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The Gross Morphology of the Central and Visceral Nervous Systems of Haplorhynchites Aeneus (Boheman) (Coleoptera: Curculionoidea: Rhynchitidae)

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THE GROSS MORPHOLOGY OF THE CENTRAL AND VISCERAL NERVOUS SYSTEMS

OF HAPLORHYNCHITES AENEUS (BOHEMAN)

(Coleoptera: Curculionoidea: Rhynchitidae)

by

Theresa Eileen Droste

A Thesis Submitted to the Faculty of the Graduate School
of Loyola University in Partial Fulfillment of
the Requirements for the Degree of
Master of Science

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INTRODUCTION

Haplorhynchites aeneus (Boheman) is a member of the family Rhynchitidae ("saw-toothed snout beetles") of the superfamily Curculionoidea. The adults live in association with several species of sunflower (Heliantheae spp.). Females cut stems below the flower heads, and eggs are deposited in the bases of the disk-flowers. Developing larvae feed on pollen and decaying tissue of the disk flowers, and bore into the ground to overwinter as fourth instar larvae; pupation and emergence occur in July (Hamilton, 1973). Although H. aeneus is not considered to be a major economic pest at this time, it is known to infest large crops of sunflowers harvested commercially for their oil.

The biology and external morphology of H. aeneus has been studied in detail primarily to determine its taxonomic position (Hamilton, 1973). Internal morphological studies have been done on scattered members of the superfamily Curculionoidea, but the nervous system has been briefly touched upon. The principal objective of this investigation is to describe the gross morphology of the Central (Somatic) and Visceral Nervous Systems of H. aeneus, including innervation of the internal organs. A second objective is to provide the basis for similar, comparative studies on internal systems in other species and genera of Rhynchitidae, with the dual purpose of determining the evolutionary position of this family with respect to other Curculionoidea, and of lending support to the theory that taxonomic characters are internal as well as external, and should be employed in classification.

This study is not a histological one, nor has there been an attempt made to identify homologous muscles and nerves with those of other insects. Rather, it provides gross anatomical information which is fundamental to future investigations in physiology and phylogeny.

REVIEW OF LITERATURE

The nervous system of insects in general has been intensively studied, with emphasis on the histology and histophysiology of the Central Nervous System. However, the gross morphology of the entire nervous system is known for only selected representative specimens, and as a result, few attempts have been made to assess the value of gross neuroanatomical characteristics in the higher classification of insect families.

Bullock and Horridge (1965) have consolidated the information known on the anatomy of both the Central and Visceral Nervous Systems in a major treatise, which includes selected illustrations on the neuroanatomy of each order as well as a comprehensive bibliography, up to 1965. Other general works relating structure and function are Roeder (1958), Rockstein (1964), Wigglesworth (1965), and Chapman (1971). Smith and Treherne (1963) discuss the physiology of the finer details of insect neuroanatomy.

The greatest single obstacle in the few detailed accounts of nerve topography which have been done is the search for a satisfactory method of nomenclature for the nerves, which in turn involves the establishment of a workable criterion of muscle homology. This situation is further complicated by the extreme diversity seen among species in nerve fusion and branching, as well as in variation in muscle origin and insertion. Pipa and Cook (1959) studied in great detail the thoracic nerves of Periplaneta americana (L.) (Dictyoptera: Blattidae), label-

ling the nerve branches according to the individual muscles innervated, based on a previous work by Carbonnell (1947) on the thoracic musculature of the same insect. Schmitt (1959) did a similar study of the thoracic nerves of Dissosteira carolina (L.) (Orthoptera: Acrididae) but here again referred to a previous work on the thoracic muscles of the same grasshopper by Snodgrass (1929) to designate individual nerves. Schmitt (1962) gives a comprehensive review of major works and the terminology employed in the thoracic and abdominal nervous systems of selected well-studied insects. Shankland (1965) reviews muscle and nerve nomenclature, and uses the terminology of Pringle (1939) for his work on the muscles and nerves of the pregenital abdominal segments of P. americana (L.). Youssef (1968 and 1971) also reviews thoroughly the historical use of muscle and nerve nomenclature, but devises a new method based on the attachment of the muscle innervated and the degree of branching the nerve has undergone before entering the muscle. Youssef's works on the pregenital abdominal morphology of Nomia melanderi (Ckll.) (Hymenoptera: Halictidae) and the nerves and muscles of the head of Apis mellifera (L.) (Hymenoptera: Apidae) are two of the more detailed and informative studies done on the subject.

