotor *a-c*; *156a-b*, musculus remotor *a-b*; *157a-c*, musculus levator *a-c*; *158a-f*, musculus depressor *a-f*; *159*, musculus reductor meropoditis; *160*, musculus abductor carpopoditis; *161*, musculus adductor carpopoditis.

on a heavy tendon attached to the upper postaxial border of the coxopodite. The leg base is pulled backward by the contraction of this muscle.

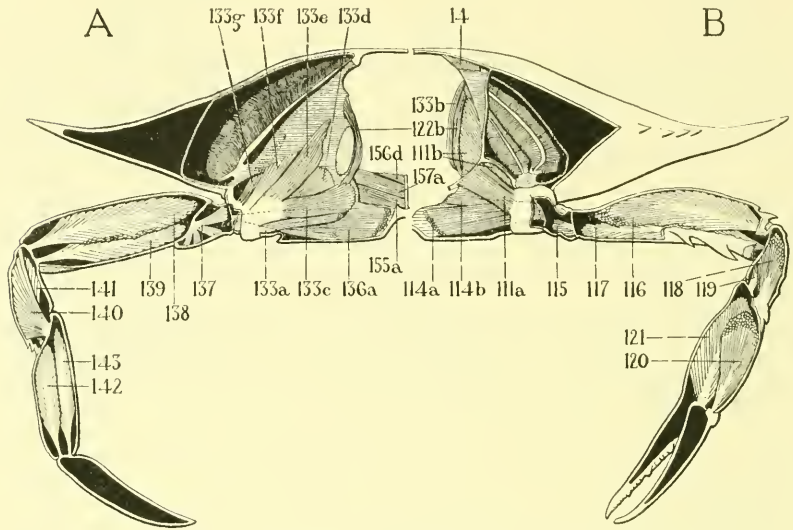


FIG. 13.—Transverse section of the thorax.

A, section through the third pereopod.

122b, branch of musculus promotor of second pereopod; 133c-g, branches of musculus promotor of third pereopod; 136a, branch of musculus depressor of third pereopod; 137, musculus reductor meropoditis of third pereopod; 138, musculus abductor carpopoditis of third pereopod; 139, musculus adductor carpopoditis of third pereopod; 140, musculus productor propoditis of third pereopod; 141, musculus reductor propoditis of third pereopod; 142, musculus abductor dactylopoditis of third pereopod; 143, musculus adductor dactylopoditis of third pereopod; 155a, branch of musculus promotor of fifth pereopod; 156d, branch of musculus remotor of fifth pereopod; 157a, branch of musculus levator of fifth pereopod.

B, section through the first pereopod.

14, musculus attractor epimeralis; 111a-b, branches of musculus promotor of first pereopod; 114a, branch of musculus depressor of first pereopod; 115, musculus reductor meropoditis of first pereopod; 116, musculus abductor carpopoditis of first pereopod; 117, musculus adductor carpopoditis of first pereopod; 118, musculus productor propoditis of first pereopod; 119, musculus reductor propoditis of first pereopod; 120, musculus abductor dactylopoditis of first pereopod; 121, musculus adductor dactylopoditis of first pereopod; 122b, branch of musculus promotor of second pereopod; 133b, branch of musculus promotor of third pereopod.

113 a-c. *Musculus levator a-c* (fig. 12 A, B).—The first branch (a) originates on the anterior border of the endosternite separating the fourth and fifth thoracic segments. It passes outward to its insertion on the upper postaxial proximal border of the coxopodite. A second and much shorter branch (b) begins on the lower rim of the inter-



mediate endopleurite. A third branch (*c*) begins behind this endopleurite on the lateral surface of the membrane holding the anterior promotor branches of the fifth pereopod which extends forward through the thorax and gives attachment to many muscles, and runs into branch *b* at their mutual insertion. These muscle parts act together in raising the leg base.

114 *a-g. Musculus depressor a-g* (figs. 12 A, B, C; 13 B).—The first branch (*a*) originates mesally on the sternum and passes outward to its insertion on the tendon attached to the membrane on the preaxial proximal border of the basi-ischiopodite. The second branch (*b*) is very indistinctly separated from the first, originating in several sections along the anterior edge of the endosternite separating the fourth and fifth thoracic segments. A third branch (*c*) which appears to be quite distinct, originates on the extreme lateral part of the same endosternite beneath 113 *a*, and comes forward to its insertion on the membrane of the lower proximal border of the basi-ischiopodite. The fourth branch (*d*) begins behind the intermediate endopleurite on the under surface of the pleural wall separating the gill chamber from the fifth thoracic segment. The remaining branches (*e*, *f*, and *g*) originate at different points in the posterior part of the coxopodite. These three last-named branches are not compact, and it is possible to subdivide them still further than this. The distinctness of these minor branches varies considerably according to the state of preservation of the tissues, and consequently appears to be much less evident in some individuals than in others. They are inserted side by side along the lower and post-axial proximal margins of the basi-ischiopodite. The depressor muscle as a whole gives a very strong downward movement to the leg base.

115. *Musculus reductor meropoditis*.—See 137.

116. *Musculus abductor carpopoditis*.—See 138.

117. *Musculus adductor carpopoditis*.—See 139.

118. *Musculus productor propoditis*.—See 140.

119. *Musculus reductor propoditis*.—See 141.

120. *Musculus abductor dactylopoditis*.—See 142.

121. *Musculus adductor dactylopoditis*.—See 143.

#### THE SECOND PEREIOPOD

122 *a-d. Musculus promotor a-d* (fig. 12 D).—The most anterior part (*a*) arises on the posterior surface of the endosternite separating the fourth and fifth thoracic segments, passing downward and outward to its insertion on a heavy tendon coming from the proximal preaxial rim of the coxopodite. The long and slender branch (*b*)

originates mesally on the prolongation of the endopleurites where they come together just below the attractor of the epimera. It travels ventrally for half its length, separated from the visceral cavity only by a very thin sheet of tissue. It passes at last into the fifth thoracic segment behind branch *a* of the promotor, where it finally attaches itself to the same tendon. The third branch (*c*) originates on the lateral part of the membrane covering the anterior promotor of the fifth pereopod, which extends forward through the thorax as previously stated. The most lateral branch (*d*) originates on the lateral anterior surface of the intermediate endopleurite, being inserted beside branch *c* on the broad tendon common to all branches of the promotor. The contraction of this muscle causes the leg base to be moved strongly forward.

123. *Musculus remotor* (fig. 12 F).—As in the first leg, this is the only unbranched muscle belonging to the leg base. It arises on the anterior surface of the endopleurite separating the fifth and sixth thoracic segments, passing downward and outward to its tendinous insertion on the upper postaxial border of the coxopodite. It opposes the promotor.

124 *a-d*. *Musculus levator a-d* (fig. 12 D, E).—This heavy muscle appears to be divided into four main parts, although the third and fourth are not very distinct from each other. The first branch (*a*) arises on the posterior surface of the endosternite between the fourth and fifth thoracic segments and is inserted by an extremely strong tendon on the upper (in this case postaxial) border of the basi-ischiopodite. A second branch (*b*) arises on the lateral part of the membrane encasing the anterior promotor of the fifth pereopod. The two remaining branches (*c* and *d*) arise close together, on the anterior surface of the endosternite between the fifth and sixth thoracic segments, and are inserted between branches *a* and *b* on the same strong tendon. The entire muscle causes the leg to be raised.

125 *a-e*. *Musculus depressor a-e* (fig. 12 D, E, F).—The first branch (*a*) originates mesally on the posterior surface of the endosternite separating the fourth and fifth thoracic segments, as well as on the sternal wall of the fifth segment. It is inserted on the lower (in this case preaxial) rim of the basi-ischiopodite. A very short branch (*b*) runs from the anterior part of the coxopodite to the same insertion, while a similar short branch (*c*) originates in the rear of the coxopodite. A slightly longer branch (*d*) begins on the outer part of the sternal wall near the endosternite between the fifth and sixth thoracic segments. The longest branch (*e*) originates on the anterior wall of the endopleurite separating the fifth and sixth segments, com-

ing forward and downward to its insertion with the other branches. The muscle as a whole opposes the levator.

126. *Musculus reductor meopoditis*.—See 137.

127. *Musculus abductor carpopoditis*.—See 138.

128. *Musculus adductor carpopoditis*.—See 139.

129. *Musculus productor propoditis*.—See 140.

130. *Musculus reductor propoditis*.—See 141.

131. *Musculus abductor dactylopoditis*.—See 142.

132. *Musculus adductor dactylopoditis*.—See 143.

#### THE THIRD PEREIOPOD

133 a-g. *Musculus promotor a-g* (figs. 12 A; 13 A).—The anterior branch (*a*) originates on the posterior surface of the endosternite separating the fourth and fifth thoracic segments, going outward to its insertion on the tendon attached to the anterior proximal rim of the coxopodite. The second branch (*b*) originates on the same prolongation of the endopleurites on which 122 *b* of the preceding segment takes origin. It travels ventrally beside 122 *b*, separated from the visceral masses only by a thin membrane, passing finally under the anterior extension of the promotor of the fifth pereio pod until it joins its tendon. Branch *c* originates mesally on the anterior upper edge of the endosternite separating the sixth and seventh segments near to its point of fusion with the endopleurite. The next two branches (*d* and *e*), not very distinct from each other, arise on the lateral part of the membrane encasing the anterior promotor of the fifth pereio pod. Branch *f* arises on the anterior lateral surface of the intermediate endopleurite, while branch *g* arises just behind it on the posterior surface of the same endopleurite. All these go to the same insertion with branch *a*. The muscle pulls the leg base forward.

134. *Musculus remotor* (fig. 12 H, I).—This unbranched muscle arises on the pleural wall and on the endosternite separating the sixth and seventh segments. Its insertion is on the proximal postaxial border of the coxopodite. Its contraction causes the leg base to be drawn backward.

135 a-c. *Musculus levator a-c* (fig. 12 H).—The most ventral branch (*a*) begins on the anterior wall of the sixth and seventh thoracic segments. The branch *b*, originating just above it on the same endosternite, is perhaps not truly distinct from it. The third branch (*c*) originates on the lateral part of the membrane covering the anterior promotor of the fifth pereio pod. These three branches are all inserted upon a heavy tendon attached to the proximal postaxial rim of the basi-ischiopodite. The leg base is raised by their contraction.

136 a-c. *Musculus depressor a-c* (figs. 12 G, H, I, 13 A).—The first (*a*) of the numerous branches to this muscle originates partly on the posterior wall of the endosternite between the fifth and sixth thoracic segments, partly on the anterior wall of the endosternite between the sixth and seventh segments, and partly on the sternal wall between. It passes to a heavy tendon attached to the tough membrane bordering the proximal anterior rim of the basi-ischiopodite. The next branch (*b*) begins on the endopleurite between the sixth and seventh segments just above the anterior prolongation of the promotor of the fifth pereopod. The next branch (*c*) lies partly behind branch *b*, originating on the endosternite near its fusion with the endopleurite separating the sixth and seventh segments. Branch *d* originates anteriorly in the coxopodite, and branch *e* posteriorly in the same segment. All these are inserted on the heavy tendon or on the membrane beside it. Their mutual contraction pulls the leg base forcibly downward.

137. *Musculus reductor meropoditis* (figs. 12 I; 13 A).—This fan-shaped muscle begins in several places on the preaxial part of the basi-ischiopodite, and is inserted postaxially on the proximal border of the meropodite. The hinge between these two segments is only slightly developed preaxially, and not much more so postaxially, so that the rearward motion imparted by this muscle is slight. It is opposed by the stiffness of the preaxial connection which causes the leg to become straightened again after its contraction.

138. *Musculus abductor carpopoditis* (figs. 12 I, 13 A).—This large muscle originates in a great many bundles of fibers attached on the whole dorsal surface of the meropodite from its anterior to its posterior walls. These bundles run together before their insertion on a long bladelike tendon which is inserted on the posterior dorsal proximal border of the carpopodite. This muscle extends the carpopodite so that it lies in a straight line with the meropodite.

