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(With Eight Plates)

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Laboratoria de Entomología, Dirección de Agronomía,
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INTRODUCTION

The cockroach has been the subject of many works in entomology. Its external anatomy is well known, and the insect is commonly used for experiments in insect physiology and investigations on insecticides. However, little has been published on its internal anatomy. Considering that a better knowledge of its anatomy could be useful to physiologists, economic entomologists, and anybody who uses the cockroach for experimental work, R. E. Snodgrass, who directed this research, proposed the musculature of the thorax as a theme.

It was found, while working on this subject, that the thoracic mus-

culature of the cockroach bears little resemblance to that of other insects. Because of these differences, and the limitation of time for the work, no comparisons have been included; the work consists chiefly of anatomical description, with an attempt at explanation of the mechanism of motion.

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I. DISCUSSION OF THE MECHANISM OF MOTION

THE CERVICAL AND VENTRAL MUSCLES

It can be observed in a living cockroach, *Periplaneta americana* (L.), that the head is capable of wide freedom of movement. The insect moves it forward or retracts it under the pronotum, or turns it to the right or left side. The head articulates on each side with the apex of the first cervical sclerites (figs. 15, 16, *1Cv*) and on such articulation swings forward and backward. The elasticity of the wide membranous areas of the neck and the folding of the first and second cervical sclerites over its articular line allows the head to make the lateral movements. The muscles responsible for the head movements can be easily seen in the dorso-ventral dissections of the thorax (figs. 17 to 20). In a general way it can be said that the muscles inserted on the tentorial bridge are retractors of the head, and the head action is aided by the muscles inserted on the ventral cervical sclerites. Of the muscles inserted on the postoccipital ridge, *52* and *53* are probably retractors too, because they insert approximately at the level of the cephalo-cervical articulations, while *56, 57,* and *58,* inserted above this level, probably swing the head on the articulations, pulling the upper part of the head backward and consequently bringing forward the lower part (mouth parts). The set of muscles moving the head does

not differ much from that described by Snodgrass (II, p. 54) [1] in the Carolina grasshopper.

The whole thorax of the cockroach, though not nearly as flexible as the cervical region, has nevertheless a certain freedom of movement, which is allowed by the partial desclerotization of its sternal plates (III, p. 171). Responsible for the thoracic movement is a complicated set of ventral muscles (fig. 54) probably working together with the dorsal oblique and longitudinal muscles and a few small sterno-phragmal muscles. The function of each one of the ventral muscles is rather obscure, and a written explanation would add but little to what can be gathered by looking at the figures.

Observing the living insect, two different kinds of movement can be seen. One is an alteration of the relative position of the thoracic segments, particularly noticeable in the prothorax, which the insect moves to a certain extent on the horizontal plane. The second type of movement is observable on the ventral side of the insect. It consists in retractions of the different sclerites and alterations of their relative positions. These movements of the thorax are probably helpful to the insect when it progresses in narrow crevices.

THE FORM OF THE THORAX AND MECHANISM OF THE LEGS

The thorax of the cockroach differs in several respects from the typical pterygote insect thorax as described by Snodgrass (I). The differences are in the first place structural. The whole body of the insect is depressed, apparently as an adaptation to living in crevices, under stones, and crawling into the narrow hiding places where blattids generally live. The three thoracic segments are as flat and broad as the rest of the body, and the flat coxae, instead of extending out from them as in a grasshopper, project from the thorax backward, in a nearly horizontal position, underlapping the ventral part of the following segments. This modifies the position of the leg, which moves in a plane nearly parallel to the longitudinal axis of the body instead of perpendicular to it. When the legs are at rest, the anterior and posterior faces of the coxa, trochanter, etc., become respectively ventral and dorsal. When the animal walks, the angle formed by the coxae and the body increases slightly, more in the middle coxae than in the hind ones, and more in the front than in the middle ones. Holding the living insect upside down between the fingers, it can be seen that it is able even to move the coxae to a position perpendicular to the axis of the body, the fore coxae having much more freedom of

[1] Roman numbers in parentheses refer to literature cited at the end of the work.

movement than the other two pairs. But though these movements are possible and actually performed by the living insect, the ordinary position of the legs is lying flat against the body, and their shape indicates that they are anatomically adapted to such position.

The articulation of the coxae with the thorax is also modified according to the described conformation of the thorax. The two regular articulations, one with the pleuron and the other with the trochantin, are both located on the anterior part of the coxal rim which is almost straight between them, curving but slightly outward. The coxae do not hang from the thorax by two opposite points as a bucket from its handle, but swing like the lid of a box on its hinges. As the line on which the two articulations are located is almost parallel to a plane passing from side to side of the insect and forms a certain angle with the median line of the body, it is evident that the only kind of movements that can be made on such articulation are a promotion-adduction and its opposite, a remotion-abduction. The adduction and abduction movements are secondary here, and are due only to the angle that the line of the hinge forms with the axis of the body, the promotion and remotion components of the movement being far more important.

More free and complete adduction and abduction movements are provided by another structure. This is a membranous fold on the ventral side of the body, between the second episternal plate (figs. 16, 34, 51, *2Eps*) and the first plate of the trochantin (figs. 16, 34, 51, *1Tn*). Both plates of the episternum are fastened together by a narrow strip of membrane, and both plates of the trochantin are actually welded together. But between the second episternal plate and the first trochantinal plate there is a wide band of flexible membrane which folds, allowing the first plate of the trochantin to glide under the second plate of the episternum. When this happens, the coxa being in its normal horizontal position, a true movement of adduction takes place, the axis of the coxa being driven toward the medial line of the body. It can be observed in the living insect that the whole trochantin swings on two articular points, one being its anterior apex which fits into the V-shaped episternum, the other being the plural-coxal process. This adds freedom to the coxal movement. In the prothorax, a cut that divides the second plate of the trochantin into two pieces (fig. 16, *2Tn*) provides an additional articulation and makes the movement of the prothoracic coxa much freer than that of the mesothorax and metathorax.

The combination of the described movements allows the coxa to move in every direction. The desclerotization characteristic of Blat-

tidae (III, p. 171) and the flexibility of the sclerites and membrane contribute to make the movement freer.

The nearly horizontal position of the coxa and leg make it also difficult to name the movements of the femur and the rest of the leg. What would be a depression of the leg if it were in a vertical plane, becomes here an almost backward movement of the leg which pushes the body forward instead of lifting it. The opposite movement brings the leg forward to its first position.

On studying the muscles responsible for the described movements, their number and complexity is amazing and it is not always possible to tell the function of a particular muscle. However, according to its origin and insertion it is possible in many cases to determine in a general way the function that a set of muscles performs. The general plan of the coxal and trochanteral muscles is almost identical in the mesothorax and metathorax, and though a little different in the prothorax, is similar enough to recognize the same scheme as in the other two thoracic segments. On account of that, the following classification has been made:

Coxal muscles.—The muscles of the coxa include promotors, remotors, adductors, and rotators.

The promotors of the coxa are: (1) Muscles that have their origin on the anterior edge of the episternum and insert on the anterior portion of the coxal rim, between the articulation with the pleural and trochantinal coxal processes. Present in mesothorax and metathorax (*126* in fig. 30; *167* in fig. 46); absent in prothorax. (2) Muscles that take their origin on the anterior edge of the episternum and under side of pleural arm and pleural ridge, and insert on a small sclerite isolated in the membrane, near the rim of the coxa and the pleurocoxal articulation. Present in the three segments (*75,* not shown in figures, *127* in fig. 31, *168* in fig. 48). (3) A muscle that originates on the tergum and inserts on the said small sclerite. Present only in the prothorax (*74* in fig. 14).

The remotors of the coxa are all the muscles inserted on the posterior part of the coxal rim and meron, which have their origins on the tergum. In the mesothorax and metathorax the powerful muscles that extend between the meron and the subalar plate work probably as remotors of the leg in addition to their function as alar muscles. In this case both the meron and the subalar plate can function as insertion and origin. A muscle that originates on the sternal arm and inserts on the posterior part of the coxal rim (present in the three segments, *83* in fig. 11, *132* in fig. 25, *172* in fig. 43) might probably act as a remotor too.

The *adductors* of the coxa are: (1) Muscles that originate on the tergum and insert on an apodemal tendon arising from the medial edge of the first plate of the trochantin, close to the coxo-trochantinal articulation. Present in the three segments. (2) Muscles that originate on the anterior edge of the first plate of the episternum (*1Eps*) and insert along the surface and the anterior edge of the first plate of the trochantin (*1Tn*). Missing in the prothorax.

The adductors of the coxa have no antagonistic set of abductor muscles, the elasticity of the sclerites being apparently the only force responsible for the abductory movements.

The *rotators* of the coxa may be supposed to include the following muscles, though it cannot be determined whether these muscles actually function as rotators or as adductors. They probably perform both movements. (1) In the prothorax, a muscle going from the mesothoracic episternum of the opposite side of the body, to the meron (*97* in fig. 54), and another muscle with the same insertion which originates on the first spina (*98* in fig. 54). (2) In the mesothorax, a muscle going from the end of the sternal arm to the ridge which limits the meron in the anterior wall of the coxa (*133* in fig. 25), and another muscle that originates on the second spina and inserts on a lower portion of the same ridge (*134* in figs. 25 and 30). (3) In the metathorax, two muscles that have their origin on different parts of the sternal arm and insert on different parts of the ridge that limits the meron on the anterior wall of the coxa. (4) In the mesothorax and metathorax, muscles going from the spina to the middle of the anterior wall of the coxa (*105* and *173* in fig. 54).