The Visceral Nervous System of insects includes the Stomogastric, Proctodeal, and Ventral Sympathetic Nervous Systems, and has been a subject of growing interest since its neuroendocrine functions have been revealed. Bordas (1900) described the retrocerebral organs of various families of Orthoptera. Zawarzin (1916) discusses the insect Stomodeal Nervous System in general. Nabert (1913) describes the corpus

allatum of a large number of insects, including representatives from four families of Coleoptera. Bickley (1942) also compared gross morphology of representative insect retrocerebral organs. The most comprehensive work on comparative stomatogastric nervous system anatomy was published by Cazal (1948) who studied that system in over 128 insect species, including 11 species of Coleoptera. Cazal's work includes histological as well as anatomical studies, emphasizing the close cellular relationship of the corpus cardiacum-corpora allatum complex of many insects with the dorsal aorta. Other descriptions of the Stomatogastric Nervous System includes Hanan (1955) on Apis mellifera (L.); McLeod and Beck (1963) on the relationship of corpus cardiacum-corpora allatum structure and its function in diapause in the European corn borer Ostrinia nubilalis (Hubner) (Lepidoptera: Pyraustidae); and Langley (1965) on the neuroendocrine complex of the tsetse fly Glossina morsitans (Diptera: Muscidae).

The problem of nerve terminology exists with the Stomatogastric Nervous System also, but to a lesser degree. Willey (1961) has standardized the nomenclature in his detailed study of the Stomodeal Nervous System of P. americana (L.), and his terminology has been followed by most subsequent authors.

Johannson (1957) described the complete nervous system of Onco-peltus fasciatus (Dallas) (Hemiptera: Lygaeidae), including the gross anatomy of the Stomodeal Nervous System, the histology of the brain, and the rate of postembryonic development of the nervous system. Quite recently, Awasthi (1972 and 1973) demonstrated in situ the neurosecre-

tory pathways of Nezara viridula (L.) (Hemiptera: Pentatomidae) and Metochus uniguttatus (Thunb.) (Hemiptera: Lygaeidae), showing the pathway of neurosecretory material as it traverses from the protocerebrum to the walls of the aorta. Srivastava (1970) published a similar study on Halys dentatus (Fab.) (Hemiptera: Pentatomidae).

Gabe (1966) summarizes the general characteristics of the structure of the retrocerebral organs for each order of insects, and discusses the relationship between gross structure of endocrine glands and their function.

Structural studies on the sympathetic or abdominal nerves of insects are given by Holste (1910) on Dytiscus marginalis (L.) (Coleoptera: Dytiscidae) and by Nesbitt (1941) on various Orthoptera. Plotnikova (1968) discusses in detail the Sympathetic Nervous System of insects in general and Locusta migratoria (L.) (Orthoptera: Acrididae) in particular, and traced the ventral, unpaired nervous tracts to the tritocerebrum, and hence to the Stomatogastric Nervous System, of the insect.

Two insect organs in which the source of innervation is in question are the heart and the salivary glands. Alexandrowisz (1926) charted the lateral and segmental cardiac nerves of the dorsal blood vessel of P. orientalis (Dictyoptera: Blattidae) and traced them to the spiracles laterally, but did not follow them anteriorly. Jones (1964) credits the corpus cardiacum for the innervation of the dorsal vessel, and discusses other anatomical and physiological phenomena of the heart of various insects. Dogra (1967) traced neurosecretory material from the protocerebrum, via the corpora cardiaca, to the dorsal aorta of Dysdercus koenigii

(Hemiptera: Pyrrhocoridae). Johnson (1966) and Miller and Thompson (1968) studied the ultrastructure of heart innervation of P. americana (L.) and found both neurosecretory and motor axons involved, but hold that neurosecretory cells in the ventral segmental ganglia give rise to the neurosecretory axons, which then reach the lateral cardiac nerves of the heart via the segmental nerves.

Whitehead (1971) found the salivary glands, ducts, and reservoirs of P. americana (L.) to be innervated by both the Stomodaeal and the Central Nervous Systems. Willey (1961), however, reports only the stomatogastric innervation of the salivary glands of that insect.