139. *Musculus adductor carpopoditis* (figs. 12 I, 13 A).—This originates in the same way as the abductor but lies ventrally in its segment and is inserted similarly by a very long tendon leading to the anterior ventral proximal border of the carpopodite. This muscle is therefore in perfect opposition to the adductor, bending the carpopodite at right angles to the meropodite.

140. *Musculus productor propoditis* (fig. 13 A).—This densely-fibered fanlike muscle originates on the entire outer border of the carpopodite, its parts coming together on a heavy leaf-shaped tendon which is inserted on the proximal median anterior border of the propodite, to which it gives a strong forward motion.

141. *Musculus reductor propoditis* (fig. 13 A).—This muscle arises on the outer and postaxial walls of the carpopodite, narrowing to its tendinous insertion on the posterior proximal border of the propodite, which is moved backward by it.

142. *Musculus abductor dactylopoditis* (fig. 13 A).—This rather slender and feather-shaped muscle arises in many small fibers on the preaxial wall of the propodite. It is inserted by a very long bladelike tendon on the outer proximal edge of the dactylopodite, which is moved outward by its action.

143. *Musculus adductor dactylopoditis* (fig. 13 A).—Very similar to the preceding in shape and size, this muscle arises largely on the postaxial part of the propodite and is inserted also on a bladelike tendon to the inner proximal border of the dactylopodite. The terminal segment is bent strongly toward the midline by this muscle.

#### THE FOURTH PEREIOPOD

144 *a-d*. *Musculus promotor a-d* (fig. 12 J).—The first branch (*a*) originates mesally on the endosternite between the seventh and eighth thoracic segments and is inserted on a heavy tendon attached to the membrane on the anterior border of the coxopodite. The second branch (*b*) originates dorsally to *a* on the same endosternite and just below the membrane covering the anteriorly extending promotor muscle of the fifth pereopod. The branch *c* originates partly on the lateral surface of the membrane of the promotor of the fifth pereopod and partly on the endosternite separating the seventh and eighth segments. The branch *d* originates on the posterior surface of the intermediate endopleurite, which in this segment is very small. All these branches are inserted with or beside the first one. The whole muscle moves the leg base forward.

145. *Musculus remotor* (fig. 12 L).—As in the three preceding pereopods, the remotor of the fourth pereopod is unbranched. It originates on the lower surface of the pleural wall, passing outward and downward to its tendinous insertion on the upper posterior rim of the coxopodite. It opposes the promotor by bringing the leg backward.

146 *a-b*. *Musculus levator a and b* (fig. 12 J, K).—The first branch (*a*) originates partly on the posterior wall of the endosternite separating the sixth and seventh segments above 147 *a*, and partly on the anterior wall of the endosternite separating the seventh and eighth segments. The second branch (*b*) originates on the anterior wall of the endosternite between the seventh and eighth segments. It would be possible to separate this part into smaller subdivisions, as several

strands go more deeply than others. The branches of this muscle go to a mutual insertion on a heavy tendon coming from the upper proximal border of the coxopodite. Their contraction causes the leg base to be elevated.

147 *a-d*. *Musculus depressor a-d* (fig. 12 J, K, L).—The first branch (*a*) originates partly on the posterior wall of the endosternite separating the sixth and seventh segments, partly on the sternal wall of the seventh segment, and partly on the anterior surface of the endosternite between the seventh and eighth segments of the thorax. The second branch (*b*) lies behind the posterior part of the first branch, spreading in a fan shape over the endosternite between the seventh and eighth segments of the thorax. It might be considered as being more than a single branch, as it is not very compact at its source. The third and fourth branches (*c* and *d*) begin on the anterior and posterior walls respectively of the coxopodite. All branches of this muscle go to the same heavy tendon fastened to the proximal ventral rim of the basi-ischiopodite. The muscle opposes the levator effectively.

148. *Musculus reductor micropoditis*.—See 137.

149. *Musculus abductor carpopoditis*.—See 138.

150. *Musculus adductor carpopoditis*.—See 139.

151. *Musculus productor propoditis*.—See 140.

152. *Musculus reductor propoditis*.—See 141.

153. *Musculus abductor dactylopoditis*.—See 142.

154. *Musculus adductor dactylopoditis*.—See 143.

#### THE FIFTH PEREIOPOD

155 *a-c*. *Musculus promotor a-c* (fig. 12 M).—The longest and heaviest branch (*a*) originates anteriorly on the median plate and passes posteriorly and laterally to its insertion on the tendon on the membrane at the anteroventral border of the coxopodite. The next branch (*b*) is very prominent, originating on the posterior surface of the membrane which projects diagonally forward through the preceding segments and on the anterior surface of which some of the branches of muscles of the second, third, and fourth pereio-pods were attached. The third branch (*c*) is the smallest. It arises on the posterior surface of the endosternite between the seventh and eighth segments, being inserted above branch *b* on its tendon. The muscle imparts a forward motion to the leg.

156 *a and b*. *Musculus remotor a-b* (fig. 12 M, O).—In this pereio-pod the remotor differs from the corresponding muscle in the other

pereiopods in that it is branched and also much more strongly developed than in the other legs, owing to the fact that it has to give a powerful backstroke to this fifth leg, which serves as the paddle and which alone causes the very effective swimming movements of the crab. The first branch (*a*) originates dorsally on a T-shaped part of the endopleurite which is attached mesally on the median plate. The posterior branch (*b*) originates on the posterior wall of the eighth segment. Both branches are inserted on a heavy tendon attached to the membrane on the proximal postaxial (in this case dorsal) border of the basi-ischiopodite. The muscle as already stated directs the leg backward.

157 *a-c*. *Musculus levator a-c* (fig. 12 M, N).—The large first branch (*a*) originates on the median plate just posterior to the first branch of the promotor. It travels laterally beneath the second branch of the promotor and beneath the dorsal half of the remotor also, to its insertion on a heavy tendon attached to the anterior (dorsal) proximal border of the basi-ischiopodite. The second branch (*b*) is small and weak. It originates on the sternum between the main branches of the promotor and the depressor, and goes upward and laterally to its insertion on the same tendon. The third branch (*c*) is a heavy and strong one, arising on the sternal wall near to the wedge formed by the first abdominal segment. The entire muscle pulls the leg strongly upward.

158 *a-f*. *Musculus depressor a-f* (fig. 12 M, N, O).—The first branch (*a*), very large and heavy, originates mesally on the sternal wall of the eighth thoracic segment. Branch *b* is very small, originating laterally on the sternal wall. Branch *c* parallels the first branch, beginning partly on the sternal wall and partly on the median plate. The fourth branch (*d*) originates on the posterior sternal wall at the end of the thorax. The fifth and sixth branches (*e* and *f*) originate on the dorsal and posterior walls respectively of the coxopodite. All these branches converge upon an extremely heavy tendon attached to the proximal preaxial (in this case posterior) border of the basi-ischiopodite. This extraordinarily powerful muscle pulls the leg base downward.

159. *Musculus reductor meropoditis*.—See 137.

160. *Musculus abductor carpopoditis*.—See 138.

161. *Musculus adductor carpopoditis*.—See 139.

162. *Musculus productor propoditis*.—See 140.

163. *Musculus reductor propoditis*.—See 141.

164. *Musculus abductor dactylopoditis*.—See 142.

165. *Musculus adductor dactylopoditis*.—See 143.

## THE PLEOPODS

## THE MALE

In the male blue crab, appendages occur only on the first two segments of the abdomen. The distal abdominal segments are much narrower than in the female, and the third, fourth, and fifth segments are fused so that their original sutures are scarcely visible, as I have pointed out earlier in this study.

In the first pleopod of the male the coxopodite is large and partially sclerotized. The basipodite is irregularly shaped, and its distal border is a membrane that attaches the long, whiplike flagellum and gives it the necessary freedom of movement. In this membrane is likewise a pocket in which the flagellum of the second pleopod normally rests.

The name "flagellum" is chosen arbitrarily for the distal part of the pleopod, as it does not show the character of a true flagellum. But neither is there sufficient evidence for considering it a highly modified endopodite or exopodite.

The second pleopod is very much weaker than the first, which completely covers it. Its coxopodite is very thin-walled and partly membranous. A small basipodite is present, controlled by a single muscle originating in the coxopodite. The basipodite and flagellum are sclerotized, but an extensive membrane lies between them, as in the first pleopod. Preaxially, the basipodite is represented only by a membrane, as its sclerotized part is entirely postaxial in position.

166. *Musculus promotor coxopoditis I pedis spurii* (fig. 14 A).—This muscle originates on the ventral surface of the last thoracic somite just lateral to the origin of the first ventral superficial abdominal muscle. It is inserted on the inner preaxial proximal border of the coxopodite, which it erects strongly. This is the only extrinsic muscle belonging to the first pleopod.

167. *Musculus abductor basipoditis I pedis spurii* (fig. 14 A).—Arising on the walls of the outer part of the coxopodite, this muscle is inserted on the outer proximal margin of the basipodite, which is pulled away from the center by its contraction.

168. *Musculus adductor basipoditis I pedis spurii* (fig. 14 A).—This is a heavy muscle arising on the inner proximal walls of the coxopodite. It is inserted on the inner proximal border of the basipodite, which is pulled toward the center by its action.

169. *Musculus abductor flagelli I pedis spurii* (fig. 14 A).—This small and compact muscle arises on the distal postaxial border of the basipodite, and is attached to the extended proximal edge of the flagellum. It causes the tip of the flagellum to move strongly outward.



170. *Musculus promotor coxopoditis II pedis spurii* (fig. 14 B).—This heavy muscle arises on the anterior margin of the second abdominal segment lying entirely beneath the first pleopod. It is inserted on the inner proximal part of the coxopodite, which is erected by its contraction.

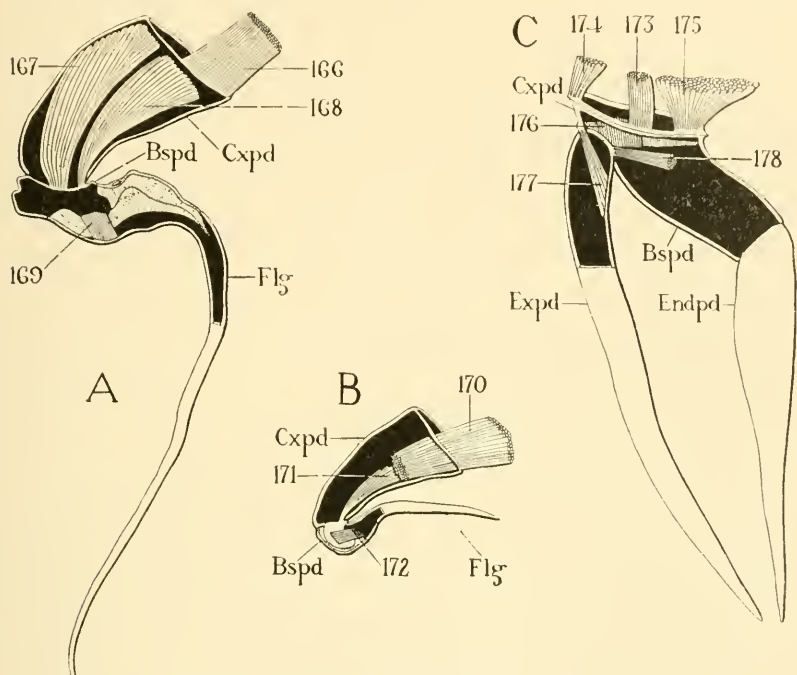


FIG. 14.—The pleopods.

A, the first pleopod of the male.

