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THE ANATOMY AND MORPHOLOGY OF THE LARVA OF
CAPNODIS MILIARIS

(COLEOPTERA: BUPRESTIDAE)

By

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PART I

INTRODUCTION

This work deals with the external and internal anatomy and morphology of the Capnodis miliaris larva. In 1945-1947 Rivnay made a survey of the species of Capnodis occurring in Palestine. He stated that Capnodis miliaris is the largest of the Capnodis species. Its host is Populus but at present it is of very little economic importance. In view of the introduction of poplars into the Huleh district, however, it may become a serious pest in the future.

True to his predictions C. miliaris is becoming a serious pest in Lebanon due to the increase of poplar plantations. This is especially the case in the Beka'a valley of Lebanon where poplars are extensively cultivated. The larvae bore into the roots of the trees and often kill the entire tree within a short period. Distinctive larval characteristics of C. miliaris are: A labrum well supplied with muscles which arise on the frons or within the labrum, heavily sclerotized mandibles and clypeus, the former of which are supplied with huge muscles and the division of the epicranium by endocarinae which lend strength and support to the weakly sclerotized head. All of these characteristics enable the larvae to live successfully within the bark of the tree forming galleries in the cambium which result sooner or later in the death of the tree.

According to Rivnay the burrowing of a neonate larva of Capnodis species into the ground is governed by positive stereostatic and chemotropic reactions and not phototropic or geotropic ones. Larvae can detect roots or twigs from a distance of 40 centimeters and distinguish between the odour of various plants.

The object of this paper is to give a description of the external and internal anatomy of the larva of C. miliaris with the hope that such information may be of assistance in controlling these potentially important insect pests.

PART II

HISTORICAL

The Coleoptera form the largest order of insects. There is no collective common name for beetle larvae but in some cases they are called grubs, worms or borers. Larvae of Coleoptera are mostly terrestrial, although a few are aquatic. The majority of them are phytophagous, living above or below the ground.

About fifty years ago A. D. Mac Gillivray published a key to the larvae of the common families of beetles (Peterson 1953). In 1930, A. W. Rymer Roberts published a more accurate key for most of the families of the order.

In 1931 Böving and Craighead published their "Illustrated synopsis of the principal larval forms of the order Coleoptera". The following classification is copied from this work:

Order COLEOPTERA

Suborder Polyphaga - "Legs five-jointed, the tarsal joint fused with a single claw into a tarsungulus; or less than five-jointed; or no legs present.

Superfamily Elateroidea

Family Buprestidae - Spiracles cribriform; tenth abdominal segment terminal, prothorax large and more or less depressed, usually covered with a plate dorsally and ventrally.

Subfamily Buprestinae (Chalcophorini, Buprestinae, Chrysobothriné).

Dorsal plate of prothorax with or without asperites, medianly marked with an inverted Y-or V-shaped groove".

The larvae of Buprestid beetles are chiefly wood-borers and may be found in the inner or outer trunk of trees, branches, or roots (Peterson 1953). In these forms the head is small and greatly withdrawn into the prothorax, the antennae are short and ocelli are absent (Imms 1957). Larvae of pine borers are known as the flat-headed type, and bore in the inner bark forming irregular channels (Porter 1930).

Buprestid larvae are easily recognized by the presence of strong branching ridges in the ental surface of the dorsal wall of the cranium. The arms of the frontal suture are present as double edged linear tracts of the cuticle extending from the vertex of the cranium to the bases of the antennae. A median ridge to the strongly sclerotized clypeal plate is present which lends support to the weakly sclerotized cranium permitting it to withstand the pull of the huge mandibular muscles which are borne upon the strong clypeal plate (Snodgrass 1947). Further, three segmented antennae, toothed mandibles, maxillae with two segmented palpi and a fused galea and lacinia or mala are present (Böving and Craighead 1931). Finally, a small labium with a spoon-shaped ligula

is present, with or without one segmented palpi.

The prothorax is expanded laterally and bears a dorsal inverted V-shaped sclerotized thickening and a ventral inverted T-shaped sclerotized thickening in its cuticle (Rees 1941).

One pair of mesothoracic spiracles is present on the cephalo-lateral surface of the mesothoracic segment and eight pairs of abdominal spiracles occur on the first eight abdominal segments. The mesothoracic spiracles are twice the diameter of the abdominal spiracles (Robert 1930).

The life cycle of buprestids usually extends for a year (Spencer 1930). Capnodis larvae are creamy white in color with a small head retracted into an expanded prothorax. The slender body is composed of the mesothorax, the metathorax and ten abdominal segments (Rivnay 1946). The legs are absent. The posterior part of the head merges with the cervix under the prothorax and both are capable of considerable freedom of movement. The larvae feed on the inner bark of trees by chewing it, extracting the juice and then discarding the remainder. It was found that a larva requires sixty days to reach pupation under laboratory conditions at a temperature of 33°C (Rivnay 1946).

The eggs of Capnodis species are white and oval in shape. Capnodis miliaris and C. tenebrionis have the

largest eggs which attain a length of 1.5 mm. and a width of 1.2 mm. Eggs require ten days to hatch at a temperature of 30°C for most species of the genus. Adults emerge from pupation in approximately ten days under optimum conditions. Experiments showed that adults descend from tree branches to oviposit. Oviposition takes place between the trunk of the tree and the soil around it. Adults live for a year and feed on the leaves of the species of trees infested by the larvae (Rivnay 1947).

Capnodis tenebrionis in Morocco was found to emerge from pupation beginning in May. Copulation occurs in July and oviposition takes place at the end of July. Sixty to one hundred eggs are laid at one time and the oviposition period lasts about thirty days (Bleton 1942).

PART III

MATERIALS AND METHODS

Capnodis miliaris larvae were collected alive from infested poplar trees and brought to the laboratory. Here they were killed either by injection with 70% alcohol or the living larvae were put directly into clean, dry jars and placed in the freezing compartment of the refrigerator until needed for dissection. To study the external anatomy of the larva it was put in a dissecting tray, covered with 70% ethyl alcohol and examined with a binocular microscope. In order to study the internal anatomy the larvae were dissected in alcohol to keep the tissue fresh and prevent deterioration. Larvae were opened along both the dorsal and the ventral median surfaces beginning with the vertical slit of the anus and extending cephalically to the head. The cuticle of the larva was then spread out to the sides with forceps and each segment was pinned down through the cuticle.

To study the head capsule, the head was removed from the rest of the body, put in 10% KOH and boiled. As a result the cuticle became transparent and sutures of the cranium were easily observable.

PART IV

DISCUSSION

I. External Anatomy

A. The Head and Prothorax

The head of Capnodis miliaris is prognathous. It is weakly sclerotized but strengthened by apodemes. The mandibles, the clypeal plate and the hypostoma are heavily sclerotized and dark brown in color while the rest of the larva is creamy white (Plate I, A and II, A).

The frontal suture (fs) is distinct, extending cephalad from the median line between the bases of the antennae (Ant) and forming internal inflections (Plate I, A and B). This median ridge extends on the ental margin of the head from the apex of the vertex (Vx) to the epistomal suture (es) (Snodgrass 1947) (Plate I, A). The hypostomal bridge (Hst) is not complete. The gula (Gu) is narrow and triangular in shape (Plate II, A).

Cephalad of the clypeus (Clp) is the labrum (lm), a membranous flap with a pair of small sclerites, the tormae (Plate I, A). On the inner surface of the labrum is the epipharynx (Ephy) which bears a fine mat of setae which are brownish-orange in color.

On the ental surface of the dorsal wall of the epicranium (ecr) is a system of strong branching ridges which strengthen

the weakly sclerotized cranium (Plate I, A and B). The epicranium extends to the ventral part of the head as two separate shelves (Plate III, B). Both dorsal and ventral parts of the epicranium are situated in the prothorax (Plate III A and B). The dorsal part extends almost to the posterior end of the prothorax, while the ventral part extends to the median portion of the prothorax.

The postoccipit (Poc) extends from the base of the vertex as a narrow rim along the margins of the separate halves of the epicranium bordering the occipital foramen (Plate I, B).

The prothorax is wider than long and is about twice the combined length of the meso- and metathorax (Plate III, A). Into it the head is retracted but can be easily extended during active feeding. The notal sclerite of the prothorax is a brownish-orange inverted V-shaped thickening which is devoid of setae. The anterior end of this sclerite almost reaches the cephalic margin of the prothorax while the posterior tip reaches the caudal margin (Plate III, A). A ventral sclerite shaped like an inverted T is also present. It too is devoid of setae and its caudal tip reaches the posterior margin of the ventral prothorax (Plate III, B).

The entire larval cuticle bears a number of small conical setae. These tend to occur in large numbers upon the

lateral aspects of the body and appear to serve as an adjunct to locomotion during active burrowing by the larvae (Rivnay, 1946).

Appendages of the Head

The Antennae (Ant)

The antennae arise in large oval antennal sockets on the lateral margins of the clypeus. They consist of two segments. The proximal segment is longer and wider than the distal segment and bears at its tip a row of fine setae which probably serve a sensory function. The bases of the antennae are large and membranous (Plate I, A).

The Mandibles (Md)

The mandibles are the outstanding feature of the larval head. They are smooth, heavily sclerotized and dark brown in color. Their function is that of grasping and tearing (Plate II, D).

Each mandible bears three cusps, a large median and two smaller lateral ones (Plate II, C). Normally the closed mandibles provide the larva with a highly sclerotized wedge formed by the anterior portion of the body. Each mandible possesses two points of articulation. Cephalically contact is maintained by a condyle which articulates on an arched

thickening (a) at the anterior margin of the clypeus (Plate I, A and B). Caudally an acetabulum which articulates with the heavily sclerotized pleurostoma constitutes the second point of contact (b) (Plate II, A).

Two tendons, which are transparent whitish in contrast to the darkly colored mandible arise from the base of the mandible; one ental and the other ectal. The abductor muscle of the mandible is attached to the ectal tendon while the adductor muscle is attached to the ental tendon (Plate II, D).

The Maxilla (Mx). The maxillae consist of the following parts:

The Cardo (Cd), in C. miliaris is a small circular sclerite surrounded by a membranous area (Plate II, A).

The Stipes (St), is the largest sclerite of the maxilla and is moderately sclerotized. Each stipes is a nearly rectangular plate bearing minute setae along its outer lateral surface and anterior tip (Plate II, A). The latter serves as the base for the attachment of the maxillary palpus and the mala (Plate II, A).

The Maxillary Palpus (Mx Plp) is composed of two segments. The proximal segment is about twice the length and width of the distal segment. At the point where the two segments join they are encircled by a row of small setae similar to the setae on the stipes (Plate II, A).

The Mala (Ma) is the mesal endite of the maxilla and bears a number of long and short setae along its inner margin and anterior tip (Plate II, A).

The Labium (lb)

The labium is a membranous flap which is supported by a pair of sclerotized rods. There is no distinction between the mentum (Mt) and the submentum (Smt) in C. miliaris. This condition is also noted by Böving and Craighead in other species of the family Buprestidae. The ligula (lig) is large and is bordered anteriorly by a brownish-orange margin bearing a large number of very minute setae and two inner lobe-like structures of the same color. These also possess a number of fine setae (Plate II, A).

On the ental surface of the labium is the hypopharynx with a pair of lateral lobes known as the superlinguae (slin), above the lateral part of each lobe is a sclerotized rod (Plate VI, A).

B. The Mesothorax and Metathorax

Both segments are composed of a dorsal tergum, a ventral sternum and narrow membranous pleurae. Both terga and sterna show vestiges of division into two primary sclerites similar to the condition found in the first eight abdominal segments. The mesothorax (2) is wider but somewhat shorter than the metathorax (3) (Plate III, A and B).

A pair of mesothoracic spiracles (Sp2) are present. They are cribriform in shape and twice the size of the abdominal spiracles. They are situated on the cephalolateral aspect of the mesothoracic segment (Plate III, A).

C. The Abdomen

There are ten abdominal segments with eight pairs of spiracles situated on the first eight segments. The first abdominal segment is slightly shorter and narrower than the following seven which are larger and of equal length and width. The ninth segment is shorter and narrower than the preceding seven abdominal segments. The tenth abdominal segment is the shortest and the anus occurs as a longitudinal slit in its terminus (Plate III, A).

II. Internal Anatomy

A. Digestive System

The alimentary canal is divided into three embryological subdivisions. These are the fore-intestine, the mid-intestine and the hind-intestine. The fore- and hind-intestines arise as ectodermal invaginations during embryological development. The anterior ectodermal invagination, termed the stomodaeum, develops into the fore-intestine, while the posterior invagination, termed the proctodaeum, develops into the hind-intestine. The stomodaeum and proctodaeum are connected by an entodermal

tube called the mesenteron which becomes the mid-intestine.

1. The Fore-Intestine

The buccal cavity or mouth is bordered anteriorly by the inner surfaces of the mouth parts which extend caudally to the pharynx. The pharynx is a tube of small diameter and is followed by the oesophagus. The two areas are not distinctly separated but it appears that the caudal boundary of the pharynx in C. miliaris is marked by the posterior margin of the supra-oesophageal ganglion. Haseman, 1910, found this condition in Psychoda alternata. At its caudal end the oesophagus is expanded into a thin walled, distensible crop which is terminated caudally by the proventriculus (Pvent). The proventriculus extends from the metathorax to the caudal half of the first abdominal segment (Plate VII, A). According to Gray (1931) the proventriculus is especially well developed in many wood-boring Coleoptera, is lined with heavily sclerotized teeth and is usually provided with folds.

In longitudinal section the proventriculus is seen to give way caudally to the cardiac or stomodeal valve (SVlv) which is circular and extends into the mid-gut (Plate VII, B). The thin inner lining of the proventriculus is continuous with that of the cardiac valve which extends into the mid-gut

as six major folds with smaller folds in between. These folds are weakly sclerotized.