Trochanteral muscles.—The function of the trochanteral muscles is much easier to interpret than that of the coxal muscles. The trochanter has, roughly, the form of a boat, hanging from the coxa by two articulations placed on the opposite sides. From the distal side of the trochanter arises the femur. If we trace a line between the two articular points, it divides the trochanter into a proximal side and a distal (femoral) side. All the muscles inserted on the proximal side will be depressors of the leg; those on the other side, levators. Figure 53 represents the trochanter of the right hind leg, seen from the coxal side. The base of the femur can be seen on the upper part of the figure. The line *A-A'* is the articular line. *180, 181, 182* are the tendons of the levators of the leg; *177, 178, 179* those of the depressors. The tendons of the middle leg follow exactly the same arrangement (see fig. 30). The fore legs show a slight variation with only two levators instead of three.

It must be understood that levators and depressors are discussed from a morphological sense. The action of the muscles will lift or depress the leg only when its position is perpendicular to the body. Since the leg is almost parallel to the body, the levators will pull it forward and slightly up, the depressors will push it back and slightly down. This is the way that the hind legs usually work in the roach. The middle legs form a slightly greater angle with the body than the hind ones, and the front legs a still greater angle than the middle legs.

All the levators of the leg have their origin within the coxa in each of the legs. Of the three depressors, the two lateral, which are the less powerful, originate also within the coxa, on the walls and rim. The middle one (the one inserted on the proximal end of the trochanter, just opposite the femur) has branches that originate within the coxa and extracoxal branches. The extracoxal branches take their origin on the tergum, pleural ridge, and pleural arm in the prothorax, and in the same places plus sternal arm and basalar plate in the mesothorax and metathorax.

THE DORSAL AND WING MUSCLES

It is in the musculature on the wings that the cockroach thorax differs widely from the normal scheme of wing-bearing segments as given by Snodgrass (I, III). The dorsal longitudinal and oblique muscles are present but they are small and "relatively unimportant elements in the wing mechanism by comparison with those of most insects" (I, p. 177). The vertical tergosternal muscles are missing entirely, and no traces of them or substituting mechanism can be found.

Cockroaches are not powerful fliers, but they do fly. Since it is extremely difficult to analyze the mechanism of the flight by looking at the alar muscles, only an enumeration is given of the muscles related directly or indirectly to the wings, which are essentially the same in both segments of the pterothorax.

Dorsal longitudinal and oblique muscles.—These are important muscles in the flight of most insects; in the cockroach they are weak and probably not very important. The dorsal longitudinals are the weaker, the obliques being stronger. Both are found also in the prothorax, where the obliques are attached to a sclerite fastened to the lateral part of the first phragma, very close to the base of the first wing.

Muscle of the basalar plate (pronator extensor of the wing).—In both wing-bearing segments this muscle is one of the more important branches of the powerful main depressor of the leg (*135c* in fig. 27, *177c* in fig. 45). The size of this muscle seems to indicate that it plays

an important role in the flight. Snodgrass (III, pp. 235 and 240) points out its role as pronator and extensor of the wing.

Muscle of the subalar plate (depressor-extensor of the wing. *128* in fig. 27, *169* in fig. 42).—Powerful muscle which originates on the meron. As in the preceding one, its size seems to indicate its importance in the flight besides its action as extensor, which has been pointed out by Snodgrass (III, p. 240). The same author (III, p. 234) shows its importance in the downstroke of the wings.

Pleuro-alar muscle (flexor of the wing. *115* in fig. 25, *158* in fig. 44).—Small muscle from the pleural ridge to the third axillary (*3Ax*, figs. 21 and 36). Its action in the wing flexion has been described by Snodgrass (III, pp. 237 to 240).

Muscles of the anterior notal wing process.—In both wing-bearing segments, a flat muscle that originates on the anterior edge of the pleural arm and pleural ridge (*116* in fig. 25, *159* in fig. 40), and inserts on the downward-bent portion of the anterior notal wing process, which articulates with the first axillary (*1Ax* in figs. 21 and 36). It is the first of a series of three muscles which ends on the posterior portion of the coxal rim, the second being between the pleural and sternal arms, the third between the latter and the coxa. Its probable action on the wing movements is difficult to explain.

II. LIST OF THE THORACIC MUSCLES

The numeral *52* has been given to the first thoracic muscle considering that 51 muscles have been found in the head. Each number in the list represents one pair of muscles located symmetrically on each side of the body.

NECK AND PROTHORAX

52. *First cervical muscle of the head* (fig. 17).—A flat, fan-shaped muscle, arising from the dorsal cervical sclerite, inserted laterally on postoccipital ridge of the head.

53. *Protergal muscle of the head* (fig. 17).—A large, flat muscle, arising from the medial line of protergum, inserted laterally on the postoccipital ridge, just below the insertion of *52*.

54. *Second cervical muscle of the head* (fig. 17).—Slender, flat muscle, arising dorsally from the cervical integument, tapering to its insertion on the tentorial bridge of the head.

55. *Longitudinal ventral muscle of the head and prothorax* (figs. 6, 17).—A medium-size, ribbon-shaped muscle, from base of the sternal arm to median part of tentorial bridge of the head.

56. Episternal muscle of the head (figs. 18, 19, 20).—Arising from the anterior external angle of episternum, inserted dorsally on postoccipital ridge of the head.

57, 58. Cephalic muscles of the cervical sclerites (figs. 19, 20).—Origins on dorsal part of postoccipital ridge, external to *56;* both extend laterally and posteriorly, *57* inserted on the first ventral cervical sclerite, *58* on the second.

59. Prothoracic longitudinal dorsal muscle (figs. 3, 18).—A flat muscle extending from the median portion of the first phragma to the integument of the neck in the point where it bends upward to join the pronotum.

60. Oblique dorsal muscle (figs. 1, 19).—Broad, flat, fan-shaped muscle. Its several bundles of fibers arise dorsally from the median part of the pronotum and converge to their insertion on a small, anvil-shaped sclerite firmly attached to the lateral portion of the first phragma, very close to the base of the fore wing.

61. Oblique dorsal muscle (figs. 1, 2, 19).—Same form as *60* but considerably smaller, lies partially underneath it, and its fibers arising from the median line of pronotum converge to their insertion on the same sclerite.

62. Transverse dorsal muscle (fig. 2).—From the medial portion of the phragma to the same insertion as *60* and *61*.

63, 64. First and second protergal muscles of the first cervical sclerite (figs. 1, 2, 3, 18).—Origins on the anterior edge of the protergum, descending vertically to insertions on the first ventral cervical sclerite. *64* is twisted around *63*.

65, 66. First and second protergal muscles of the pleural arm (figs. 2, 3, 4, 5, 6, 8, 9, 10).—From the protergum to the end of the pleural arm. Both short, small muscles arising from different parts of the protergum and converging to their insertion on the end of the pleural arm at its articulation with the sternal arm.

67. Third protergal muscle of the pleural arm (figs. 3, 5, 6, 7, 8, 9, 10, 11).—Origin on anterior edge of the protergum, goes obliquely downward and backward to the upper surface of the pleural arm.

68. Fourth protergal muscle of the pleural arm (figs. 1, 2, 3, 4, 5, 6, 8, 9, 10, 11, 12).—Origin near the anterior margin of protergum, goes downward and backward to the under surface of the pleural arm.

69. Protergal muscle of the neck (figs. 3, 5, 6, 8, 19, 20).—Arises from the anterior part of the protergum and goes downward to its insertion on a fold of the ventral integument of the neck.