166, *musculus promotor coxopoditis I pedis spurii*; 167, *musculus abductor basipoditis I pedis spurii*; 168, *musculus adductor basipoditis I pedis spurii*; 169, *musculus abductor flagelli I pedis spurii*.

B, the second pleopod of the male.

170, *musculus promotor coxopoditis II pedis spurii*; 171, *musculus adductor basipoditis II pedis spurii*; 172, *musculus abductor flagelli II pedis spurii*.

C, the first pleopod of the female.

173, *musculus promotor coxopoditis I pedis spurii*; 174, *musculus abductor coxopoditis I pedis spurii*; 175, *musculus adductor coxopoditis I pedis spurii*; 176, *musculus reductor basipoditis I pedis spurii*; 177, *musculus abductor exopoditis I pedis spurii*; 178, *musculus adductor exopoditis I pedis spurii*.

171. *Musculus adductor basipoditis II pedis spurii* (fig. 14 B).—Arising in numerous strands on the inner postaxial wall of the coxopodite, this muscle is attached to the inner proximal border of the basipodite, which is brought toward the center by its contraction. No abductor of the basipodite is present in this appendage, as the elasticity of the membrane apparently gives the necessary opposition to the adductor.

172. *Musculus abductor flagelli II pedis spurii* (fig. 14 B).—Like the corresponding muscle in the first abdominal appendage, this muscle arises on the lateral part of the wall of the basipodite and terminates on the proximal preaxial border of the flagellum, which is brought away from the center as well as slightly forward by its action.

THE FEMALE

The first and sixth abdominal segments of the female blue crab lack appendages. The second, third, fourth, and fifth segments each have pleopods which become increasingly smaller posteriorly. The coxopodite and basipodite are separated by a membrane on the post-axial surface; preaxially the two are fused. A description of the muscles pertaining to the first abdominal appendage, attached to the second abdominal segment, applies to the other three pairs of abdominal appendages, in which the muscles are similar but weaker.

173. *Musculus promotor coxopoditis I pedis spurii* (fig. 14 C).—This muscle arises on the dorsal border of the second abdominal segment and is inserted on the middle of the preaxial proximal border of the coxopodite, which it brings strongly forward.

174. *Musculus abductor coxopoditis I pedis spurii* (fig. 14 C).—This muscle likewise originates on the dorsal border of the second abdominal segment lateral to the origin of the promotor. It passes slightly outward to its insertion on the extreme lateral proximal border of the coxopodite. The appendage is moved away from the midline by its action. In the three pleopods which follow this one, the abductor of the coxopodite takes its origin below and behind that of the promotor muscle, so that in the last pleopod it is nearly obscured by the promotor when viewed preaxially. This is the only noteworthy difference in any of the muscles of the following three appendages as compared with those of the first appendage, except that they become smaller as the appendages themselves decrease in size.

175. *Musculus adductor coxopoditis I pedis spurii* (fig. 14 C).—This muscle is much larger than its opponent, the abductor. It arises on the median dorsal border of the second abdominal somite from almost the midline to the origin of the promotor. It is inserted at the extreme median proximal margin of the coxopodite, which it pulls inward and forward.

176. *Musculus reductor basipoditis I pedis spurii* (fig. 14 C).—This is a very short but rather powerful muscle arising laterally along the proximal posterior border of the coxopodite at the only place where the fusion is not complete between basipodite and coxopodite.

It runs inward without narrowing to its insertion along the proximal posterior wall of the basipodite, which is moved backward by its action.

177. *Musculus abductor exopoditis I pedis spurii* (fig. 14 C).—Arising on the lateral anterior border of the basipodite near the insertion of the abductor of the basipodite, the abductor of the exopodite is inserted on the lateral wall of the exopodite, on which it produces a feeble outward pull.

178. *Musculus adductor exopoditis I pedis spurii* (fig. 14 C).—This rather slender muscle arises on the median proximal preaxial wall of the basipodite and extends outward to its insertion on the inner proximal end of the exopodite, which is moved inward by its pull.

There are no muscles to govern the endopodite, which moves only as the basipodite moves.

179. *Musculus promotor coxopoditis II pedis spurii*.—See 173.

180. *Musculus abductor coxopoditis II pedis spurii*.—See 174.

181. *Musculus adductor coxopoditis II pedis spurii*.—See 175.

182. *Musculus reductor basipoditis II pedis spurii*.—See 176.

183. *Musculus abductor exopoditis II pedis spurii*.—See 177.

184. *Musculus adductor exopoditis II pedis spurii*.—See 178.

185. *Musculus promotor coxopoditis III pedis spurii*.—See 173.

186. *Musculus abductor coxopoditis III pedis spurii*.—See 174.

187. *Musculus adductor coxopoditis III pedis spurii*.—See 175.

188. *Musculus reductor basipoditis III pedis spurii*.—See 176.

189. *Musculus abductor exopoditis III pedis spurii*.—See 177.

190. *Musculus adductor exopoditis III pedis spurii*.—See 178.

191. *Musculus promotor coxopoditis IV pedis spurii*.—See 173.

192. *Musculus abductor coxopoditis IV pedis spurii*.—See 174.

193. *Musculus adductor coxopoditis IV pedis spurii*.—See 175.

194. *Musculus reductor basipoditis IV pedis spurii*.—See 176.

195. *Musculus abductor exopoditis IV pedis spurii*.—See 177.

196. *Musculus adductor exopoditis IV pedis spurii*.—See 178.

#### THE SKELETON

A brief survey of some of the skeletal peculiarities found in the blue crab is not out of place in a study of its myology, since the shape of the skeleton and the arrangement of the muscles attached upon it are mutually interdependent.

The segments of the head and thorax of the crab are immovably ankylosed, as I have repeatedly emphasized. To some extent, this fact simplifies the musculature, as it at once precludes the presence of

true trunk muscles which are necessary only when the segments move individually. (See figs. 15 and 16.)

The muscles of the last five thoracic segments are separated internally by a series of irregularly shaped partitions. Each of these partitions consists of two thin plates, formed by the anterior wall of one segment closely applied to the posterior wall of the preceding segment.

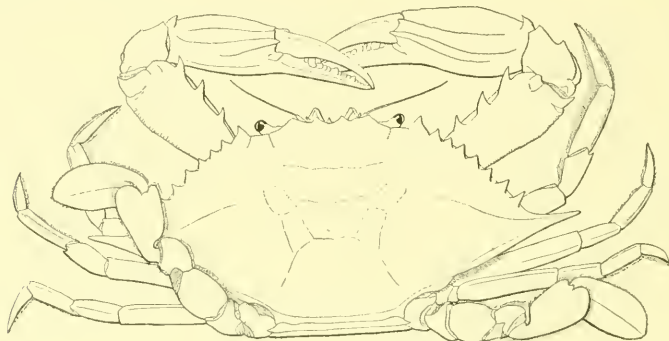


FIG. 15.—Dorsal view of the blue crab.

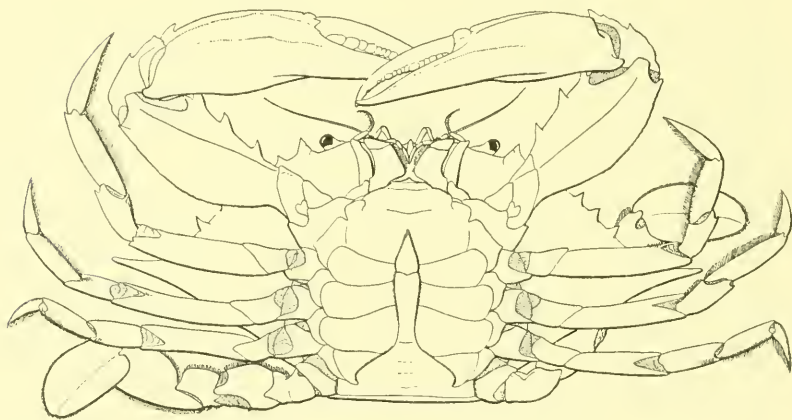


FIG. 16.—Ventral view of the blue crab.

The lower half of each partition is formed by a pair of the plates arising from the sternal borders of neighboring segments and is called an endosternite. The upper half of each partition is similarly formed by a pair of the plates which originate on the pleural walls of neighboring segments and is called an endopleurite. Each endosternite coalesces with its corresponding endopleurite, and it is at this line of coalition that the break occurs during ecdysis to allow the crab to molt completely. (See figs. 17 and 18.)

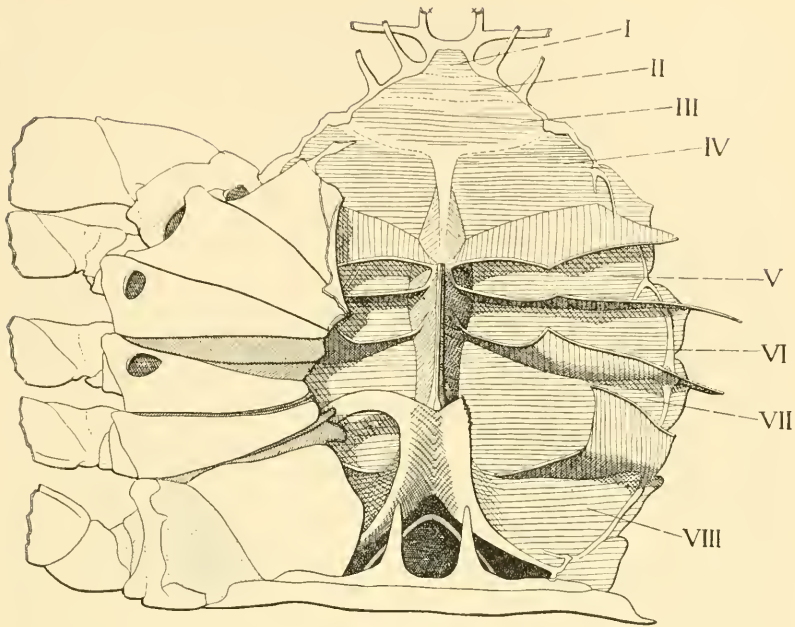


FIG. 17.—Dorsal view of thorax with carapace removed to show internal skeletal parts.

*I-VIII*, first through eighth somites of thorax.

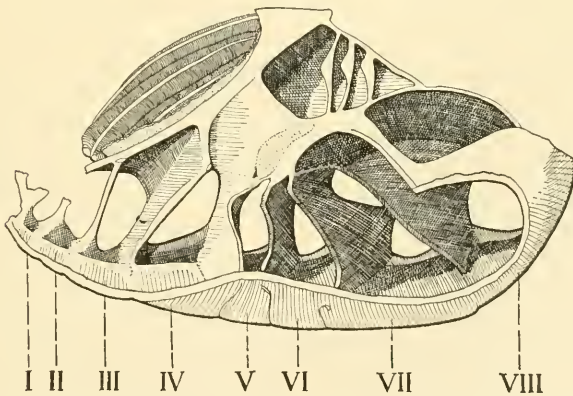


FIG. 18.—Lateral section of thorax showing internal skeletal parts.

*I-VIII*, first through eighth somites of thorax.

The endosternites and endopleurites formed in the manner just described are entirely intersegmental. A secondary infolding of the pleural wall occurs, however, in the fourth, fifth, sixth, and seventh thoracic segments. To this infolded structure, which is strictly intra-segmental, I have given the name of secondary endopleurite. No corresponding infolding occurs in the sternal parts of these segments. The secondary endopleurite is firmly attached at its inner margin to the anterior surface of the membrane encasing the promotor of the fifth pereopod. The remotor muscle always finds its origin behind the secondary endopleurite, while some of the branches of the depressor and levator do so likewise in certain segments. This indicates that these partitions are in truth only secondary, since the remotor of a particular segment would not arise outside its own segment.