2. The Mid-Intestine or Mesenteron

The mesenteron is a straight tube of constant diameter which extends from the anterior end of the second abdominal segment to the anterior end of the sixth abdominal segment. It is distinctly set off from the hind-intestine. The most characteristic feature of the mid-intestine is the presence of two gastric caeca, one on each side of the anterior end. These caecae surround the stomodeal valve and extend obliquely to the caudo-lateral region of the prothorax (Plate VII, A).

3. The Hind-Intestine

The hind-intestine is the tube which forms the posterior portion of the alimentary canal. It is separated from the mid-intestine by the pyloric valve. At the cephalic end of the hind-intestine are six Malpighian tubules (Mal). (Plate VII, A), each arising separately. Two of these arise from the dorsum of intestine, two from the pleural aspects and two from the ventral surface. They all extend cephalad to the caudal region of the prothorax and then return, projecting posteriorly to the anterior part of the hind-intestine. The caudal portion of the hind-intestine is differentiated into a rectum which is surrounded by muscles. The rectum is terminated in the tenth segment by the anus

which takes the form of a longitudinal slit (Plate III, A).

B. The Nervous System

The Central Nervous System - The central nervous system is composed of two main subdivisions, the brain and its nerves and the ventral nerve cord.

The Brain and Its Nerves

The brain is composed of two conspicuous masses of the supra (Br) and the suboesophageal ganglia (SOe Gng) Plate IV, A and B). The supraoesophageal ganglion is situated above the pharynx and is formed by the coalescence of the first three embryonic neuromeres. These three parts of the supraoesophageal ganglion are the protocerebrum, the deutocerebrum and the tritocerebrum.

The protocerebrum innervates the compound eyes and ocelli when the latter are present. The deutocerebrum innervates the antennae and their muscles, while the tritocerebrum innervates the labrum and the fore-intestine.

In C. miliaris the supraoesophageal ganglion consists of two ovoid ganglia joined mesally and protected from external injury by the roof of the cranium. Nerves project from the anterior end of the supraoesophageal ganglion but due to thorough fusion of the neuromeres, their origin cannot be determined with accuracy (Plate IV, A).

1. The Antennal Nerve (Ant Nv). The antennal nerve arises from the anterior lobe of the supraoesophageal ganglion and extends above the cephalic end of the mandibular muscle. It branches just before the antennal base. Branch a innervates the base of the antennae while branch b innervates the muscles of the antennae (Plate IV, A).

2. The Labro-Frontal Nerve. This nerve originates from the cephalic part of the supraoesophageal ganglion adjacent to the antennal nerve. It soon divides into a frontal ganglion connective (fr Con) and a labral nerve (Lm Nv) (Plate IV, A). The labral nerve extends anteriorly giving rise to three branches. Branch c innervates the labrum and divides into two sub-branches; Nerves d and e project into the clypeus and are shorter in length than branch c.

3. The Circumoesophageal Connectives (Coe Com). These connectives arise from the anterior end of the supraoesophageal ganglion below the labrofrontal nerve. They proceed caudo-ventrad to the suboesophageal ganglion (Plate VI, A).

4. The Suboesophageal Commissure (Soe Com). The suboesophageal commissure arises as a ventral branch of the tritocerebrum. In C. miliaris the commissure arises next to the circumoesophageal connectives which embrace the pharynx and connect both sides of the supraoesophageal ganglion (Plate VI, A).

The Suboesophageal Ganglion (Soe Gng). This ventral nerve mass below the pharynx is oval in shape (Plate IV, B). Six pairs of branches arise from it. They are as follows:

1. The Mandibular Nerve (Md Nv). The mandibular nerve arises from the anterior region of the suboesophageal ganglion and projects cephalolaterally to the mandibular muscle. The nerve trunk divides into four branches as it reaches the mandibular muscle. Nerve f runs anteriorly over the mandibular muscle and divides into two sub-branches caudad of the base of the mandibles. Branch g enters the mandibular muscles and supplies the anterior part of this muscle. Branch h and i also enter the mandibular muscles and give off fine sub-branches to the various levels of muscle fibers (Plate IV, B).

2. The Maxillary Nerve (Mx Nv). The maxillary nerve arises ventrad of the mandibular nerve from the cephalo-lateral part of the suboesophageal ganglion (Plate IV, B). It runs cephalically for a short distance then divides into three branches. Branch j and k pass into the maxillary muscles while branch l supplies the base of the maxilla.

3. The Labial Nerve (Lb Nv). The labial nerve arises from the cephalo-lateral end of the suboesophageal ganglion, ventrad of the origin of the maxillary nerve. It is smaller

in diameter than the former and extends cephalad, crossing over the maxillary nerve to the labium. At the base of the labium it divides into two branches both of which extend to the labial muscles.

4 & 5. Lateral Nerves. Two pairs of lateral nerves, lateral nerve No.4 and lateral nerve No.5, arise from the sides of the suboesophageal ganglion. The fourth pair arises cephalad of the fifth pair (Plate IV, B).

Pair No.4 projects posteriorly over the ventral prothoracic muscles. They extend above the longitudinal and oblique ventral muscles and then each divides into two nerves. Nerve m extends cephalically to supply the anterior prothoracic and head muscles. Nerve n passes under the longitudinal ventral muscles to supply the ectal surface of the ventral muscles (Plate IV, B).

Pair No.5 arises slightly caudad of lateral nerve pair No.4 and runs posteriorly for a short distance (Plate IV, B). Here it bifurcates. Branch o passes under the longitudinal and oblique ventral muscles of prothorax dividing into two sub-branches. Each sub-branch sends several fine branches to the cuticle and prothoracic muscles.

Nerve p passes over the longitudinal and oblique ventral muscles, then passes under them to send off fine

branches to innervate the ventral prothoracic muscles (Plate IV, B).

6. Caudo-lateral Nerve Trunk or Pair No.6. The sixth pair of nerves arises from the caudo-lateral portion of the suboesophageal ganglion. These extend beneath the ventral prothoracic muscles and split into two nerves. Branch q runs caudo-laterally and ends in two fine branches which surround the base of mesothoracic spiracle. Branch m extends along branch q and gives off two sub-branches which surround the ventral tracheal trunk of the head which supplies the head at the posterior end of prothorax (Plate IV, B).

Ganglia and Connectives of the Thorax

The suboesophageal ganglion and the three thoracic ganglia are connected with each other by pairs of connectives. The distance between the suboesophageal ganglion and the prothoracic ganglion (1) is twice the distance between the latter and the mesothoracic ganglion (2) while the distance between the meso- and metathoracic ganglion (3) is half the distance between the preceding ganglia (Plate V, A).

The prothoracic ganglion gives rise to a pair of nerves, one on each side. Each prothoracic nerve runs caudally to the inner anterior part of the mesothoracic segment where it divides into two distinct nerves (Plate V, A). Nerve 1

passes over the ventral tracheal commissure joining one side of the trachea with the other under the longitudinal muscles. Here it gives off two fine branches. Branch s innervates the anterior portion of the dorsal muscle and branch t innervates the posterior portion of the dorsal mesothoracic muscles (Plate VI, B).

Nerve 2 gives off three fine branches. Branch u runs to the ventral muscles, branch w supplies the lateral muscles and branch x runs under the ventral tracheal commissure to the spiracular muscle.

Mesothoracic ganglion

The mesothoracic ganglion gives rise to a pair of nerves, one from each side of the ganglion, which extends posteriorly to supply the metathoracic segment. The mesothoracic nerve passes over the ventral tracheal commissure giving off four branches. Each supplies a part of the metathoracic segment as shown in (Plate V, A and VI, B).

Metathoracic Ganglion

The metathoracic ganglion resembles the mesothoracic ganglion in giving rise to a pair of nerves. Each nerve runs posteriorly to the first abdominal segment and has the same nerve branches as the mesothoracic ganglion (Plate V, A and VI, B).

Abdominal Ganglia

There are seven abdominal ganglia which differ in shape from the thoracic ganglia in being smaller and less oval in shape. The first six abdominal ganglia lie at the median anterior end of abdominal segments Nos. II - VII. A pair of nerves arises from each abdominal ganglion and each gives off branches similar to the metathoracic and first abdominal branches.

The Seventh Abdominal Ganglion

The seventh abdominal ganglion or (No.10) lies at the posterior end of the seventh abdominal segment, and extends to the anterior end of the eighth abdominal segment (Plate V, A). It is almost twice the size of the preceding six abdominal ganglion. Four pairs of nerves arise from the seventh abdominal ganglion. Pair A or intestinal nerve (Int Nv, A) extends to the anterior portion of the hind intestine, giving off several branches posteriorly (Plate V, B). Pair B supplies the eighth abdominal segment and is similar to the other abdominal nerves (Plate V, A). Pair C projects posteriorly to abdominal segment nine giving rise to several fine branches to the muscles (Plate V, A). Pair D projects posteriorly next to the preceding nerve. Each nerve passes through abdominal segment number nine and extends to segment ten where it gives

off a number of fine branches which supply the muscles of the tenth segment and to the muscles surrounding the rectum (Plate V, A).

From each thoracic (Plate XI) and abdominal ganglion a pair of very thin respiratory branches extends from the caudo-lateral part of the ganglion beneath the ganglionic nerve (Plate VI, A). Both nerve and respiratory branch extend posteriorly to enter the same segment. The respiratory branch joins the ventral tracheal commissure of the segment, while the ganglionic nerve passes over the ventral tracheal commissure.

The Oesophageal Sympathetic Nervous System

The oesophageal sympathetic system is commonly called the stomatogastric or anterior nervous system. In C. miliaris this system is composed of a frontal ganglion (Fr Gng) lying cephalad of the supraoesophageal ganglion and connected with it by the arched frontal nerve (Fr Con) (Plate IV, C). This ganglion gives off two very small lateral branches which extend over the pharynx and a recurrent nerve (R Nv) which arises from the caudal region of the frontal ganglion. The latter extends posteriorly along the mid-dorsal line of the pharynx below the brain for a short distance (Plate IV, A). Then it divides into two nerves above the crop each of which divides into two sub-branches.

Two lateral ganglia occur on either side of the oesophagus behind the supraoesophageal ganglion. Each lateral ganglion appears to be composed of two fused parts, an anterior round end and a posterior oval body (Plate IV, A).

A pair of nerves extend from each ganglion (Plate VI, A). Branch No.1, arising from the anterior side of the ganglion, extends cephalo-ventrad until it joins the maxillary nerve. Branch No.2 extends from the posterior end of the lateral ganglion and follows the same direction until it joins the ventral head trunk of the respiratory system.

C. Respiratory System

There are nine pairs of spiracles present in the larva of C. miliaris. The first pair occurs on the mesothorax (Sp₂) and the remaining eight pairs are abdominal (Plate III, A).

The Tracheation of the Head and Thorax

The tracheal tubes of the right and left sides of the mesothorax arise from a short spiracular atrium which gives rise to the following branches.

1. The dorsal head trunk

The dorsal head trunk (D Tra) extends from the mesothoracic spiracular atrium directly to the mesal region of the mesothoracic segment. From here it extends cephalo-dorsally into the prothorax. Before passing into the prothorax the

dorsal head trunk gives off a side branch (a) that extends to the dorsal prothoracic muscles (Plate VIII). At the posterior end of prothorax a small branch (b) arises from the dorsal head trunk to supply the dorsal side of the digestive tube in the prothorax (Plate VIII). It extends anteriorly between the two halves of the epicranium into the head passing under the frons (Plate VIII) and giving off a number of branches to the cephalic portion of the mandibular muscle, the labrum, the dorsal part of the anterior digestive system, the fat bodies and a very fine branch to the supraesophageal ganglion (Plate IX). The two dorsal head trunks are united by a dorsal commissural trachea (D Com) before passing under the frons (Plate VIII and IX).

2. The Ventral Head Trunk

The ventral head trunk (V Tra) follows a similar course except that it extends ventrally and gives off two distinct major branches (A and B) (Plate X, A). Branch A enters the mandibular muscle while branch B extends anteriorly giving off branches to the ventral sides of the digestive tube, the fat bodies and the suboesophageal ganglion (Plate IX and X, A). In the head it supplies the maxillae, the fat bodies, the labium and the mandibular muscles. The two ventral head trunks are connected by a ventral commissure (V Com), before passing into the head (Plate X, A).

Nos. 3 and 4 are median tracheae extending between the dorsal and ventral head trunks (Plate VIII, IX and X).

3. The Median Tracheae No.3

Median trachea No.3 (M Tra) divides into two major branches (C and D) (Plate X, A). Laterally a small branch (c) arises which extends to the dorsal muscles of the prothorax. The major branch of it, however, progresses over the outer ventral portion of the epicranium, giving off three branches (d, e, f) in the process. Branch d passes over the ventral part of epicranium to supply the ventral muscles of the prothorax (Plate X, A). Branches e and f pass over the ventral part of the epicranium until they reach the ental margin of the epicranium where they turn, passing under the mandibular muscle. Branch D divides into two distinct branches. Each of these branches extends anteriorly dividing again to supply the ventral muscles (Plate X, A).

4. The Median Trachea No.4

Median Trachea No.4 (4-Tra) runs anteriorly into the prothorax where it divides into two branches (E and F), each of which divides again before passing under the ventral part of the epicranium into the posterior mandibular muscle (Plate X, B).

5. The Lateral Longitudinal Trunk

The lateral longitudinal trunk (L Tra) extends caudad from the mesothoracic spiracle to the spiracular opening of the first abdominal segment. It thus passes completely through the metathoracic segment. In the mesothoracic segment a small branch (g) (Plate XI) arises from the lateral trunk to supply the dorsal and ventral portions of the digestive tube in this segment. Fine branches also project from the lateral trunk in the mesothoracic segment to supply the muscle of this segment.

6. The Ventral Tracheal Commissure

The ventral tracheal commissure (V Com) connects the lateral longitudinal trunk on both sides of the mesothoracic segment passing beneath the ventral longitudinal muscles (Plate XI and XV). This ventral tracheal commissure is smaller in diameter than the lateral longitudinal trunk. On either side of the mesothoracic segment the ventral tracheal commissure of the mesothorax is connected with the ventral tracheal commissure of the metathorax by a small transverse tracheal branch (h) which arises from the cephalo-lateral sides of both commissures (Plate XI).