70. *First tergal muscle of the trochantin* (figs. 2, 3, 5, 18, 19, 20).—Arises from the tergum near the median line, goes to the anterior part of the apodemal tendon on the edge of the first plate of trochantin (figs. 15, 16, *1Tn*).
71. *Second tergal muscle of the trochantin* (figs. 2, 5, 6, 8, 20).—Arises from the tergum, near the origin of *70;* goes to the posterior part of the apodemal tendon on the edge of the first plate of trochantin (figs. 15, 16, *1Tn*).
72. *Third tergal muscle of the trochantin* (figs. 1, 2, 3, 4, 5, 6, 8, 9).—Two branches, *a* and *b,* arise from different places on the tergum but soon unite to form one muscle which inserts on first plate of the trochantin (figs. 15, 16, *1Tn*), near its posterior end.
73. *Fourth tergal muscle of the trochantin* (figs. 1, 2, 4, 5, 6, 7, 8, 20).—Arises laterally from the tergum. It is a broad, flat muscle at its origin, tapering downward to its insertion on the posterior end of the surface of trochantin.
74. *Tergal promotor of the coxa* (figs. 1, 2, 4, 6, 8, 9, 10, 11, 12, 13, 14, 18, 19, 20).—Rather broad, flat muscle, arising from the anterior edge of tergum, tapering to its insertion in small sclerite near the coxo-epimeral articulation.
75. *Sterno-pleural promotor of the coxa* (not shown in figures).—Originates on the anterior edge of episternum and under side of pleural edge; goes to the same sclerite as *74.*
76. *First tergo-meral muscle* (figs. 2, 3, 5, 6, 7).—Arises from the tergum and goes to the meron. Acts probably as a remotor of the coxa.
77. *Second tergo-meral muscle* (figs. 2, 3).—From tergum to meron. Acts probably as a remotor of the coxa.
78. *Third tergo-meral muscle* (figs. 2, 3).—Arises from tergum, internal to *76,* goes to meron. Acts probably as a remotor of the coxa.
79. *Fourth tergo-meral muscle* (figs. 1, 3).—Arises from the tergum near the median line, goes to the meron. Acts probably as a remotor of the coxa.
80. *Tergal remotor of the coxa* (figs. 2, 3, 4).—Arises from the tergum near the median line, goes to the basicosta of the coxa.
81. *Main tergal remotor of the coxa* (figs. 1, 2, 3, 4, 5, 17, 18, 19).—Powerful, flat muscle; arises from the anterior edge of the tergum, turns around most of the thoracic muscles, goes to the posterior (dorsal) portion of the basicosta of the coxa.
82. *Sternal adductor of the coxa* (figs. 5, 6).—Flat muscle arising on the sternal arm, inserted on the basicosta of the coxa.

83. Sternal muscle of the coxa (figs. 8, 9, 10, 11).—Arises on the sternal arm, goes to the basicosta of the coxa. Acts probably as a remotor.

84. Prosternal muscle of the cervical sclerite (figs. 17, 54).—A slender muscle, going horizontally from its origin on the sternal arm to the second cervical sclerite (figs. 15, 61, *2Cv*).

85. Main depressor of the leg (figs. 1 to 12).—It is the most powerful muscle in the fore leg and prothorax. From several origins on different parts of the prothorax and coxa, its branches converge to a broad apodemal tendon arising from the proximal angle of the trochanter. Its branches are:

a. First tergal branch (figs. 1 to 10).—Origin on the anterior edge of the protergum.

b. Second tergal branch (figs. 1 to 10).—Origin on the tergum, posterior to branch *a*.

c. Pleural branch (fig. 11).—Its origin covers partly the posterior edge of the pleural arm and advances over part of the upper surface of the pleural ridge and the epimeron.

d. Pleural branch (fig. 12).—Origin on the under surface of the pleural arm and pleural ridge.

e. First coxal branch (fig. 8).—Origin on the medial portion of the wall of the coxa.

f. Second coxal branch (figs. 8, 9).—Origin on the posterior (dorsal) wall of the coxa.

g. Third coxal branch (fig. 13).—Origin on the anterior (ventral) wall of coxa and basicosta of the coxa.

h. Fourth coxal branch (figs. 9, 10, 11, 12).—Arises from the medial portion of the wall of coxa.

86. Posterior depressor of the leg (fig. 7).—Origin on the posterior (dorsal) wall of coxa, goes to apodemal tendon on the trochanter.

87. Anterior depressor of the leg (figs. 13, 14).—Origin on the inner portion of the anterior (ventral) wall of the coxa, goes to apodemal tendon of trochanter.

88. Main levator of leg (figs. 7 to 14).—Two branches converge on a common apodemal tendon on the trochanter. .

a. Anterior branch (figs. 7 to 14).—Arises from anterior (ventral) wall of coxa.

b. Posterior branch (figs. 7 to 13).—Arises from posterior (dorsal) wall of coxa.

89. Secondary levator of the leg (fig. 7).—Small, weak muscle arising from posterior (dorsal) wall of the coxa, goes to apodemal tendon of trochanter (tendon shown in figs. 8 to 13).

Numbers *90* to *95* have been left for the muscles of the rest of the fore leg.

96. Phragmal muscle of the sternal arm (figs. 17, 54).—Slender muscle from the lateral portion of the first phragma to the sternal arm.

97. Episternal muscle of the coxa (figs. 5, 6, 54; in figs. 5 and 6 it is cut).—Flat, ribbonlike muscle, arises from the internal edge of the mesepisternum, goes to prothoracic coxa on opposite side, where it inserts on a ridge that begins at coxo-pleural articulation. Its fibers divide into two or more bundles in the midline of the body, where they cross with those of the corresponding muscle from the opposite side. Acts probably as a rotator.

98. Spinal muscle of the coxa (figs. 5, 6, 54; in figs. 5 and 6 it is cut).—Flat muscle, arises from first spina, inserts on the same ridge as *97*. Acts probably as a rotator.

99. Sterno-spinal muscle (fig. 54).—From sternal arm to first spina. The following muscles (*100* to *106*) are intersegmental.

100. Ventral longitudinal muscle (fig. 54).—Extends between prothoracic and mesothoracic sternal arms.

101. Sternal-spinal intersegmental muscle (fig. 54).—From sternal arm of the prothorax to second spina.

102. Ventral oblique muscle (fig. 54).—Slender muscle, extends from prothoracic sternal arm to the edge of mesepisternum of the opposite side.

103. Transverse ventral muscle (fig. 54).—Broad, flat, short bundle of fibers from the first spina to the medial edge of the mesepisternum.

104. Spino-sternal muscle (fig. 54).—From first spina to base of mesothoracic sternal arm.

105. Spinal rotator of the mid-coxa (fig. 54).—Long, flat, slender muscle arising from first spina, inserted on the ridge which limits the meron of the mid-coxa.

106. Spinal longitudinal ventral muscle (fig. 54).—Very slender, threadlike muscle, going along the median line from the first to the second spina.

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107. Closing muscle of the first spiracle (fig. 35).—Small flat, triangular muscle arising from the anterior part of the chitinous ring that surrounds the spiracle, going upward to its insertion on the median part of the anterior lip.

108. First phragmal muscle of the episternum (figs. 29, 30).—Short, flat muscle inserted on the anterior edge of the episternum, slants inward to the medial part of the phragma.

109. Second phragmal muscle of the episternum (figs. 29, 30).—Much weaker than *108*. Its insertion on the episternum lies close to that of *108*, but the muscle slants outward to the lateral part of the phragma.

110. Dorsal longitudinal muscle (fig. 23).—Flat bundle of fibers that extends along the median line from first to second phragma.

111. First oblique dorsal muscle (figs. 22, 23).—Small, triangular muscle going from median portion of second phragma to median line on the tergum.

112. Second oblique dorsal muscle (fig. 22).—Broad, flat muscle going from second phragma to tergum.

113. Third oblique dorsal muscle (fig. 22).—Broad, flat muscle, going from lateral portion of the second phragma to the tergum.

114. Tergo-pleural muscle (figs. 22, 23, 24).—From the tergum, goes downward to the upper surface of pleural ridge.

115. Pleuro-alar muscle, flexor of the wing (figs. 22, 23, 24, 25).—Arises from the under side of the pleural ridge, goes dorsally to its insertion on the 3rd axillary (fig. 21, *3Ax*).

116. Tergo-pleural muscle (figs. 22, 23, 24, 25).—Broad bundle of short fibers going from a broad insertion along the anterior edge of pleural ridge and pleural arm to the downward-bent part of the anterior notal wing process which articulates with the first axillary (*1Ax* in fig. 21).

117. Pleuro-sternal muscle (fig. 25).—Broad, short muscle, from the anterior edge of the pleural arm to the anterior edge of the sternal arm.

118. First tergal muscle of the trochantin (figs. 22 to 28).—Powerful muscle, from a broad origin on the anterior edge of the tergum, goes tapering backward and downward to its insertion on the surface of the first plate of the trochantin (figs. 33, 34, *1Tn*) very close to the articulation with the coxa.

119. Second tergal muscle of the trochantin (figs. 22 to 28).—Originates on the anterior part of the tergum, inserts on apodeme on the edge of the first plate of trochantin.

120. Third tergal muscle of the trochantin (figs. 22 to 28).—Originates on the tergum posterior to *119*, goes to apodeme on the edge of the first plate of trochantin.

121. Phragmal muscle of the basisternum (figs. 28, 29).—Narrow muscle; origin on the lateral portion of the phragma; goes

downward and backward to its insertion on the lateral portion of the basisternum.

122. *First episternal muscle of the trochantin* (figs. 29, 30, 31).—From its origin on the anterior edge of the episternum goes ventrally to insert on the surface of the first plate of trochantin (figs. 33, 34, *1Tn*), just before the insertion of *118*.

123. *Second episternal muscle of the trochantin* (figs. 29, 30, 31, 32).—Origin on the anterior edge of the episternum; goes ventrally to a broad insertion along the anterior edge of the first plate of the trochantin.

124. *Third episternal muscle of the trochantin* (fig. 32).—From its origin, near the anterior edge of the episternum, goes ventrally to a broad insertion on the anterior edge of the first plate of the trochantin.

125. *Phragmal muscle of the sternal arm* (fig. 54).—Origin on lateral part of the second phragma; goes inward and downward to the upper surface of basal part of sternal arm.

126. *Sternal promotor of the coxa* (figs. 28, 29, 30).—Origin on lateral part of anterior edge of episternum; goes ventrally to anterior edge of coxa, between the coxal articulations with the epimeron and trochantin.

