SMITHSONIAN MISCELLANEOUS COLLECTIONS VOLUME 103, NUMBER 7

# THE MUSCULATURE OF THE LABRUM, LABIUM, AND PHARYNGEAL REGION OF ADULT AND IMMATURE COLEOPTERA

(WITH 24 PLATES)

BY

CARL KESTER DORSEY Bureau of Entomology and Plant Quarantine U. S. Department of Agriculture



(PUBLICATION 3697)

CITY OF WASHINGTON PUBLISHED BY THE SMITHSONIAN INSTITUTION JANUARY 20, 1943



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## By CARL KESTER DORSEY

Bureau of Entomology and Plant Quarantine, U. S. Department of Agriculture (WITH 24 PLATES)

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#### INTRODUCTION

This paper presents the results of a comparative study of the muscle arrangement in certain regions of the insect head and stomodaeum. A preliminary study was made in Orthoptera, Dermaptera, Hymenoptera and Neuroptera, and was followed by a similar but more inclusive study of representatives of adult and immature stages of the order Coleoptera.

Several species of orthopteroid insects were dissected to determine the muscular arrangement in a generalized form of insect. The other orders are included to observe similarities with and variations from the type of muscle system in Orthoptera, of which *Periplaneta americana* L. is chosen as the most generalized form.

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In order to observe carefully the places of origin and insertion of the labral, labial, hypopharyngeal, and pharyngeal muscles it is necessary to remove the maxillae and mandibles and their muscles. The maxillary, mandibular, and antennal muscles are not included in this study.

This particular work evolved from an interest as to how chewing insects actually accomplish the feat of getting the food into the true mouth, which, of course, is located in the posterior region of the cibarium. Much is known as to how these insects procure and chew their food, but the hypopharynx though tonguelike in position could not be very efficient in accomplishing the work done by the tongue of a vertebrate. In many insects the hypopharynx, for all practical purposes, can be considered to be absent; such insects also ingest food and thrive, so the hypopharynx alone cannot be responsible for the act of placing the food in the mouth from which point it can be swallowed.

It is difficult and often impossible to identify corresponding muscles on a functional basis. A muscle, for example, as found in one species may be an adductor while its homolog in another species is perhaps a retractor because of some slight change in the position of the point of insertion. For this reason the general application of functional names to insect muscles is limited; a careful study of each species individually is necessary to ascertain muscle functions.

It is hoped that the facts of the arrangement of muscles, and certain anatomical observations herein presented will contribute to a better understanding of the means of ingestion of food by chewing insects, and also of the homologies of muscles between orders of insects, or between families within an order.

The Leng system of classification as modified by Böving and Craighead (1930) is followed, and at least one family from each superfamily selected from which a genus is chosen for study. When possible the immature stage of the same genus is used. The species of Coleoptera included in this study are not considered as representative, necessarily, of their respective families.

This work is presented in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Graduate School, Entomology Department, University of Maryland. The study was carried on under the direct supervision of R. E. Snodgrass of the United States Department of Agriculture, Bureau of Entomology and Plant Quarantine, who is also a member of the staff of the University of Maryland, Entomology Department. The writer is sincerely grateful to Mr. Snodgrass for his guidance and encouragement throughout this entire study, and also to Dr. Ernest N. Cory, head of the Entomology Department, University of Maryland, for his helpful criticisms. The assistance of the United States National Museum in the loan of certain immature stages of Coleoptera for study is appreciated as is also that of several specialists in the Division of Insect Identification, Bureau of Entomology and Plant Quarantine, for their help in the identification of certain species.

## I. GENERAL DISCUSSION OF THE MUSCULATURE

Among the orthopteroid insects there is apparently, with minor variations, a general plan of muscle arrangement. The American cockroach, *Periplaneta americana* L., is selected as a representative of Orthoptera exhibiting the generalized plan of musculature. The muscles included in this work are numbered for convenience of study and their homologies in other species and orders are considered.

The muscles are considered as occurring in definite pairs unless indicated as otherwise. The muscles in the dorsal region of the head inserted on the stomodaeum posterior to the paired nerve (frontal connective) that connects the frontal ganglion with the brain are considered as belonging properly to the frons; those muscles that are anterior to this nerve belong to the clypeal region proper.

1. Compressor muscle of the labrum (fig. 1).—An asymmetrical muscle arising in the posterior region of the dorsal wall of the labrum; inserted along the lateral margin of the ventral wall of the labrum.

2. Dilator muscle group of the labrum (figs. 1, 2).—A transverse band of fibers extending across the ventral wall of the labrum.

3. Ventral (posterior) muscle of the labrum (fig. 2).—Arises in the posterior region of the frons adjacent to the inner margin of the antennal rim and is inserted laterally at the base of the labrum on the torma.

4. Dorsal (anterior) muscle of the labrum (fig. 2).—Arises near the center in the posterior region of the frons and is inserted medially on the posterior dorsal margin of the labrum.

5, 6, and 7. Dorsal dilator muscles of the cibarium (figs. 1, 2).— Arise on the clypeal region slightly laterally and, with the exception of muscle 7, are inserted in the anterior region of the dorsal wall of the cibarium. Muscle 7 is inserted on the dorsal wall of the cibarium, midregion, between the transverse muscles, 12, of this area.

8. Dorsal dilator muscle of the cibarium (figs. 1, 1A, 2).—Arises centrally in the anterior clypeal region; it surrounds muscle 4 (fig. 1A) and extends ventrad to be inserted in the anterior region of the dorsal surface of the cibarium. This muscle was found only in *Periplaneta* americana L.

9. Dorsal dilator muscle of the anterior region of the pharynx (figs. 1, 2).—Arises on the frons anterior to muscle 11 and is inserted on the dorsal wall of the pharynx immediately behind the frontal ganglion connective.

10. Muscle of hypopharyngeal bar Y (figs. 1, 2).—A branched muscle: branch a arises on the frons immediately laterad of muscle II (fig. 1); branch b arises laterally in the anterior region of the frons. Both branches are inserted on the dorsal end of the sclerotized bar Y (fig. 1), branch b laterally.

11. Dorsal dilator muscle of the pharynx (figs. 1, 2).—Arises on the frons immediately laterad of the dorsal muscle of the labrum, 4, and is inserted slightly laterally on the dorsal wall of the pharynx.

12. Compressor muscle group of the cibarium (fig. 2).—Arises on one side of the dorsal wall of the cibarium, central region, and extends transversely across the surface to be attached on the opposite side.

13. Compressor muscles of the anterior region of the cibarium (fig. 2).—Arise laterally on the dorsal wall of the cibarium in the anterior region of muscle group 12; they extend diagonally anteriorly to be inserted on the dorsal surface of the cibarium mesad of one of the dorsal dilator muscles of the cibarium, 5.

14. Hypopharyngeal muscle of the mandible (fig. 1).—Arises on the lateral wall of the mandible and is inserted on the distal end of sclerite X (fig. 1). This muscle was found only in Orthoptera; it is, of course, common in apterygote insects and other arthropods.

15. Anterior dorsal dilator muscle of the salivarium (fig. 1).— Arises on sclerite X adjacent to muscle 16 and is inserted laterally on the ventral wall of the hypopharynx.

16. Dorsal salivary cup muscle (fig. 1).—Arises on the inner surface of sclerite X and is inserted, near the center, on the dorsal surface of the salivary cup.

17. Anterior salivary cup muscle (fig. 1).—Arises laterally on the ventral wall of the labium adjacent to the palpal base and is inserted laterally in the anterior region of the salivary cup anterior to muscle 18.

18. Lateroventral salivary cup muscle (fig. 1).—Arises laterally at the base of the prementum near the dorsal surface and is inserted laterally in the anterior region of the salivary cup.

19. Muscle of the hypopharynx (fig. 1).—Arises on the tentorial bridge immediately dorsad of muscle 20 and is inserted laterally on the base of the hypopharynx.

20. Dorsal (anterior) muscle of the labium (figs. 1, 3).—Arises on the tentorial bridge immediately dorsad of muscle 21 and is inserted laterally in the anterior region of the dorsal wall of the labium. 21. Ventral (posterior) muscle of the labium (figs. 1, 3).—Arises laterally on the tentorial bridge at the posterior end of the anterior tentorial arm and is inserted laterally on the base of the prementum.

22. Muscle of the prementum (figs. 1, 3).—Arises medially in the posterior region of the submentum and is inserted slightly laterally on the base of the prementum.

23. Depressor muscle of the labial palpus (figs. 1, 3).—Arises centrally on the dorsal wall of the labium at the base of the glossa and is inserted dorsally on the base of the palpus.

24. Levator muscle of the labial palpus (figs. 1, 3).—Arises laterally at the base of the prementum and is inserted posteriorly on the base of the labial palpus.

25. Muscle of the labial palpus (figs. 1, 3A).—Arises laterally on the prementum and is inserted basally and somewhat dorsally on the second palpal segment.

26. Muscle of the labial palpus (figs. 3, 3A).—Arises in the middle region of the ventral (posterior) wall of the first palpal segment and is inserted ventrally (posteriorly) in the middle region of the base of the third segment.

27. Muscle of the labial palpus (figs. 3, 3A).—Arises anteriorly at the base of the first palpal segment, inserted on the third segment basally on the anterior margin.

28. Flexor muscle of the glossa (fig. 3).—Arises medially at the base of the prementum and is inserted on the ventral wall of the labium at the base of the glossa.

29. Flexor muscle of the paraglossa (fig. 3).—Arises on the ventral wall of the labium at the base of the prementum and is inserted basally on the ventral wall of the paraglossa.

30. Ventral dilator muscle of the pharynx (fig. 1).—Arises on the tentorium and is inserted medially on the pharyngeal region just within the mouth.

31. Lateral dilator muscles of the pharynx (fig. 2).—Arise laterally on the dorsal head region adjacent to the inner margin of the compound eye posterior to the muscle of hypopharyngeal bar Y, 10, branch A, and are inserted on the side of the pharynx ventrad of the dosal dilator muscle of the pharynx, 11 (fig. 1).

32. Dorsal appressor muscle group of the cibarium (fig. 2).— Arises on the dorsal pharyngeal surface posterior to the frontal ganglion and extends anteriorly beneath the compressor muscle group of the cibarium, 12, to be inserted on the dorsal wall of the cibarium adjacent to the anterior limits of muscle 12. These muscles are found in a well-developed state in the specimens used in this work only in Orthoptera, Dermaptera, and Neuroptera. Two other Orthoptera were studied, the cricket Gryllus assimilis Fab. and the grasshopper Melanoplus differentialis (Thos.). In the latter there are no essential differences in the musculature. In Gryllus the muscle arrangement is practically the same as that found in Periplaneta except for a few minor variations; the dilator muscle group of the labrum, 2, is absent, the ventral muscle of the labrum, 3, is branched, and the muscle of hypopharyngeal bar Y, 10, is not branched.

As a representative of Dermaptera, Anisolabis maritima Gene was chosen (figs. 4, 5, 6). The dorsal (anterior) muscle, 20, of the labium (fig. 5), the ventral (posterior) muscle, 21, of the labium (fig. 5), and the muscle of the prementum, 22 (figs. 5, 6), are essentially the same as those in Periplaneta except that muscle 20 arises posterior to muscle 21. The muscle of the hypopharynx, 19 (figs. 5, 6), arises centrally in the middle region of the mentum instead of on the tentorial structure as it does in the cockroach; this is an unusual origin for this muscle, as it usually arises at some point on the posterior tentorial structure. The insertion of this muscle, however, does not vary. The flexor muscle of the glossa, 28 (fig. 1), and the depressor muscle of the labial palpus, 23 (fig. 1), are absent. The muscles of the labrum, cibarium, and hypopharynx are similar to those of Periplaneta.

In Neuroptera, Corydalus cornutus L. adult and larval stages were studied. The salivary muscles, in the adult form (figs. 8. 9), are similar to those of Periplaneta; the anterior dorsal dilator muscle of the salivarium, 15 (fig: 1), is absent. The full complement of labial muscles is present. The muscle of the hypopharynx, 19 (figs. 8, 9), arises laterally in the posterior region of the gula and is inserted at the base of the hypopharynx, but not on the sides of the salivary cup as is the case in Periplaneta. In addition to the usual compressor muscle of the labrum, I (fig. 8), there is another muscle that arises immediately posterior to muscle I and is inserted in the anterior region of the cibarium on the dorsal wall; this muscle is probably only a division of muscle 1. The ventral muscle of the labrum, 3, and the dorsal muscle of the labrum, 4 (fig. 8), are of the general form and arrangement. Of the dorsal dilator muscles of the cibarium, 5, 6, 7 (fig. 8), muscle 5 is represented by a single pair of muscles; muscle 6 consists of two pairs, and muscle 7 is also made up of two groups of muscles on each side of the dorsum of the cibarium. The dorsal dilator muscle of the anterior region of the pharynx, 9 (fig. 7), arises laterad of the muscle of hypopharyngeal bar Y, 10, instead of mesad which is the usual way.

In the larval stage of *Corydalus* (figs. 10, 11, 12) the muscles vary little from those of the adult, with a few exceptions and variations. Of the salivary muscles, 17 is absent. The *dorsal dilator muscles*, 5 and 7 (figs. 10, 12), are represented by a single pair of muscle groups. The ventral wall of the cibarium is furnished with well-developed transverse, longitudinal, and diagonal muscle groups (fig. 11, 33). These muscles were observed only in Neuroptera.