In the metathoracic segment is a small tracheal branch (i) (Plate XI), arising from the cephalo-lateral part

of the lateral longitudinal trunk to supply the dorsal and ventral surfaces of the digestive tube in this segment. Cephalad of branch (i) three more distinct tracheal branches (j, k, l) arise from the lateral longitudinal trunk (Plate XI and XV). Tracheal branches j and k pass anteriorly under the transverse muscles along the intersegmental fold. Branch j supplies the dorsal muscles of the metathoracic segment while branch k passes under the oblique tergo-sternal muscle, supplying it and the lateral oblique muscles, (Plate XI, XV).

Tracheal branch (l) or the ventral commissure, joins the ventral mesothoracic commissure by a transverse branch (h) connecting both ventral commissures (Plate XI).

Tracheation of the Abdomen

The First Abdominal Segment - The segment contains the following tracheal branches.

1. The Lateral Longitudinal Trunks

The lateral longitudinal trunks extend on each side of the segment from the mesothoracic spiracle to the eighth abdominal spiracle (VIII, XI).

2. The Visceral Trunks

A pair of visceral trunks occur on each side of the first abdominal segment (1 and 2). Visceral trachea (No. 1) (Vs Tra 1) extends to the ventral part of the

digestive system while (No. 2) (Vs Tra 2) extends to the dorsal part of the digestive tube (Plate XI).

3. Tracheal Branches of the First Abdominal Segment

Arising from the lateral longitudinal trunk are three branches which project anteriorly passing beneath the transverse muscles along the intersegmental fold into the posterior part of the metathoracic segment (Plate XI and XV). Branch (m) passes beneath the dorsal longitudinal muscle. Branch (n) extends to the lateral metathoracic muscle. Branch (o) passes beneath the longitudinal ventral muscles of the metathoracic segment.

4. The Lateral Commissure

The lateral commissure (L Com) arises from the lateral aspect of the ventral visceral trachea of the first abdominal segment. It passes over the internal longitudinal dorsal muscles and supplies them with fine branches (Plate XI and XV). From this point it projects caudally until it reaches the second abdominal spiracle passing over the cephalo-dorsal longitudinal muscles of the second abdominal segment on the way.

The second to seventh abdominal segments have the same tracheation as the first abdominal segment except that the

lateral longitudinal trunk gives off only one tracheal branch (p) instead of three (Plate XI and XV). Branch (p) extends anteriorly under the transverse muscle breaking into two branches. One passes under the ventral longitudinal muscle and the other branch passes to the lateral muscles of the preceding segment.

The Eighth Abdominal Segment

The eighth abdominal segment has the same tracheation as the preceding segment except that the visceral tracheae are somewhat thicker in diameter and more branched (Plate XII). Also, a new pair of tracheal trunks occur on each side.

1. The Longitudinal Visceral Trunk

The longitudinal visceral trunk of (No. 1) extends from the eighth spiracle of the tenth segment along the side of the digestive tube. It gives off branches to both the dorsal and the ventral portions of the hind-intestine (Plate XII).

The lateral longitudinal trunks (L Tra) extend posteriorly to the cephalic margin of the ninth segment giving off tracheal branches to the dorsal and lateral muscles of the ninth segment (Plate XII).

2. The Inner Lateral Longitudinal Trunk

The inner lateral longitudinal trunk or (No.2) extends

caudally on each side of the segment above the lateral and ventral longitudinal muscles of the eighth and ninth segment. The two inner longitudinal trunks fuse with each other on the cephalic margin of the tenth segment (Plate XII), giving rise to two small branches on each side of the segment which supply the muscles of the tenth segment and the rectum.

D. The Muscular System

The Head Muscles

The muscles of the head include those of the labrum, the stomodaeum, the antennae, the mandibles, the maxillae and the labium. Each of these muscle groups is further subdivided into their minor constituents.

The Labral Muscles

The labral muscles include the following:

1. The Compressor of the Labrum

The compressor of the labrum is formed of a pair of contiguous muscles arising on the cephalo-dorsal wall of the labrum and inserting on its caudo-ventral wall (Plate I, B and II, B).

2. The Anterior Labral Muscles

The anterior labral muscles consist of a pair of median muscles which arise in front of the frontal suture

and extend to the anterior margin of the base of the labrum (Plate I, Band II, B).

3. The Posterior Labral Muscles

The posterior labral muscles consist of a pair of muscles which arise on the frons laterad of the anterior labral muscles. They attach at the base of the labral tormae (Plate I, B and II, B).

The Muscles of the Stomodaeum

The muscles of the stomodaeum consist of the following:

4. The Dorsal Dilators of the Buccal Cavity

A pair of dorsal dilators arise in the clypeus cephalad of the buccal cavity and extend to the anterior end of the stomodaeum (Plate II, B).

5. The Dorsal Dilators of the Pharynx

A pair of dorsal dilators of the pharynx arising from the cephalic portion of the frons extend to and insert upon the pharynx cephalad of the supraesophageal ganglion (Plate II, B).

6. The Ventral Dilators of the Pharynx

A pair of ventral muscles arise upon the ventro- cephalic aspect of the epicranium and insert upon the lateral aspect of the pharynx directly beneath the dorsal dilators (Plate II, B).

7. The Antennal Muscles

A pair of antennal muscles arise on the inner wall of the head caudad of the frontal suture and insert at the base of the antennae (Plate XIII).

The Mandibular Muscles

The mandibular muscles include the following two major bundles:

8. The Abductor Muscles

A pair of slender abductor muscles arise upon the inner dorso-lateral region of the epicranium and insert on the ectal apodemes of the mandibles (Plate II, D).

9. The Adductor Muscle

A pair of large, powerful muscles arise upon the ental dorsal region of the epicranium and insert on the ental apodemes of the mandibles. Each adductor muscle is divided into two groups composed of numerous fibers. They insert upon a tendon which arises from the inner base of the mandible (Plate II, D).

10. The Maxillary Muscles

A pair of maxillary muscles from each maxilla arises upon the lateral margin of the cephalo-ventral portion of the epicranium and inserts at the base of the stipes (Plate XIV).

11. The Labial Muscles

Labial muscles consist of a pair of muscles arising upon the ental margin of the ventral aspect of the epicranium just cephalad of the maxillary muscles. They insert on the median lateral aspect of the labium (Plate XIV).

The Prothoracic Muscles

12. The First Prothoracic Dorsal Longitudinal Muscles

The first prothoracic longitudinal muscles consists of a pair of muscles (12-1) arising upon the vertex. These extend caudad between the two separate halves of the dorsal epicranium and insert upon the median portion of the first intersegmental fold which is sclerotized to form an apodeme. Below this muscle is a secondary longitudinal muscle (12-2) which inserts slightly above the first but which has the same origin. There is also a tertiary dorsal longitudinal muscle (12-3) below the (12-2) with the same origin (Plate XIII).

13. The Second Prothoracic Longitudinal Muscles

The second prothoracic dorsal longitudinal muscles consist of a pair of slender muscles arising upon the vertex with the first dorsal longitudinal muscles. They insert, however, upon the intersegmental fold laterad of the first dorsal longitudinal muscle and dorsad of the third dorsal

oblique muscles (Plate XIII).

14. The Transverse Dorsal Muscles

The pair of broad transverse dorsal muscles in the prothorax arise upon the ental posterior surface of the epicranium and extend between the first and second dorsal longitudinal muscles. They insert upon the inner median region of the tergum of the prothorax (Plate XIII).

15. The First Dorsal Oblique Muscles

The first dorsal oblique muscles arise upon the cephalo-dorsal surface of the epicranium in the region of the vertex. They extend obliquely covering a part of the second dorsal oblique and the anterior portion of the third dorsal oblique muscles. The first dorsal oblique muscles insert upon the caudo-lateral portion of the prothoracic tergum (Plate XIII).

16. The Second Dorsal Oblique Muscles

The second pair of dorsal oblique muscles arise from the dorsal epicranium on each side of the vertex below the first pair of oblique muscles. They insert upon the lateral surface of the prothoracic tergum above the first dorsal oblique muscles (Plate XIII).

17. The Third Dorsal Oblique Muscles

The third dorsal oblique muscles arise upon the dorsal epicranium below the anterior end of the first dorsal

oblique muscles and insert upon the intersegmental fold adjacent to the first pair of dorsal longitudinal muscles (Plate XIII).

18. The First Pair of Ventral Longitudinal Muscles

The first pair of ventral longitudinal muscles are ribbon-shaped and originate upon the cephalo-ventral part of the epicranium. They insert upon the median sclerotized portion of the ventral inter-segmental fold (Plate XIV).

19. The Second Pair of Ventral Longitudinal Muscles

The second pair of ventral longitudinal muscles arise jointly with the first pair of ventral longitudinal muscles and insert upon the lateral surface of the ventral inter-segmental fold (Plate XIV).

20. The Oblique Ventral Muscles

A pair of slender oblique ventral muscles is present in the prothorax which arises from the cephalo-lateral surface of the ventral epicranium laterad of the ventral longitudinal muscles. They insert upon the median intersegmental fold, covering a small portion of the first ventral longitudinal muscles (Plate XIV).

21. The Ventral Transverse Muscles

Ventral transverse muscles arise upon the median lateral surface of the ventral epicranium and extend over the

central portion of the first longitudinal muscles. They pass between the ventral oblique and the first ventral longitudinal muscles and insert upon the median portion of the prothoracic sternum (Plate XIV).

22. The Ventral Vertical Muscles

In the prothorax a fan-shaped pair of vertical muscles arises from the inner surface of the postocciput. They extend downward and insert upon the prothoracic sternum between the attachments of the first and second longitudinal ventral muscles (Plate XIV).

The Mesothoracic Muscles

23. The Internal Dorsal Longitudinal Muscles

The internal dorsal longitudinal muscles consist of a pair of muscles which extend from the first to the second intersegmental membranes (Plate XV).

24. The External Dorsal Longitudinal Muscles

The external dorsal longitudinal muscles arise beneath the internal muscles and extend from the first to the second intersegmental membrane.

25. The Dorsal Oblique Muscles

The dorsal oblique muscles extend from the posterior median region of the mesothorax to the second intersegmental fold. They are found beneath the external dorsal longitudinal

muscles (Plate XVII).

26. The Internal Ventral Longitudinal Muscles

The internal ventral longitudinal muscles possess an arrangement similar to that of the dorsal internal longitudinal muscles (Plate XV).

27. The External Ventral Longitudinal Muscles

These muscles are of an arrangement similar to the external dorsal longitudinal muscles or (No. 24) (Plate XVI).

28. The Ventral Oblique Muscles

The ventral oblique muscles appear to be arranged similarly to the dorsal oblique muscles (or No.25) (Plate XVII).

29. The Transverse Muscles

The transverse muscles extend along the intersegmental fold. A pair of intersegmental muscles is present upon each of the intersegmental folds, (Plate XV and XVI).

30. The Oblique Tergo-Sternal Muscles

The oblique tergo-sternal muscles arise upon the apodeme of the first intersegmental fold and extend over the cephalo-lateral portion of the dorsal longitudinal muscles. They insert upon the second intersegmental fold above the cephalo-lateral end of the ventral longitudinal muscles (Plate XV).

31. The Transverse Muscles

The transverse muscles arise upon the tergum below the dorsal longitudinal muscles and insert upon the sternum below the ventral longitudinal muscles (Plate XV and XVI).

32. The Occluser of the Mesothoracic Spiracle

The occluser muscle of the mesothoracic spiracle arises upon the first intersegmental fold above the cephalolateral end of the internal aspect of the spiracle (Plate SVI).

33. The Dilator Muscles of the Mesothoracic Spiracle

The dilator muscle of the mesothoracic spiracle arises upon the first intersegmental fold below the cephalolateral end of the internal ventral longitudinal muscles and inserts above the lateral aspect of the spiracle (Plate XVI).

34. The Lateral Oblique Muscles

A pair of lateral oblique muscles from each side of the mesothoracic segment arises from the second intersegmental fold. These converge upward until their ends meet below the spiracle, where they insert.

The Metathoracic Muscles

The metathoracic muscles are similar to the mesothoracic muscles except for the absence of the oblique tergo-sternal

muscles or (No. 30) (Plate XV, XVI, XVII).

The Abdominal Muscles

The abdominal musculature of C. miliaris consists of the following:

The Muscles of the First Abdominal Segment

The first segment of the abdomen has been found to be supplied by six sets of muscles. These include the following muscles.

35. The Dorsal Longitudinal Muscles

Most of the dorsal longitudinal muscle fibers, except for a few, are of segmental length and extend from the anterior to the posterior intersegmental folds (Plate XV).

36. The Dorsal Oblique Muscles

The dorsal oblique muscles are not of segmental length. They arise upon the median region of the tergum and insert upon the intersegmental fold (Plate XVI).

37. The Ventral Longitudinal Muscles

The ventral longitudinal muscles of the first abdominal segment are similar to the dorsal longitudinal muscles or (No. 35) (Plate XV).

38. The Ventral Oblique Muscles

The ventral oblique muscles of the first abdominal segment are similar to the dorsal oblique muscles or (No. 36) (Plate XVI).

39. The Transverse Muscles

The transverse muscles of the first abdominal segment are all similar to the meso- or metathoracic transverse muscles or (No. 31). They arise upon the tergum below the longitudinal and oblique muscles and insert upon the sternum beneath the ventral longitudinal and oblique muscles (Plate XV and XVI).

40. The Occlusor Muscles of the Spiracles

These muscles appear to be similar to the occlusor muscles of the mesothoracic spiracles (Plate XVI).

41. The Oblique Lateral Muscles

These muscles appear to be similar to the meso- or metathoracic oblique lateral muscles or (No. 34) (Plate XVI).

When the muscles of the second through the eighth abdominal segments were studied it was found that the dorsal and ventral muscles of these seven segments are very similar to these discussed for the first abdominal segment. The only difference was found in the lateral muscles (Plate XVI).