127. *Sterno-pleural promotor of the coxa* (figs. 29, 31, 32).—Origin on surface of episternum and under surface of pleural ridge; goes tapering posteriorly to small plate near coxo-pleural articulation.

128. *Subalar muscle of the fore wing* (figs. 22 to 27).—Powerful muscle, originates on the meron of the mid-coxa, goes forward and upward to insert on the subalar plate (*Sa*). Corresponds to the depressor-extensor of the fore wing in other insects.

129. *First tergal remotor of the coxa* (figs. 22, 23, 24).—Origin on the tergum; goes dorsally to the posterior (dorsal) portion of the coxal rim.

130. *Second tergal remotor of the coxa* (figs. 22, 23, 24).—Powerful muscle, lies partially underneath *129*. Originates on the anterior part of the tergum, goes dorsally to the posterior (dorsal) portion of the coxal rim.

131. *Third tergal remotor of the coxa* (figs. 22, 23, 24).—Powerful muscle, originates on anterior median part of the tergum, goes dorsally to the posterior (dorsal) portion of the coxal rim.

132. *Sternal remotor of the coxa* (fig. 25).—Broad, flat muscle, going from the posterior edge of the sternal arm to the posterior (dorsal) portion of the coxal rim.

133. *Sternal muscle of the coxa* (fig. 25).—From the end of the sternal arm to the ridge which limits the meron on the anterior (ventral) wall of the coxa. Acts probably as a rotator.

134. *Spinal muscle of the coxa* (figs. 25, 30).—Long, flat muscle, originates on second spina, goes to the ridge which limits the meron on the anterior (ventral) wall of the coxa. Acts probably as a rotator.

135. *Main depressor of the leg* (figs. 22 to 28).—The most powerful muscle of the leg and mesothorax. Originates on several parts of mesothorax and coxa; its branches converge to a broad apodeme inserted on the proximal angle of the trochanter.

   a. *Tergal branch* (figs. 22 to 26).—Origin on antero-lateral part of the tergum.

   b. *Sternal branch* (fig. 26).—Origin on downward-bent flange of the anterior edge of the sternal arm.

   c. *Basalar muscle of the fore wing* (fig. 27).—This large bundle of fibers is attached anteriorly to an apodemal tendon arising from the anterior edge of the basalar plate (fig. 33, *Ba*) (edge which articulates with the edge of the episternum), inserts posteriorly on the broadest portion of the trochanteral tendon. Corresponds to the pronator-extensor of the fore wing in other insects.

   d. *Coxal branch* (fig. 26).—Origin on mesal part of coxal wall.

   e. *Coxal branch* (fig. 28). Origin on the anterior part of coxal rim, near coxo-trochantinal articulation.

136. *Posterior coxal depressor of the leg* (fig. 25).—Broad muscle which originates on the posterior (dorsal) wall of the coxa, near the rim. Its fibers converge to apodeme attached to the trochanter.

137. *Anterior coxal depressor of the leg* (figs. 27, 28, 30).—Arises from the mesal part and mesal angle of the coxa, its fibers converge on apodemal tendon attached to the proximal end of trochanter.

138. *Anterior coxal levator of the leg* (fig. 30).—Slender, weak muscle, from the anterior wall of the coxa to a thin apodemal tendon attached to the femoral part of the trochanter.

139. *Main coxal levator of the leg* (figs. 25 to 28).—With several origins on the coxal wall, its fibers converge on apodemal tendon attached to the trochanter.

   a. (figs. 25, 26).—Has its origin on the posterior wall of the coxa, toward the meral angle.

b. (figs. 27, 28).—Origin on the anterior part of the coxal rim and on the ridge which limits the meron.

c. (fig. 28).—Origin on the anterior wall of coxa and coxal rim.

140. Posterior coxal levator of the leg (fig. 25).—Rather small muscle with four branches (*a, b, c, d*) which originate on the posterior wall of the coxa. All branches converge on apodemal tendon which is attached to the trochanter very near to the tendon of *139*.

Numbers *141* to *146* have been left for the muscles of the rest of the middle leg.

METATHORAX

147. Closing muscle of the second spiracle (fig. 52).—Small, fan-shaped muscle. Origin on the inferior part of the spiracular plate. Its fibers converge on a lever arising from the inferior commissure of the spiracular opening.

148. Ventral longitudinal muscle (fig. 54).—Long, flat band of fibers going ventrally from the sternal arm of the mesothorax to the sternal arm of the metathorax.

149. Transverse ventral muscle (fig. 54).—Flat ribbon from the second spina (*2Spn*) to a small plate near the edge of the metepisternum.

150. Phragmal muscle of the episternum (fig. 54).—Broad, short, flat muscle going from the second phragma to the anterior edge of the metathoracic episternum.

151. Spino-sternal oblique muscle (fig. 54).—Flat bundle of fibers extending from the second spina to the anterior edge of the sternal arm.

152. Spino-sternal longitudinal muscle (fig. 54).—Very slender, threadlike bundle of fibers running along the medial line from the second spina to the base of the metathoracic sternal arm.

153. Dorsal longitudinal muscle (figs. 37, 38).—Flat bundle of fibers between the second phragma and the first abdominal tergum.

154. First dorsal oblique muscle (fig. 37).—Small, short muscle which originates on the median line of the tergum and goes to the medial part of the first abdominal tergum.

155. Second dorsal oblique muscle (fig. 37).—Two broad bunches of fibers (*a* and *b*) which take their origin near the median line of the tergum and go to the lateral part of the anterior edge of the first abdominal tergum.

156. Third dorsal oblique muscle (fig. 37).—Very short muscle. Origin on the tergum, insertion on an upward-bent flange on the lateral part of the edge of the first abdominal tergum.

157. Tergo-pleural muscle (figs. 37, 38, 39).—Broad, powerful muscle; origin on lateral part of the tergum, goes downward and outward to its insertion on the upper surface of the pleural ridge.

158. Pleuro-alar muscle, flexor of the wing (figs. 37 to 42, 44).—Arises from the under surface of the pleural ridge, goes upward to its insertion on the third axillary (fig. 36, *3Ax*).

159. Tergo-pleural muscle (figs. 37 to 43).—Broad, flat bundle of short fibers going from a broad origin on the anterior edge of the pleural arm to its insertion on a downward-bent part of the anterior notal wing process which articulates with the first axillary (*1Ax* in fig. 36).

160. Pleuro-sternal muscle (figs. 40 to 43).—Broad, flat, short muscle going from the anterior edge of the pleural arm to the anterior edge of the sternal arm.

161. First tergal muscle of the trochantin (figs. 37 to 46).—From a broad insertion on the anterior edge of the tergum goes tapering backward and downward to its insertion on the surface of the posterior end of the first plate of the trochantin (*1Tn* in fig. 50).

162. Second tergal muscle of the trochantin (figs. 37 to 46).—Origin on the anterior edge of the tergum, mesal of *161;* goes in the same direction as *161* to its insertion on apodemal tendon of the mesal edge of the first plate of trochantin.

163. Third tergal muscle of the trochantin (figs. 37 to 46).—Origin on anterior portion of the tergum, goes in the same direction as *162* to the same apodemal tendon.

164. First episternal muscle of the trochantin (fig. 47).—Broad, flat muscle. Origin near anterior edge of the episternum, goes ventrally to its insertion on the surface of the first plate of trochantin.

165. Second episternal muscle of the trochantin (figs. 47, 48).—Flat bundle of fibers which has its origin near the anterior edge of the episternum and goes ventrally to a broad insertion on the anterior edge of the first plate of the trochantin.

166. Third episternal muscle of the trochantin (figs. 48, 49).—Flat, short, fan-shaped muscle arising from the surface of the episternum, inserts on the anterior edge of the first plate of the trochantin, lateral of the insertion of *165*.

167. First episternal promotor of the coxa (fig. 46).—Very broad, flat muscle which originates on the anterior margin of the episternum and goes ventrally to the anterior edge of the ventral wall of the coxa, between the epimeral and trochantinal articulations.

168. Second episternal promotor of the coxa (figs. 47, 48).—Origin on the postero-lateral portion of the episternum and the under surface of the pleural ridge and pleural arm; insertion on apodemal tendon attached to a small plate near the edge of the coxa and the coxo-pleural articulation.

169. Subalar muscle of the hind wing (figs. 37 to 42).—Powerful muscle which originates on the meron and goes upward and forward to insert on the subalar plate (*Sa*). Corresponds to the depressor-extensor of the wing in other insects.

170. First sternal muscle of the coxa (figs. 40 to 43).—Slender muscle. Origin on the end of the sternal arm. Insertion on the ridge which limits the meron, very close to the coxo-pleural articulation. Probably acts on rotator or rotator-adductor of the coxa.

171. Second sternal muscle of the coxa (figs. 40, 41, 42).—Flat muscle, from a broad origin on the posterior edge of the sternal arm, goes to its insertion on the ridge which limits the meron. Probably acts as rotator or rotator-adductor of the coxa.

172. Sternal remotor of the coxa (figs. 41, 42, 43).—Broad, flat, short bundle of fibers which originates on the posterior edge of the sternal arm and inserts on the posterior (dorsal) part of the coxal rim.