In Hymenoptera, Sphecius speciosus (Dru.) adults were selected for study (figs. 13, 14, 15, 16). This species possesses muscles that are massive and somewhat complicated in arrangement, and which are not easy to homologize with muscles of Periplaneta, though certain of them can be considered homologous. The flexor muscle of the paraglossa, 29 (fig. 13), arises basally on the ventral wall of the prementum and is inserted at the base of the paraglossa. There is present only one labial-palpus muscle, 24 (fig. 16); it is similar to that found in Periplaneta. The dorsal salivary cup muscle, 16 (fig. 13), arises on the inner surface of sclerite X (fig. 14) and is inserted laterally on the salivary cup. The anterior salivary cup muscle. 18 (figs. 13, 16), which arises immediately posterior to the levator muscle of the labial palpus, 24, on the ventral wall of the prementum, is inserted laterally in the anterior region of the salivary cup. The muscle of the hypopharynx, 10 (fig. 13), arises in the posterior region of the head and is inserted in the posterior region of the salivary cup immediately ventrad and caudad of the dorsal salivary cup muscle, 16. The ventral muscle of the labium, 21 (fig. 13), takes its origin on the inner side of the base of the anterior tentorial arm and is inserted centrally at the base of the prementum. The apparent dorsal muscle of the labium, 20A (fig. 13), arises on the anterior tentorial arm slightly above the ventral muscle of the labium, 21, and is inserted on the base of the cardo proximally, so it probably belongs to the maxilla and not to the labium. The ventral muscle of the labrum, 3 (figs. 14, 15), arises and is inserted in the usual manner. The dorsal dilator muscles of the cibarium, 5, 6, 7 (figs. 14, 15), are powerful and specialized. Muscle 5 arises centrally in the anterior region of the clypeus and is inserted centrally in the anterior region of the dorsal wall of the cibarium. Muscle 6 arises laterally in the anterior region of the clypeus adjacent to the clypeal suture and is inserted on the dorsal wall of the mid-region of the cibarium. Muscle 7 is posterior to muscle 6 in origin and insertion. The compressor muscle group of the cibarium, 12 (figs. 14, 15), is similar to that of Periplaneta. The specialized muscle 34 (figs. 14, 15) arises centrally on the dorsal surface of the modified bar Y (fig. 14) and extends slightly diagonally and anteriorly to become inserted on the dorsal wall of the cibarium, anterior region; this is a compressor muscle of this region that may be homologous with the compressor muscles of the anterior region of the cibarium, 13 (fig. 2), in the cockroach. The two modified sclerites, bars Y (fig. 14), support the sides of the cibarium and stomodaeum; they are united by a continuously sclerotized area that strengthens the ventral wall of the stomodaeum. Muscle 34 (fig. 15) is inserted laterally on the distal end of the bar Y; this muscle extends laterally and anteriorly to its point of origin in the posterior region of the frons adjacent to the inner margin of the compound eye. The dorsal dilator muscle of the pharynx, II (figs. 14, 15), consists of a compact group of fibers and probably is a homolog of muscle 11 in orthopteroid forms. The ventral dilator muscle of the pharynx, 30 (fig. 14), is especially large and powerful; it arises on a sclerotized central projection from the anterior (dorsal) surface of the tentorial bridge by means of a tendon; it is inserted medially on the ventral surface of the continuous sclerotized area that supports the stomodaeum. This is a dilator muscle of the stomodaeum. It was thought on first examination that muscle 35 (figs. 14, 15) was homologous with the muscle of hypopharyngeal bar Y, 10 (fig. 1), in Periplaneta; this is not the case because the small frontal ganglion with its connectives lies posterior to this muscle, the function of which is not certain. In the honeybee, Apis mellifera L., there is a muscle which undoubtedly is homologous with the muscle of the hypopharyngeal bar Y, 10, found in Periplaneta; it consists of an anterior and a posterior branch inserted on the distal end of bar Y, and is posterior to the frontal connective nerve.

## II. MUSCLE ARRANGEMENT IN COLEOPTERA

The muscles of adult and immature Coleoptera included in this work are numbered as in *Periplaneta* and are considered to be homologous with those of the same designation in the orthopteroid forms unless indicated as being otherwise.

Certain muscles appear generally and consistently throughout the adult and immature stages in the order, though there are specialized muscles found in certain species and also generalized muscles that are greatly modified in size, shape, origin, and insertion. By considering the muscles of each superfamily separately it is easier to interpret homologies and the probable function of the various muscles.

#### III. CARABOIDEA

In this group adult Harpalus caliginosus F., Carabidae (figs. 17, 18, 19), Tetracha carolina (L.), Cicindelidae, and Lacoophilus sp., Dytiscidae, were selected for study. The labral muscles are absent in the three genera studied. In *Harpalus* the muscles of the cibarium 5. 6, and 7 (figs. 17, 19) and those of the dorsal and lateral pharyngeal regions are similar to those found in Periplaneta. Bar Y (fig. 19) is attached to a subpharyngeal brace. The lateral dilator muscle of the pharynx, 31 (fig. 19), is not considered, necessarily, as a homolog of 31 in Periplaneta or in any of the other species of Coleoptera since it varies greatly in size, form, and position; but the function being the same, it is given the same number. The place of origin of the labial and hypopharyngeal muscles is unusual. In the anterior region of the gula, caudad of the posterior tentorial pits there is a central invagination, or apodeme (fig. 19, PTN), which is finlike and of considerable size. The muscle of the hypopharynx, 19, the dorsal and ventral muscles of the labium, 20 and 21 respectively, and muscle 21A (fig. 19), arise on this apodeme and not on the tentorial structure as is the usual manner. It is possible that this apodeme represents a greatly modified tentorial bridge and tentorial arms. The dorsal muscle of the labium, 20 (figs. 18, 19), is inserted centrally on a projection that extends inward from the ventral labial wall in the basal region; it possibly performs the same function as muscle 20 in Periplaneta. Muscle 21A (figs. 18, 19) was found only in this species; it probably in some way supplements the action of the other labial muscles.

In Tetracha only the dorsal and ventral muscles of the labium, 20 and 21, respectively, and the muscle of the prementum, 22, are present; they arise centrally in the posterior gular region. The dorsal dilator muscles of the cibarium, 5, 6, and 7, are similar to those of Harpalus; the compressor muscle group of the cibarium, 12, is more strongly developed. The dorsal dilator muscle of the pharynx, 11, is powerfully developed. The tormae of the labrum extend posteriorly and then bend sharply ventrad to form a rigid lateral support on each side of the mouth; this rigid brace is continuous with the ventral head structure. Bar Y projects from the posterior dorsal region of this torma modification; the muscle of hypopharyngeal bar Y, 10, is inserted on its distal end.

In Laccophilus the ventral muscle of the labium, 21, originates in the posterior gular area. The muscle of the hypopharynx, 19, is single, broad, thin, and arises by means of a bifurcate tendon high on each anterior tentorial arm. The compressor muscle group of the cibarium, 12, is well developed. The dorsal dilator muscles of the cibarium, 5, 6, and 7, are essentially the same as those in Harpalus.

For the larval forms in this superfamily, Amara sp. and Galerita sp. were studied. In Amara (figs. 20, 21, 22) the levator muscle of the labial palpus, 24 (fig. 22), is strong and the dorsal and ventral muscles of the labium, 20 and 21 respectively, are large. The dorsal dilator muscles of the cibarium, 5, 6, and 7 (figs. 21, 22), are well developed. The pharynx is small; the dorsal dilator muscle of the pharynx, 11, is absent. Bar Y extends posteriorly along the sides of the cibarium and is connected with the one on the opposite side by a long, subpharyngeal, sclerotized area. In Galerita the dorsal and ventral muscles of the labium, 20 and 21 respectively, are similar to those in Amara. The dorsal dilator muscles of the cibarium, 5, 6, and 7, are grouped together to form a massive unit of muscle fibers. The muscle of hypopharyngeal bar Y, 10, is similar to that of Amara.

#### IV. GYRINOIDEA

The adults studied in this superfamily are Dineutes discolor Aubé and D. vittatus (Germ.), Gyrinidae. In D. discolor (figs. 23, 24, 25) the labral muscles are absent. The dorsal dilator muscles of the cibarium, 5, 6, and 7, the dorsal dilator muscle of the anterior region of the pharynx, 9 (fig. 24), the muscle of hypopharyngeal bar Y, 10 (fig. 23), and the compressor muscle group of the cibarium, 12 (fig. 24), are all similar to those in Harpalus. The dorsal dilator muscle of the pharynx, 11, is absent. Bar Y is also continuous with a subpharyngeal support. There is an apodeme originating in the anterior gular region essentially the same as the one in Harpalus; however, only the dorsal and ventral muscles of the labium, 20 and 21 respectively (fig. 23), arise on it. The muscle of the hypopharynx, 19 (figs. 23, 25), arises by means of a **T**-shaped tendon, the lateral arms of which originate on the walls of the gular suture. The musculature of D. vittatus is practically the same as that in D. discolor.

The larvae used for study are *Dineutes* sp. (figs. 26, 27, 28). The dorsal dilator muscles of the cibarium, 5, 6, and 7, and the muscle of hypopharyngeal bar Y, 10 (figs. 26, 28), are similar to those of the larva of Amara sp.; they are proportionately much more massive. The dorsal dilator muscle of the pharynx, 11, is present and the compressor muscle group of the cibarium, 12, is either absent or so poorly developed that it is not noticeable. The labial muscles are essentially the same as those of Amara with some variation as to shape. The muscle of the prementum, 22 (figs. 27, 28), is present in *Dineutes*.

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## V. STAPHYLINOIDEA

The adults studied in this superfamily are Silpha americana L., Silphidae (figs. 29, 30, 31), and Creophilus villosus Grav., Staphylinidae. In Silpha the labral muscles are present. The compressor muscle of the labrum, I, is well developed (fig. 31), and the ventral muscle of the labrum, 3 (fig. 31), is inserted on the labrum by means of a long, thin tendon. The dorsal dilator muscles of the cibarium, 5, 6, and 7 (figs. 29, 31), the compressor muscle group of the cibarium, 12 (figs. 29, 31), the dorsal dilator muscles of the pharynx, 9 and II (figs. 29, 31), and the muscle of hypopharyngeal bar Y, IO (figs. 29, 31), are all massive and undoubtedly furnish the power for a strong and efficient sucking mechanism. The musculature of the labium is essentially the same as that found in *Periplaneta*, excepting the salivary muscles, which are not found in Coleoptera. The muscle of the hypopharynx, 19 (figs. 30, 31), the dorsal and ventral muscles of the labium, 20 and 21 (figs. 30, 31), the muscle of the prementum, 22 (figs. 30, 31), and the levator muscle of the labial palpus, 24 (fig. 30), are present. The preoral cavity is provided with a sizeable, narrow lobe (fig. 31) that extends downward from the cibarial wall and also is equipped with a suboral grooved shelf (fig. 31) that originates in the posterior dorsal region of the labium, and which receives the cibarial lobe in somewhat of a semi-piston-and-cylinder relationship, possibly to facilitate sucking operations.

In Creophilus the labial muscles are the same in number and arrangement as in Silpha; they arise slightly more posteriorly on the gular sutures. The labral muscles are similar also except that the ventral muscle of the labrum, 3, arises on the anterior surface of the distal end of the anterior tentorial arm at the junction of the arm and the head wall. The muscles of the cibarial and pharyngeal regions are practically the same as those found in Silpha.

Silpha americana L., Silphidae (figs. 32, 33, 34), and a specimen of Staphylinae of the Staphylinidae are the two larval forms used for study. The muscles in Silpha are very well developed. The compressor muscle of the labrum, I, is absent and the ventral muscle of the labrum, 3 (figs. 32, 34), is strong. The dorsal dilator muscles of the cibarium, 5, 6, and 7 (figs. 32, 34), have become grouped together in a large mass. The compressor muscle group of the cibarium, I2 (figs. 32, 34), is well developed as are the dorsal dilator muscles of the pharynx, 9 and II (figs. 32, 34). The muscle of hypopharyngeal bar Y, I0 (fig. 34), is strong and multibranched. Muscle IIA (fig. 34), is an additional dorsal dilator of the pharynx which possibly belongs to the dorsal dilator muscle group of the pharynx, 11. The labium is a good example of the prementum with two divisions I and 2 (fig. 33). The muscle of the hypopharynx, 19 (figs. 33, 34), the dorsal and ventral muscles of the labium, 20 and 21 (figs. 33, 34), and the muscle of the prementum, 22 (fig. 34), are all present, well developed, and take their origin on the tentorial structure. In the specimen of Staphylinae the muscle of the prementum, 22, is inserted on the prementum at the base in the same plane as the dorsal and ventral muscles of the labium, 20 and 21. The prementum is not divided into two parts as in Silpha. The cibarial, pharyngeal, and hypopharyngeal muscles are much the same as those in Silpha, with a few variations. The labral muscles are absent; a tendon arises on the anterior tentorial arm, dorsal region, and extends anteriorly to be inserted basally and laterally on the nasale in a manner very similar to the insertion of the ventral muscle of the labrum, 3, in the adult Creophilus villosus Grav.

## VI. HYDROPHILOIDEA

Sphaeridium scaraboides Linn., Hydrophilidae (figs. 35, 36, 37), is the adult form studied. The muscles, though well developed, are reduced in number. Muscle I (fig. 35) possibly corresponds with the compressor muscle of the labium, I, in Periplaneta; the insertion has become changed from the ventral wall of the labrum to a sclerotized mesal extension of the torma which is continuous with the dorsal wall of the anterior region of the cibarium. The ventral muscle of the labrum, 3 (figs. 35, 37), arises on the distal end of the dorsal branch of the anterior tentorial arm and is inserted in the usual way. The dorsal dilator muscles of the cibarium, 5, 6, and 7, are absent. The anterior tentorial arms are joined by a sclerotized suboesophageal brace, SB (fig. 37); a lateral dilator muscle of the pharynx arises on this brace. The dorsal and ventral muscles of the labium, 20 and 21 (figs. 36, 37), both take their origin in the anterior area of the postmental region.

Sphaeridium bipustulatum Fabr. (figs. 38, 39, 40) and Hydrous triangularis (Say) are the larvae studied in the family Hydrophilidae. In Sphaeridium the labral muscles are absent. The dorsal dilator muscles of the cibarium, 6 and 7 (figs. 38, 39), are present; muscle 6 is long, 7 compact and linear. The dorsal dilator muscles, 9 and 11 (fig. 39), are well developed as is also the muscle of hypopharyngeal bar Y, 10 (fig. 39). Bar Y is continuous with the sclerotized sub-pharyngeal area. The three muscles 36, 37, and 38 (fig. 39) are probably maxillary muscles. Muscle 36 arises laterally from the posterior region of this sclerotized subpharyngeal area and 37 and 38

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arise on a median apodeme in the posterior gular region; all these muscles are inserted at the base of the maxilla. There is a small labial muscle, probably the *ventral muscle of the labium*, 21 (figs. 39, 40), that arises at the base of the postmentum adjacent to the posterior tentorial pits; it is inserted medially and basally on the prementum.