42. The Lateral Muscles of the Abdomen

The lateral muscles of the abdomen are present between the dorsal and ventral longitudinal muscles without coming in contact with either of these muscles sets. Such muscles extend transversely along the entire length of each abdominal segment.

They are shorter in length in the region of the spiracle but wider as they pass below it. There are three sets of transverse muscles lined up over each other along each side of the segments. These form an inner (42 a) a middle (42 b) and external set of muscles (42 c). The inner transverse lateral set of muscles appears to be broadest while those of the external set are the narrowest (Plate XV and XVI).

43. Oblique Lateral Muscles

The oblique lateral muscles of the abdomen appear singly along the side of each segment and extend cephalically to the base of the abdominal spiracle (Plate XVI).

The Muscles of the Ninth Abdominal Segment

The ninth abdominal segment lacks the dorsal and ventral oblique muscles observed in the preceding abdominal segments but possesses similar dorsal, ventral, longitudinal and lateral dorso-ventral muscles. Only one set of transverse lateral muscles is present.

The Muscles of the Tenth Abdominal Segment

The muscles of the tenth abdominal segment include the following muscles:

44. The Longitudinal Muscles

Three pairs of longitudinal muscles are present which do not appear clearly. One pair of these extends ventrally (44 a), another extends laterally (44 b) and a third pair runs dorsally (44 c) (Plate XVII, B).

E. Fat Bodies

Fat bodies are present above and below the nervous, digestive, respiratory and muscular systems and even occur below successive layers of muscles.

F. Circulatory System

In living larvae a dorsal blood vessel is visible extending from the prothorax to the ninth or tenth abdominal segment. In the prothorax it is not possible to determine exactly where the dorsal vessel ends due to the dorsal thickening of the pronotum. In dissected larvae the dorsal blood vessel is not visible.

PART V

SUMMARY

1. The external structure of C. miliaris larvae has been shown to agree with the general characteristics of the family Buprestidae and the sub-family Buprestinae in having the dorsal plate of the prothorax medianly marked with an inverted Y or V-shaped groove. The presence of a frontal suture as a double edged linear tract distinguishes the head of Buprestid larvae from the head of other beetle larvae.

2. The digestive system is a straight tube except for a small loop in the anterior end of the hind intestine. The digestive tube is distinctly divided into the three embryonic parts which are visible in the mature larvae; the fore-intestine, the mid-intestine and the hind-intestine. The characteristic features of the digestive tube are as follows: Six major folds in the proventriculus which are slightly sclerotized, two gastric caecae which extend from the most anterior end of mesenteron, six separate Malpighian tubules arising at the anterior end of the hind-intestine and a vertical terminal anus.

3. Nine pairs of spiracles are present. There is one pair of mesothoracic spiracles and eight pairs of abdominal spiracles situated near the anterior margin of each pleuron. The respiratory system is well developed with a pair of dorsal

head trunks, a pair of ventral head trunks, a lateral longitudinal trunk, a pair of visceral trunks and ventral and lateral commissures. Each segment is well supplied with respiratory branches and tracheoles which extend to all areas of the body.

4. The muscular system is well developed in the prothorax and parts of the head such as the labrum and the mandibles. The muscles of the meso- metathoracic and first abdominal segment are less complex than the prothoracic muscles while the muscles of abdominal segments II - VIII are even more simple in their distribution. In the ninth and tenth segments the muscles are reduced. In general the muscular system is simple except for the prothoracic muscles.

PART VI

PLATE I

- A. Dorsal view of the Head and Epicranium.
- B. Ental Dorsal View of the Head and Epicranium.

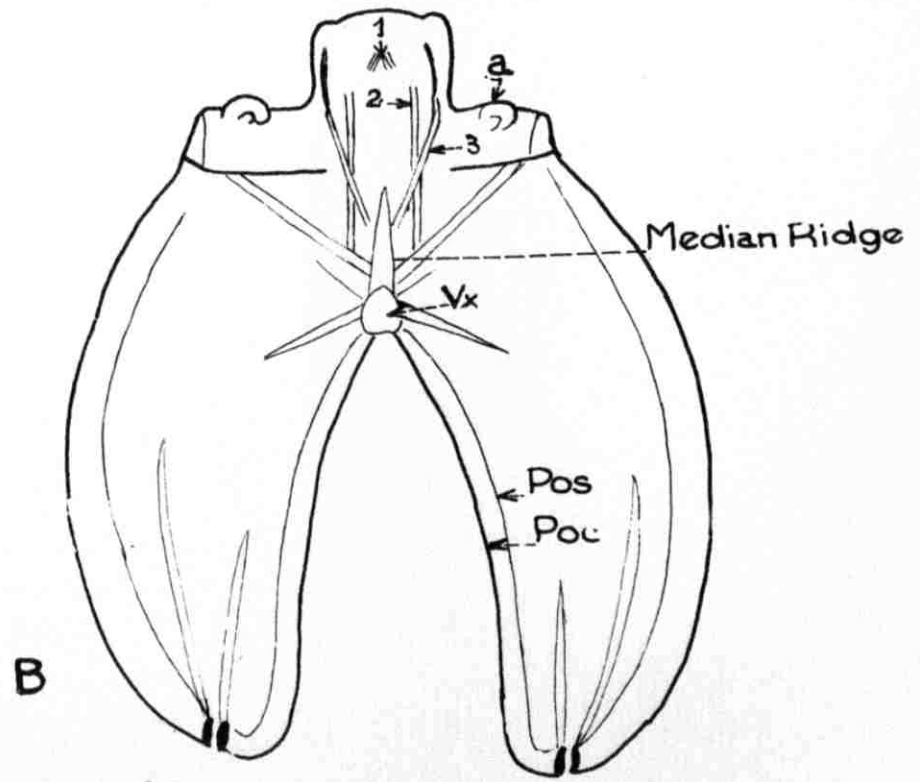
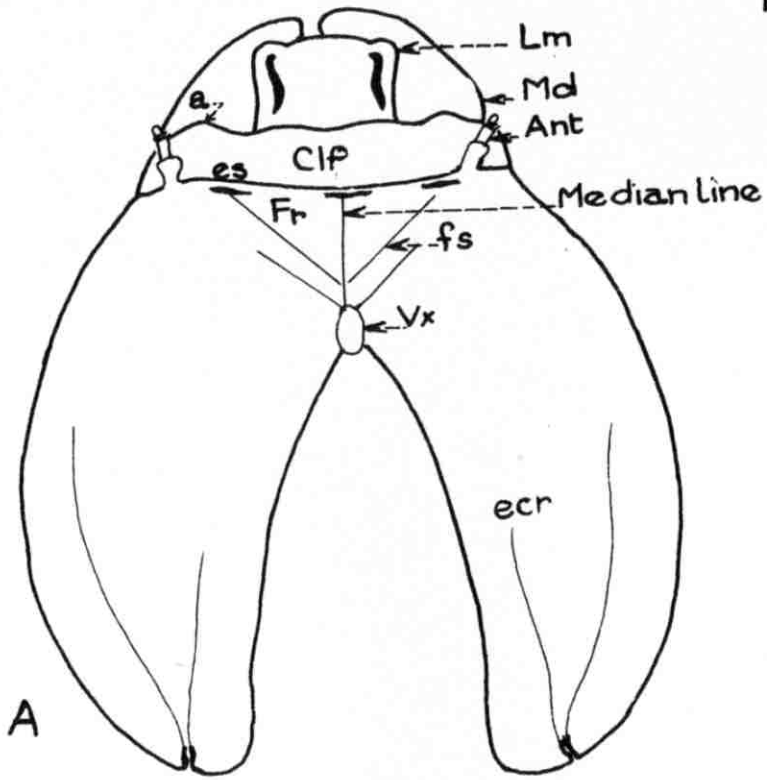


PLATE II

- A. Ventral View of the Head
 B. Dorsal View of the Labrum and the Pharyngeal Muscles
 C. Ental View of the Mandible
 D. Dorsal View of the Mandible and Its Muscles

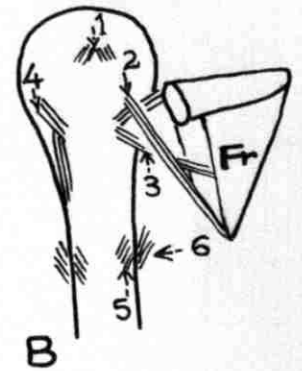
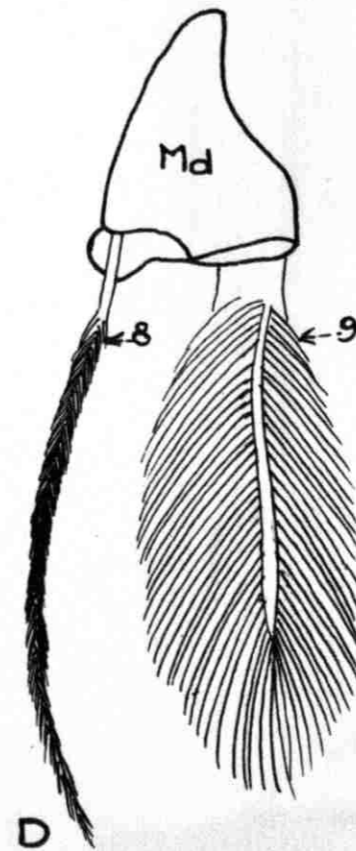
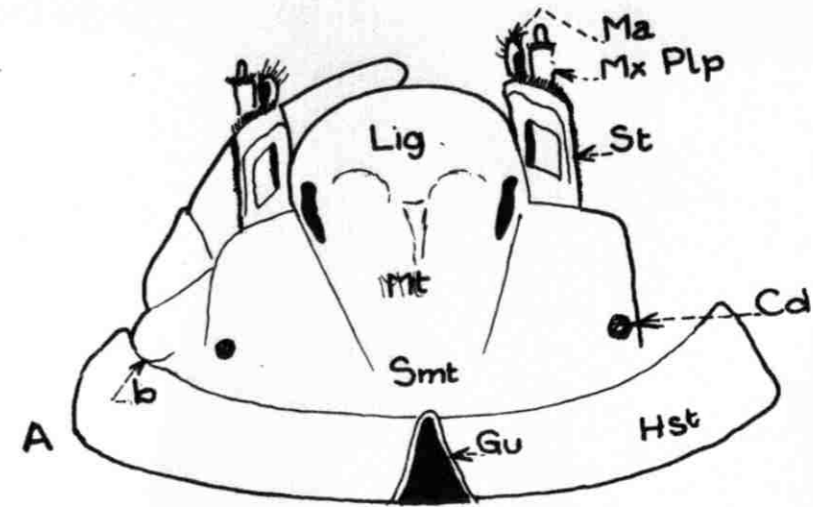


PLATE III

- A. External Dorsal View of the Entire Larva
- B. External Ventral View of the Head and Thorax

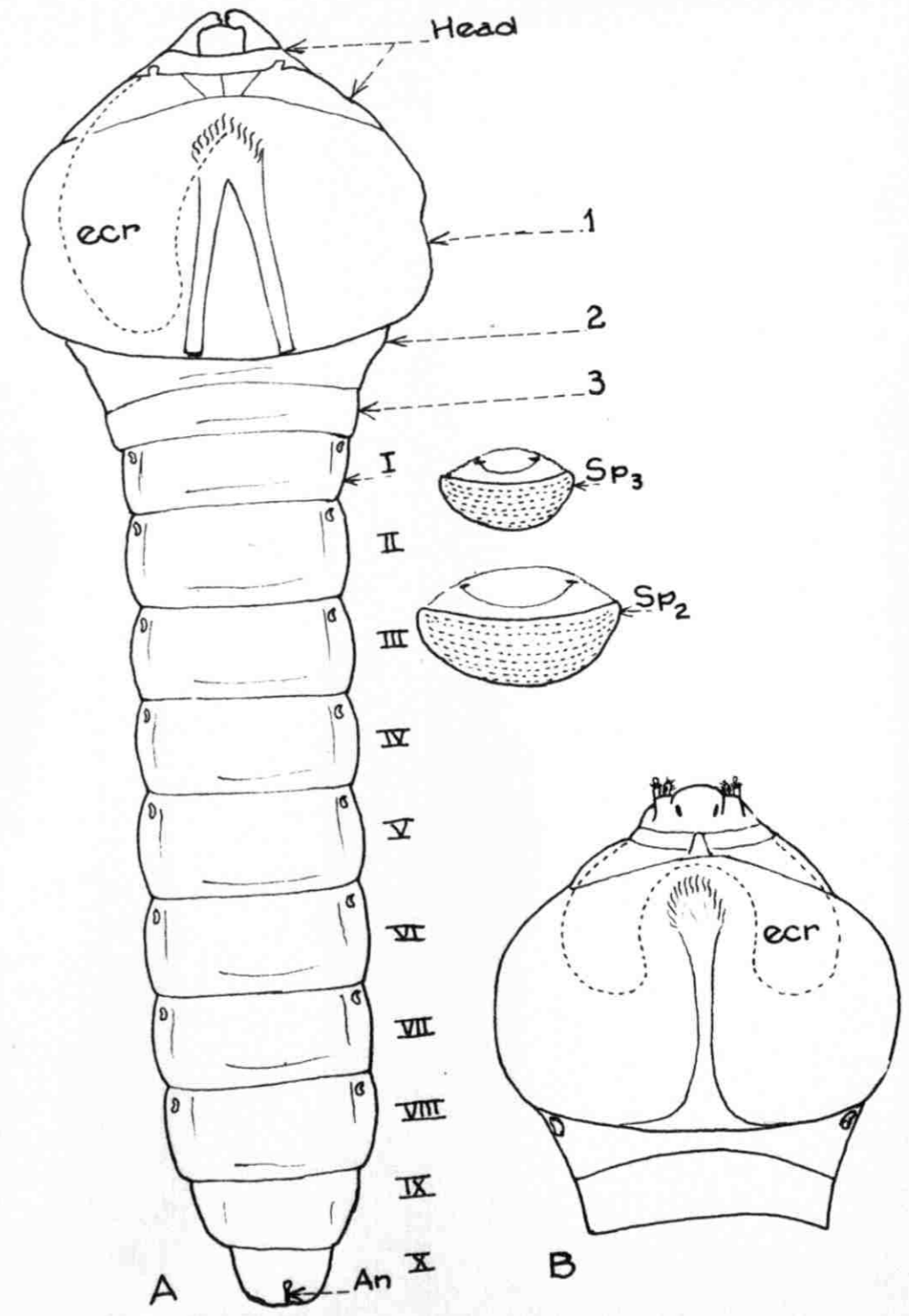
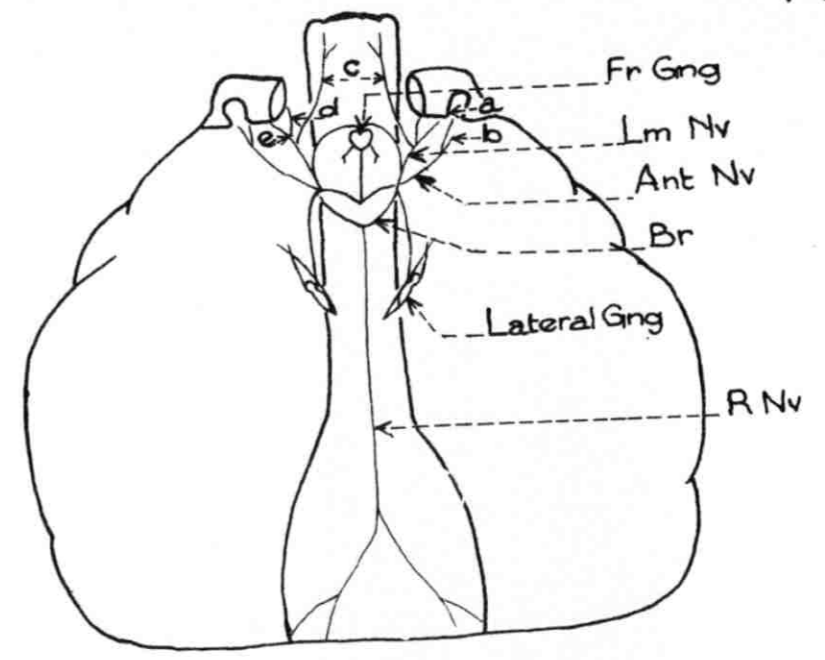
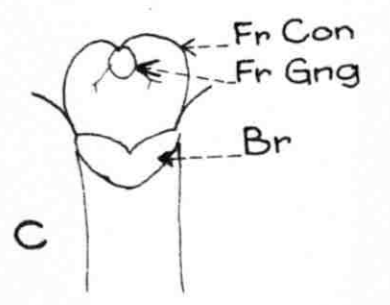