The endoskeletal partitions of the last five segments of the thorax present an interesting complexity due to the overdevelopment of the fifth pereopod, as I have already noted. The muscle attachments of this pereopod have been increased by the forward prolongation of a branch of the promotor muscle through the three preceding segments. The pocketlike membrane that encases this part of the muscle serves as a place of attachment for the several endopleurites where they meet the endosternites, as well as for the secondary endopleurites, and these attachments hold it firmly in place to resist the heavy pull which the muscle exerts upon it. The anterior termination of this prolongation may be seen upon the posterior wall of the fourth thoracic segment, where it appears as an oval, semi-transparent window partly separating the endopleurite and endosternite lying between the fourth and fifth thoracic segments.

Although the median plate extends forward as far as the endosternite separating the first and second pereopods, it serves exclusively as a place of origin for branches of the four basal muscles of the telopodite of the fifth pereopod. Some part of each of these muscles originates upon the median plate, although none of the muscles originates entirely upon it.

The third maxilliped and the first pereopod bear a pair of gills, which lie side by side in the gill chamber. The second maxilliped likewise possesses two gills, one of which lies in the extreme anterior part of the gill chamber in front of the gills belonging to the pereopods, and which can be distinguished from them only by its smaller size and its anterior position. The other gill of the second maxilliped lies at right angles to the first, extending outward and backward from the anterior corner of the gill chamber. The second and third pereopods each possess a single gill. The first maxilliped and the fourth and fifth pereopods lack gills.

## THE GENERAL STRUCTURE OF THE CRUSTACEAN APPENDAGE

In order to understand the true relationships between the exceedingly diverse and often highly specialized crustaceans that exist today, it is a matter of importance to attempt to reconstruct a generalized ancestral type, from which all these existing divergences may have arisen by various evolutionary processes.

A typical leg of any of the higher crustaceans consists of not more than seven segments, including the basal segment called the coxopodite, which is followed by the basipodite bearing the endopodite of five segments, each segment having a pair of muscles to move it. Any or all of these seven segments may be provided with exites—lobes growing on the external part of the limb, or endites—lobes growing on the internal part of the limb. These exites and endites, when they are large and movable, may have special muscles of their own.

In the insects the basal segment of the leg is obviously divided into a coxa and a subcoxa, the latter forming sclerotized plates in the pleural wall of the thorax. In the crustaceans it is possible to trace a similar development of the limb basis. Consequently, we may look upon the coxopodite as being equivalent to the coxa of the insect, while the sternal and possibly the pleural regions of the thorax in the blue crab represent the subcoxal regions of the legs of the insect.

The coxopodite is sometimes ankylosed with the basipodite, in which case the resulting structure goes by the name of protopodite. The coxopodite may exist by itself, as in the mandible and the two maxillae of the isopod and the amphipod (fig. 21 A, B, C; fig. 22 A, B, C), or it may give rise to a basipodite with or without an exopodite and endopodite. The coxopodite may have one or more epipodites (fig. 24 E, F), which are usually gill-like, nonsegmented structures forming a part of the respiratory system.

In the lower crustaceans the leg has an exopodite as well as an endopodite, both of which always arise from the basipodite. In the higher crustaceans the exopodite still persists in the maxillipeds and the pleopods.

The exopodite may have any number of joints, and its distal part may be modified to form a flagellum, as in the maxilliped and true legs of the mysid (fig. 19 D; fig. 20 A, B, C). The endopodite, on the contrary, is very definitely limited to a maximum of five segments. Frequently, the distal segments are not present, and some of the proximal ones may have ankylosed. The endopodite exists in its typical form as a walking leg in the higher crustaceans, the names of its segments being the ischiopodite, the meropodite, the carpopodite, the propodite, and the dactylopodite. The typical crustacean leg has two principal places for bending—one at the basal joint between

the coxopodite and the basipodite, and the other at the "knee" joint between the meropodite and the carpopodite. Hence there are typically three segments between the basal joint and the "knee" joint, and three

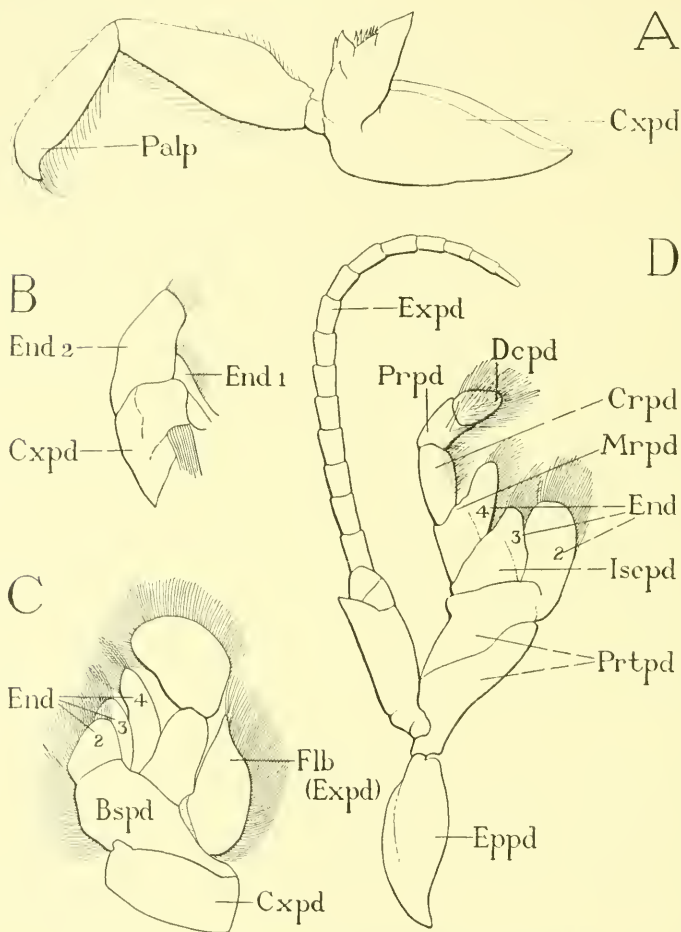


FIG. 19.—Appendages of *Michtheimysis stenolepis*.

A, the mandible.

B, the first maxilla.

C, the second maxilla.

D, the first maxilliped.

*Bspd*, basipodite; *Carpd*, carpopodite; *Cxpd*, coxopodite; *Dcpd*, dactylopodite; *End*, endite; *Eppd*, epipodite; *Expd*, exopodite; *Flb*, flabellum; *Iscpd*, ischiopodite; *Mrpd*, meropodite; *Prpd*, propodite; *Prtpd*, protopodite.

more beyond the "knee" joint. When fewer segments occur in either section, we may know that the leg is not entirely typical. For instance, in the second maxilliped of the amphipod (fig. 23 A), only two seg-



ments occur distal to the "knee" joint, and therefore we know that the dactylopodite is absent or fused. In the leg of the blue crab (fig. 12 A, B), two movable segments occur between the basal joint and the "knee" joint. One can easily see in this case that the

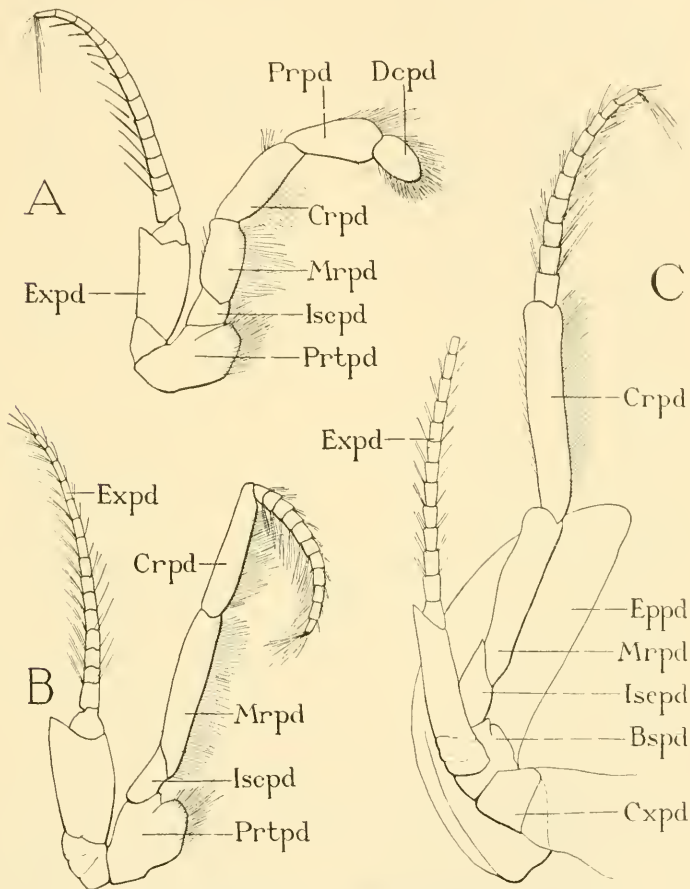


FIG. 20.—Appendages of *Michtheimysis stenolepis*.

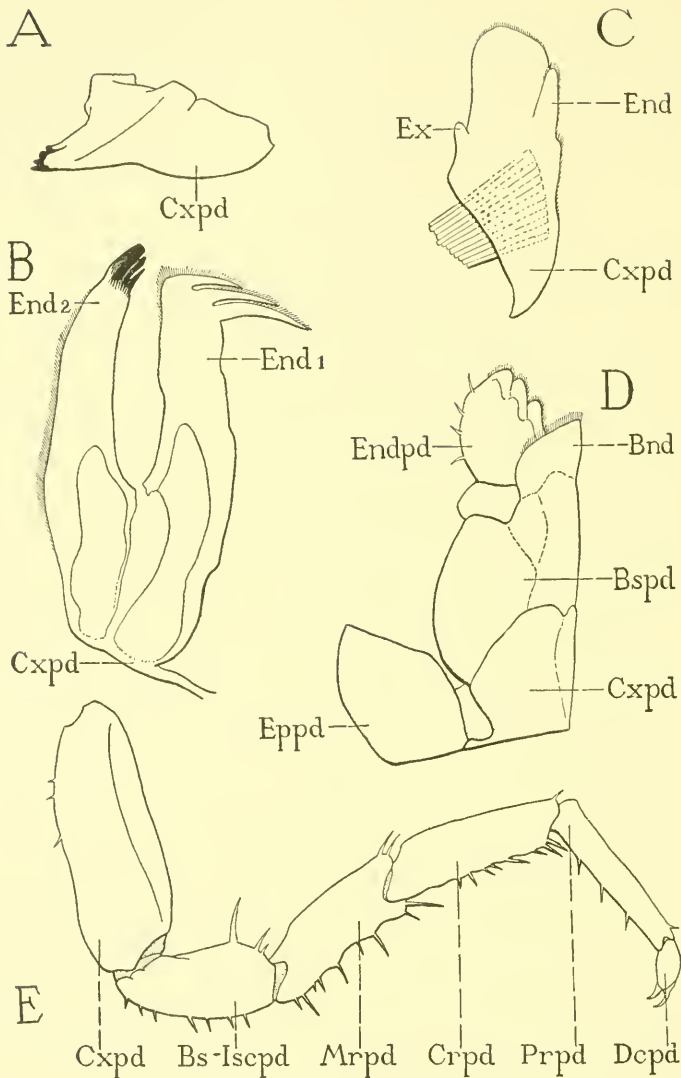
A, the second maxilliped.

B, the third maxilliped.