In Hydrous there are five pairs of powerful muscles that arise on the anterior tentorial arm and are inserted at the base of the maxilla. There is a muscle present, probably the ventral muscle of the labium, 21, and another that is inserted on the dorsal region of the labium which may be the dorsal muscle of the labium, 20. The dorsal dilator muscles of the cibarium, 6 and 7, the dorsal dilator muscles of the pharynx, 9 and 11, the muscle of hypopharyngeal bar Y, 10, and the compressor muscle group of the cibarium are all similar to those in Sphaeridium though they are much more massive. The ventral muscles of the pharynx are large and complicated in arrangement.

#### VII. CUCUJOIDEA

In this group Scotobates calcaratus (Fab.), Tenebrionidae, and Epilachna corrupta Muls., Hippodamia convergens Guer., Coccinellidae, adults were used for study. In Scotobates (figs. 41, 42, 43) the labral, cibarial, pharyngeal, and hypopharyngeal muscles are present and well developed. Bar Y (fig. 41) is connected with the anterior, distal edge of the anterior tentorial arm by means of a flat, sclerotized band. The ventral muscle of the labium, 21 (figs. 41, 42), may be homologous with that of Periplaneta, but its origin is on the anterior region of the postmentum and not on the tentorium. The dorsal muscle of the labium, 20 (figs. 41, 42), arises in the usual manner, but it is inserted medially on the inner side of the anterior labial wall and might easily be interpreted as the muscle of the hypopharynx, 19.

In Epilachna there is only one labial muscle; it corresponds with the ventral muscle of the labium, 2I, in Scotobates. The muscles of the labrum, cibarium, and pharynx are essentially the same as those in Scotobates, with a slight variation in arrangement. The muscle of hypopharyngeal bar Y, 10, lies laterad of the ventral muscle of the labrum, 3. The dorsal dilator muscles of the pharynx are very powerful.

In *Hippodamia convergens* Guer. the musculature is practically the same as in *Epilachna*. The *compressor muscle group of the cibarium*, 12, is well developed.

Scotobates calcaratus (Fab.), Tenebrionidae, Hippodamia convergens Guer., Coccinellidae, and Synchroa puncta Newn., Syn-

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chroidae, larvae were studied. In Scotobates (figs. 44, 45, 46) the muscles are well developed. The compressor muscle of the labrum, I, the dorsal dilator muscle of the pharynx, II, and the compressor muscle group of the cibarium, 12, are absent. The dorsal dilator muscles of the cibarium, 5, 6, and 7 (figs. 44, 46), have become grouped together and are indicated only by 7. The muscle of hypopharyngeal bar Y, 10 (fig. 44), has numerous subdivisions. There is a large, heavily sclerotized median cuspidate sclerite (CPS) on the dorsal surface of the hypopharynx (fig. 46). An arm extends posteriorly and ventrally from each side of the posterior region of this sclerite to become joined to a heavily sclerotized intralabial brace the lateral limits of which are the sides of the posterior hypopharyngeal region. The ventral muscle of the labium, 21 (figs. 45, 46), arises and is inserted in the usual manner; the dorsal muscle of the labium, 20 (fig. 46), arises in the posterior lateral region of the submentum just anterior to the posterior end of the anterior tentorial arm. The muscle of the prementum, 22 (fig. 45), is a broad, powerful muscle.

In Hippodamia only the ventral muscle of the labium, 21, is present. The ventral muscle of the labrum, 3, is absent; the tormae are slender and rodlike and extend posteriorly to become united with hypopharyngeal bar Y. The dorsal dilator muscles of the pharynx, 9 and 11, are especially powerful.

In Synchroa the musculature is similar to that of Scotobates though the compressor muscle group of the cibarium, 12, is present and the muscle, of hypopharyngeal bar Y, 10, is not so profusely branched.

#### VIII. BYRRHOIDEA

Only larval forms were available for study in the family Byrrhidae. In Byrrhus (figs. 47, 48, 49) the labral muscles are absent. The dorsal dilator muscles of the cibarium, 5, 6, and 7 (figs. 47, 48), are reduced in size and are grouped together. The dorsal dilator muscle of the anterior region of the pharynx, 9 (figs. 47, 48), is small; the muscle of hypopharyngeal bar Y, 10 (figs. 47, 48), consists of two large branches, 10 and 10A. The labial muscles are somewhat confusing because of an additional labial muscle, 22A (figs. 48, 49). The regular labial muscles, 20 and 21, occur as usual and the muscle of the prementum, 22 (figs. 48, 49), is consistent. The additional labial muscle, 22A, may be a second muscle of the prementum inserted at the base of prementum 1 (figs. 48, 49).

## IX. DASCILLOIDEA

From this superfamily adult and immature stages of Nosodendron californicum Horn, Nosodendridae, and Heterocerus sp., Heteroceridae, larvae were studied. In the adult Nosodendron (figs. 50, 51, 52), of the labral muscles only the ventral muscle of the labrum, 3 (figs. 51, 52), is present. The cibarial, pharyngeal, and hypopharyngeal muscles are well developed. The muscle of hypopharyngeal bar Y, 10 (figs. 51, 52), is especially massive. Bar Y (fig. 52) is greatly modified; it forms a strong, lateral support to the mouth and is continuous with a broad, thin, sclerotized structure that extends ventrally and posteriorly to become united with the ventral head wall. The dorsal and ventral muscles of the labium, 20 and 21 (figs. 50, 52), are present; they originate in the gular area posterior to the submentum. The mentum completely covers the prementum in this species (fig. 52).

In the larval Nosodendron (figs. 53, 54, 55) the labral muscles are absent as is also the compressor muscle group of the cibarium, 12 (fig. 54). The dorsal dilator muscles of the cibarium, 5, 6, and 7, the muscle of hypopharyngeal bar Y, 10, and the dorsal dilator muscles of the pharynx, 9 and 11, are all massive and are collected more or less in the region of the posterior area of the cibarium (figs. 53, 54). Bar Y (fig. 54) is large and forms a strong support on the sides of the mouth; it extends ventrally on the sides of the posterior hypopharyngeal region. The full complement of labial muscles is present.

In Heterocerus the labral, cibarial, pharyngeal, and hypopharyngeal muscles are similar to those of Nosodendron; the muscle of hypopharyngeal bar Y is trifurcate. The dorsal muscle of the labium, 20, arises at the posterior end of the anterior tentorial arms and is inserted on the dorsal wall of the labium at what is probably the base of the hypopharynx. The ventral muscle of the labium, 21, takes its origin medially in the posterior region of the postmentum and is inserted medially at the base of prementum 1. Muscle 22 (probably the muscle of the anterior tentorial arms; it is inserted laterally in the posterior region of prementum 2.

#### X. DRYOPOIDEA

Helichus fastigiatus (Say), Dryopidae (figs. 56, 57, 58), is the adult form selected for study from this superfamily. The musculature in this species is, with some modification, of the generalized plan. The compressor muscle group of the cibarium, 12, is absent

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as also is the anterior dorsal dilator muscle of the pharynx, 9, and the dorsal dilator muscle of the cibarium, 5. Hypopharyngeal bar 3' (fig. 57) is very weakly sclerotized. The labial muscles consist of two pairs, the dorsal and ventral muscles of the labium, 20 and 21 (figs. 57, 58).

The larvae considered from the family Ptilodactylidae are Ptilodactyla serricollis (Say) (figs. 59, 60, 61). The ventral muscle of the labrum, 3, two dorsal dilator muscles of the cibarium, 6 and 7, and the muscle of hypopharyngeal bar Y, 10 (figs. 59, 61), are present and well developed. The dorsal and ventral muscles of the labium, 20 and 21 (figs. 60, 61), are present. Muscle 20 originates medially at the inner base of the anterior tentorial arms; muscle 21 arises on the base of the submentum between the posterior ends of the anterior tentorial arms.

## XI. CANTHAROIDEA

Adults from two families in this group were studied, *Chauliogna*thus pennsylvanicus Deg., Cantharidae, and *Plateros timidus* Lec., Lycidae.

In Chauliognathus (figs. 62, 63, 64) the muscles are very well developed; those of the labrum, cibarium, pharynx, and hypopharynx are massive (figs. 62, 63). The transverse compressor muscle group of the cibarium, 12, is absent. Hypopharyngeal bar Y (fig. 62) is continuous with the greatly modified tentorial structure that forms a strong support to withstand the action of the powerful muscles of this region; it unites the dorsal and ventral head walls rigidly. One side of the structure is joined with the other by means of a subpharyngeal sclerotized area. The posterior (ventral) ends are continuous with the ventral head wall. The epipharyngeal region of the labrum and the posterior dorsal labial region are equipped with a lobe and a grooved receptacle respectively, similar to that already described in the adult Silpha americana L., but in Chauliognathus it is more definitely associated with the epipharyngeal area. The labial muscles are much the same as those of the generalized form and are not nearly so powerful proportionately as are those of the dorsal head regions. Each lateral posterior margin of the labium is furnished with a slender, sclerotized resilient bar, RB (fig. 62), which abuts against the anterior external face of the rigid tentorial structure. This resilient bar probably assists the labium in returning to its normal resting position after contractions of the labial muscles have disturbed its position.

In *Plateros* there is only one pair of labial muscles, the ventral pair, 21; they arise on the posterior ends of the anterior tentorial arms and are inserted medially on the base of the prementum. The *lecator muscle of the labial palpus, 24,* is present. The rigid tentorial structure that was found in *Chauliognathus* is absent in *Plateros*. The labral, cibarial, pharyngeal and hypopharyngeal muscles are all essentially the same as in *Chauliognathus*.

Chauliognathus pennsylvanicus Deg., Cantharidae (figs. 65, 66, 67), and Photuris sp., Lampyridae, are the larval forms considered.

In Chauliognathus (figs. 65, 66) muscle 5 does the same work as the dorsal dilator muscle of the cibarium, 5 (figs. 1, 2), in the generalized form; it is considered homologous though it is greatly modified in origin and somewhat in its insertion. The other dorsal dilator muscles of the cibarium, 6 and 7 (figs. 65, 67), form a compact, linear group as do also the dorsal dilator muscles of the pharynx, 11 (fig. 67). There is a heavy tentorial modification present, but it is less extensive than that of the adult; it is also continuous with the subpharyngeal plate. Hypopharyngeal bar Y (fig. 67) extends posteriorly from the dorsal region of the structure. There is a heavily sclerotized postoral subpharyngeal support that joins the head on each side laterad of the mouth. The labial muscles are similar to those of the adult and the posterior lateral sclerotized resilient bar, RB (fig. 67), that was described in the adult form is also present in the larvae.

In *Photuris* sp. the musculature is similar to that of *Chauliognathus;* the muscles, however, are less well developed.

#### XII. ELATEROIDEA

Neotrichophorus carolinensis (Schfr.), Elateridae, and Chrysobothris femorata (Oliver), Buprestidae, are the adult forms from this group used for study.

In Neotrichophorus (figs. 68, 69, 70) the full complement of labral muscles is present. Upon first examination it was thought that only the ventral muscle of the labrum, 3 (figs. 68, 70), was present, but it was later determined that muscle 3 and the dorsal muscle of the labrum, 4, are so closely appressed as to appear as one. Muscle 4 is inserted laterally on the posterior dorsal rim of the labrum while muscle 3 is inserted ventrally and laterally as is the usual manner. This is the only species in the order Coleoptera, examined in this work, that exhibited any indication of an anterior (dorsal) labral muscle. Another elaterid adult, Heteroderes nicholsi Notman, was

examined, but only the *ventral muscle of the labrum*, 3, was found to be present; muscle 3 in this species is unusual in that it originates laterally in the anterior clypeal region (fig. 74). This condition has been observed only in this species.

In Neotrichophorus the cibarial, pharyngeal, and hypopharyngeal muscles are of the usual form (figs. 68, 70). Hypopharyngeal bar Y more or less parallels the lateral margins of the cibarium and is joined to the bar Y on the opposite side by a subpharyngeal supporting area on which are inserted strong ventral dilator muscles of the pharynx, 30 (fig. 68). The labial and hypopharyngeal muscles are of generalized form, though the ventral muscle of the labium, 21, is absent unless the muscle of the prementum, 22 (figs. 68, 69), has been misinterpreted as 21, in which case, of course, muscle 22 would be absent.

In Chrysobothris the labial and palpal muscles are similar to those in Neotrichophorus; the muscle of the prementum, 22, is absent. The labral muscles are also similar except that the dorsal muscle of the labrum, 4, is absent; the ventral muscle of the labrum, 3, arises in the midfrontal region on the inner (mesal) surface of the suture that separates the inner margin of the compound eye from the frons. The cibarial, pharyngeal, and hypopharyngeal muscles are essentially the same, but are all poorly developed.

Parallelostethus attenuatus (Say) (figs. 71, 72, 73), Alaus sp., Elateridae, and Cebrio antennatus Schfr., Cebrionidae, are the larvae studied in this superfamily.

In *Parallelostethus* the labral muscles are absent. The cibarial, pharyngeal, and hypopharyngeal muscles are powerful, but otherwise similar to those found in the adult *Neotrichophorus;* hypopharyngeal bar Y is also similar. The labial muscles, except for being long and thin (figs. 72, 73), are of the generalized form. The extra length is made possible by a posterior, spurlike extension of the anterior tentorial arm (fig. 73); the *dorsal and ventral muscles of the labium, 20* and 21, arise on the inner surface on the posterior tip of this spurlike extension.

In *Alaus* sp. the musculature is essentially the same as that in *Parallelostethus*, and in the cebrionid larva, *Cebrio*, the muscles were found to be practically the same as those in the two elaterid larvae studied.

#### XIII. SCARABAEOIDEA

The adults of *Popillia japonica* Newman and *Macrodactylus sub-spinosus* (Fab.), Scarabaeidae, and *Lucanus placidus* Say, Lucanidae, were selected for study in this superfamily.