173. Spinal muscle of the coxa (fig. 54).—Very slender and long bunch of fibers. Origin on the second spina. Insertion on anterior wall of the coxa, between *181b* and *181c*. Acts probably as adductor and rotator.

174. First tergal remotor of the coxa (figs. 37, 38, 39).—Flat muscle, originates on the anterior part of the tergum, goes dorsally to the posterior part of the coxal rim.

175. Second tergal remotor of the coxa (figs. 37, 38, 39).—Originates on the anterior part of the tergum, goes dorsally underneath *174* to insert on the posterior part of the coxal rim.

176. Third tergal remotor of the coxa (figs. 37, 38, 39).—Powerful muscle, originates on the anterior part of the tergum, inserts on the posterior part of the coxal rim.

177. Main depressor of the leg (figs. 37 to 46).—The most powerful muscle of the leg and metathorax. It has several origins on dif-

ferent parts of the metathorax and coxa, and its different branches insert on a broad common apodemal tendon attached to the proximal angle of the trochanter (*177T*).

a. Tergal branch (figs. 37 to 44).—Origin on anterior part of the tergum.

b. Sternal branch (fig. 44).—Short, flat bundle of fibers. Origin on downward-bent flange of the anterior margin of the sternal arm.

c. Basalar muscle of the fore wing (fig. 45).—This large bunch of fibers is attached anteriorly to an apodemal tendon arising from the edge of the basalar plate which articulates with the episternum. Corresponds to the promotor-extensor of the hind wing in other insects.

d. First coxal branch (figs. 41 to 45).—Origin on mesal angle of coxa.

e. Second coxal branch (fig. 46).—Origin on the anterior wall of the coxa and anterior part of the coxal rim.

178. Posterior coxal depressor of the leg (fig. 40).—Broad, flat muscle. Origin on the posterior wall of the coxa and posterior part of the coxal rim. Insertion on apodemal tendon attached to the posterior part of the proximal end of the trochanter.

179. Anterior coxal depressor of the leg (figs. 46, 47).— Flat muscle. Origin on anterior wall of the coxa and anterior part of the coxal rim. Insertion on apodemal tendon attached to the anterior part of the proximal end of the trochanter.

180. Anterior coxal levator of the leg (fig. 47).—Slender muscle, originates on the anterior wall of the coxa, inserts on apodemal tendon attached to the anterior part of the distal half of the trochanter.

181. Main levator of the leg (figs. 40 to 43, 46).— From three origins on the posterior and anterior walls of the coxa, its branches converge on apodemal tendon attached to the distal part of the trochanter.

a. Posterior branch (figs. 40, 41).—Origin on lateral angle of posterior wall of the coxa.

b. First anterior branch (figs. 42, 43, 46).—Has its origin on anterior part of coxal rim and ridge which limits the meron on the anterior wall of the coxa.

c. Second anterior branch (fig. 46).—Origin on anterior portion of coxal rim. The insertion of *173* (fig. 54) separates this branch from *b*.

182. Anterior coxal levator of the leg (fig. 40).—From different origins on the posterior wall of the coxa, its four branches converge to an apodemal tendon attached to the trochanter very closely to that of *181*.

a and *b*. (fig. 40).—Origin on posterior wall of coxa.

c and *d*. (fig. 40).—Origin on posterior part of coxal rim.

Numbers *183* to *188* have been left for the muscles of the rest of the leg.

The following muscles, going from the metathorax to the abdominal sclerites, must be considered intersegmental.

189. Spino-sternal muscle (fig. 54).—Very slender bunch of extremely long fibers going from the second spina to the second abdominal sternum.

190. Tergo-sternal muscle (figs. 38, 39).—From the upper surface of the sternal arm to the first abdominal tergum.

191. Oblique ventral muscle (fig. 54).—From the base of the sternal arm to the anterior edge of the first abdominal sternum.

192. First longitudinal ventral muscle (fig. 54).—From the under surface of the sternal arm to the anterior edge of the first abdominal sternum.

193. Second longitudinal ventral muscle (fig. 54).—Two branches having their origin on both sides of *190* converge to form a single flat muscle which goes backward overlapping *192* to insert on the anterior edge of the second abdominal sternum.

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ABBREVIATIONS USED ON THE FIGURES

For numbers of the muscles refer to part II (list of muscles).

Ax, axillaries. *1Ax*, first axillary; *2Ax*, second axillary; *3Ax*, third axillary.

Ba, basalare, basalar plate.

Bs, basisternum.

Cv, cervical plates. *1Cv*, first cervical; *2Cv*, second cervical; *3Cv*, third cervical; *4Cv*, fourth cervical.

Cx, coxa.

Epm, epimeron.

Eps, episternum. *1Eps*, first plate of the episternum; *2Eps*, second plate of the episternum.

Fm, femur.
Fs, furcasternum.
Hd, head.
Hp, humeral plate.
Ju, jugal region.
m, first median plate.
m', second median plate.
Mer, meron.
PlA, pleural arm.
PlR, pleural ridge.
SA, sternal arm.
Sa, subalare, subalar plate.
Spn, spina. *1Spn*, first spina; *2Spn*, second spina.
T, tendon (used after the number of a muscle).
Tg, tegula.
Tn, trochantin (*1 Tn*, first trochantinal plate; *2 Tn*, second trochantinal plate).
Tr, trochanter.

EXPLANATION OF PLATES

Plate 1

Fig. 1. Right half of the prothorax, dorsal view. The right half of the head can be seen in the upper part of the figure. The muscles appear as they are seen when the pronotum is removed.
2. Same. Some of the muscles which appear in the preceding figure have been removed to show the muscles underneath.
3. Same, some muscles removed.
4. Same. Right coxa, trochanter, and part of the femur are seen in the lower part of the figure. Some muscles removed.
5. Same, some muscles removed.
6. Same, some muscles removed.
7. Same, some muscles removed. Posterior wall of coxa removed to show muscles inside.
8. Same, some muscles removed in thorax and coxa.
9. Same, some muscles removed.

Plate 2

Fig. 10. Right half of the prothorax and right coxa seen from above. Some muscles removed.
11. Same, some muscles removed.
12. Same, some muscles removed.
13. Same, some muscles removed.
14. Same, some muscles removed.
15. Skeleton of the right side of the prothorax seen from above. The pronotum has been removed. Coxa, trochanter, and femur are seen in the lower part of the figure. (See explanation of abbreviations.)
16. Skeleton of the left side of the prothorax seen from below.
17. Left half of the prothorax, mesal view.

Plate 3

Fig. 18. Left half of the prothorax, mesal view. Some of the muscles which appear in figure 17 have been removed.
19. Same, some muscles removed.
20. Same, some muscles removed.
21. Articulation of the right fore wing with the mesothorax, dorsal view. Only the right half of the mesonotum and the basal part of the wing appear on the figure. (See explanation of abbreviations.)
22. Right half of the mesothorax, dorsal view. Muscles seen as they appear when the mesonotum is removed.
23. Same, some muscles removed.
24. Same, showing the coxa in the lower part of the figure. Some muscles removed.

Plate 4

Fig. 25. Right side of the mesothorax and right coxa, dorsal view. The posterior wall of the coxa has been removed to show the muscles inside.
26. Same, some muscles removed.
27. Same, some muscles removed.
28. Same, some muscles removed.
29. Same, some muscles removed.
30. Same, some muscles removed.
31. Same, some muscles removed.
32. Same, some muscles removed.
33. Skeleton of the right side of the mesothorax, dorsal view. The mesonotum has been removed. Coxa, trochanter, and femur are shown. (See explanation of abbreviations.)

Plate 5

Fig. 34. Skeleton of the left half of the mesothorax, left coxa, trochanter, and femur, ventral view. (See explanation of abbreviations.)
35. Right mesothoracic spiracle, mesal view.
36. Articulation of the right hind wing with the metathorax, dorsal view. Only the right half of the metanotum and the basal part of the wing appear in the figure. (See explanation of abbreviations.)
37. Left half of the metathorax, dorsal view. The muscles appear as they are seen when the metanotum is removed. The first abdominal tergum is shown in the lower part of the figure.
38. Same, first abdominal tergum and some muscles removed.
39. Same, some muscles removed. Coxa, trochanter, and femur shown in the lower part of the figure.

Plate 6

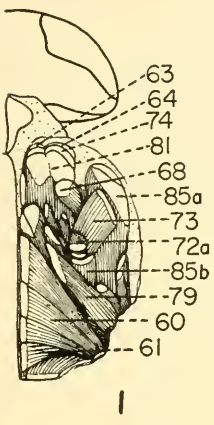
Fig. 40. Right half of the metathorax and right coxa, dorsal view. Posterior wall of the coxa has been removed to show the muscles inside.
41. Same, some muscles removed.
42. Same, some muscles removed.
43. Same, some muscles removed.