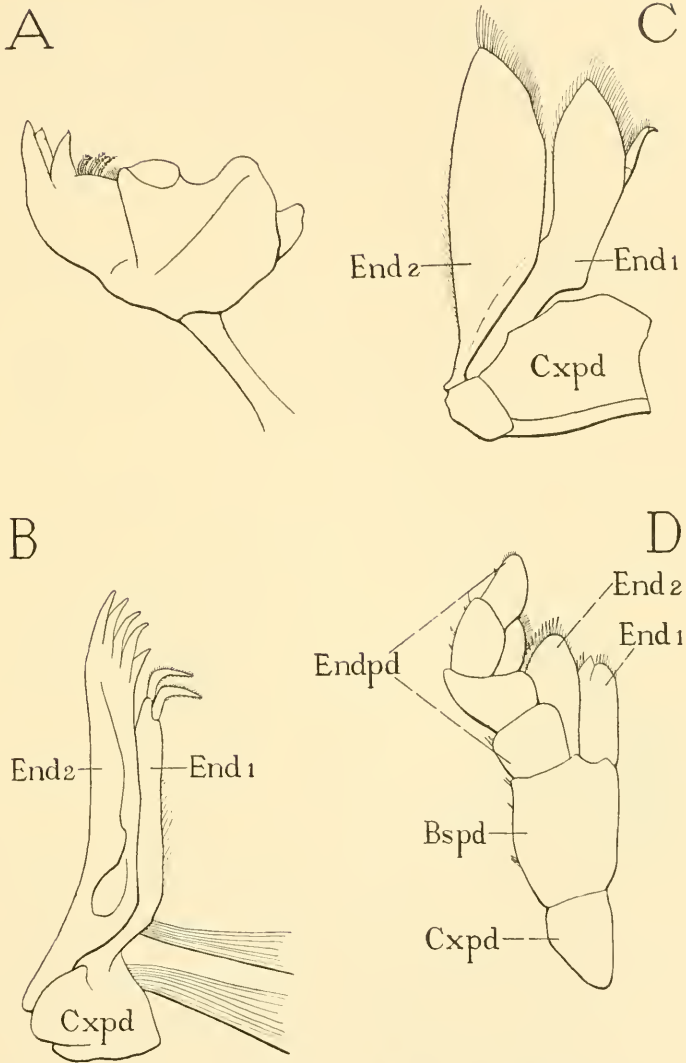
C, the fifth pereopod.

*Bspd*, basipodite; *Crpd*, carpopodite; *Cxpd*, coxopodite; *Dcpd*, dactylopodite; *Eppd*, epipodite; *Expd*, exopodite; *Iscpd*, ischiopodite; *Mrpd*, meropodite; *Prpd*, propodite; *Prtpd*, protopodite.

basipodite is nearly ankylosed with the ischiopodite, the resulting structure thereby becoming a basi-ischiopodite. In the leg of the higher crustaceans the exopodite is absent. The basipodite plus the endopodite is often referred to as the telopodite.

FIG. 21.—Appendages of *Ligia exotica*.

- A, the mandible.  
 B, the first maxilla.  
 C, the second maxilla.  
 D, the maxilliped.  
 E, the first pereopod.  
*Bnd*, endite of the basipodite; *Bs-Iscpd*, basi-ischiopodite; *Bspd*, basipodite;  
*Dcpd*, dactylopodite; *End*, endite; *Endpd*, endopodite; *Eppd*, epipodite; *Ex*,  
 exite; *Mrpd*, meropodite; *Prpd*, propodite.

FIG. 22.—Appendages of *Orchestoidea californiana*.

A, the mandible.

B, the first maxilla.

C, the second maxilla.

D, the first maxilliped.

*Bspd*, basipodite; *Cxpd*, coxopodite; *End*, endite; *Endpd*, endopodite.

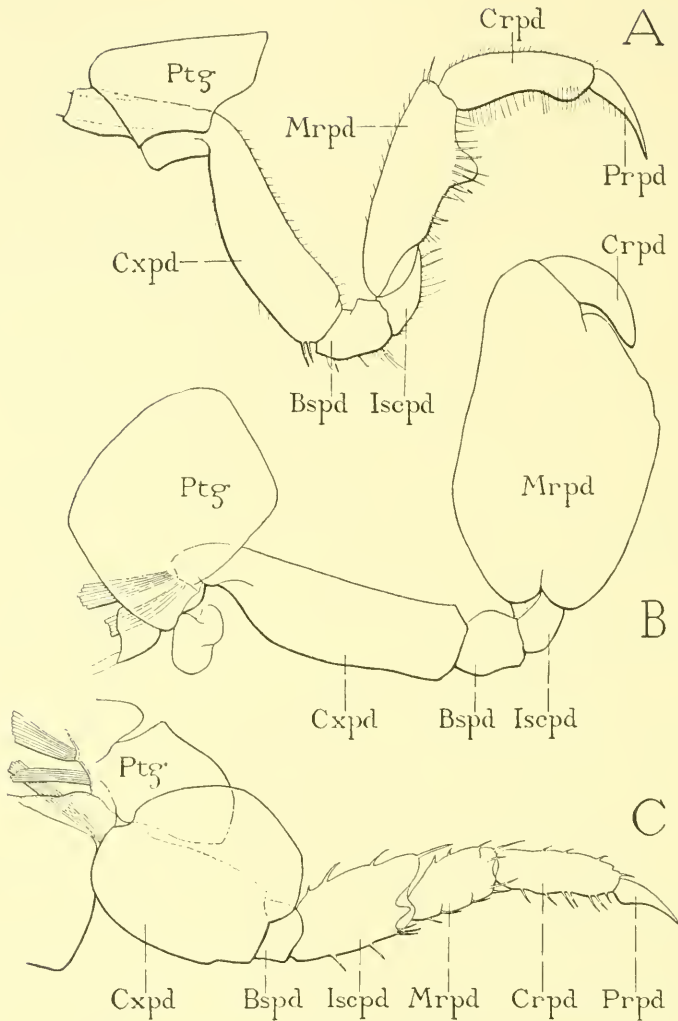


FIG. 23.—Appendages of *Orchestoidea californiana*.

A, the second maxilliped.

B, the third maxilliped.

C, the fifth pereopod.

*Bspd*, basipodite; *Crpd*, carpopodite; *Cxpd*, coxopodite; *Isepd*, ischiopodite; *Mrpd*, meropodite; *Prpd*, propodite; *Ptg*, paratergite.

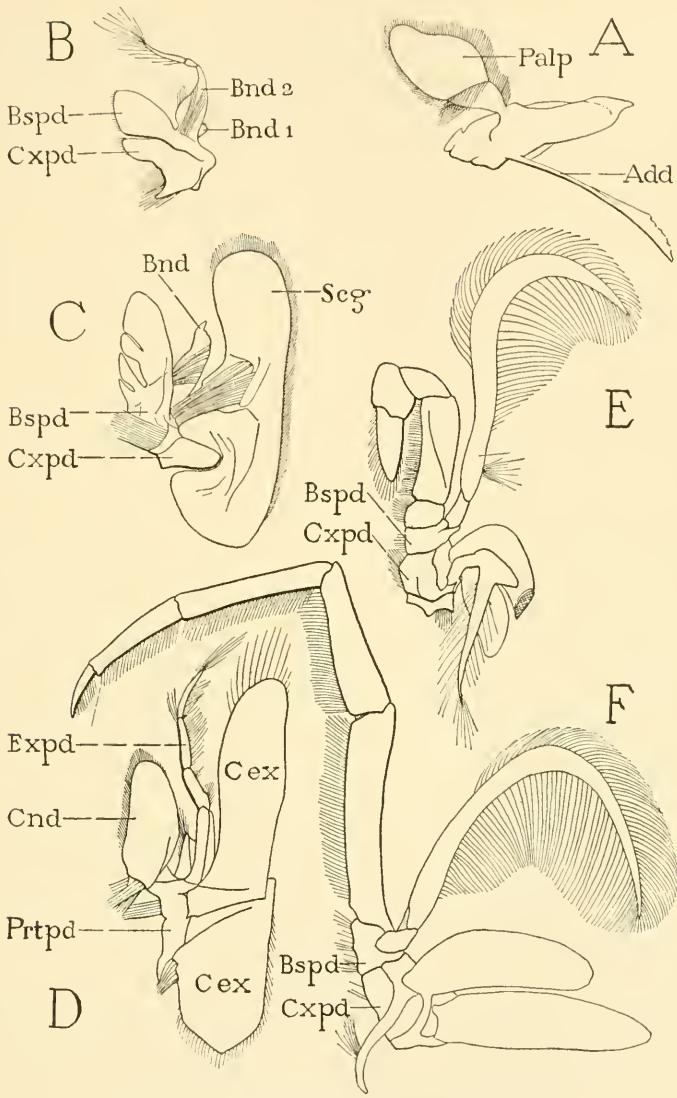


FIG. 24.—Appendages of *Penaeus setiferus*.

- A, the mandible.
- B, the first maxilla.
- C, the second maxilla.
- D, the first maxilliped.
- E, the second maxilliped.
- F, the third maxilliped.

*Add*, tendon of the adductor muscle of the mandible; *Bnd*, endite of the basipodite; *Bspd*, basipodite; *Cex*, exite of the coxopodite; *Cxpd*, coxopodite; *Expd*, exopodite; *Prtpd*, protopodite; *Scg*, scaphognathite.

When more than seven segments appear to be visible externally, as is the case in the syncarid *Anaspides*, the additional supposed segments are due to slight creases or furrows in the body wall and are not true segments with their necessary complement of muscle. Some shrimps also apparently have many additional segments in the distal part of the legs, but neither are these true segments, as their myology proves.

The so-called exopodite of the trilobite leg arises on the actual basal segment of the limb, and the question has been raised as to whether it is a true exopodite or an epipodite. If it is an exopodite homologous with that of living crustaceans, then it throws the trilobite definitely into the class Crustacea. If, on the other hand, it is an epipodite, then it makes the trilobite ancestral to all the Arthropoda so far as the structure of its legs is concerned.

## PART II. THE OSSICLES AND MUSCLES OF THE STOMACH

Although it was not at first intended to do more than list the muscles of the appendages, the structure of the stomach appeared to be so interesting that I have prepared a second part to my paper including the muscles of the stomach and listing the ossicles on which they find their attachment. The literature on the stomach muscles is even less extensive than is that on the appendage muscles, and I find that some of the muscles of the pyloric region of the stomach of decapod crustaceans have not been figured or described.

It is logical to include the stomach muscles in the same paper with the muscles of the appendages that originate on the body wall, for developmental studies of invertebrates have demonstrated that the gastric mill is merely an invaginated part of the body wall, so that the muscles pertaining to it are as truly "skeletal" as are those of the appendages.

The word "stomach" is, as a matter of fact, a misnomer. The enlarged part of the alimentary canal immediately following the esophagus, although popularly referred to as a stomach, is a part of the stomodaeum of arthropods and performs the same function as does the gizzard in birds—that is, to pulverize the fragments of food and render them small enough to be acted upon effectively by the true digestive juices, which are secreted in the pylorus, a relatively small section of the alimentary canal which follows the stomodaeum.

But it is convenient to speak of the whole structure from the mouth to the beginning of the intestine as the "stomach." As this has been done in most of the preceding discussions by former authors, the term has been used in the present discussion in the same broad sense.

## OSSICLES OF THE STOMACH

In order to give the necessary rigidity to the stomach in the breaking up of food particles to aid in their rapid assimilation, the stomach is equipped with a complicated mechanism composing the so-called "gastric mill." A series of strategically placed ossicles gives places of attachment externally to the muscles, and inside the stomach most of the ossicles are tooth-bearing so that they may effectively pulverize the food before it passes on to the next stage of digestion. These ossicles may be considered under separate headings according to their function and position.

## OSSICLES OF THE "GASTRIC MILL"

*I. Mesocardiac ossicle. Single.*—This small median ossicle lies in the dorsal wall of the cardiac region of the stomach and is almost completely fused with the urocardiac ossicle, which lies behind it. In front it is bounded on either side by the pterocardiac ossicles. It gives a firm attachment to the anterior ends of the cardiopyloric muscles, since it is especially thickened at this point. (Figs. 25 A, 27, 28.)

*II. Pterocardiac ossicles. One pair.*—These ossicles lie on either side of the foregoing and meet each other in front of it, projecting on either side with their wing-shaped outer ends nearly at right angles to the midline of the stomach. One of the pair of anterior gastric muscles (197) is inserted on the widened inner border of each ossicle. The attenuate tip of the ossicle approaches the outer border of the zygo-cardiac ossicle, with which it is closely connected. (Figs. 25 A, 27, 28.)