In Popillia (figs. 75, 76, 77), of the labral muscles only the ventral muscle of the labrum, 3 (figs. 75, 76), is present. The cibarial, pharyngeal, and hypopharyngeal muscles are similar to those of the generalized plan except that the dorsal dilator muscle of the pharynx, 11, is absent. Muscle group 13 (figs. 75, 76) may or may not be homologous with the compressor muscles of the anterior region of the cibarium, 13 (fig. 2), in Periplaneta; they are well-developed diagonal muscles inserted on the anterior dorsal wall of the cibarium and they apparently have the same function. The compressor muscle group of the cibarium, 12 (fig. 75), is wide, but not long and it is confined to the posterior dorsal region of the cibarium. There is only one labial muscle present, 39 (figs. 76, 77); it is a single unit of fibers arising centrally in the middle region of the labium and extending slightly anteriorly and dorsally to become inserted medially on the dorsal labial wall. The function, probably, is to assist in moving the hypopharyngeal region in some manner. The levator muscle of the labial palpus, 24 (fig. 77), arises on an intralabral tormalike process extending mesad from the lateroventral base of the labium; this structure extends in a hoop form dorsally and is joined to the process on the opposite side of the labium. The tendonous insertion end of one of the maxillary muscles enters the intralabial region (fig. 77) and extends through the modified, hooplike structure to be inserted on the maxillary base; it has no effect on the movement of the labium.

In Macrodactylus the median labial muscle, 39, is absent; a muscle probably corresponding to the ventral muscle of the labium, 21, of the generalized form arises rather medially in the anterior region of the postmentum and is inserted ventrally on the base of the prementum. The cibarial, pharyngeal, and hypopharyngeal muscles are similar to those in *Popillia*; the compressor muscles of the anterior region of the cibarium, 13, are absent as is also the ventral muscle of the labrum, 3.

In Lucanus the median labial muscle, 39, and the ventral muscle of the labrum, 3, are absent; the ventral muscle of the labium, 21, is similar to that in Macrodactylus. The muscle of hypopharyngeal bar Y, 10, is large and branched because of the fact that bar Y has a wide, thin, multibranched distal end, and muscle 10 is, of course, inserted on these distal branches. There is a muscle group present that possibly is homologous with the compressor muscles of the anterior region of the cibarium, 13, in Popillia; the fibers are arranged on the dorsal wall of the cibarium more longitudinally than diagonally, which is the case in Popillia. The cibarial muscles are all rather slender and the oesophagus is small considering the size of the insect.

The larval forms of Scarabaeoidea studied pertain to *Popillia japonica* Newman and *Cotinis nitida* (L.), Scarabaeidae.

In Popillia (figs. 78, 79, 80) the ventral muscle of the labrum, 3 (figs. 78, 79), is strong; the muscle of hypopharyngeal bar Y, 10 (figs. 78, 79), is massive. All of the cibarial muscles are absent. The dorsal dilator muscle of the anterior region of the pharynx, 9 (fig. 78), is so weak as to be almost threadlike. The compressor muscle group of the cibarium, 12 (fig. 78), is poorly developed. There is a large, heavily sclerotized cuspidate sclerite on the posterior dorsal surface of the labium. The dorsal and ventral muscles of the labium, 20 and 21 (figs. 78, 80), and the muscle of the prementum, 22 (figs. 78, 80), are well developed.

In Cotinis the labral and labial muscles are similar to those in *Popillia*; the muscle of hypopharyngeal bar Y, 10, is also similar. There is only one pair of weak muscles inserted on the dorsum of the cibarium just anterior to the frontal connective nerves; it is probably one of the dorsal dilator muscles of the cibarium, 5, 6, or 7. A pair of weak dorsal pharyngeal muscles, probably 9, is present.

## XIV. CLEROIDEA

Dermestes caninus Germ., Dermestidae, and Enoclerus spinolae Lec., Cleridae, are the adult forms studied in this superfamily.

In Dermestes (figs. \$1, \$2, \$3) the labral, cibarial, pharyngeal, and hypopharyngeal muscles are all well developed. The compressor muscle of the labrum, I, and 5 of the dorsal dilator muscles of the cibarium are absent. The muscle of hypopharyngeal bar Y, 10 (figs. \$1, \$2), is branched as in the generalized form. Bar Y is rather heavy and is continuous ventrally with a sclerotized subpharyngeal rod that connects the bar Y of one side with that of the other. In the labium a muscle is present that might be considered either as the muscle of the prementum, 22, or as the ventral muscle of the labium, 21 (figs. \$1, \$3). It arises medially in the anterior region of the submentum and is inserted medially on the base of the prementum. The muscle 20 (figs. \$1, \$3) may in reality be homologous with the muscle of the hypopharynx, 19; it arises on the inner surface of the posterior end of the anterior tentorial arm and is inserted medially on the dorsal labial wall in the anterior region by means of a tendon.

In *Enoclerus* the musculature is similar to that in *Dermestes*, with a few variations. One additional pair of ventral muscles of the labium is present.

For the larval stages, *Dermestes caninus* Germ., Dermestidae, and *Tenebriodes* sp., Ostomatidae, were chosen for study.

In Dermestes (figs. 84, 85, 86) the labral muscles are absent; the dorsal dilator muscle of the cibarium, 5, the dorsal dilator muscle of the pharynx, 11, and the compressor muscle group of the cibarium, 12, are also absent. The other cibarial, pharyngeal, and hypopharyngeal muscles are present and well developed. The muscle of hypopharyngeal bar Y, 10 (figs. 84, 85), is branched and especially massive. Bar Y (fig. 84) is heavily sclerotized and forms a rigid lateral support to the dorsal cibarial region and to the mouth. As is the case in the adult Dermestes, the labial muscle, 21 (figs. 84, 86), is difficult to homologize with those of the generalized form; the selection of their numerical designations (names), in this case, is influenced entirely by their points of insertion.

In Tenebriodes sp. the ventral muscle of the labrum, 3, is present. The cibarial, pharyngeal, hypopharyngeal, and labial muscles are similar to those of Dermestes; the ventral muscle of the labium, 21, arises on the tentorial structure and not on the submentum as it does in Dermestes.

## XV. MELOIDEA

Macrobasis immaculata (Say), Meloidae (figs. 87, 88, 89), is the adult studied in this superfamily. The labral muscles, I and 3 (figs. 87, 88), are present and well developed. The dorsal dilator of the cibarium, 5, is absent; the compressor muscle group of the cibarium,  $I^2$ , is weak; the other cibarial and pharyngeal muscles are strong. The proximal (ventral) region of bar Y (fig. 88) supports the ventral pharyngeal wall and the sides of the mouth. In the labium the levator muscle of the labial palpus, 24 (figs. 88, 89), takes its origin on the intralabial sclerotized bar, IR (fig. 88), that terminates laterally in a broad lateral hypopharyngeal sclerite. The muscle of the hypopharynx, I9 (figs. 88, 89), arises in the usual area and is inserted medially on a short apodeme process by means of a tendon.

The larva studied is Zonabris phalerata (Pall.) (figs. 90, 91, 92). The muscles are well developed in this species, though the compressor muscle of the labrum, 1, and the dorsal dilator muscle of the cibarium, 5, are absent. The dorsal muscle of the labium, 20 (figs. 91, 92), arises in the posterior region of the submentum and the ventral muscle of the labium, 21 (figs. 91, 92), originates medially in the anterior region. Hypopharyngeal bar Y (fig. 91) is continuous with a long sclerotized subpharyngeal structure that joins the two bars together in the posterior region of the ventral wall of the cibarium.

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#### XVI. MORDELLOIDEA

Mordella quadripunctata (Say), Mordellidae (figs. 93, 94, 95), is the adult form used for study in this superfamily. The muscles are powerful and well developed. The cibarial, pharyngeal, and hypopharyngeal muscles are of the generalized form. Hypopharyngeal bar Y (fig. 93) is weakly sclerotized. The muscle of the prementum, 22 (fig. 95), might be the ventral muscle of the labium, 21, with the origin moved anteriorly from the tentorial structure rather than muscle 22, though it is difficult to interpret a condition like this. The ventral dilator muscle of the pharynx, 30 (fig. 93), and the lateral dilator muscle of the pharynx, 31 (fig. 93), are present, the latter being very large. There is a sclerotized subpharyngeal rod (fig. 93) that lies immediately under the mouth opening; it terminates laterally in the integument of the posterior dorsal hypopharyngeal area.

The larvae studied are of the same species as the adult (figs. 96, 97, 98). The musculature is, as the figures indicate, well developed and unusual. There is a large, thin, sclerotized apodeme that extends ventrally from the center of the middle region of the frons on which the ventral muscle of the labrum, 3 (fig. 97), the muscle of hypopharyngeal bar Y, 10, 10A, 10B (fig. 97), and the dorsal dilator muscle of the pharynx, 11 (fig. 97), all take their origin. The ventral muscle of the labrum, 3 (figs. 96, 97), is inserted on the distal end of a modified torma that originates on the ventral labral wall and which extends laterally and dorsally. The dorsal dilator muscles of the cibarium, 6 and 7 (fig. 97), are thin and very long; the muscle of hypopharyngeal bar Y, 10, 10A, 10B (fig. 97), is divided into three branches and the dorsal dilator muscle of the pharynx, II (fig. 97), originates on the ventral margin of the posterior region of the apodeme. The labial muscles, 20 and 22 (figs. 97, 98), do not require special comment as the figures are self-explanatory. There is present a rigid, heavily sclerotized, subpharyngeal intralabial structure, IR (fig. 97). The crosspiece that lies beneath the anterior region of the pharynx terminates in the lateral integumental wall of the posterior labial or hypopharyngeal region.

#### XVII. CERAMBYCOIDEA

The adults studied in this superfamily are *Cyllene robiniae* (Forst.), Cerambycidae, Cerambycinae, and *Prionus pocularis* Dalm., Prioninae.

In Cyllene (figs. 99, 100, 101) the muscles are well developed and are of the generalized plan. The muscle of hypopharyngeal bar Y,

10 (figs. 99, 100), is especially massive. The dorsal wall of the cibarium is decidedly dome-shaped and appears to be able to accommodate the suboral lobe, SL (fig. 99). The *dorsal muscle of the labium, 20* (figs. 99, 101), is inserted laterally on the prementum near the dorsal surface. In the posterior lateral region of the sub-pharyngeal area the integument of one side is joined with that of the opposite by a sclerotized intralabial rod, IR (fig. 99). The anterior tentorial arm (fig. 99, AT) is broad but thin. The suboral lobe (SL) is probably the hypopharynx; a muscle interpreted as the *muscle of the hypopharynx*, 19 (figs. 99, 101), is inserted medially at its base.

In Prionus the compressor muscle of the labrum, 1, is absent; the muscle of hypopharyngeal bar Y, 10, is branched. The labral, cibarial, pharyngeal, and hypopharyngeal muscles are similar to those in Cyllenc. The labial muscles are similar also, except that the muscle of the prementum, 22, is absent and the ventral muscle of the labium, 21, is present.

In the larval Cyllene robiniae (Forst.), Cerambycinae (figs. 102, 103, 104), the muscles are powerful and in the dorsal head region are usually multibranched or subdivided. The labral muscles are absent; the dorsal dilator muscles of the cibarium, 5, 6, and 7 (figs. 102, 104), occur in groups and the muscle of hypopharyngeal bar Y, 10 and 10A (fig. 104), consists of two main branches each of which is subdivided into several units. The compressor muscle group of the cibarium, 12 (figs. 102, 104), is strong; immediately beneath this group the dorsal wall of the posterior region of the cibarium and the anterior pharyngeal region invaginates to form a pouch which, when viewed laterally, is somewhat obovate. This pouch or lobe extends down into the region of the mouth opening. There is a median muscle, 40, beneath the compressor muscle group of the cibarium, 12 (figs. 102, 104), that arises medially in the posterior region of the pouch and is inserted centrally in the anterior region of the same. The dorsal dilator muscle of the pharynx, II (fig. 104), is inserted on the posterior dorsal region of the pouch and the dorsal dilator muscle of the cibarium, 7, in the anterior dorsal region. By the combined action of muscles 7, 11, 12, and 40 (fig. 104) it would seem that the lobe formed by the ventral wall of the pouch could pull food into the mouth from the shelflike hypopharynx, HY, that lies immediately anterior to it. In the ventral head region the muscle of the hypopharynx, 19, the dorsal and ventral labial muscles, 20 and 21, the ventral and lateral dilator muscles of the pharynx, 30 and 31

#### NO. 7 MUSCULATURE OF COLEOPTERA—DORSEY

(figs. 103, 104), are all well developed and conform rather closely to the generalized plan of musculature.

## XVIII. BOSTRICHOIDEA

*Apatides fortis* (Lec.), Bostrichidae, adult and immature forms, were used for study in this superfamily.

In the adult Apatides (figs. 105, 106, 107) the epipharynx is large and conelike; the compressor muscle of the labrum, I (fig. 106), is elongate and is inserted laterally near the tip of the epipharynx. The epipharynx (fig. 106, EP) is supported laterally by a slender sclerotized rod (SR) arising dorsally on a tormalike process that extends mesad from the side of the labrum anterior to the base of the normal torma. The ventral muscle of the labrum, 3 (figs. 105, 106), is inserted on the distal end of the torma which is more elongate than usual. The cibarial, pharyngeal, and hypopharyngeal muscles are strong. The dorsal dilator muscle of the cibarium, 7 (figs. 105, 106), apparently has a branch, 7A (fig. 105), the point of origin of which has migrated anteriorly to the posterior surface of the epistomal suture. The labial muscles are well developed; the ventral muscle of the labium, 21 (figs. 106, 107), possibly in reality is the muscle of the prementum, 22, since it takes its origin laterally in the posterior region of the submentum.

The larval Apatides (figs. 108, 109, 110) exhibits the first labral compressor muscle, I (figs. 108, 109), observed in immature Coleoptera. The powerful ventral muscle of the labrum, 3 (figs. 108, 109), is inserted on the distal end of an elongate torma; the muscle of hypopharyngeal bar Y, I0 and I0A (fig. 108), is branched and strong. The ventral and lateral dilator muscles of the pharynx, 30 and 3I (fig. 108), are especially well developed. In the labium the dorsal and ventral labial muscles, 20 and 2I (figs. 108, 110), lie so close together that superficially they appear to be one nuscle. The unusual muscle 4I (figs. 108, 110) was observed only in this species; it arises laterally in the anterior region of the submentum and extends dorsally almost vertically to become inserted laterally at the base of the labium near the dorsal surface.

## XIX. CHRYSOMELOIDEA

Leptinotarsa decimlineata (Say), Chrysomelidae, Donacia distincta Lec., Donaciidae, and Galerucella xanthomelaena (Schr.), Galerucidae, are the specimens of adults studied in this superfamily.