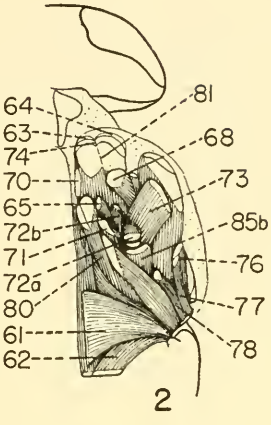
Plate 7

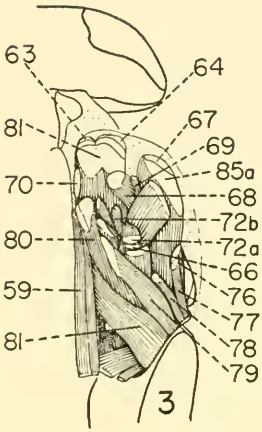
Fig. 44. Right half of the metathorax and right coxa, dorsal view. Posterior wall of coxa removed to show muscles inside. Some muscles removed.
45. Same, some muscles removed.
46. Same, some muscles removed.
47. Same, some muscles removed.

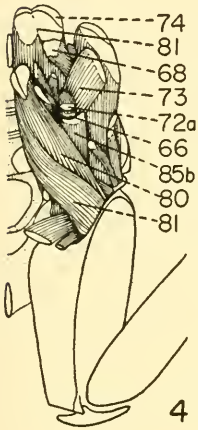
Plate 8

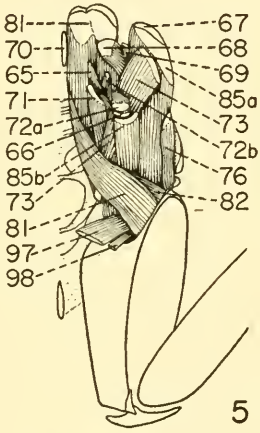
Fig. 48. Right half of the metathorax, dorsal view, some muscles removed.
49. Same, some muscles removed.
50. Skeleton of the right half of metathorax, right coxa, trochanter, and femur, dorsal view. (See explanation of abbreviations.)
51. Skeleton of the left half of metathorax, left coxa, trochanter, and femur, ventral view. (See explanation of abbreviations.)
52. Right metathoracic spiracle, mesal view.
53. Trochanter of the right hind leg, dorsal view.
54. Right half of the whole thorax (nota removed), dorsal view. Only ventral muscles are shown.

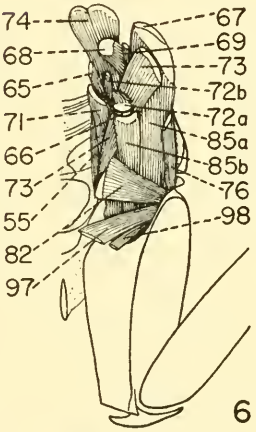


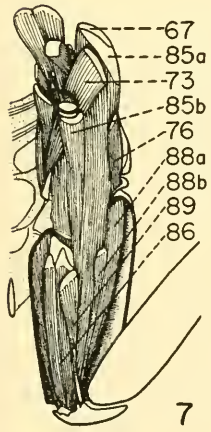


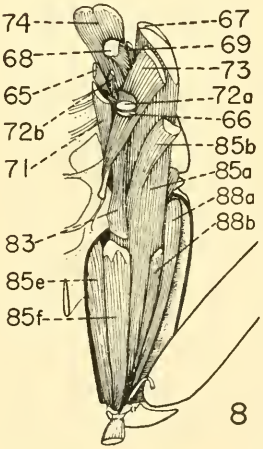


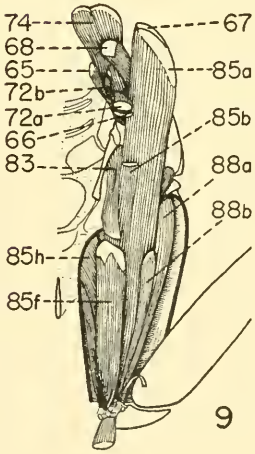












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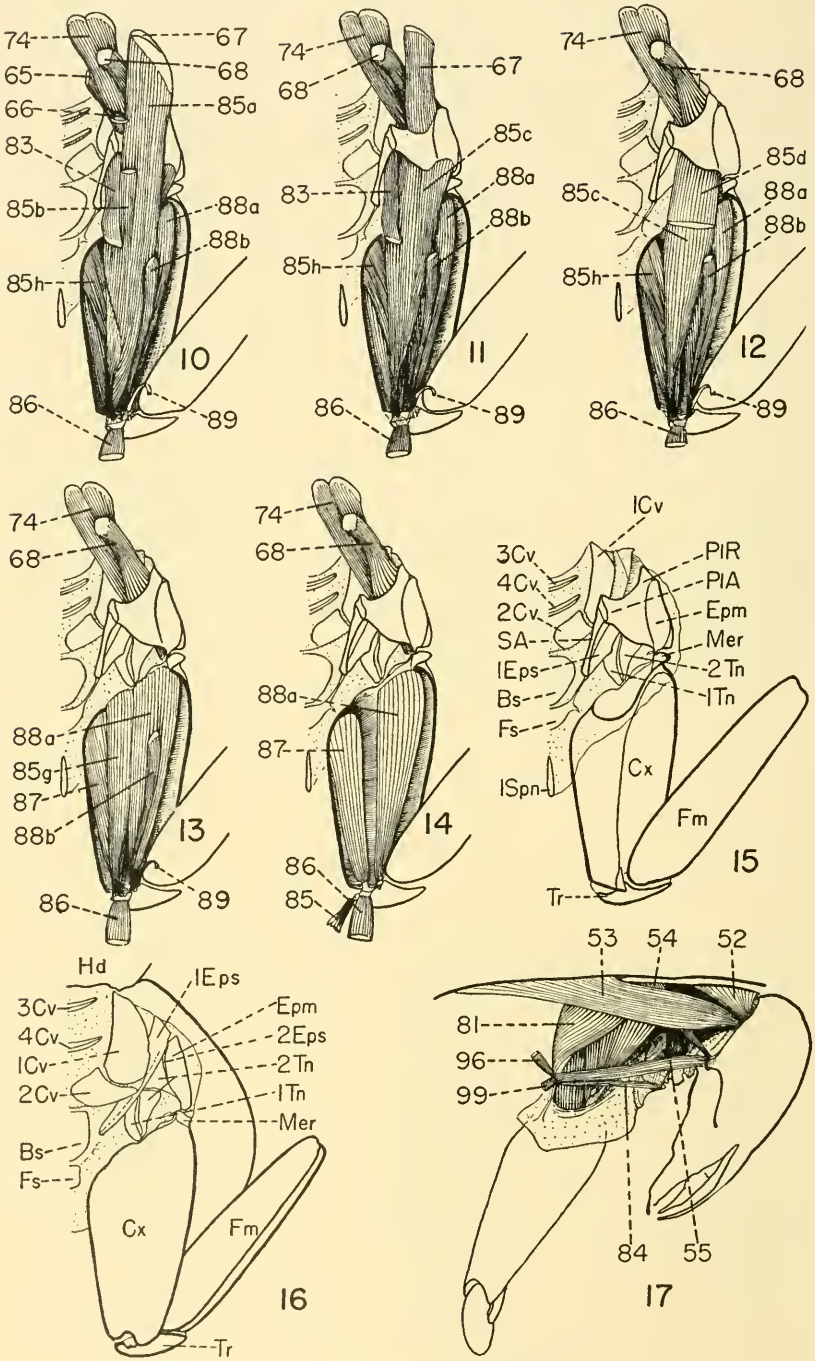

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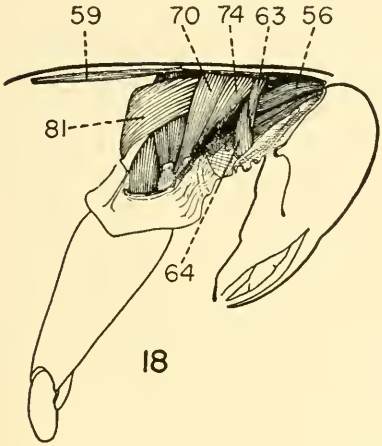

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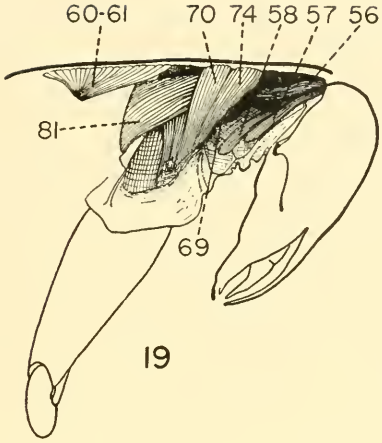

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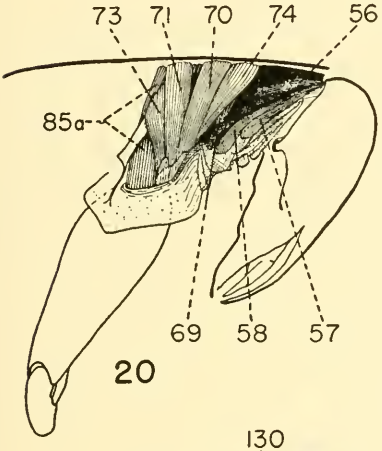