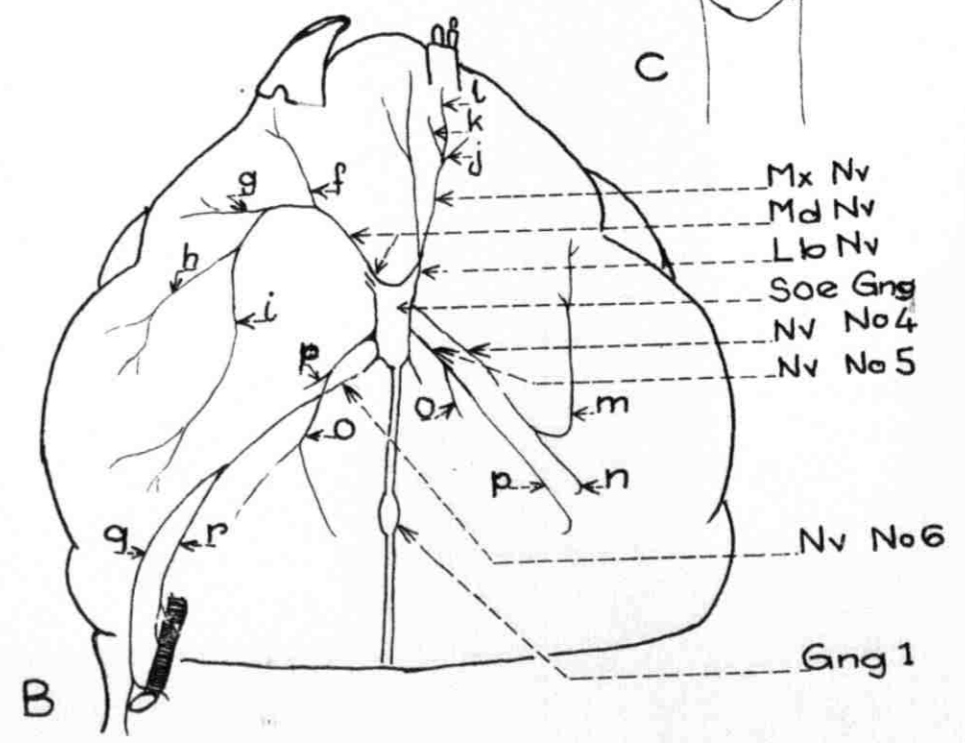
PLATE IV



A



C



B

- A. Dorsal View of the Supraesophageal Ganglion and Its Nerves
- B. Dorsal View of Subesophageal Ganglion and Its Nerves
- C. Dorsal View of Supraesophageal Ganglion and Frontal Ganglion

PLATE V

A. Dorsal View of the Suboesophageal Ganglion and the Ventral Nerve Cord

B. Dorsal View of the Seventh Abdominal Ganglion and the Intestinal Nerve

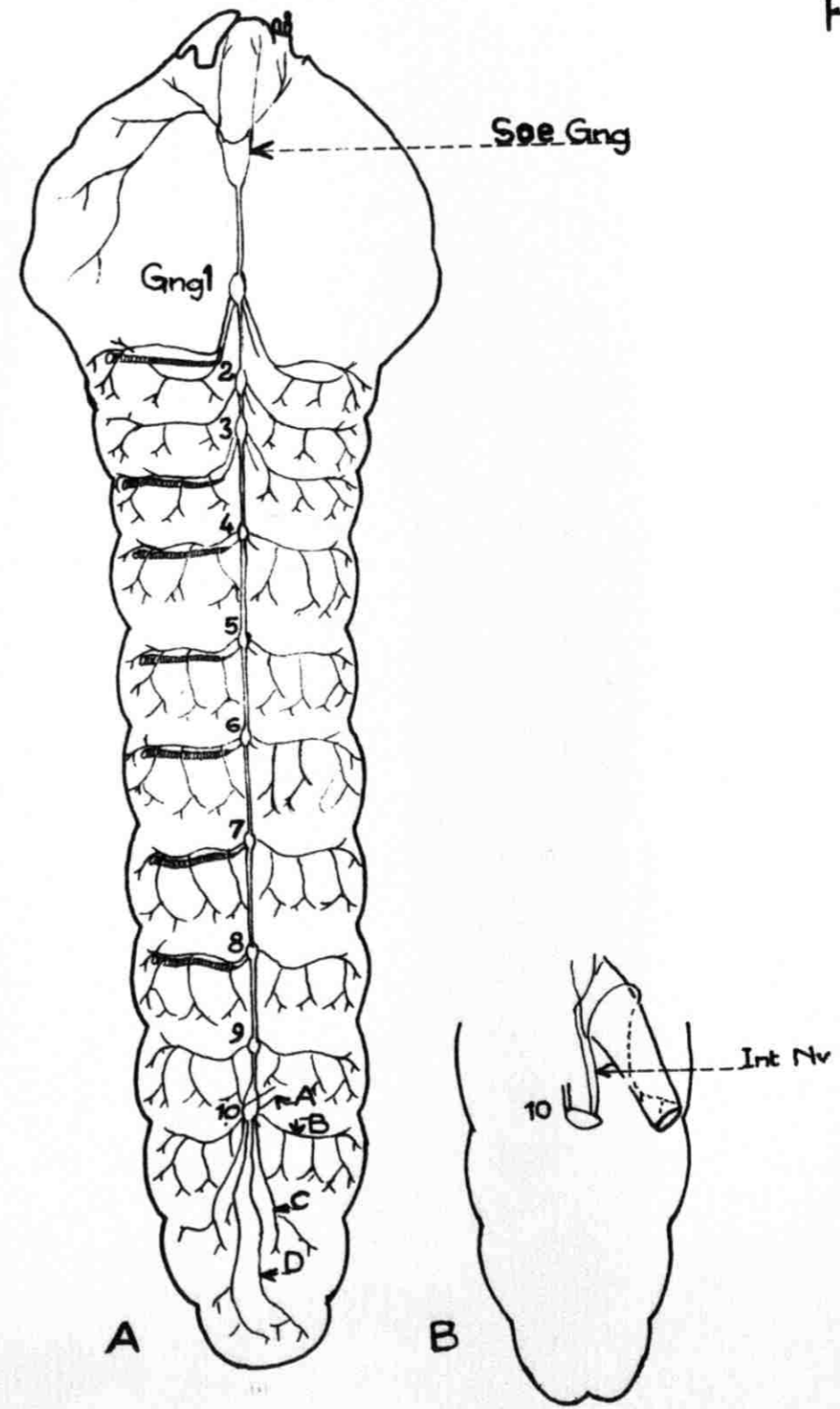


PLATE VI

- A. Lateral View of the Hypopharynx, Supraoesophageal and Lateral Ganglia
- B. Dorsal View of the Thoracic, First and Second Abdominal Segments and Their Relation to the Musculature