In Leptinotarsa (figs. 111, 112, 113) the muscles of the dorsal head region are well developed. The muscle of hypopharyngeal bar Y,

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10 (figs. 111, 112), is branched; the anterior branch 10A arises laterally in the anterior frontal area on the posterior surface of the epistomal suture. The labial muscles are strong, especially the *dorsal muscle of the labium*, 20 (figs. 112, 113). There is an unusual tendonous structure (fig. 112, TS) that arises broadly, medially and basally from the ventral labial wall; it extends anteriorly to be inserted medially on the dorsal wall of the labium in the anterior region. A contraction of the *dorsal labial muscle*, 20 (fig. 112), would exert a pull on the labium at the point of insertion; this tendon that joins the anterior dorsal labial surface with that of the posterior ventral region probably retracts the anterior labial area when muscle 20 contracts. There is a strongly sclerotized intralabial brace, IR (fig. 112), in the posterior region of the labium that terminates laterally in the integument.

' In Donacia the compressor muscle of the labrum, I, is absent; the anterior branch of the muscle of hypopharyngeal bar Y, 10A, arises as it does in Leptinotarsa. The cibarial, pharyngeal, hypopharyngeal, labral, and labial muscles are apparently homologous with those found in Leptinotarsa.

In Galerucella the compressor muscle of the labrum, I, is absent; the anterior branch of the muscle of hypopharyngeal bar Y, IOA, arises as it does in Leptinotarsa. The cibarial, pharyngeal, and labial muscles are homologous with those found in Leptinotarsa.

For the larvae in this superfamily Leptinotarsa decimlineata (Say) and Typophorus viridicyaneus (Cr.), Chrysomelidae, were selected for study.

In Leptinotarsa (figs. 114, 115, 116) the muscles are very well developed. The compressor muscle of the labrum, I (figs. 114, 115), is present; the cibarial muscles, 6 and 7, and pharyngeal muscles, II (fig. 114), are long because of the space between the dorsal wall of the stomodaeum and the head wall. The muscle of the hypopharyngeal bar Y, IO (fig. 114), is subdivided into many units. The ventral dilator muscle of the pharynx, 30 (fig. 114), is especially massive; the dorsal and ventral labial muscles, 20 and 21 (figs. 114, 116), and the muscle of the prementum, 22 (figs. 114, 116), are all strong. The latter muscle is inserted on the ventral wall of the labium on an area in which the division of the prementum is indistinct; the dorsal and ventral labial muscles, 20 and 21, are inserted on the base of prementum I (fig. 116). The muscle of the prementum, 22 (fig. 116), is inserted on the base of the prementum, 22 (fig. 116), is inserted on the base of the prementum, though the dividing suture is indistinct.

The musculature in *Typophorus* is similar to that of *Leptinotarsa* except that the *compressor muscle of the labrum*, *I*, is absent.

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## XX. PLATYSTOMOIDEA

Euparius marmoreus (Oliv.), Platystomidae (figs. 117, 118, 119), is the adult form studied in this superfamily. The labral muscles are absent; the cibarial, pharyngeal, and hypopharyngeal muscles are not well developed. The hypopharyngeal bar Y (fig. 118) is modified into a flat plate. There is a heavily sclerotized subpharyngeal rod, IR(fig. 118), present that supports the ventral region of the mouth and also strengthens the posterior lateral labial walls in which region the ends of the rod terminate. The labial muscles are well developed. The dorsal muscle of the labium, 20 (figs. 118, 119), is an unusual muscle in this species; it arises laterally in the posterior gular area as a thickened, powerful group of muscle fibers that quickly converge to become inserted on the end of a thin tendon in the anterior gular region. The tendon extends anteriorly and is inserted somewhat laterally in the dorsal region of the posterior labial area.

In the larva of this species (figs. 120, 121, 122) the ventral muscle of the labrum, 3 (figs. 120, 121), is present. The muscle of hypopharyngeal bar Y, 10 (fig. 10), is massive; the dorsal dilator muscles of the pharynx, 9 and 11, are absent in this species. The hypopharyngeal bar Y (fig. 121) is large; it supports the mouth opening laterally and is continuous with a heavily sclerotized suboral lobe that is joined on each side by a heavily sclerotized bar, IR (fig. 121), that terminates in the integumental wall of the posterior dorsal lateral region of the labium. The ventral muscle of the labium, 21 (figs. 121, 122), arises on the tentorium at the base of the tentorial arm; it is inserted medially on the base of the prementum. There is a division of the muscle of the prementum, 22 (figs. 121, 122), into two parts; each arises laterally in the anterior region of the submentum and each is inserted laterally at the base of the prementum.

## XXI. CURCULIONOIDEA

From this superfamily *Pantomorus godmani* (Crotch), Curculionidae, and *Dendroctonous valens* Lec., Scolytidae, were selected for study of the adults.

In *Pantomorus* (figs. 123, 124, 125) the muscles are reduced in number and those present are poorly developed. The *labial muscles* are absent and the *cibarial muscles*, 7 (figs. 123, 124), are represented by a row of weak fibers inserted through the transverse *compressor muscle group of the cibarium*, 12 (figs. 123, 124), and, since they all do insert through 12, are probably divisions of 7. The muscle of *hypopharyngeal bar Y*, 10 (fig. 123), is also weak and bar Y (fig.

123) has practically disappeared; it is very lightly sclerotized. There is a large, soft suboral lobe, *SL* (fig. 123), present that extends anteriorly into the cibarium in a tonguelike manner (fig. 123). The labium is furnished with a single pair of muscles (figs. 123, 125) that probably correspond with the *muscle of the prementum*, 22, in the generalized form.

In *Dendroctonous* the musculature is similar to that of *Pantomorus* with a few minor variations.

Pantomorus leucoloma Boh. and Listroderes obliquus Klug., Curculionidae, and Eupsalis minuta Drury, Brentidae, are the larval species studied.

In Pantomorus (figs. 126, 127, 128) the ventral muscle of the labrum, 3 (fig. 127), and the muscle of hypopharyngeal bar Y, 10 (fig. 127), are very well developed; the cibarial and pharyngeal muscles are rather weak. The pharyngeal muscles, 11 (fig. 127), are probably homologous with the dorsal dilator muscles, 11, in the generalized plan; they are inserted dorsally on the wall of the pharynx posterior to the frontal connective. *Hypopharyngeal bar Y* (fig. 127) is continuous with a broad lateral and ventral sclerotized plate that passes beneath the anterior region of the pharynx to become joined with the bar Y of the other side. A median, flat, sclerotized posterior extension arises from the posterior dorsal margin of the labrum (fig. 127, ME); it is a resilient piece. When the ventral muscle of the labrum, 3 (fig. 127), is retracted, the labrum is depressed and the sclerotized dorsal extension, ME, abuts against the posterior inner surface of the epistomal suture (fig. 127, ES). When the ventral muscle of the labrum, 3, relaxes, the resiliency of the extended process, ME (fig. 127), pushes the labrum back into its normal position thus doing the work of a muscle. There is a heavily sclerotized intralabial rod, IR (fig. 127), present that terminates laterally on the posterior lateral walls of the labium and which is joined to the dorsal labial wall adjacent to the mouth opening. The labial muscles conform with those of the generalized form in origin and insertion.

In Listroderes the muscles are essentially the same as those in *Pantomorus*. The posterior dorsal margin of the labrum is furnished with the median posterior extension, *ME*, also. The *dorsal muscle* of the labium, 20, is inserted laterally on the dorsal wall of the labium.

The muscles in *Eupsalis* are similar to those of *Pantomorus*. The *dorsal muscle of the labium*, 20, is inserted as in the case of *Listroderes*. The *dorsal dilator muscle of the anterior region of the pharynx*. 9, is present in this species.

#### XXII. LYMEXYLOIDEA

*Hylecoetus lugubris* Say, Lymexylidae, adults and larvae were selected for study in this superfamily.

The muscles of the labrum in the adult (figs. 129, 130) are represented only by the ventral muscle of the labrum, 3. The pharyngeal muscles, 9 and 11 (figs. 129, 130), occur in paired groups. The muscle of hypopharyngeal bar Y, 10 (fig. 129), lies between the two branches of pharyngeal muscle, o. A small, longitudinal band of muscles, 13 (figs. 129, 130), is present; it possibly is homologous with the compressor muscles of the anterior region of the cibarium, 13 (fig. 2), of the general plan. They arise medially, adjacent to the anterior margin of compressor muscle group of the cibarium, 12 (figs. 129, 130), and are inserted medially and dorsally on the cibarium a short distance anterior to the point of origin. Hypopharyngeal bar Y (fig. 130) is rather large and furnishes a strong support to the sides of the mouth and to the posterior lateral cibarial region. The lateral dilator muscle of the pharynx, 31 (fig. 130), is long and powerful. The muscle of the prementum, 22 (figs. 130, 131), is the only muscle present in the labium.

In the larvae of *Hylecoetus* (figs. 132, 133, 134) the labral muscles are absent; the muscle of hypopharyngeal bar Y, 10, and its branch 10A (figs. 132, 133), are especially massive; the cibarial and pharyngeal muscles are comparatively long and slender. Muscle 10 (fig. 133) arises by means of a tendon in the posterior region of the frons. The posterior lateral labial region is furnished with a heavily sclerotized intralabial brace, IR (fig. 132), the ends of which terminate in the integumental wall. Externally there is a heavily sclerotized Ushaped area present that extends over the dorsal surface of the posterior labial region and is continuous laterally with the ends of the intralabial brace, IR (fig. 132). The labial muscles present an unusual plan of arrangement. The prementum is elongate and possesses a small median sclerite in the anterior region (fig. 134). The muscle of the prementum, 22 (figs. 132, 134), which is short and very broad, arises medially along the posterior margin of the tentorial bridge; it is inserted along the base of the prementum. The ventral muscle of the labium, 21 (figs. 132, 134), originates medially on the posterior margin of the tentorial bridge and it is inserted rather medially on the posterior edge of the median premental sclerite. The dorsal muscle of the labium, 20 (figs. 132, 134), arises laterally on the inner surface of the posterior end of the anterior tentorial arm; it is inserted laterally in the anterior region of the median sclerite of the prementum.

#### SUMMARY

A general plan of muscle arrangement can be recognized in orthopteroid insects, and the same plan is found in representatives of other orders. It is possible to discover apparent homologies among muscles on the basis of origin and insertion, though one or both attachments may vary considerably among the different species. There are certain muscles that evidently are homologous with those of the generalized plan, but which because of some variation or modification in origin or insertion are difficult to identify. On the other hand, some muscles are aberrant and cannot be reconciled with any plan.

Some unusual muscles and structures, and relationships between muscles and skeletal parts, were encountered in this study.

The following muscles occurred only in the species of Orthoptera included in this work: the hypopharyngeal muscle of the mandible, 14 (fig. 1); the anterior dorsal dilator muscle of the salivarium, 15 (fig. 1); the depressor muscle of the labial palpus, 23 (fig. 1); the muscles of the labial palpus, 25, 26, and 27 (figs. 1, 3A); and the flexor muscle of the glossa, 28 (figs. 1, 3).

In Periplaneta americana L., Orthoptera, the compressor muscle of the labrum, I (fig. 2), is asymmetrical; the dilator muscle group of the labrum, 2 (fig. 2), and the dorsal dilator muscle of the cibarium,  $\delta$  (figs. 1, 1A, 2), were observed only in this species.

The muscle of the hypopharynx, 19 (figs. 5, 6), in Anisolabis maritima Gené, Dermaptera, arises centrally in the midregion of the mentum and not on the tentorial bridge as is the usual manner.

In both the adult and larval forms of *Corydalus cornutus* L., Neuroptera (figs. 9, 11), the prementum is divided into three sclerites. The muscle group 33 (fig. 11) was observed to be especially well developed only in the larva of *Corydalus*.

The two muscles 34 and 35 (figs. 14, 15) were observed only in the adult *Sphecius speciosus* (Dru.), Hymenoptera. The *muscle of hypopharyngeal bar Y*, 10, of the generalized plan is absent; this is the only case in which this condition was observed. The *dorsal muscle* of the labium, 20A (fig. 13), was found only in this species.

In Harpalus caliginosus F., Carabidae (adult), muscle 2IA (fig. 19) is an additional labial muscle that is not found in the other insects included in this work. It is in this species also that the posttentorial apodeme, PTN (fig. 19), occurs; all of the labial muscles arise on this structure, as does also the *muscle of the hypopharynx*, 19 (fig. 19). A similar apodeme is found in *Dineutes discolor* Aube., Gyrinidae

(adult) (fig. 23, *PTN*), but the *hypopharyngeal muscle*, 19, does not originate on it in this species.

The prementum is divided into two sclerites in the coleopterous larvae of: Silpha americana L., Silphidae; Byrrhus sp., Byrrhidae; Nosodendron californicum Horn., Nosodendridae; Hylecoetus lugubris Say, Lymexylidae; and Leptinotarsa decimlineata (Say), Chrysomelidae. The muscle of the prementum, 22, occurs in all of these larvae; and the muscle of prementum 1, 22A (fig. 48), was found only in the larvae of Byrrhus sp., Byrrhidae.

In Sphaeridium scarabaeoides L., Hydrophilidae (adult), the ventral muscle of the labrum, 3 (figs. 35, 37), arises on the distal end of the anterior tentorial arm instead of on the dorsal head wall as is the usual manner. In S. bipustulatum Fabr. (larva) muscle 37 (fig. 39) arises on the posterior lateral margin of the subpharyngeal supporting area and is inserted on the base of the cardo; this muscle was not observed in other insects.

It was found that in *Scotobates calcaratus* (Fab.), Tenebrionidae (adult), the anterior tentorial arm, AT (fig. 41), is connected with *hypopharyngeal bar* Y by means of a thin, flat, sclerotized band.

A heavily sclerotized intralabial brace or rod (IR) that terminates laterally in the integument of the posterior lateral labial region is to be found in Coleoptera in: Cyllene robiniae (Forst.), Cerambycidae (adult) (fig. 99, IR); Macrobasis immaculata (Say), Meloidae (adult) (fig. 88, IR); Leptinotarsa decimlineata (Say), Chrysomelidae (adult) (fig. 112, IR); Scotobates calcaratus (Fabr.), Tenebrionidae (larva) (fig. 46, IR); Mordella quadripunctata (Say), Mordellidae (larva) (fig. 97, IR); Pantomorus leucoloma Boh., Curculionidae (larva) (fig. 127, IR); Hylecoetus lugubris Say, Lymexylidae (larva) (fig. 132, IR).