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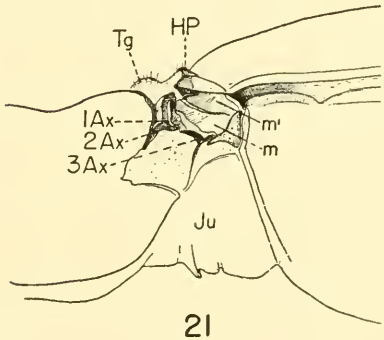

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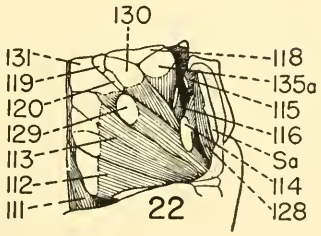

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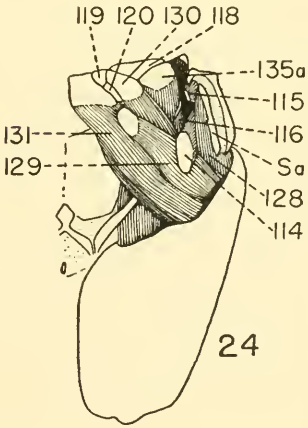

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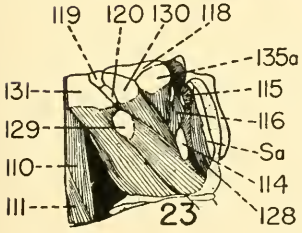

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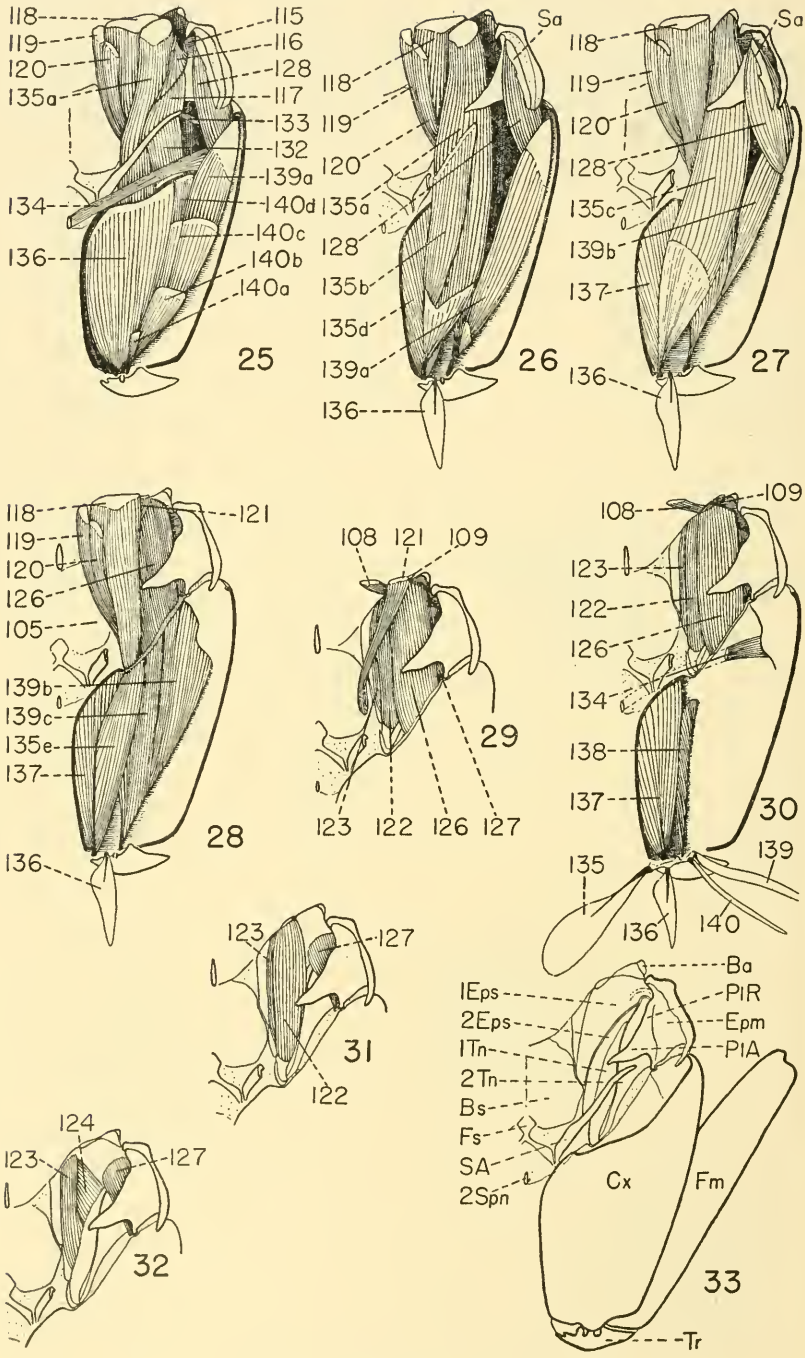
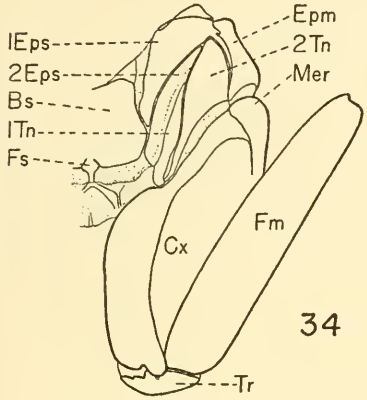
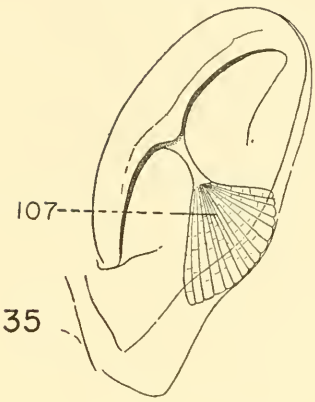
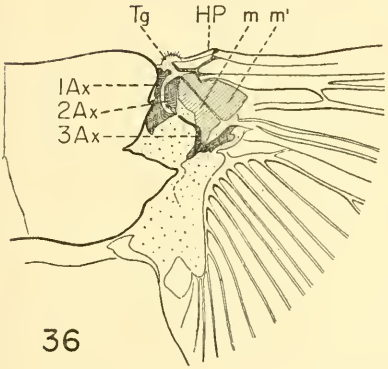
(For explanation, see p. 22.)

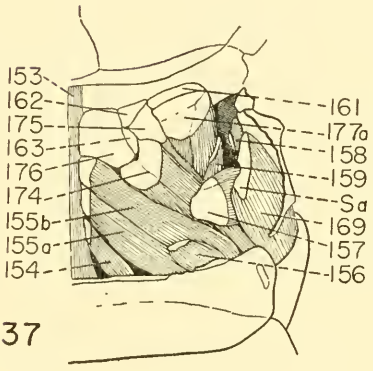


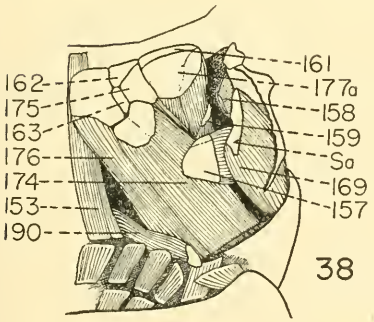
(For explanation, see p. 22.)