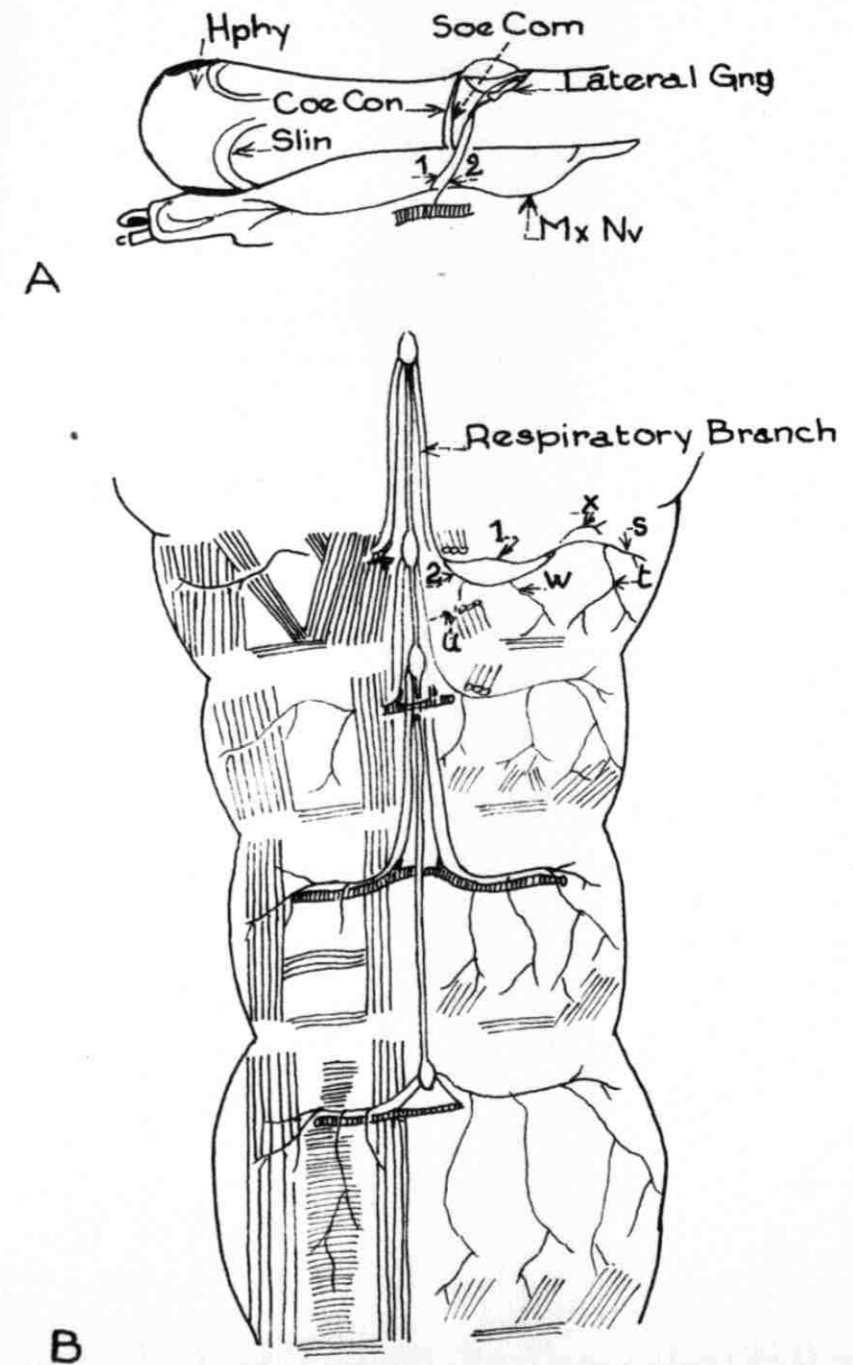


PLATE VII

A. Dorsal View of the Digestive System

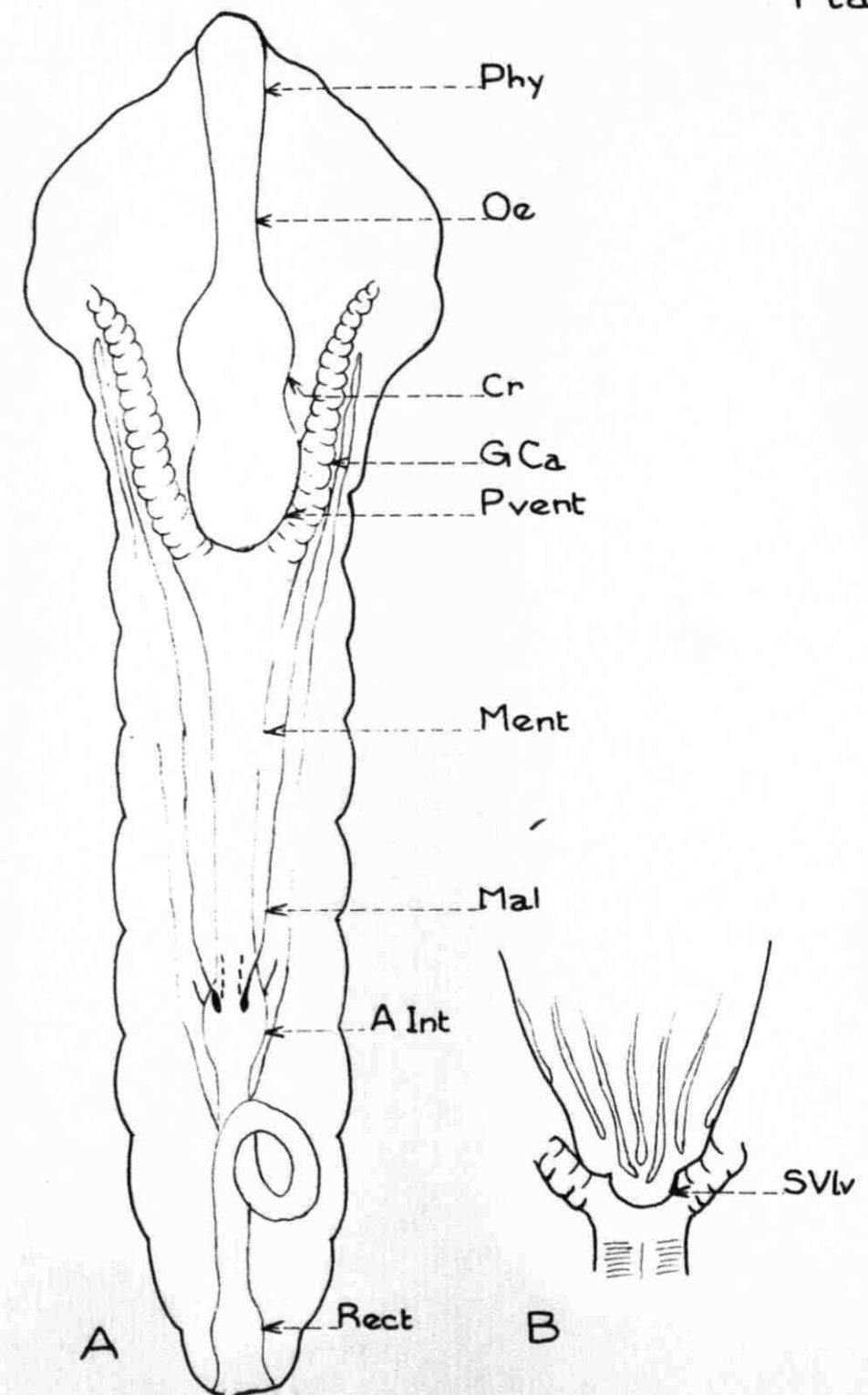
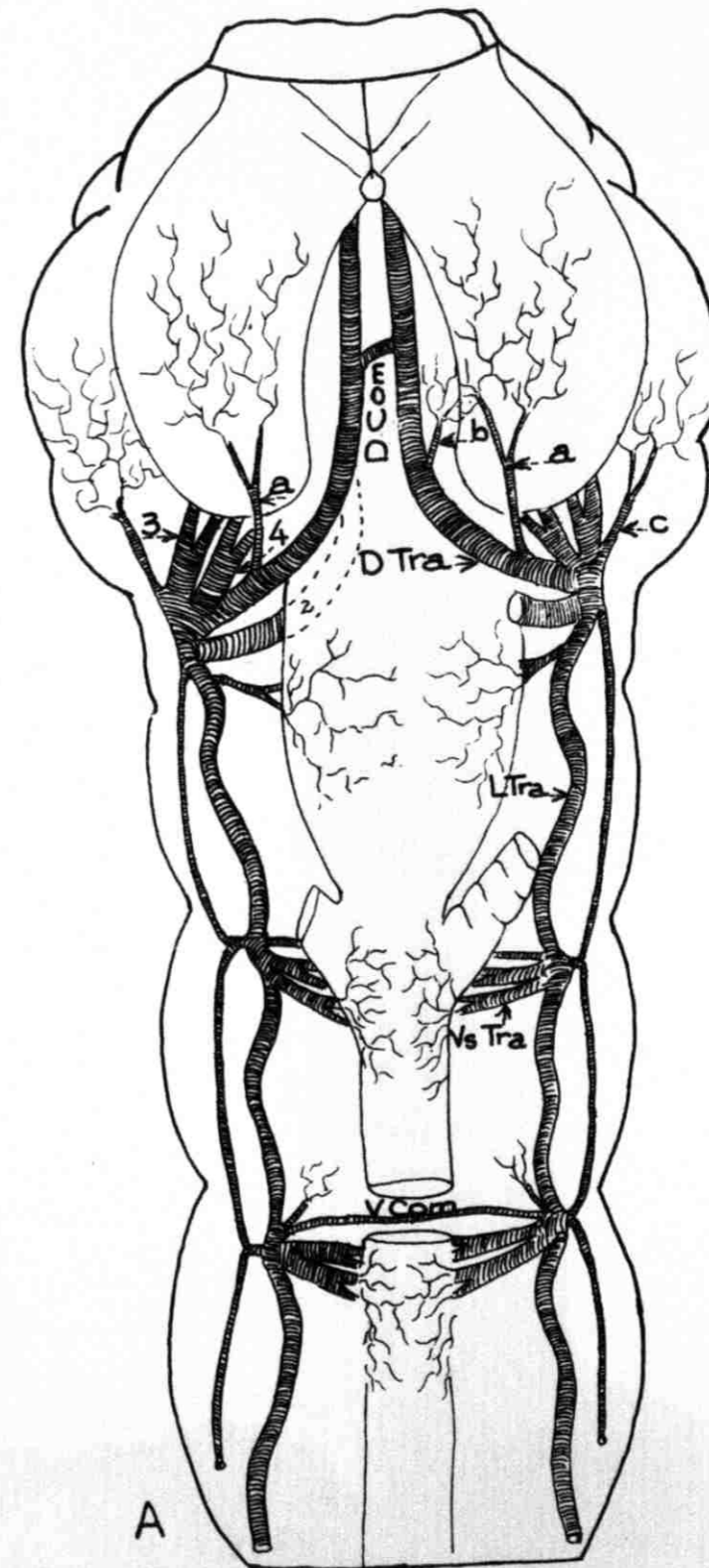
B. Longitudinal Section of the Proventriculus Showing Major
Folds

PLATE VIII

A. Dorsal View of the Respiratory System



1

2

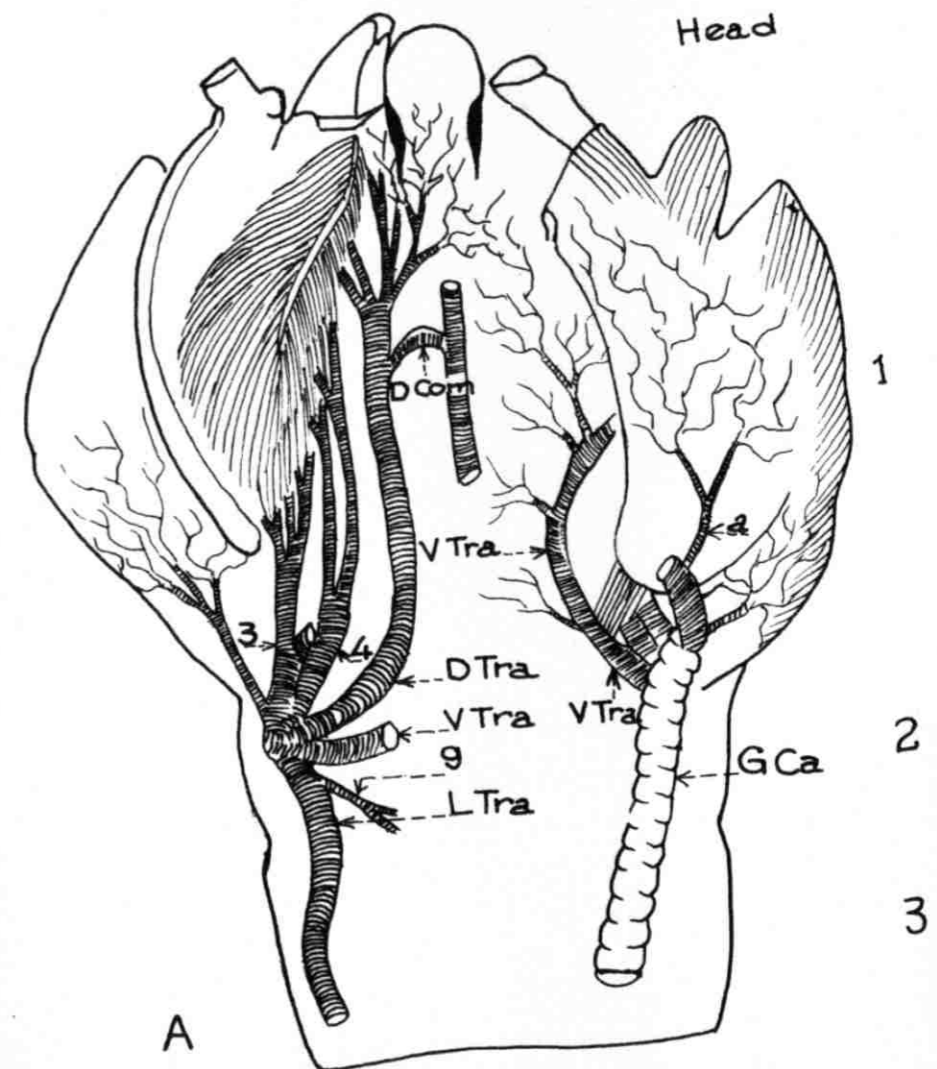
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I

II

PLATE IX

A. Dorsal View of the Respiratory System of the Head, and
Thoracic Segment 1, 2 and 3.



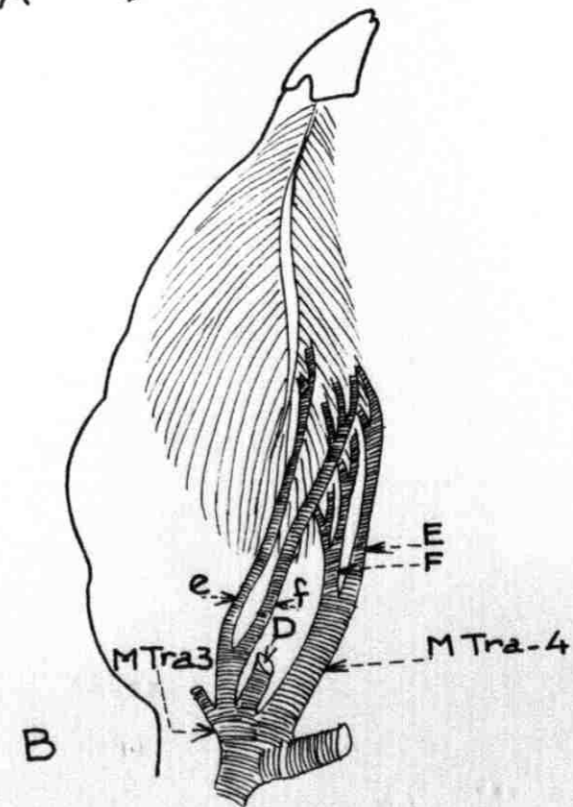
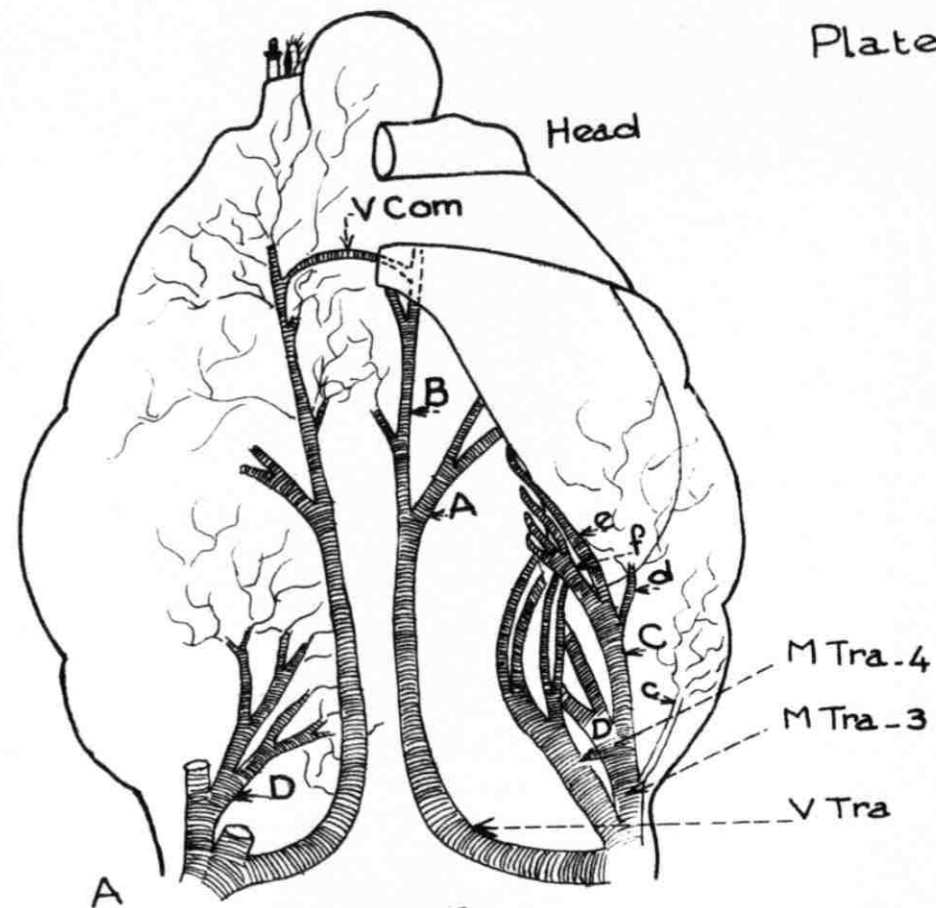