In Nosodendron californicum Horn, Nosodendridae (adults and larvae), the hypopharyngeal bar Y (figs. 52, 54) is greatly modified and enlarged (more so in the adult) and is continuous with the tentorial structure. In the adult form the mentum covers the prementum (figs. 50, 52).

In Chauliognathus pennsylvanicus Deg., Cantharidae (adults and larvae), the tentorial structure (figs. 62, 67, TN) is greatly modifield (more so in the adult); a sclerotized resilient bar is present in the integument of the posterior lateral margin of the labium.

Only in *Neotrichophorus carolinensis* (Schfr.), Elateridae (adult), of the Coleoptera studied, were both the *dorsal* (anterior) and *ventral* (posterior) *labral muscles*, 4 and 3 (figs. 68, 70), present. In

Heteroderes nicholsi Notman (adult) the ventral muscle of the labrum, 3 (fig. 74), arises laterally on the anterior region of the clypeus; this is an unusual point of origin for this muscle. In the larval Parallelostethus attenuatus (Say) there are posterior extensions of the anterior tentorial arms that provide the points of origin for the long labial muscles, 20 and 21 (figs. 72, 73).

In *Popillia japonica* Newman, Scarabaeidae (adult) (figs. 75, 76, 77), the labial muscles are absent and an unusual muscle in the labium, 39 (figs. 76, 77), is to be found only in this species.

The levator muscle of the palpus, 24 (figs. 88, 89), in Macrobasis immaculata (Say), Meloidae (adult), arises on the intralabial brace (IR).

In the larvae of *Mordella quadripunctata* (Say), Mordellidae, there is present a thin apodeme (fig. 97, AP) that arises medianly in the posterior region of the frons and extends deeply into the head cavity. All the labral, cibarial, dorsal pharyngeal muscles, and the *muscles of* the hypopharyngeal bar Y, 10, 10A, 10B (fig. 97), arise on this apodeme.

In the larva of *Cyllene robinae* (Forst.), Cerambycidae, there is an uusual lobe that extends ventrally from the dorsal cibarial wall into the mouth region (figs. 102, 104); the lobe is furnished with muscle 40 and probably assists in some manner in food ingestion.

The epipharynx is large and unusual in structure in the adult *Apatides fortis* (Lec.), Bostrichidae (fig. 106, EP). In the larva of this species muscle 4I (fig. 108) is unusual in that it is not found in the other insects studied in this work.

In the adult of Leptinotarsa decimlineata (Say), Chrysomelidae, branch 10A of the muscle of hypopharyngeal bar Y, 10 (figs. 111, 112), arises on the posterior surface of the epistomal suture (fig. 111, ES). In this species the ventral part of the labial wall is connected with the anterior dorsal wall by means of an intralabial tendonous structure (fig. 112, TS).

The dorsal muscle of the labium, 20 (figs. 118, 119), in Euparius marmoreus (Oliv.), Platystomidae (adult), arises laterally in the posterior region of the head, posterior to the tentorium, and is inserted on the labium by means of a very long tendon.

In the larva of *Pantomorus leucoloma* Boh., Curculionidae, the resilient median process (fig. 127, ME) that extends posteriorly from the dorsal margin of the labrum probably does the work of a muscle in assisting in the return of the labrum to its resting position after the *ventral muscle of the labrum*, 3, relaxes.

Further investigations are necessary to determine the nature of the complete act of the ingestion of food by chewing insects. The facts presented in this paper indicate, however, that the cibarial, pharyngeal, and hypopharyngeal muscles, which are powerfully developed in many species, play an important part in ingestion. The action of these muscles is undoubtedly supplemented by that of the labial muscles to a varied degree depending on the species.

# MUSCLES CONSIDERED IN THIS STUDY

1. Compressor muscle of the labrum.

2. Dilator muscle group of the labrum.

3. Ventral (posterior) muscle of the labrum.

4. Dorsal (anterior) muscle of the labrum.

5, 6, 7. Dorsal dilator muscles of the cibarium.

8. Dorsal dilator muscle of the cibarium.

9. Dorsal dilator muscle of the anterior region of the pharynx.

10. Muscle of hypopharyngeal bar Y.

11. Dorsal dilator muscle of the pharynx.

11A. Dorsal dilator muscle of the pharynx.

12. Compressor muscle group of the cibarium.

13. Compressor muscles of the anterior region of the cibarium.

14. Hypopharyngeal muscle of the mandible.

15. Anterior dorsal dilator muscle of the salivarium.

16. Dorsal salivary cup muscle.

17. Anterior salivary cup muscle.

18. Lateroventral salivary cup muscle.

19. Muscle of the hypopharynx.

20. Dorsal (anterior) muscle of the labium.

21. Ventral (posterior) muscle of the labium.

21A. Muscle of the labium.

22. Muscle of the prementum 2.

22A. Muscle of the prementum 1.

23. Depressor muscle of the labial palpus.

24. Levator muscle of the labial palpus.

25. Muscle of the labial palpus.

26. Muscle of the labial palpus.

27. Muscle of the labial palpus.

28. Flexor muscle of the glossa.

29. Flexor muscle of the paraglossa.

30. Ventral dilator muscle of the pharynx.

31. Lateral dilator muscles of the pharynx.

32. Dorsal appressor muscle group of the cibarium.

33. Muscles of the ventral wall of the cibarium.

34. Laterodorsal muscle of the cibarium.

35. Lateral muscle of the posterior cibarial region.

36, 37, 38. Maxillary muscles.

39. Median muscle of the labium.

40. Retractor muscle of anterior pharyngeal region.

41. Muscle of the labium.

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# ABBREVIATIONS USED ON THE FIGURES

AF, antennal fossa. ANT, antenna. AT, anterior tentorial arm.

CD, cardo. CIB, cibarium. CL, clypeus. CPS, cuspidate sclerite. CS, coronal suture.

*E*, compound eye. *EP*, epipharynx. *ES*, epistomal suture.

FC, frontal connective nerve. FGN, frontal ganglion. FR, frons. FS, frontal suture.

GL, glossa. GU, gula.

HY, hypopharynx.

IR, intralabial rod or brace.

LB, labium. LBP, labial palpus. LIG, ligula. LM, labium.

*M*, true mouth opening. *MD*, mandible. *ME*, median posterior extension. MT, mentum. MX, maxilla. MXP, maxillary palpus.

NA, nasale.

*O*, ocellus. *OE*, oesophagus.

PGL, paraglossa. PH, pharynx. PMT, prementum. PSMT, postmentum. PT, posterior tentorial pits. PTN, posttentorial structure.

RB, resilient bar.

SB, suboesophageal brace. SC, salivary cup. SD, salivary duct. SL, suboral lobe. SMT, submentum. SR, sclerotized rod. ST, stomodaeum.

T, torma. TB, tentorial bridge. TN, tentorium. TS, tendinous structure.

Y, hypopharyngeal bar Y.

# EXPLANATION OF PLATES

## PLATE I

- 1. Periplaneta americana L., Orthoptera, sagittal section of head slightly to the left of median plane.
- 1A. Same, diagrammatic detail of the relation of the dorsal dilator muscle of the cibarium, 8, to the dorsal muscle of the labrum, 4.
  - 2. Same, dorsal view of head with part of head wall removed to expose muscles.
  - 3. Same, ventral view of labium and posterior head region with part of integument removed to expose muscles.
- 3A. Same, diagrammatic detail of relationship of the muscles of the labial palpus, 25, 26, and 27.

#### PLATE 2

- 4. Anisolabis maritima Gené, Dermaptera, dorsal view of head with part of head wall removed to expose muscles.
- 5. Same, sagittal section of head slightly to the left of median plane.
- 6. Same, ventral view of head with part of integument removed to expose muscles.
- 7. Corydalus cornutus L., Neuroptera (adult), dorsal view of part of head with integument removed to expose muscles.
- 8. Same, sagittal section of head slightly to the left of median plane.
- Same, ventral view of head with part of integument removed to expose muscles.

## PLATE 3

- 10. Corydalus cornutus L., Neuroptera (larva), dorsal view of head with part of integument removed to expose muscles.
- Same, ventral view of head with part of integument removed to expose muscles.
- 12. Same, sagittal view of head slightly to the left of median plane.
- 13. Sphecius speciosus (Dru.), Hymenoptera (adult), lateral view of labium with part of integument removed to expose muscles and also portion of anterior tentorial arm with points of muscle origin.
- 14. Same, sagittal section of anterior (dorsal) head region slightly to the left of the median plane.
- 15. Same, dorsal view of anterior region of head with part of integument removed to expose muscles.
- 16. Same, ventral view of labium and tentorium with part of integument removed to expose muscles.

#### Plate 4

- 17. Harpalus caliginosus F., Carabidae (adult), dorsal view of head with part of integument removed to expose muscles.
- Same, ventral view of labium with part of integument removed to expose muscles.

- 19. Same, sagittal section of head slightly to the left of median plane.
- 20. Amara sp., Carabidae (larva), ventral view of labium with part of integument removed to expose muscles.
- 21. Same, dorsal view of head with part of integument removed to expose muscles.
- 22. Same, sagittal section slightly to the left of median plane.

#### PLATE 5

- 23. Dineutes discolor Aubé, Gyrinidae (adult), sagittal section of head slightly to the left of median plane.
- 24. Same, dorsal view of head with part of integument removed to expose muscles.
- Same, ventral view of labium with part of integument removed to expose muscles.
- 26. Dineutes sp., Gyrinidae (larva), dorsal view of head with part of integument removed to expose muscles.
- 27. Same, ventral view of labium with part of integument removed to expose muscles.
- 28. Same, sagittal section of head slightly to the left of the median plane.

#### Plate 6

- 29. Silpha americana L., Silphidae (adult), dorsal view of head with part of integument removed to expose muscles.
- 30. Same, ventral view of head with part of integument removed to expose muscles.
- 31. Same, sagittal section of head slightly to the left of median plane.
- 32. Silpha americana L., Silphidae (larva), dorsal view of head with part of integument removed to expose muscles.
- Same, ventral view of labium with part of integument removed to expose muscles.
- 34. Same, sagittal section of head slightly to the left of median plane.

#### PLATE 7

- 35. Sphaeridium scarabacoides L., Hydrophilidae (adult), dorsal view of head with part of integument removed to expose muscles.
- 36. Same, ventral view of head with part of integument removed to expose muscles.
- 37. Same, sagittal section of head slightly to the left of median plane.
- 38. Sphaeridium bipustulatum Fabr., Hydrophilidae (larva), dorsal view of head with part of integument removed to expose muscles.
- 39. Same, sagittal section of head slightly to the left of median plane.
- Same, ventral view of labium with part of integument removed to expose muscles.
- 41. Scotobates calcaratus (Fab.), Tenebrionidae (adult), modified sagittal section of head slightly to the left of median plane.

## PLATE 8

42. Scotobates calcaratus (Fab.), Tenebrionidae (adult), ventral view of head with part of integument removed to expose muscles.

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#### NO. 7

- 43. Same, dorsal view of head with part of integument removed to expose muscles.
- 44. Scotobates calcaratus (Fab.), Tenebrionidae (larva), dorsal view of head with part of integument removed to expose muscles.
- 45. Same, ventral view of anterior portion of head with part of integument removed to expose muscles.
- 46. Same, sagittal section of head slightly to the left of median plane.

#### PLATE 9

- 47. Byrrhus sp., Byrrhidae (larva), anterior portion of head with part of integument removed to expose muscles.
- 48. Same, sagittal section of head slightly to the left of median plane.
- 49. Same, ventral view of head with part of integument removed to expose muscles.
- 50. Nosodendron californicum Horn, Nosodendridae (adult), ventral view of head with part of integument removed to expose muscles.
- 51. Same, dorsal view of head with part of integument removed to expose muscles.
- 52. Same, sagittal section of head slightly to the left of median plane.

## PLATE 10

- 53. Nosodendron californicum Horn, Nosodendridae (larva), dorsal view of head with part of integument removed to expose muscles.
- 54. Same, sagittal section of head slightly to the left of median plane.
- 55. Same, ventral view of head with part of integument removed to expose muscles.
- 56. *Helichus fastigiatus* (Say), Dryopidae (adult), dorsal view of head with part of integument removed to expose muscles.
- 57. Same, sagittal section of head slightly to the left of median plane.
- Same, ventral view of head with part of integument removed to expose muscles.

#### PLATE II

- 59. Ptilodactyla serricollis (Say), Ptilodactylidae (larva), dorsal view of head with part of integument removed to expose muscles.
- 60. Same, ventral view of head with part of integument removed to expose muscles.
- 61. Same, sagittal section of head slightly to the left of median plane.
- 62. Chauliognathus pennsylvanicus (Deg.), Cantharidae (adult), sagittal section of head slightly to the left of median plane.
- 63. Same, dorsal view of head with part of integument removed to expose muscles.
- 64. Same, ventral view of head with part of integument removed to expose muscles.

#### PLATE 12

- 65. Chauliognathus pennsylvanicus (Deg.), Cantharidae (larva), dorsal view of head with part of integument removed to expose muscles.
- 66. Same, ventral view of head with part of integument removed to expose muscles.

- 67. Same, sagittal section of head slightly to the left of median plane.
- 68. Neotrichophorus carolinensis (Schfr.), Elateridae (adult), sagittal section of head slightly to the left of median plane.
- 69. Same, ventral view of head with part of integument removed to expose muscles.
- 70. Same, dorsal view of head with part of integument removed to expose muscles.

#### PLATE 13

- 71. Parallelostethus attenuatus (Say), Elateridae (larva), dorsal view of head with part of integument removed to expose muscles.
- 72. Same, ventral view of head with part of integument removed to expose muscles.
- 73. Same, sagittal section of head slightly to the left of median plane.
- 74. Heteroderes nicholsi Notman, Elateridae (adult), lateral view of labrum and clypeus with part of head wall removed to expose muscles.
- 75. Popillia japonica Newman, Scarabaeidae (adult), dorsal view of head with part of integument removed to expose muscles.
- 76. Same, sagittal section of head slightly to the left of median plane.