*III. Zygocardiac ossicles. One pair.*—This pair of ossicles lies in the superolateral wall of the cardiac region of the stomach and is the largest and strongest of the ossicles. Externally, they appear as slender curved structures, the anterior end in close connection with the tips of the pterocardiac ossicles, and their posterior end with the exopyloric ossicles. When the stomach is opened, the zygocardiac ossicles are found to project inward, thickening greatly and bearing on their inner opposed surfaces the "lateral teeth," consisting of one very heavy denticle of tough chitinous material followed by two smaller single ones and by a double row composed altogether of about 20 very pointed small denticles, directed inward and growing smaller in size posteriorly, the area between them without ridges. (Figs. 25 A, B, 26, 27.)

*IV. Exopyloric ossicles. One pair.*—These ossicles appear externally as short and nearly straight structures lying diagonally near the lateral posterior border of the stomach. The outer end of each ossicle

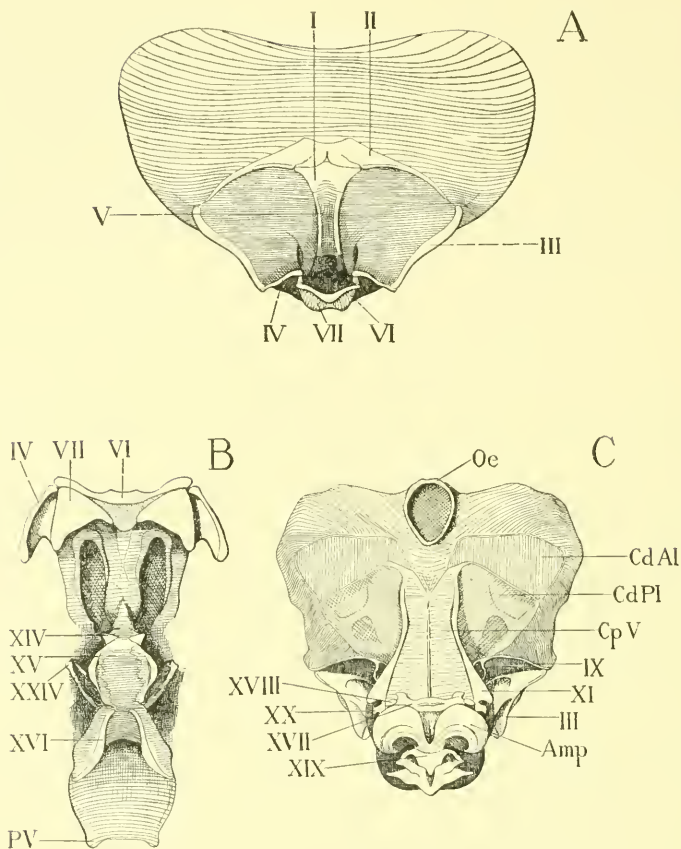


FIG. 25.—External views of stomach showing ossicles.

A, ossicles of the fully distended stomach viewed from above, all muscles removed.

*I*, mesocardiac ossicle; *II*, pterocardiac ossicle; *III*, zyocardiac ossicle; *IV*, exopyloric ossicle; *V*, urocardiac ossicle; *VI*, propyloric ossicle; *VII*, pyloric ossicle.

B, ossicles of the posterior wall of stomach and dorsal pyloric region.

*IV*, exopyloric ossicle; *VI*, propyloric ossicle; *VII*, pyloric ossicle; *XIV*, anterior mesopyloric ossicle; *XV*, posterior mesopyloric ossicle; *XVI*, urpyloric ossicle; *XXIV*, middle pleuopyloric ossicle; *PV*, pyloric valve.

C, ventral view of stomach, walls partly collapsed, all muscles removed.

*III*, zyocardiac ossicle; *IX*, prepectineal ossicle; *XI*, inferolateral cardiac ossicle; *XVII*, antero-inferior pyloric ossicle; *XVIII*, pre-ampullary ossicle; *XIX*, postero-inferior pyloric ossicle; *XX*, anterior supra-ampullary ossicle.

*Amp*, ampulla; *CdAl*, anterolateral cardiac plates; *CdPl*, posterolateral cardiac plates; *CpV*, cardiopyloric valve; *Oe*, esophagus.



is directly behind the posterior termination of the zygocardiac ossicle, to which it is closely articulated, and its inner upper border is the point of insertion for the outer cardiopyloric muscle (210 a). Inwardly, the ossicles project as small triangular plates lying below the median tooth of the urocardiac ossicle. (Figs. 25 A, B, 26, 27.)

*V. Urocardiac ossicle. Single.*—This ossicle is a broad, shield-shaped median plate which is almost completely fused with the mesocardiac ossicle on its anterior border. It projects backward and finally

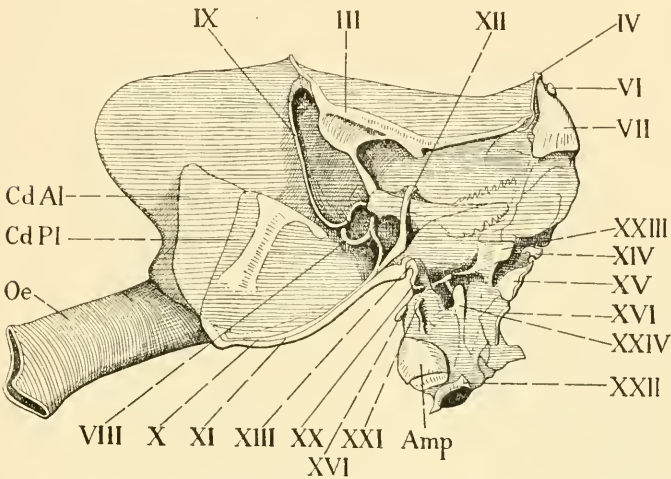


FIG. 26.—Lateral view of stomach showing ossicles after removal of all muscles.

*III*, zygocardiac ossicle; *IV*, exopyloric ossicle; *VI*, propyloric ossicle; *VII*, pyloric ossicle; *VIII*, pectinal ossicle; *IX*, prepectinal ossicle; *X*, postpectinal ossicle; *XI*, inferolateral cardiac ossicle; *XII*, subdentary ossicle; *XIII*, lateral cardiopyloric ossicle; *XIV*, anterior mesopyloric ossicle; *XV*, posterior mesopyloric ossicle; *XVI*, uropyloric ossicle; *XVIII*, pre-ampullary ossicle; *XX*, anterior supra-ampullary ossicle; *XXI*, middle supra-ampullary ossicle; *XXII*, posterior supra-ampullary ossicle; *XXIII*, anterior pleuropyloric ossicle; *XXIV*, middle pleuropyloric ossicle.

*Amp*, ampulla; *CdAl*, anterolateral cardiac plate; *CdPl*, posterolateral cardiac plate; *Oe*, esophagus.

downward as an elongate, heavy plate, articulating with the inner termination of the propyloric ossicle. On its ventral (inner) surface it bears the heavy, ridged median tooth which opposes the lateral teeth of the zygocardiac ossicles. (Figs. 25 A, 27, 28.)

*VI. Propyloric ossicle. Single.*—This appears externally as a small, curved, median ossicle lying in the dorsal wall of the stomach, its outer end just behind the inner terminations of the exopyloric ossicles and articulating closely with them by a short bar of cartilagelike tissue. Upon dissection, the inner part of this ossicle appears triangular in shape, its inner point meeting the uropyloric ossicle at its posterior end

and serving to give rigidity to the median tooth. (Figs. 25 A, B, 26, 27.)

*VII. Pyloric ossicles. One pair.*—These strongly convex, triangular structures lie between the exopyloric ossicles, with which they articulate on either side, and extend behind the propyloric ossicle, entirely on the surface of the stomach. They give attachment to the inner posterior gastric muscles. There is a ligamentous connection

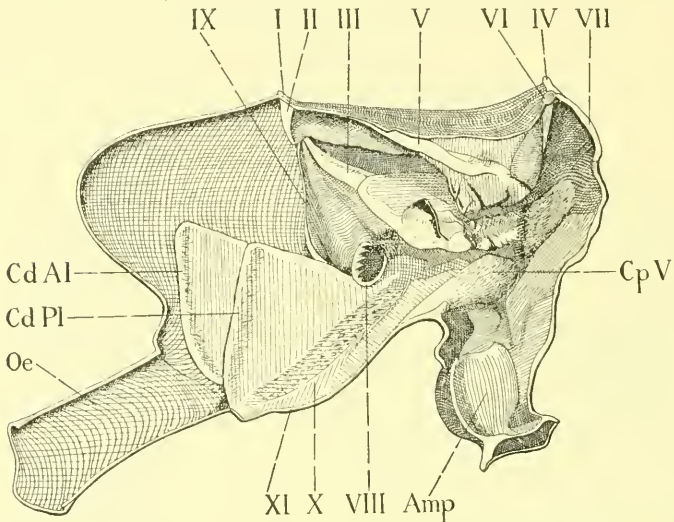


FIG. 27.—Internal view of stomach cut slightly to one side of the median line to show relative positions of the "teeth."

*I*, mesocardiac ossicle; *II*, pterocardiac ossicle; *III*, zyocardiac ossicle; *IV*, exopyloric ossicle; *V*, urocardiac ossicle; *VI*, propyloric ossicle; *VII*, pyloric ossicle; *VIII*, pectineal ossicle; *IX*, prepectineal ossicle; *X*, postpectineal ossicle; *XI*, inferolateral cardiac ossicle.

*Amp*, ampulla; *CdAl*, anterolateral cardiac plate; *CdPl*, posterolateral cardiac plate; *CpV*, cardiopyloric valve; *Oe*, esophagus.

between them, but they do not appear to be fused into one structure, as in the case in the European *Cancer pagurus*. (Figs. 25, A, B, 26, 27.)

#### CARDIAC "SUPPORTING OSSICLES"

*VIII. Pectineal ossicles. One pair.*—These ossicles lie in the lateral wall of the stomach between the lower posterior end of the prepectineal and the upper posterior end of the postpectineal ossicles. Externally, they appear as relatively small, semicircular structures, but internally, they are seen to bear a distinct brushlike cluster of six or seven long

clawlike teeth, which are called the "lateral accessory teeth." (Figs. 26, 27, 28.)

*IX. Prepectineal ossicles. One pair.*—These slender, curved, rod-like ossicles, lying entirely on the lateral stomach wall, extend upward and forward from the pectineal ossicle to the outer anterior end of the zygo-cardiac ossicle with which they articulate by a cartilagelike tissue. (Figs. 25 C, 26, 27, 28.)

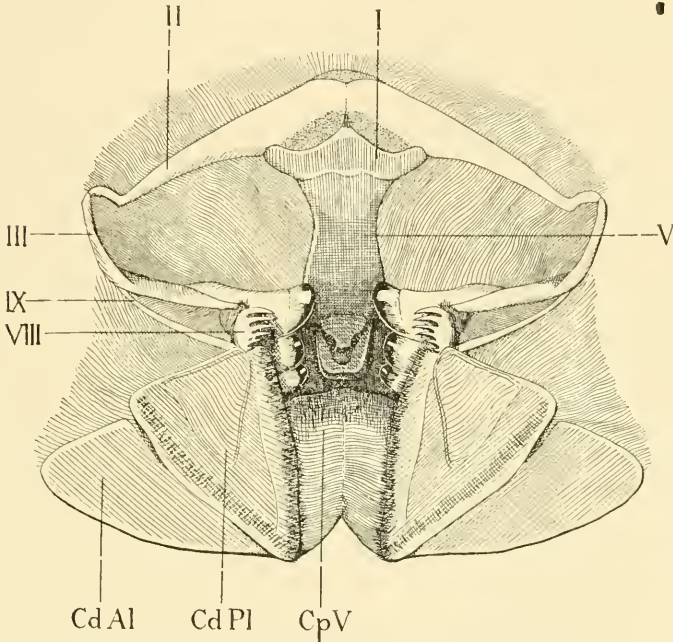


FIG. 28.—Internal view of posterior part of stomach, the anterior parts being dissected away to show the "gastric mill."