PLATE X

A. Ventral View of the Respiratory System of the Head and Thoracic Segments 1 and 2.

B. Ventral View of the Middle Trachea No. 3 and No.4.

PLATE XI

A. Dorsal View of the Respiratory System of Thoracic Segments
1 and 2 and Abdominal Segments I and II.

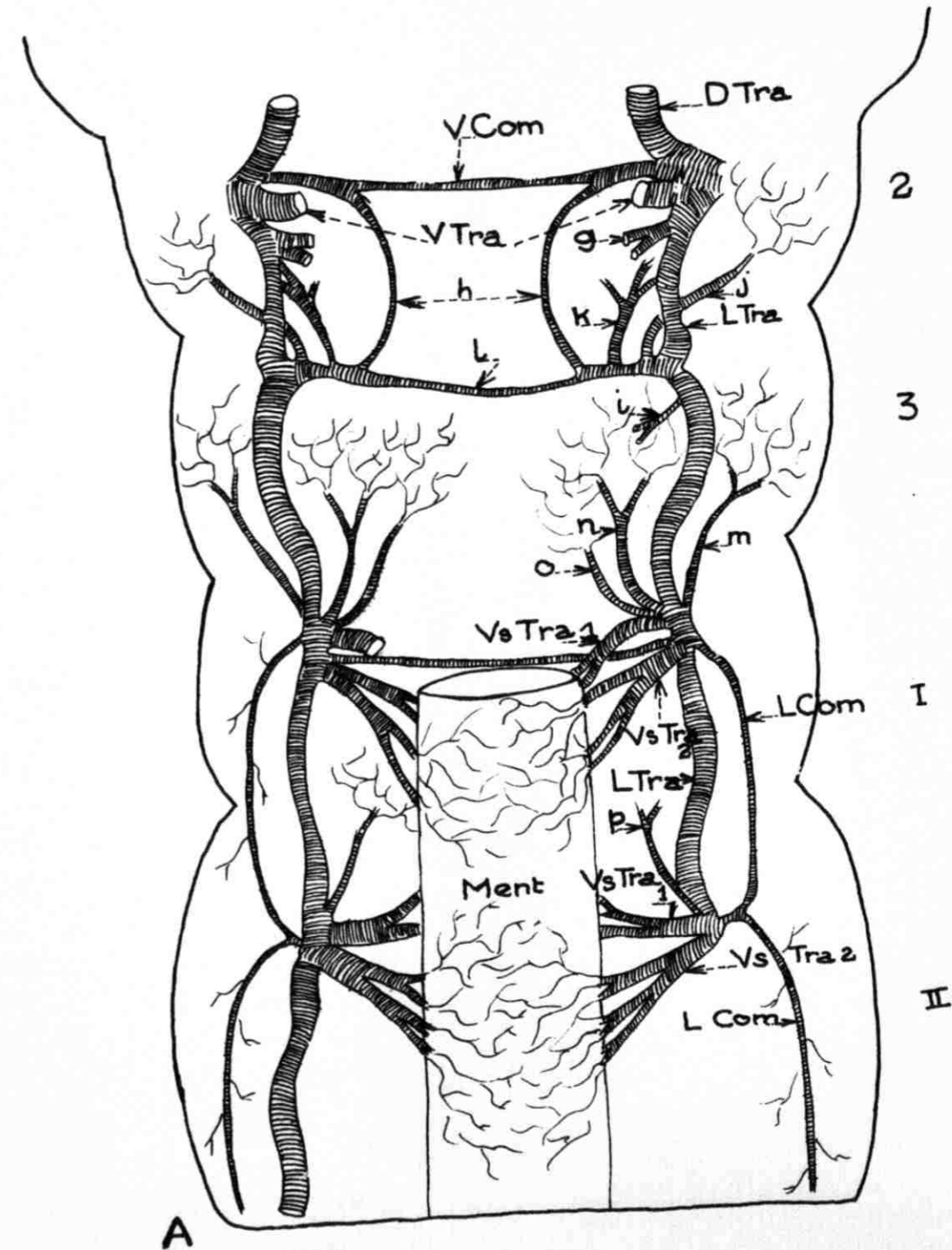
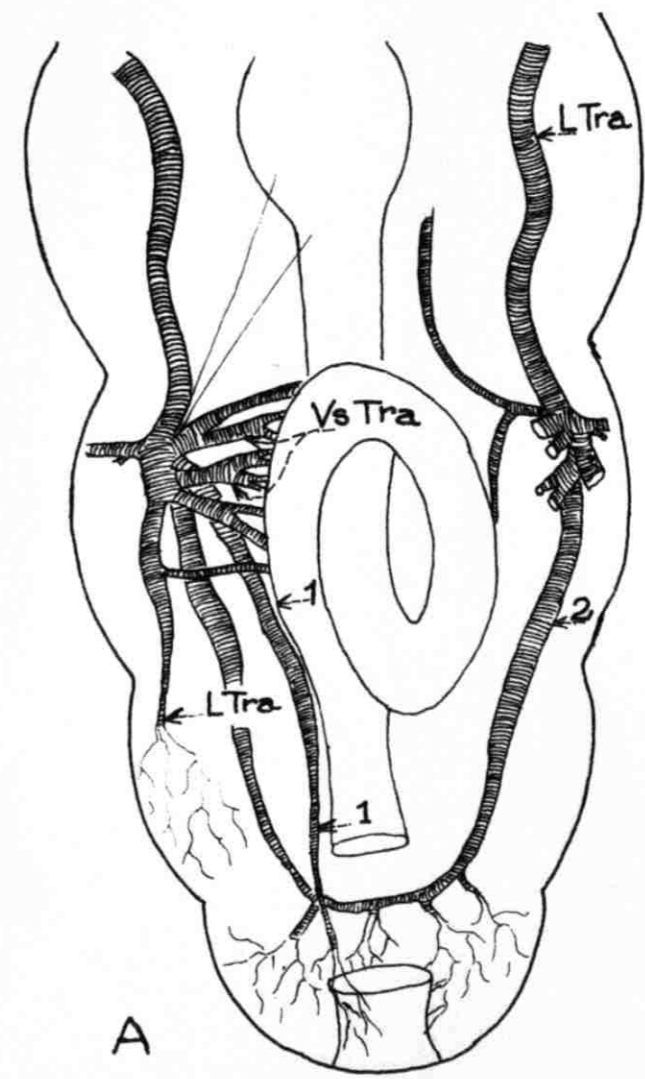


PLATE XII

A. Dorsal View of the Respiratory System of the Abdominal Segments VIII - X.



VII

VIII

IX

X

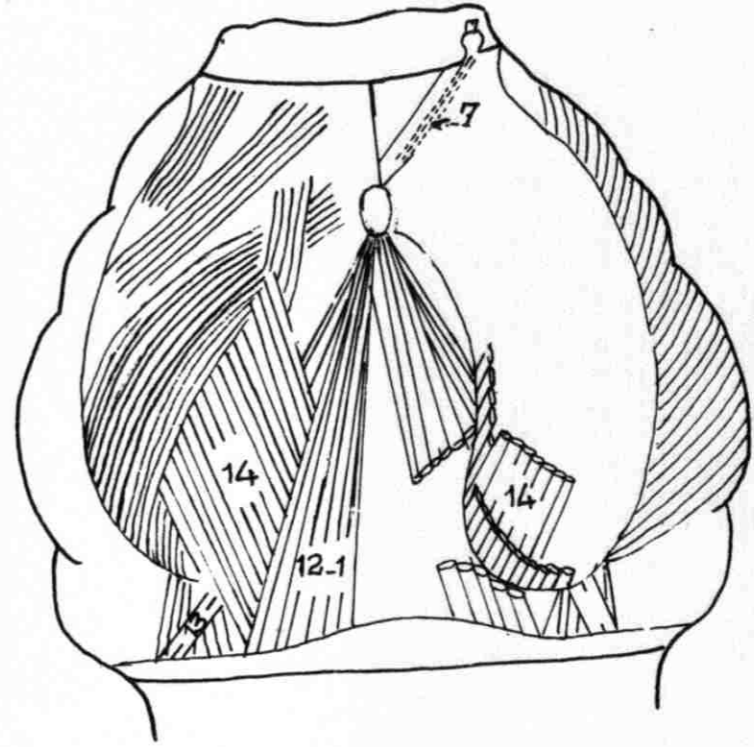
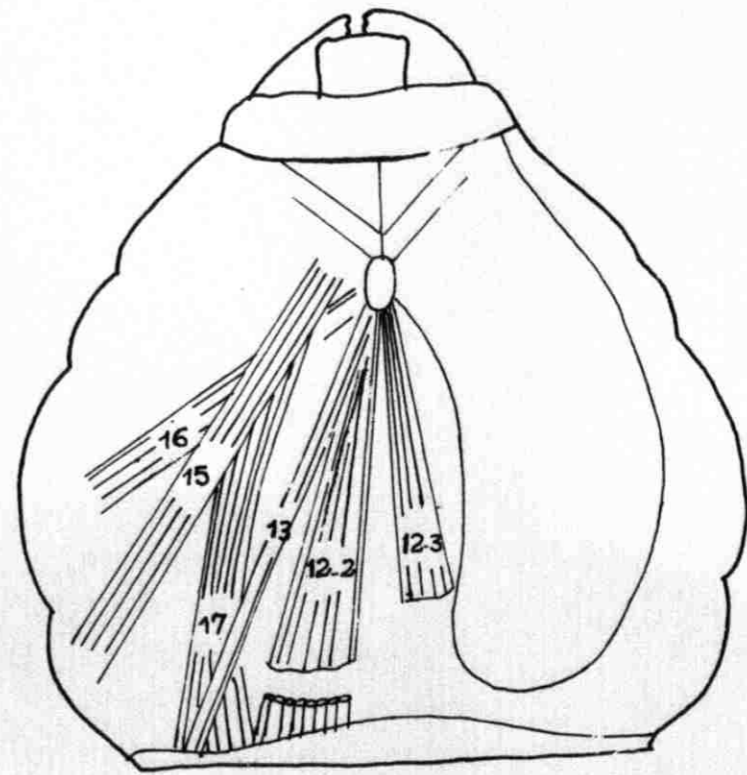