## PLATE 14

- 77. Popillia japonica Newman, Scarabaeidae (adult), ventral view of head with part of integument removed to expose muscles.
- 78. Same (larva), sagittal section of head slightly to the left of median plane.
- 79. Same, dorsal view of head with part of integument removed to expose muscles.
- 80. Same, ventral view of head with part of integument removed to expose muscles.
- 81. Dermestes caninus Germ., Dermestidae (adult), sagittal section of head slightly to the left of median plane.
- 82. Same, dorsal view of head with part of integument removed to expose muscles.

## PLATE 15

- 83. Dermestes caninus Germ., Dermestidae (adult), ventral view of head with part of integument removed to expose muscles.
- 84. Same, sagittal section of head slightly to the left of median plane.
- 85. Same, dorsal view of anterior portion of head with part of integument removed to expose muscles.
- Same, ventral view of head with part of integument removed to expose muscles.
- 87. Macrobasis immaculata (Say), Meloidae (adult), dorsal view of head with part of integument removed to expose muscles.
- 88. Same, sagittal section of head slightly to the left of median plane.

## Plate 16

- 89. Macrobasis immaculata (Say), Meloidae (adult), ventral view of head with part of integument removed to expose muscles.
- 90. Zonabris phalerata (Pall.), Meloidae (larva), dorsal view of head with part of integument removed to expose muscles.

## NO. 7 MUSCULATURE OF COLEOPTERA—DORSEY

- 91. Same, sagittal section of head slightly to the left of median plane.
- 92. Same, ventral view of head with part of integument removed to expose muscles.
- 93. Mordella quadripunctata (Say), Mordellidae (adult), sagittal section of head slightly to the left of median plane.
- 94. Same, dorsal view of head with part of the integument removed to expose muscles.

## PLATE 17

- 95. Mordella quadripunctata (Say), Mordellidae (adult), ventral view of head with part of integument removed to expose muscles.
- 96. Same (larva), dorsal view of head with part of integument removed to expose muscles.
- 97. Same, sagittal section of head slightly to the left of median plane.
- 98. Same, ventral view of head with part of integument removed to expose muscles.
- 99 Cyllene robiniae (Forst.), Cerambycidae (adult), sagittal section of head slightly to the left of median plane.

## PLATE 18

- 100. Cyllene robiniae (Forst.), Cerambycidae (adult), dorsal view of head with part of integument removed to expose muscles.
- 101. Same, ventral view of head with part of integument removed to expose muscles.
- 102. Same (larva), dorsal view of head with part of integument removed to expose muscles.
- 103. Same, ventral view of head with part of integument removed to expose muscles.
- 104. Same, sagittal section of head slightly to the left of median plane.

## PLATE 19

- 105. Apatides fortis (Lec.), Bostrichidae (adult), dorsal view of head with part of integument removed to expose muscles.
- 106. Same, sagittal section of head slightly to the left of median plane.
- 107. Same, ventral view of head with part of integument removed to expose muscles.
- 108. Same (larva), sagittal section of head slightly to the left of median plane.
- 109. Same, dorsal view of head with part of integument removed to expose muscles.

## Plate 20

- 110. Apatides fortis (Lec.), Bostrichidae (larva), ventral view of portion of head with part of integument removed to expose muscles.
- 111. Leptinotarsa decimlineata (Say), Chrysomelidae (adult), dorsal view of head with part of integument removed to expose muscles.
- 112. Same, sagittal section of head slightly to the left of median plane.
- 113. Same, ventral view of portion of head with part of integument removed to expose muscles.
- 114. Same (larva), sagittal section of head slightly to the left of median plane.

## PLATE 21

- 115. Leptinotarsa decimlincata (Say), Chrysomelidae (larva), dorsal view of head with part of integument removed to expose muscles.
- 116. Same, ventral view of head with part of integument removed to expose muscles.
- 117. Euparius marmoreus (Oliv.), Platystomidae (adult), dorsal view of head with part of integument removed to expose muscles.
- 118. Same, sagittal section of head slightly to the left of median plane.
- 119. Same, ventral view of anterior portion of head with part of integument removed to expose muscles.
- 120. Same (larva), dorsal view of head with part of integument removed to expose muscles.

#### PLATE 22

- 121. Euparius marmoreus (Oliv.), Platystomidae (larva), sagittal section of head slightly to the left of median plane.
- 122. Same, ventral view of head with part of integument removed to expose muscles.
- 123. Pantomorus godmani (Crotch), Curculionidae (adult), sagittal section of head slightly to the left of median plane.
- 124. Same, dorsal view of head with part of integument removed to expose muscles.
- 125. Same, ventral view of anterior portion of head with part of integument removed to expose muscles.

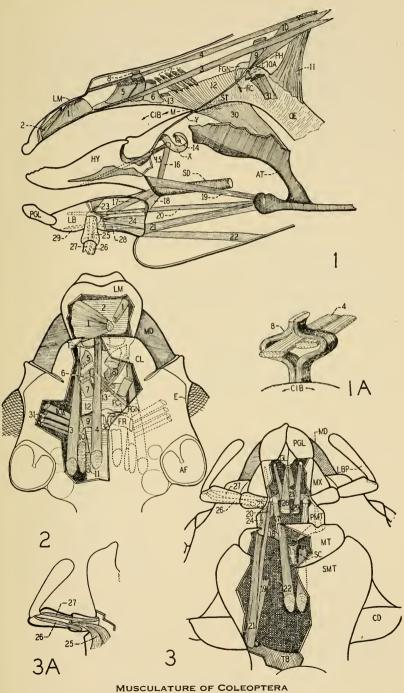
#### PLATE 23

- 126. Pantomorus leucoloma Boh., Curculionidae (larva), dorsal view of anterior region of head with part of integument removed to expose muscles.
- 127. Same, sagittal section of head slightly to the left of median plane.
- 128. Same, ventral view of head with part of integument removed to expose muscles.
- 129. *Hylecoetus lugubris* Say, Lymexylidae (adult), dorsal view of head with part of integument removed to expose muscles.

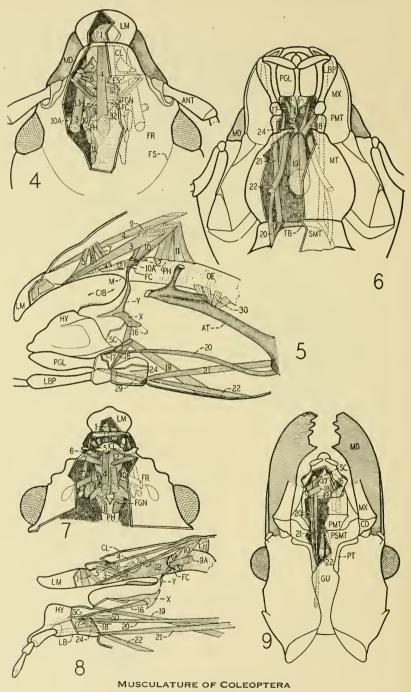
#### PLATE 24

- 130. Hylecoetus lugubris Say, Lymexylidae (adult), sagittal section of head slightly to the left of median plane.
- 131. Same, ventral view of head with part of integument removed to expose muscles.
- 132. Same (larva), sagittal section of head slightly to the left of median plane.
- 133. Same, dorsal view of anterior portion of head with part of integument removed to expose muscles.
- 134. Same, ventral view of head with part of integument removed to expose muscles.

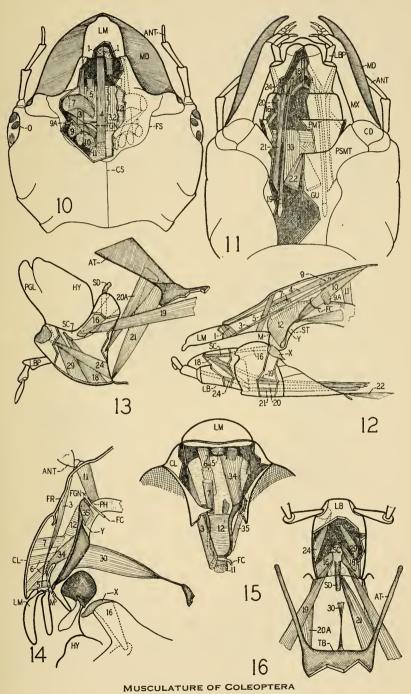
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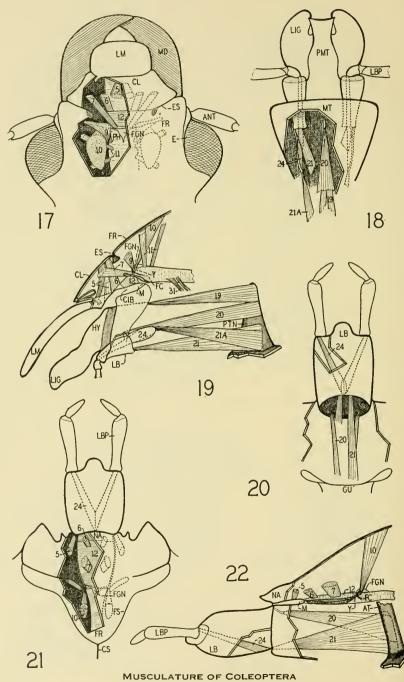
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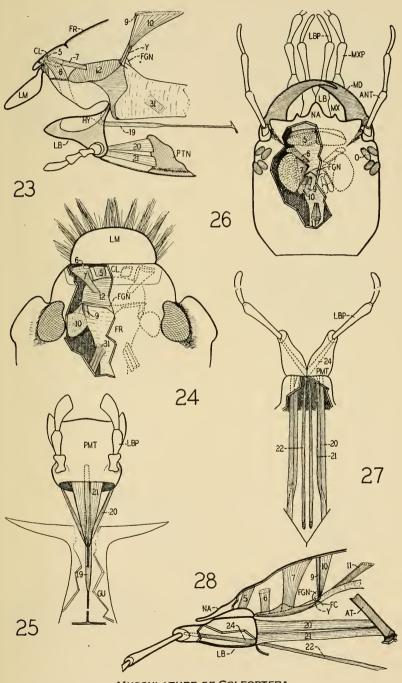
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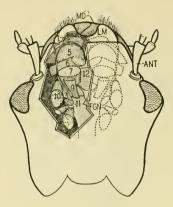
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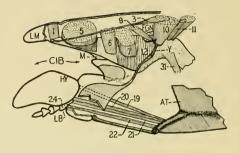


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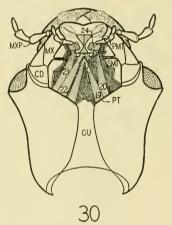
MUSCULATURE OF COLEOPTERA (For explanation of plate see page 38.)

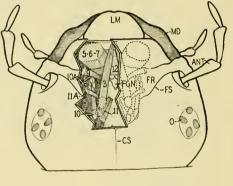




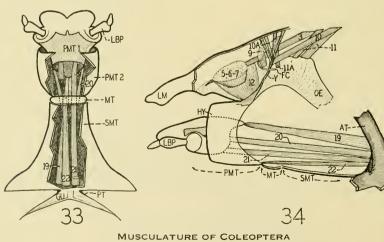


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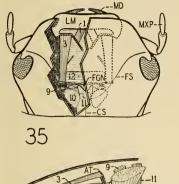


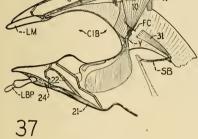
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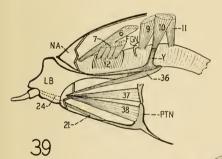


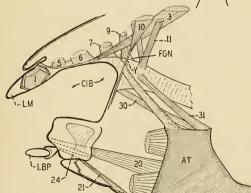
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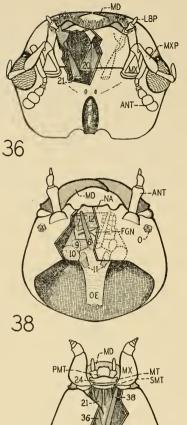






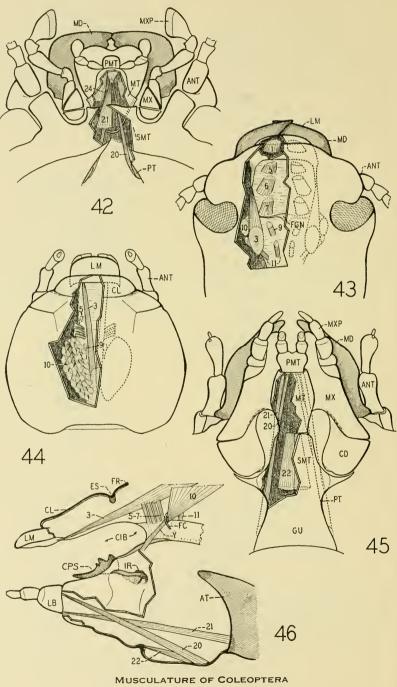


MUSCULATURE OF COLEOPTERA (For explanation of plate see page 38.)