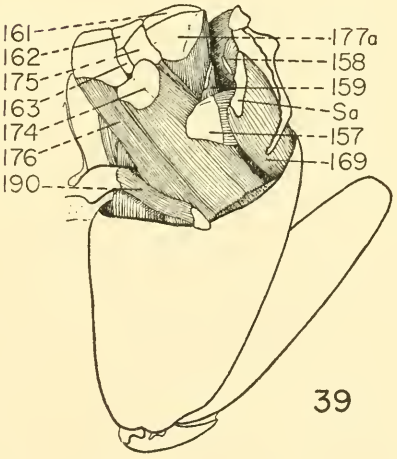




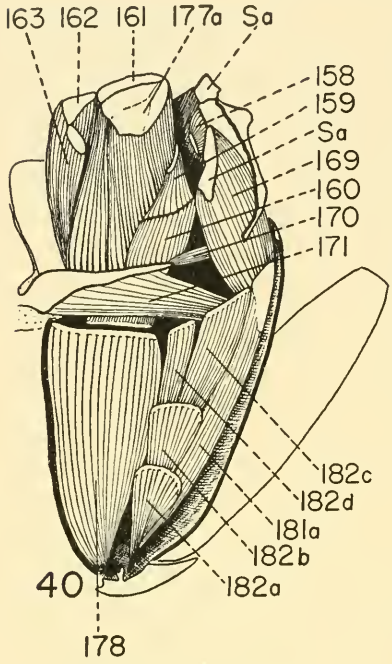


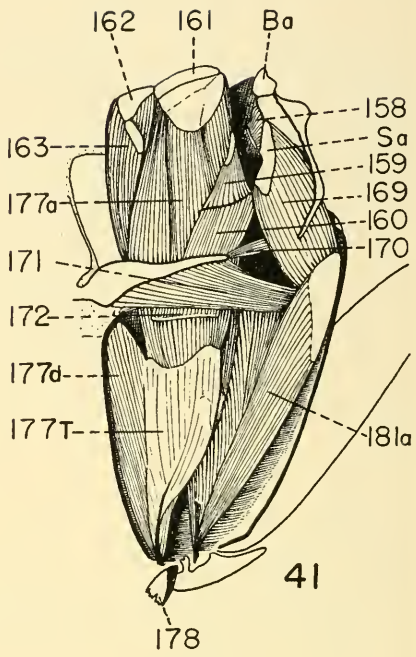


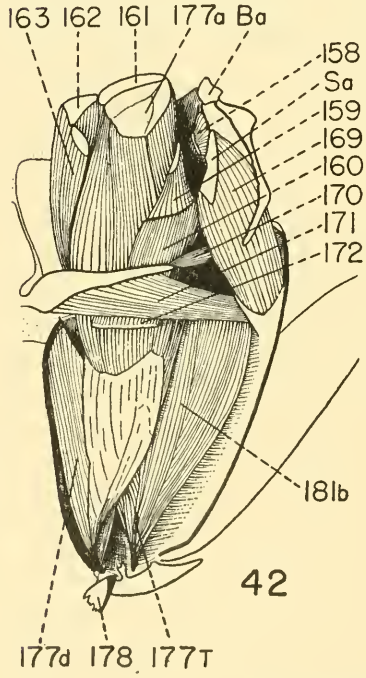


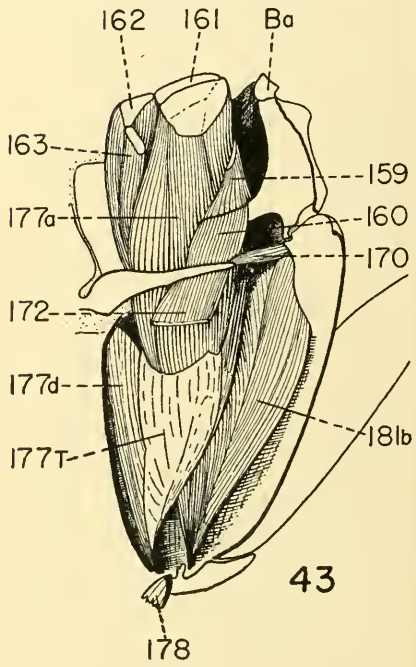


(For explanation, see p. 22.)









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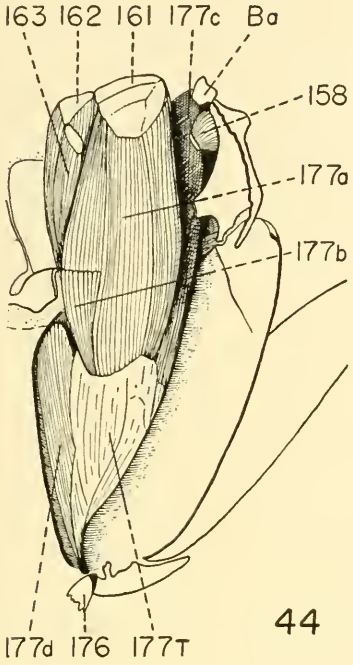
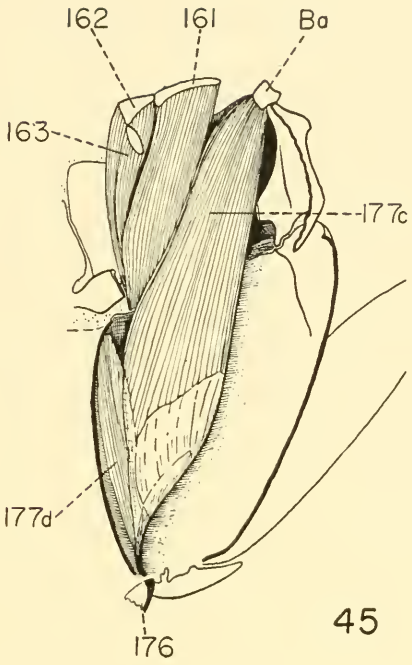
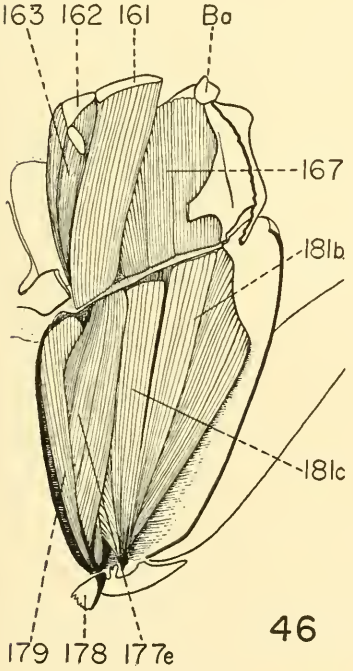
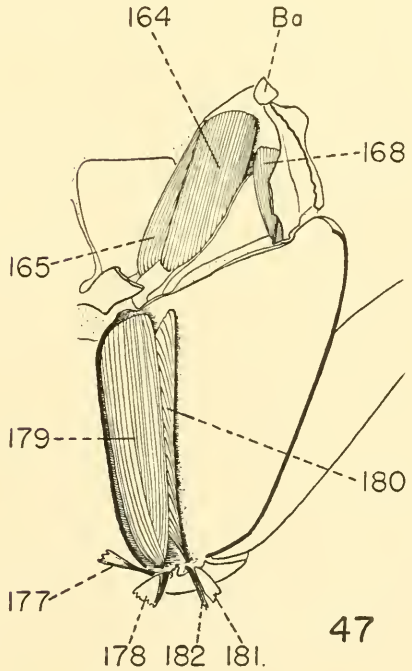
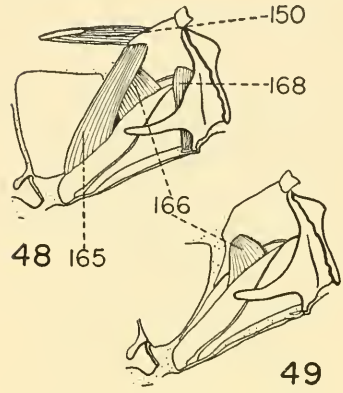


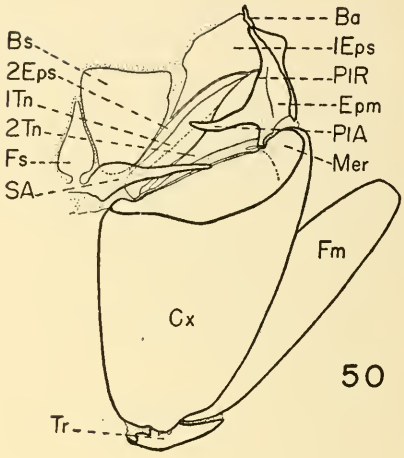


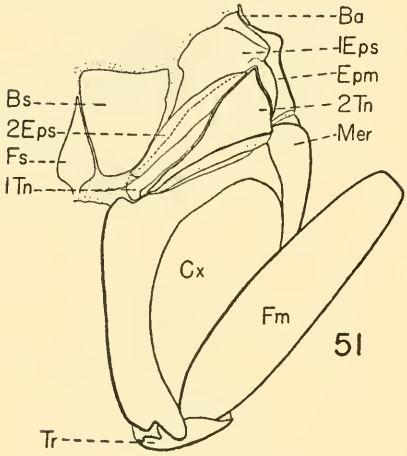


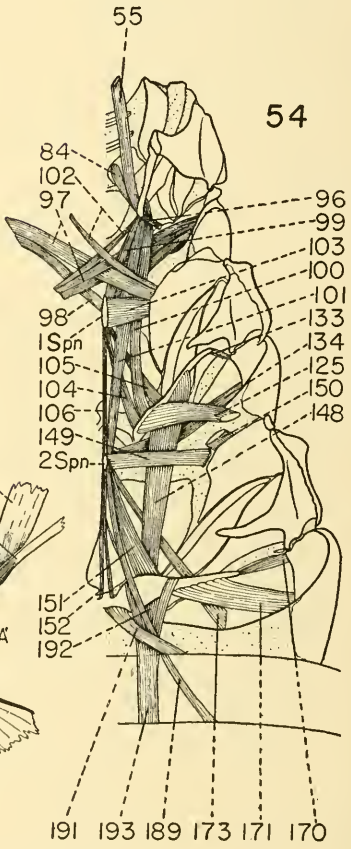


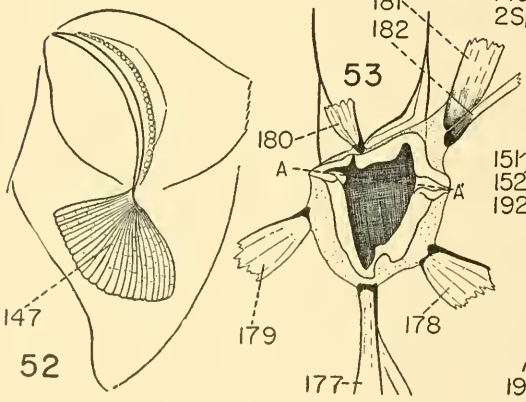
(For explanation, see p. 23.)











(For explanation, see p. 23.)