*I*, mesocardiac ossicle; *II*, pterocardiac ossicle; *III*, zygo-cardiac ossicle; *V*, urocardiac ossicle; *VIII*, pectineal ossicle; *IX*, prepectineal ossicle.

*CdAl*, anterolateral cardiac plate; *CdPl*, posterolateral cardiac plate; *CpV*, cardiopyloric valve.

*X. Postpectineal ossicles. One pair.*—Passing downward and forward from the posterior margin of the pectineal ossicle, these ossicles, also slender and rodlike, merge with the ventral wall of the stomach below the posterolateral cardiac plates. For the greater part of their length they lie closely in contact with the inferolateral cardiac ossicles, which can scarcely be distinguished from them at their anteroventral termination. (Figs. 26, 27.)

*XI. Inferolateral cardiac ossicles. One pair.*—These ossicles are in contact with the subdentary ossicles near their posterior termination,

but as they go forward and downward along the ventral wall of the stomach, they soon join the postpectineal ossicles, as noted in the preceding paragraph. Seen from below, these ossicles are found to be wide posteriorly, tapering as they converge anteriorly. (Figs. 25 C, 26, 27.)

*XII. Subdentary ossicles. One pair.*—Each of these ossicles, somewhat curved and boomerang-shaped externally, is in contact on its upper margin with the zygo-cardiac ossicle. Ventrally each is attached by a cartilagelike tissue to the inferolateral cardiac ossicle just at its posterior point of attachment to the postpectineal ossicle. (Fig. 26.)

*XIII. Lateral cardiopyloric ossicles. One pair.*—These extremely small curved ossicles lie behind the inferolateral cardiac ossicles and are attached on their lower posterior border to the anterior suprampullary ossicles. (Fig. 26.)

*Cd Al. Anterolateral cardiac plates. One pair.*—These rhombic membranous plates lie directly in front of the posterolateral cardiac plates but are much less clearly defined. There is no heavy calcification in these plates, but the anterodorsal margin is stiffened into a ridge that is slightly thicker than the remaining membrane of the plate. (Figs. 25 C, 26, 27, 28.)

*Cd Pl. Posterolateral cardiac plates. One pair.*—These broad plates, nearly triangular in shape, lie above and in front of the postpectineal ossicle. Although most of the surface is membranous, each plate has a hammer-shaped calcification extending along its upper and anterior borders, to give attachment to the lateral cardiac muscles. The inner posterior border of each plate has several rows of bristles, which project into the stomach. (Figs. 25 C, 26, 27, 28.)

*Cp V. Cardiopyloric valve.*—This valve lies in the ventral posterior part of the stomach, bounded at each side by a posterolateral cardiac plate. It is approximately tongue-shaped, and the thickened posterior end is provided with bristles. It regulates the entrance of triturated material into the intestine. (Figs. 25 C, 27, 28.)

#### PYLORIC "SUPPORTING OSSICLES"

The three following pairs of ossicles are found in the dorsal wall of the pyloric foregut, which is bent so that it is now directed posteriorly.

*XIV. Anterior mesopyloric ossicles. One pair.*—These small angular ossicles project sharply from the membrane surrounding them. They are near the median line and below and posterior to the pyloric ossicle (VII). (Figs. 25 B, 26.)

*XV. Posterior mesopyloric ossicles. One pair.*—These ossicles lie directly below the preceding. They are roughly crescentic in shape and are connected by a thin membrane. (Figs. 25 C, 26.)

*XVI. Uropyloric ossicles. One pair.*—These very slender, angularly-bent ossicles are found behind the posterior mesopyloric ossicles in the roof of the pyloric region, now forming the posterior termination of the stomach. (Figs. 25 B, 26.)

*PV. Pyloric valves. One pair.*—These valves project posteriorly from the cartilagelike tissue which lies posteriorly behind the uropyloric ossicles (*XVI*) in the dorsal wall of the pyloric region. (Fig. 25, B.)

The ventral wall of the pyloric foregut bears the following ossicles:

*XVII. Antero-inferior pyloric ossicle. Single.*—This median rhomboid plate is transversely widened and lies immediately in front of the ampullae. Its widest base is anteriorly in contact with the cardiopyloric valve. (Fig. 25 C.)

*XVIII. Pre-ampullary ossicles. One pair.*—These two very small ossicles project from the region just behind the outer border of the antero-inferior pyloric ossicle and a short distance in front of the pyloric ampullae. (Figs. 25 C, 26.)

*XIX. Postero-inferior pyloric ossicle. Single.*—This small bow-shaped ossicle lies behind the inter-ampullary groove. It is not heavily calcified and therefore is not very apparent at first glance. (Fig. 25 C.)

*XX. Anterior supra-ampullary ossicles. One pair.*—Each one of this pair of ossicles is a small semicircular, heavily calcified projection, which appears just below and in contact with the lateral cardiopyloric ossicle and behind the supra-ampullary ossicle. (Figs. 25 C, 26.)

*XXI. Middle supra-ampullary ossicles. One pair.*—Each one of this pair of short, straight ossicles lies in a vertical position below the preceding and above the ampullae. (Fig. 26.)

*XXII. Posterior supra-ampullary ossicles. One pair.*—These semicircular ossicles lie close together below the ampullae, and terminate the series of ossicles supporting the pyloric region posteriorly. (Fig. 26.)

The following ossicles occur in the pleuopyloric walls:

*XXIII. Anterior pleuopyloric ossicles. One pair.*—This very heavily calcified, triangular structure projects strongly from the side wall of the stomach in front of the anterior mesopyloric ossicle (*XIV*). It is continued as a long forked calcareous projection leading forward and downward externally along the stomach wall. (Fig. 26.)

*XXIV. Middle pleuopyloric ossicles. One pair.*—Attached to one of the forks of the calcareous projection of the preceding ossicle is

a rounded but equally prominent ossicle, which is arbitrarily called the middle pleuropyloric. The posterior pleuropyloric ossicle seems to be lacking in the blue crab. It is named but not figured by Pearson (1908) in his study of *Cancer pagurus* (p. 103). (Figs. 25 B, 26.)

#### MUSCLES OF THE ALIMENTARY SYSTEM

For the sake of conformity with the writings of other authors, the muscles of the alimentary system are discussed according to their origin, following the definition of Mocquard,<sup>4</sup> who recognized two sets of muscles—first, the *extrinsic*, in which the points of origin are on some part of the body skeletal system and which are inserted on ossicles lying in the walls of the stomach, and second, the *intrinsic*, which are attached at both ends to stomach ossicles or to thickened parts of the stomach membrane.

#### EXTRINSIC MUSCLES

The following three sets of muscles help to work the gastric mill:

197. *Musculus gastricus anterior. One pair.*—Each muscle of this pair has its origin on the cervical membrane and extends backward, gradually convergent toward the midline. They are attached side by side on the inner anterior part of the pterocardiac ossicle (*II*). These muscles are the most readily detected of any of the stomach muscles, as their large size and dorsal position bring them conspicuously to view as soon as the carapace is broken in that region. (Figs. 29, 30.)

198. *Musculus gastricus posterior mesalis. One pair.*—These muscles arise from two small calcareous projections on the under side of the carapace at the median part of the mesogastric region. There is a distinct transverse indentation or channel on the outside of the carapace, which indicates the position of attachment of these muscles, as well as that of the external posterior gastric muscles and the dorsal pyloric muscles to be mentioned later. The inner posterior gastric muscles extend forward and downward to their attachment on the pyloric ossicle (*VII*). These muscles are not so heavy as the anterior gastric muscles (197) just described. (Figs. 29, 30.)

199 *a and b. Musculus gastricus posterior lateralis. Two pairs a and b.*—These muscles arise from the under side of the mesogastric region in the outer part of the same channel which marks the origin of the inner posterior gastric muscles (198) discussed above. They extend downward and forward, converging as they go, and the median

<sup>4</sup> Mocquard, F., Recherches anatomiques sur l'estomac des Crustacés podophthalmaires. Ann. Sci. Nat., 6 ser., Zool., vol. 16, p. 238, 1883.

ones (199 *b*) are inserted just below the inner end of the exopyloric ossicle (*IV*) near the end of the propyloric ossicle (*VI*), while the external pair (199 *a*) are inserted on the outer half of the exopyloric ossicle (*VI*). The outer and inner posterior gastric muscles seen in their natural positions resemble the spokes of an opened fan, being nearly alike in size and length and converging at somewhat similar angles to their respective points of insertion. (Figs. 29, 30.)

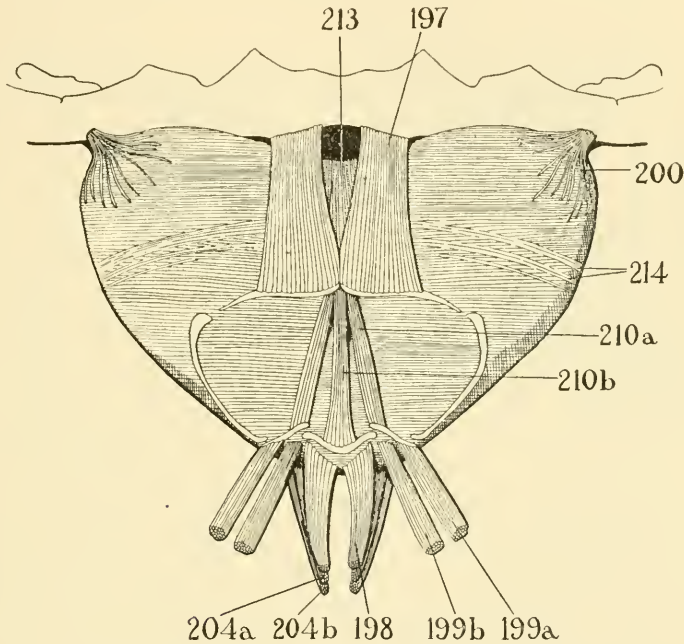


FIG. 29.—Muscles of the stomach viewed from above.

197, musculus gastricus anterior; 198, musculus gastricus posterior mesalis; 199*a* and *b*, musculus gastricus posterior lateralis *a* and *b*; 200, musculus dilatator anterior superior ventriculi; 204*a* and *b*, musculus dilatator dorsalis pylorici anterior *a* and *b*; 210*a* and *b*, musculi cardiopylorici *a* and *b*; 213, musculus cardiacus anterior mesalis; 214, musculus cardiacus anterior lateralis.

The following muscles dilate the stomach:

200. *Musculus dilatator anterior superior ventriculi*. One pair.—Each muscle arises from the inner side of the cervical membrane immediately behind the orbit. The body of the muscle extends inward and backward, dividing very soon into a dozen or more slender fibers which diverge widely to their points of insertion at various places on the anterior upper and outer walls of the stomach. These fibers are exceedingly delicate. (Figs. 29, 30.)