PLATE XIII

Dorsal View of the Prothoracic Muscles



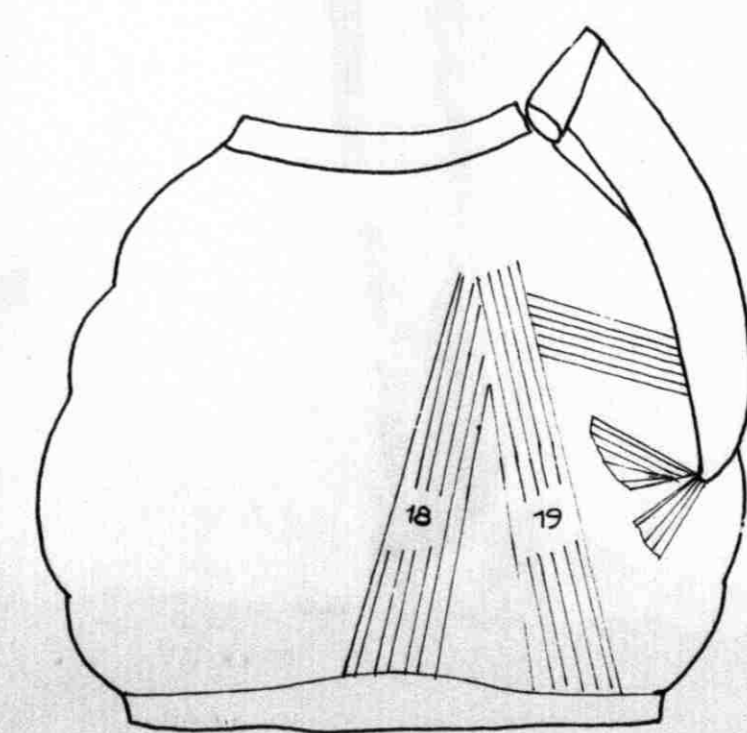
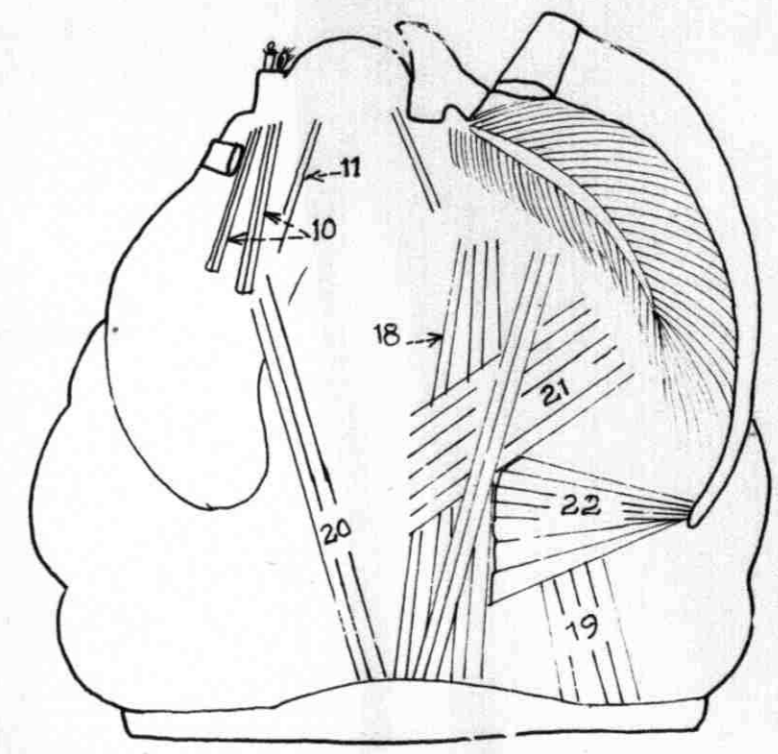
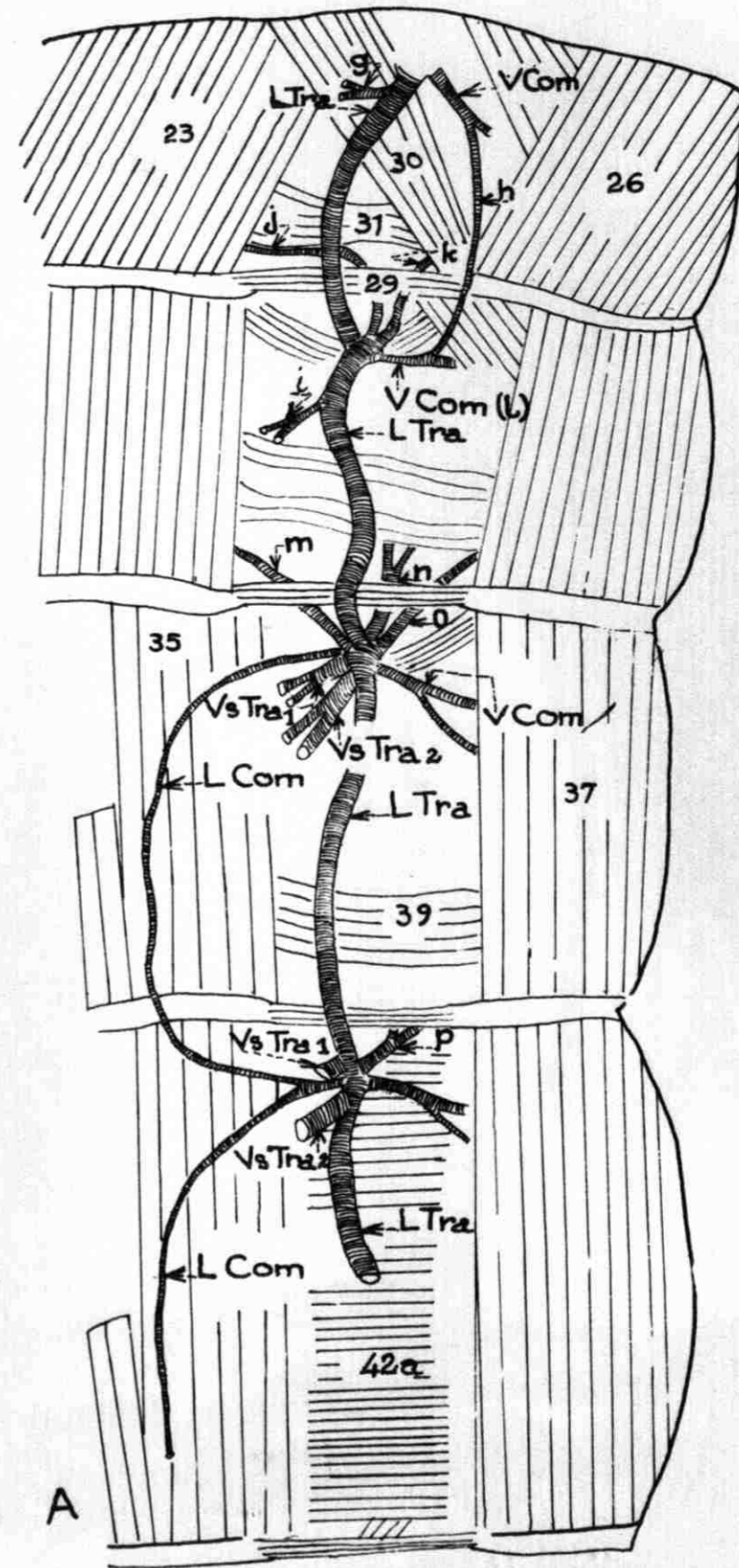


PLATE XIV

Ventral View of the Prothoracic Muscles

PLATE XV

Ventral View of the Muscles of Thoracic Segments 2 and 3 and Abdominal Segment I and II.



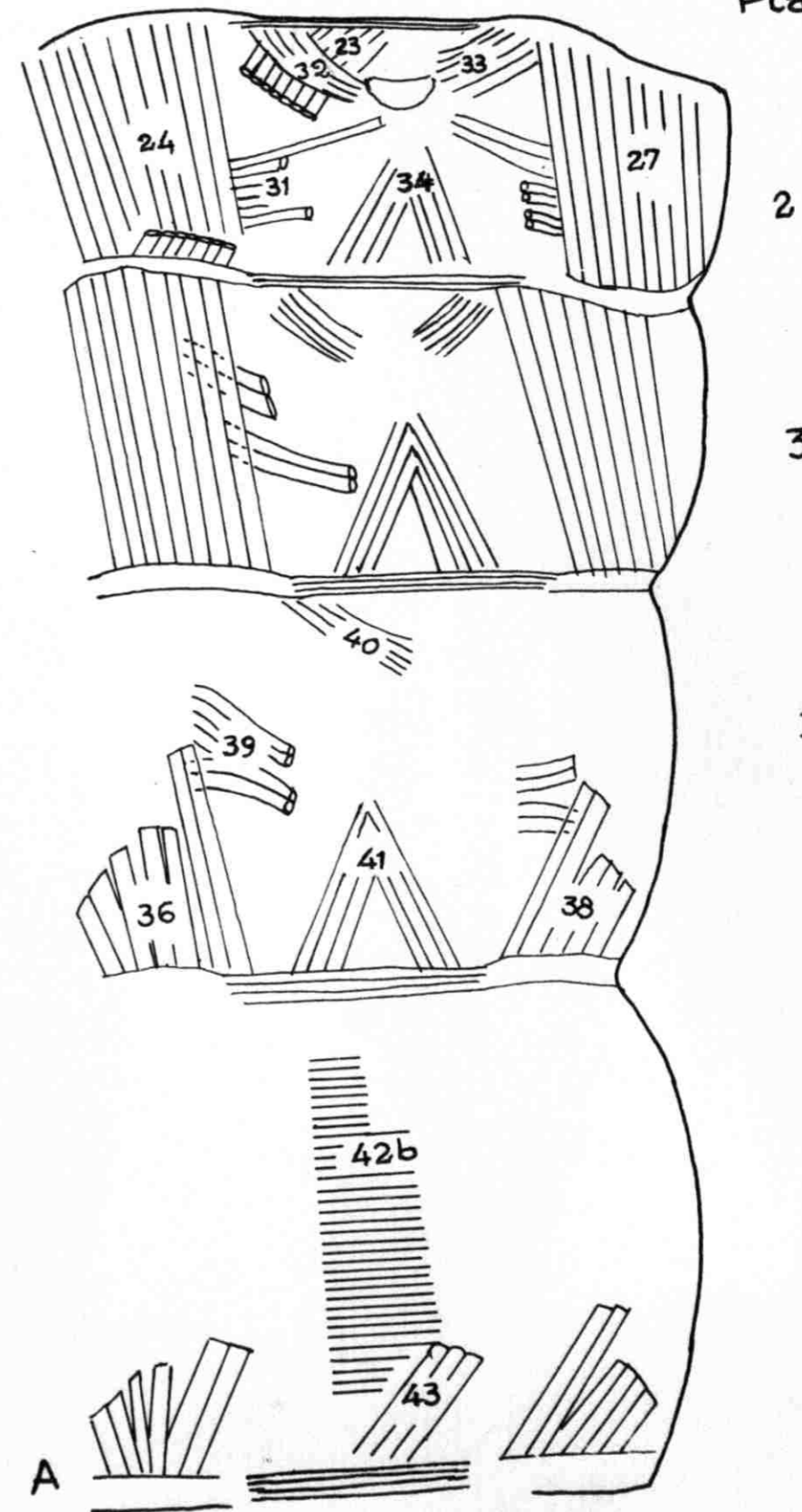
2

3

I

II

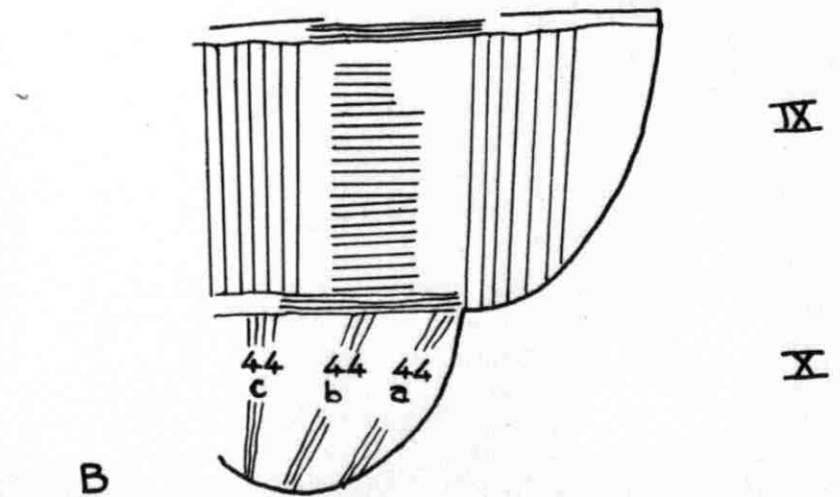
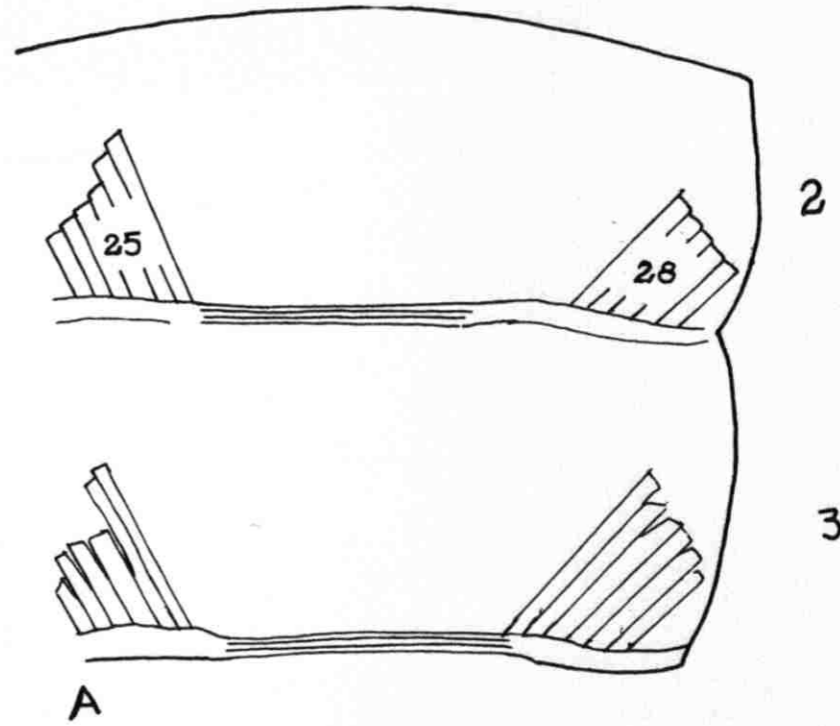
A

PLATE XVI

Ventral View of The Muscles of Thoracic Segments
2 and 3 and Abdominal Segments I and II. Muscles
Beneath Those Shown in Plate XV.

PLATE XVII

- A. Ventral View of Thoracic Segments 2 and 3. Muscles
Beneath those Shwon in Plate XVI.
- B. Ventral View of the Muscles of Abdominal Segments IX
and X.



PART VII

Explanation of Abbreviations

Abbreviations of words are taken from:

1. Snodgrass 1935. Insect Morphology
2. Böving and Craighead 1931. Ent. amer. 11.

A Int	=	Anterior Intestine
Ant	=	Antenna
An	=	Anus
Br	=	Supraoesophageal Ganglion
Bu C	=	Buccal Cavity
Cd	=	Cardo
Clp	=	Clypeus
Coe Con	=	Circumoesophageal Connectives
Com	=	Commissure
Con	=	Connectives
Cr	=	Crop
D Com	=	Dorsal Commissure
D Tra	=	Dorsal Tracheal Trunk
ecr	=	Epicranium
es	=	Epistomal suture
Fr	=	Frons
Fr Con	=	Frontal Ganglion Connectives
Fr Gng	=	Frontal Ganglion
Fs	=	Frontal Suture

G Ca	=	Gastric Casca
Gng	=	Ganglion
Gu	=	Gula
Hphy	=	Hypopharynx
Hst	=	Hypostoma
Int	=	Intestine
L Com	=	Lateral Commissure
Lb	=	Labium
Lm	=	Labrum
Lig	=	Ligula
Ltra	=	Lateral Tracheal Trunk
Ma	=	Mala
Mal	=	Malpighian Tubule
Md	=	Mandible
Ment	=	Mesenteron
Mt	=	Mentum
Mx	=	Maxilla
Nv	=	Nerve
Oe	=	Oesophagus
Phy	=	Pharynx
Plp	=	Palpus
Poc	=	Postocciput
Pos	=	Post occipital suture
Pvent	=	Proventriculus
Rect	=	Rectum
RNv	=	Recurrent Nerve

Slin	=	Superlinguae
Smt	=	Submentum
Soe Com	=	Suboesophageal Commissure
Soe Gng	=	Suboesophageal Ganglia
Sp	=	Spiracle
St	=	Stipe
Stom	=	Stomodaeum
SVlv	=	Stomodeal Valve
Tra	=	Trachea
V Com	=	Ventral Commissure
V Tra	=	Ventral Tracheal Trunk
Vs Tra	=	Visceral Trachea
Vx	=	Vertex

PART VIII

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Listed below are selected references consulted during the process of this investigation. References cited in the text are indicated by an asterisk (*). Abbreviations follow those listed in the World List of Scientific Periodicals.

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