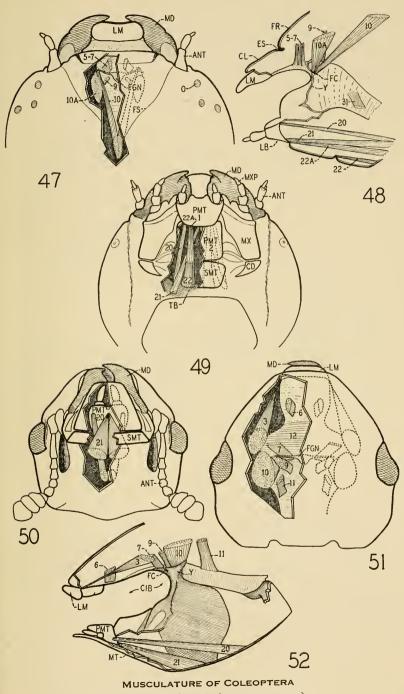


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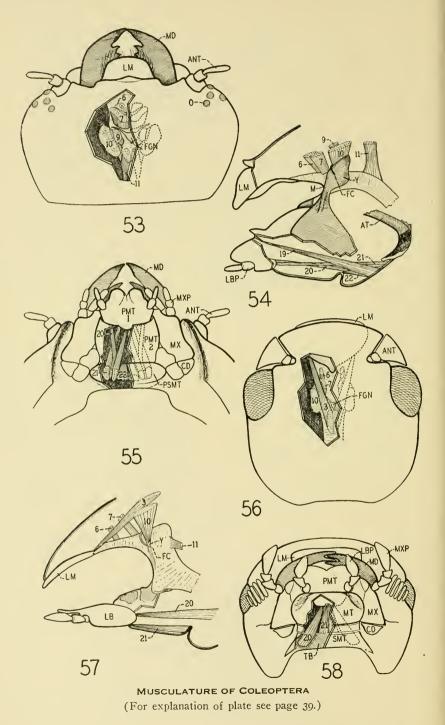
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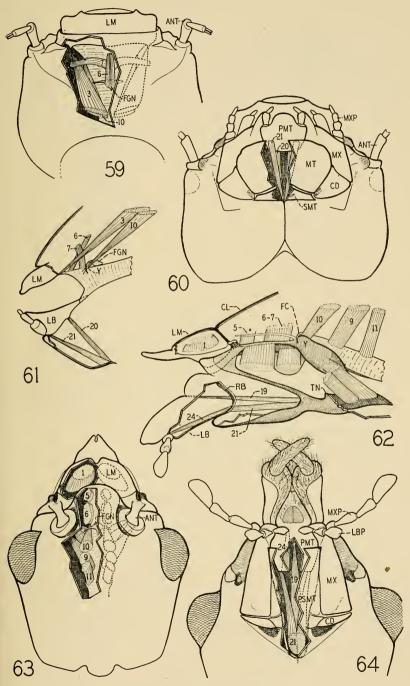


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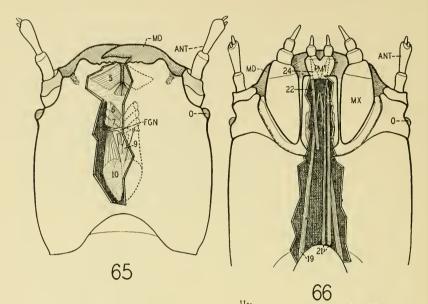


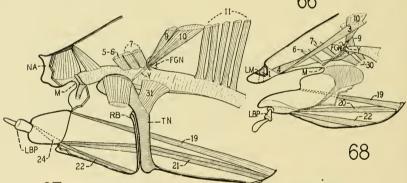
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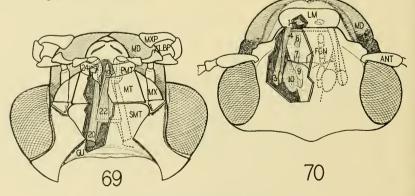


MUSCULATURE OF COLEOPTERA (For explanation of plate see page 39.)

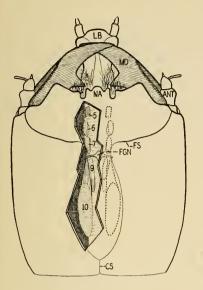


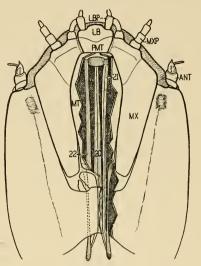






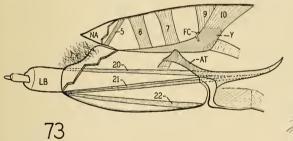
MUSCULATURE OF COLEOPTERA (For explanation of plate see pages 39-40.)



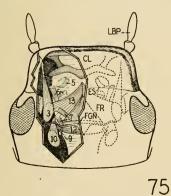


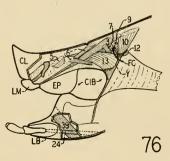
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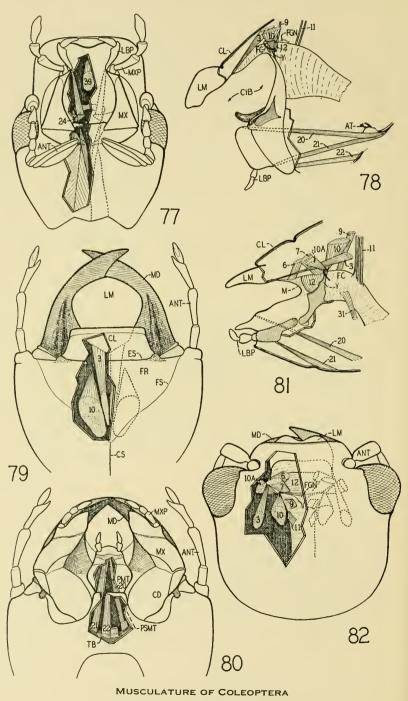




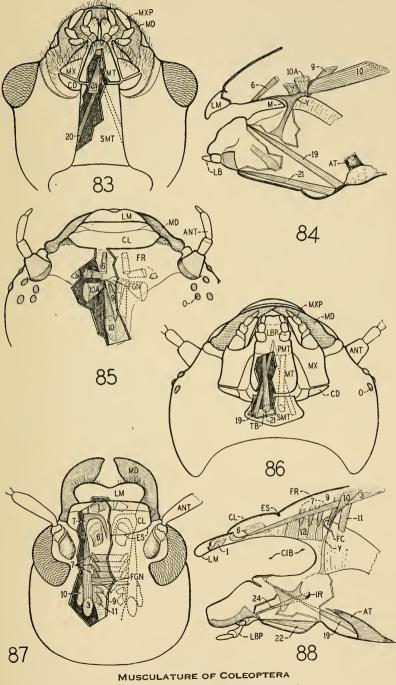


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MUSCULATURE OF COLEOPTERA (For explanation of plate see page 40.)



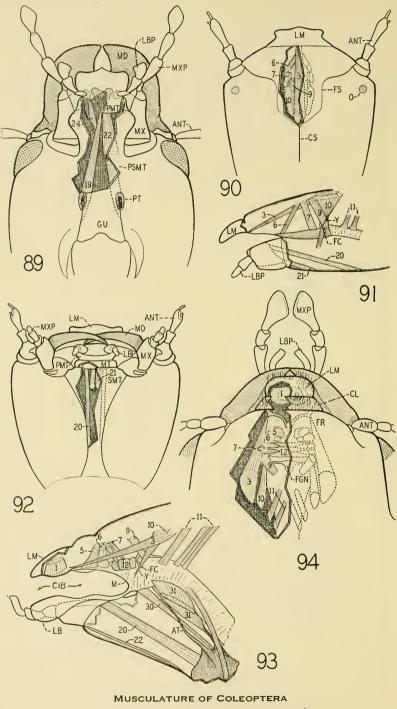
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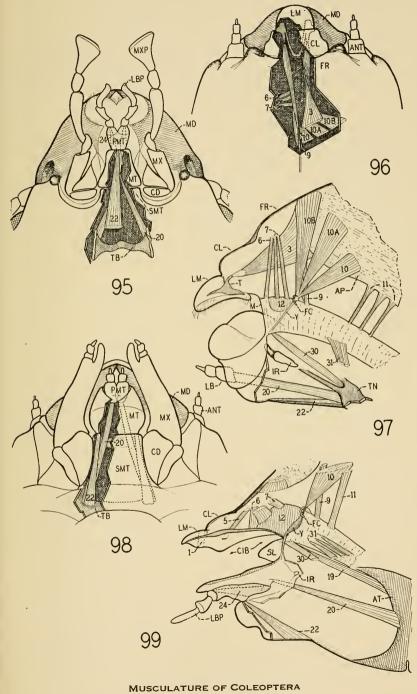
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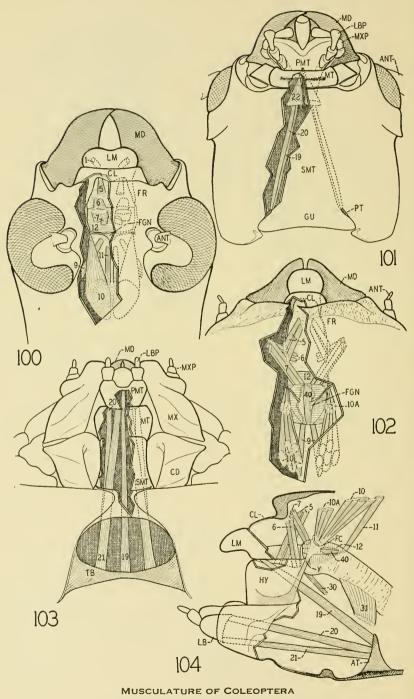
SMITHSONIAN MISCELLANEOUS COLLECTIONS



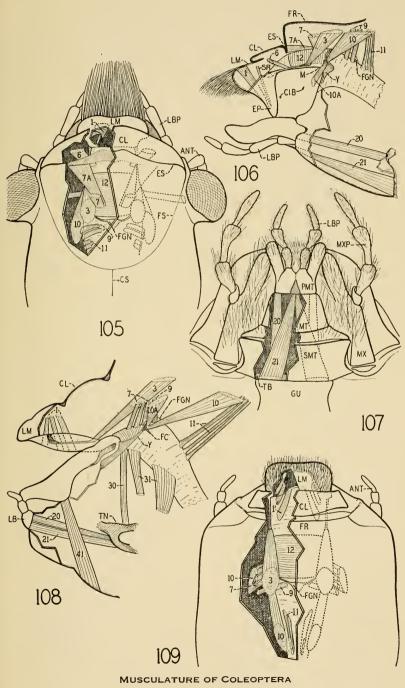
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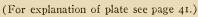


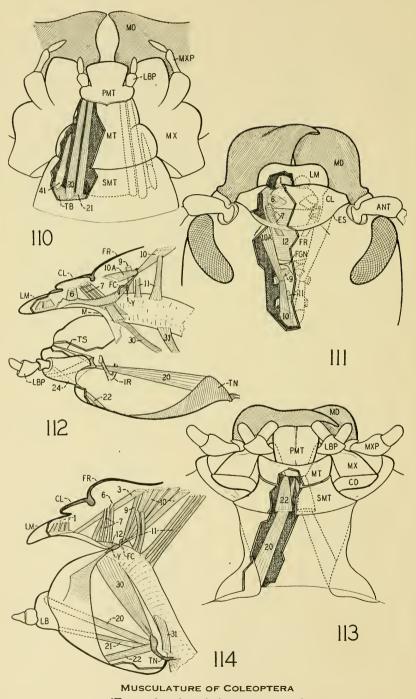
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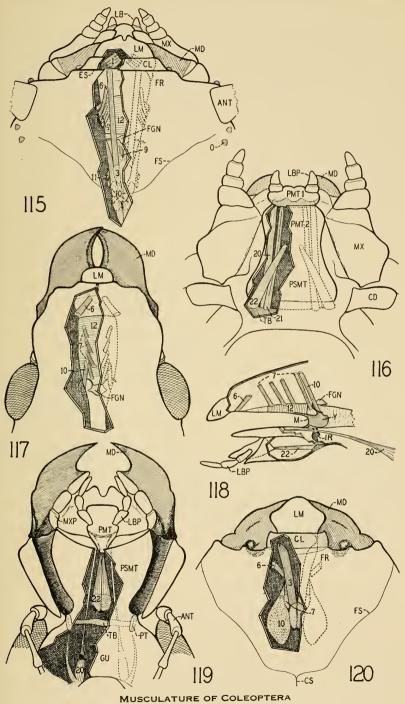
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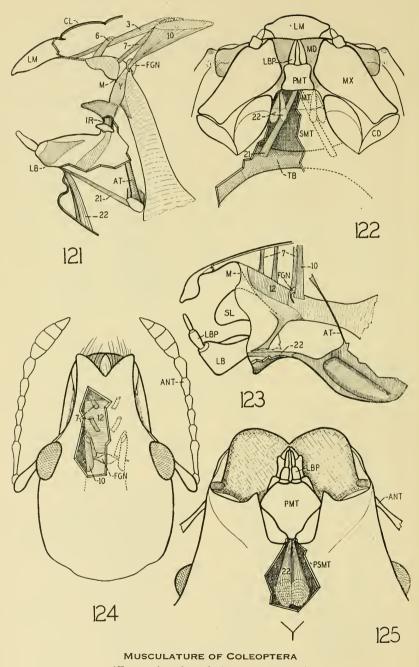




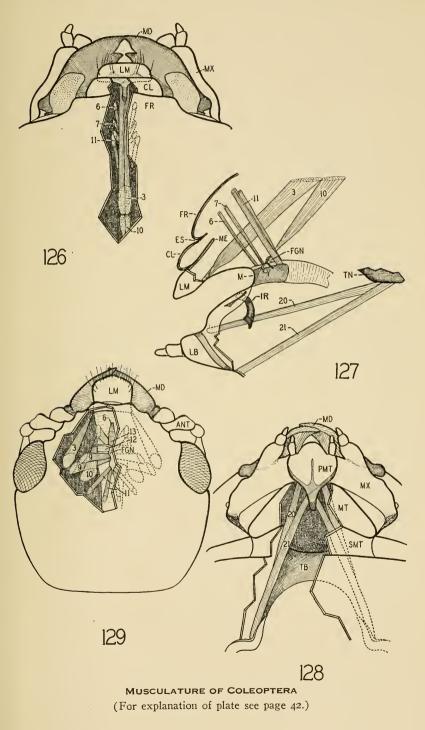
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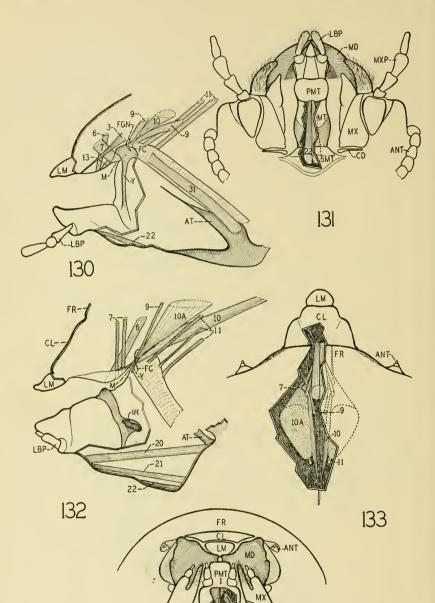


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(For explanation of plate see page 42.)





MUSCULATURE OF COLEOPTERA (For explanation of plate see page 42.)

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