201. *Musculus dilatator anterior inferior ventriculi*. One pair.—The muscles of this pair are extremely attenuate and difficult to separate from the antero-superior dilator muscle of the foregut (206) at their common origin on the upper part of the epistome. A careful tracing shows that the former pair is inserted on the lower anterior wall of the ventriculus above and behind the termination of the esopha-

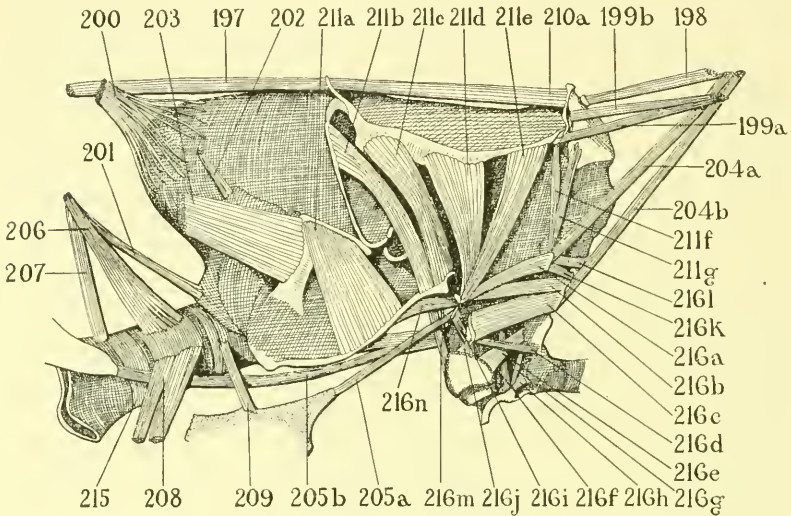


FIG. 30.—Lateral view showing muscles of the stomach.

197, musculus gastricus anterior; 198, musculus gastricus posterior mesalis; 199a and b, musculus gastricus posterior lateralis a and b; 200, musculus dilatator anterior superior ventriculi; 201, musculus dilatator anterior inferior ventriculi; 202, musculus dilatator lateralis anterior ventriculi; 203, musculus dilatator lateralis posterior ventriculi; 204a and b, musculus dilatator dorsalis pylorici anterior a and b; 205a and b, musculus dilatator pylorici inferior a and b; 206, musculus dilatator anterior superior oesophagei; 207, musculus dilatator anterior inferior oesophagei; 208, musculus dilatator lateralis oesophagei; 209, musculus dilatator posterior oesophagei; 210a, musculus cardiopylorici a; 211a-g, musculi interiores cardiaci laterales a-g; 215, musculi circumoesophagei; 216a-n, musculi pylorici a-n.

gus. The connectives of the cerebral ganglion pass diagonally across them. (Fig. 30.)

202. *Musculus dilatator lateralis anterior ventriculi*. One pair.—These muscles arise on the roof of the prebranchial chamber and pass inward and downward to their insertion on the upper margin of the anterolateral cardiac plate (*Cd Al*). They are not very firmly knit and may be torn away with the tissues surrounding the stomach. (Fig. 30.)

203. *Musculus dilatator lateralis posterior ventriculi*. One pair.—Arising on the roof of the prebranchial chamber, these muscles pass



inward through the sheetlike sinus tissue, widening somewhat as they approach their insertion along the anterior edge of the hammer-shaped calcification in the posterolateral cardiac plate (*Cd Pl*). (Fig. 30.)

204 *a* and *b*. *Musculus dilatator dorsalis pylorici anterior a* and *b*. *Two pairs*.—The two muscles on each side run close together at their origin, so that they are not readily separable. They arise directly below the origin of the inner posterior gastric muscle (198), being attached to the lower end of the same calcareous projection of the inner surface of the carapace at the median part of the mesogastric region. Both pairs of dorsal pyloric muscles pass downward and forward as ribbon-like bundles of muscle fibers. The anterior and upper of the two pairs (204 *a*) is inserted on the anterior pleuropyloric ossicle (*XXIII*), while the posterior and lower pair (204 *b*) terminates on the posterior mesopyloric ossicle (*XV*); thus at their insertions they are entirely separate. (Figs. 29, 30.)

205 *a* and *b*. *Musculus dilatator pylorici inferior a* and *b*. *Two pairs*.—Each slender muscle of the outer pair (205 *a*) originates on the endopleurite of the first maxillary segment, passing backward and upward to its insertion on the pre-ampullary ossicle (*XVIII*). The muscles of the inner pair (205 *b*), much longer than the outer but equally attenuate, arise near the base of the mandibular apophysis, thence passing close to the sides of the esophagus and the posterior wall of the cardiac region, and are inserted on the antero-inferior pyloric ossicles (*XVII*) in the ventral wall of the pyloric region. For the last half of their course, the muscles of this inner pair lie so near together that the two appear to be one. (Fig. 30.)

The following muscles dilate the esophagus:

206. *Musculus dilatator anterior superior oesophagei*. *One pair*.—Each of these muscles arises from the epistome near the midline and just beside the median projection from which spring the basal ocular muscles. Diverging backward and downward, the muscles widen considerably at their insertion on the upper wall of the esophagus. (Fig. 30.)

207. *Musculus dilatator anterior inferior oesophagei*. *One pair*.—These muscles are nearly indistinguishable from the preceding at their origin on the epistome, but they pass straight downward to an insertion in a more anterior position on the esophagus. (Fig. 30.)

208. *Musculus dilatator lateralis oesophagei*. *One pair*.—This muscle springs from the posterior angle of the epistome, diverging considerably as it approaches the esophagus, on the lateral wall of which the various fibers find their attachments, just below those of the preceding muscle. (Fig. 30.)

209. *Musculus dilatator posterior oesophagei*. *One pair*.—This muscle is small and not easily distinguishable, lying as it does within the web of tissues surrounding the stomach. It arises on the endopleurite of the first maxillary segment, passing backward and over the inner ventral pyloric dilator (205 *b*) to its insertion on the lateral wall of the esophagus just posterior to the insertion of the lateral dilator of the esophagus (208). (Fig. 30.)

#### INTRINSIC MUSCLES

210 *a* and *b*. *Musculi cardiopylorici a* and *b*. *A median and two lateral*.—The median muscle (*b*) extends from the thickened posterior border of the mesocardiac ossicle (*I*) to the upper central edge of the propyloric ossicle (*VI*). The lateral muscles (*a*) extend from the mesocardiac ossicle (*I*) to the inner end of the exopyloric ossicle (*IV*), diverging slightly posteriorly. These muscles oppose the movements of the extrinsic gastric muscles. (Figs. 29, 30.)

211 *a-g*. *Musculi interiores cardiaci laterales a-g*. *Seven pairs*.—These muscles all run more or less dorsoventrally on the lateral wall of the stomach. (Fig. 30.) In the following list, the dorsal insertion is named first:

*a*. Hammer-shaped ossicle in the posterolateral cardiac plate (*Cd Pl*) to the inferolateral cardiac ossicle (*XI*).

*b*. Prepectineal ossicle (*IX*) to inferolateral ossicle (*XI*).

*c*. Zygocardiac ossicle (*III*) to inferolateral ossicle (*XI*).

*d*. Zygocardiac ossicle (*III*) to anterior supra-ampullary ossicle (*XX*).

*e*. Zygocardiac ossicle (*III*) to anterior supra-ampullary ossicle (*XX*); perhaps this and the preceding should be considered as parts of the same muscle because they have their origins and insertions on the same ossicles, although not on the same points of the ossicles.

*f*. Exopyloric ossicle (*IV*) to anterior pleuropyloric ossicle (*XXIII*).

*g*. Pyloric ossicle (*VII*) to anterior pleuropyloric ossicle (*XXIII*).

212. *Musculus cardiacus posterior inferior*. *One pair*.—This muscle is composed of short fibers attached on the sides to the inferolateral cardiac ossicle (*XI*) and coming almost together at the median line, where they are attached to each side of a projecting ridge running down the center of the cardiopyloric valve. These muscles cannot be seen until the outer and inner lower dilators of the pylorus have been removed, as well as the obscuring branches *m* and *n* of the pyloric muscle. (Not figured.)

213. *Musculus cardiacus anterior mesalis*. *Single*.—If one detaches the anterior gastric muscles carefully, the weak and poorly developed strands of the anterior cardiac muscle may be seen. It arises underneath the former, in front of the anterior median part of the mesocardiac ossicle (*I*), passing forward and downward over the anterior wall of the stomach, and dividing into numerous fibers before it reaches its attachment above the esophagus. (Fig. 29.)

214. *Musculus cardiacus anterior lateralis*. *One pair*.—The fine strands of this muscle arise on the anterior border of the anterolateral cardiac plate (*Cd Al*) and go upward as a thin sheet of very loosely-knit fibers to their attachment near the median line just above the esophagus, close to that of the preceding muscle. (Fig. 29.)

215. *Musculi circumoesophagei*. *Many*.—Taken all together, these numerous muscle fibers go to make up a band surrounding the esophagus. Individually they are very small. (Fig. 30.)

216 a-n. *Musculi pylorici a-n*. *Fourteen pairs*.—It is most convenient to list these numerous small muscles controlling the constriction of the pylorus in tabular form, giving the ossicles between which each muscle extends. The numbering of each individual muscle has been purely arbitrary and without other significance than one of identification. (Fig. 30.)

a. Lateral cardiopyloric ossicle (*XIII*) to anterior pleuropyloric ossicle (*XXIII*).

b. Lateral cardiopyloric ossicle (*XIII*) to posterior mesopyloric ossicle (*XV*).

c. Middle supra-ampullary ossicle (*XXI*) to posterior mesopyloric ossicle (*XV*).

d. Middle supra-ampullary ossicle (*XXI*) to uropyloric ossicle (*XVI*).

e. Ampulla (*Amp*) to uropyloric ossicle (*XVI*).

f. Posterior supra-ampullary ossicle (*XXII*) to middle pleuropyloric ossicle (*XXIV*).

g. Posterior supra-ampullary ossicle (*XXII*) to uropyloric ossicle (*XVI*).

h. Posterior supra-ampullary ossicle (*XXII*) to pyloric valve. (*PV*).

i. Pre-ampullary ossicle (*XVIII*) to middle supra-ampullary ossicle (*XXI*).

j. Middle supra-ampullary ossicle (*XXI*) to ampulla (*Amp*).

k. Anterior pleuropyloric ossicle (*XXIII*) to posterior mesopyloric ossicle (*XV*).

*l.* Anterior pleuropyloric ossicle (*XXIII*) to anterior mesopyloric ossicle (*XIV*).

*m.* Ampulla (*Amþ*) to antero-inferior pyloric ossicle (*XVII*).

*n.* Lateral cardiopyloric ossicle (*XIII*) to inferolateral cardiac ossicle (*XI*).

#### ABBREVIATIONS USED ON THE FIGURES

<i>a-b</i> , primitive dorsoventral axis of appendage.	<i>Flb</i> , flabellum.
<i>A Cxpd</i> , anterior part of coxopodite.	<i>Flg</i> , flagellum.
<i>Add</i> , tendon of adductor of mandible.	<i>I</i> , dorsal promotor muscle.
<i>Ant</i> , anterior border.	<i>Iscpd</i> , ischiopodite.
<i>Aþpd</i> , appendage.	<i>J</i> , dorsal remotor.
<i>Bnd</i> , endite of basipodite.	<i>K</i> , ventral promotor.
<i>Bs-Iscpd</i> , basi-ischiopodite.	<i>L</i> , ventral remotor.
<i>Bspd</i> , basipodite.	<i>Mrpd</i> , meropodite.
<i>Ccx</i> , exite of coxopodite.	<i>Palp</i> , palp.
<i>Cnd</i> , endite of coxopodite.	<i>P Cxpd</i> , posterior part of coxopodite.
<i>Crpd</i> , carpopodite.	<i>Post</i> , posterior border.
<i>Cxpd</i> , coxopodite.	<i>Prpd</i> , propodite.
<i>Dcpd</i> , dactylopodite.	<i>Prtpd</i> , protopodite.
<i>End</i> , endite.	<i>Ptg</i> , paratergite.
<i>Endpd</i> , endopodite.	<i>Scg</i> , scaphognathite.
<i>Eþpd</i> , epipodite.	<i>St</i> , statocyst.
<i>Ex</i> , exite.	<i>Stn</i> , sternum.
<i>Expd</i> , exopodite.	<i>T</i> , tergum.
	<i>Tn</i> , telson.

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