Very little work has been done on the innervation of the genital musculature and reproductive organs, or of the hindgut, of insects, with the exception of Snodgrass (1936) on Orthoptera and Atkins and Chapman (1957) on Dendroctonus pseudotsugae (Hopk.) (Coleoptera: Scolytidae). Davey (1964) summarizes theories on the nervous control of visceral muscles in insects, including the heart, Malpighian tubules, and the three divisions of the alimentary canal.

Our knowledge of the neuroanatomy of Coleoptera is far from complete. Dytiscidae is the best known family, due to the work of Holste (1910) on the entire nervous and muscular system of Dytiscus marginalis (L.) and Joly (1942) on the retrocerebral complex of the same insect. Cazal (1948), mentioned earlier, compared Stomatogastric Nervous System anatomy of 11 species of Coleoptera, none of which, however, are members of Curculionoidea. Arvy and Gabe (1953) studied the retrocerebral organs of Tenebrio molitor (L.) (Coleoptera: Tenebrionidae). Siew (1965) demon-

strated the gross anatomy of the Stomatogastric Nervous System of Gal-
eruca tanacetii (L.) (Coleoptera: Chrysomelidae) and emphasized the in-
timate nervous connections of the brain-corporum cardiacum, corporum card-
iacum-corporum allatum, corporum cardiacum-hypocerebral ganglion, and cor-
porum allatum-subesophageal ganglion. Berberet and Helms (1972) treat
the metamorphosis of selected systems, including the Central Nervous
System, of Phyllophaga anxia (LeConte) (Coleoptera: Scarabeidae).

The external anatomy of the superfamily Curculionoidea has been
studied extensively for taxonomical purposes, but only selected econom-
ically important members have been studied internally in any detail.
The most comprehensive work was done by Aslam (1961) who compared the
gross morphology of selected systems of representative members, for the
purpose of comparing internal differences with taxonomical divisions.
In this study, the digestive and reproductive systems from 60 species
representing 44 genera and 25 subfamilies, and the Central Nervous Sys-
tem of 16 species from 14 genera and 12 subfamilies were charted. As-
lam's treatise includes the only internal anatomical studies published
on members of the family Rhynchitidae, Deporaus betulae (L.) and Rhyn-
chites pauxillus (Germ.) (European), other than the present study on H.
aeneus. Unfortunately, these species were not among the 16 species in
which Aslam charted the Central Nervous System.

The digestive and reproductive systems of various members of
the family Curculionidae have been compared in individual studies:
Naupactus leucoloma (Boheman) by Tissot (1938); Anthonomus grandis (Boh-
eman) by Burke (1959) and Sundman and King (1963); Graphognathus striatus

(Buchanan), G. fecundus (Buchanan), and G. peregrinus (Buchanan) by Stone, Herman and Brady (1971). Only brief reference was made to the nervous systems in these studies.

Murray and Tiegs (1953) studied the metamorphosis of Calandra oryzae (L.) describing in detail the internal organs including the nervous elements. Panji and Chhibba (1972) studied the morphology of the rostrum of the same weevil, mentioning the possible taxonomic use of the position of the frontal ganglion. Donges (1954) published a thorough and detailed study of the head of Cionis scrophulariae (L.). The ultra-structure of the neuroendocrine glands of the alfalfa weevil Hypera postica (Fab.) was published by Tombes and Smith (1970) and Tombes (1972) published scanning electron micrographs of the corpus cardiacum-corpora allatum complex of Hypera punctata (Fab.).

The works of Donges (1954) on C. scrophulariae (L.), Willey (1961) on P. americana (L.), and Youssef (1971) on A. mellifera (L.) give by far the most detailed accounts of the numerous intimate connections of the stomatogastric nervous structures with the supra- and sub-esophageal ganglia of insects.

MATERIALS AND METHODS

Adult specimens of H. aeneus were collected from Heliantheae spp. along roads and railroad banks in Skokie, Illinois during the month of July 1973. The weevils were killed and preserved in Weaver's fixative (formaldehyde-acetic acid-chloral hydrate) (Weaver and Thomas, 1956), then stored at 7° C until dissection. It was found that the insects remained in excellent condition for fine detail up to 10 months later, whether or not the body cavity had been punctured.

Twenty females and fifteen males were dissected. Dissections were performed under distilled water with the insect partially embedded in Sticky Wax (Kerr Mfg. Co., Romulus, Michigan). Specimens were bisected on various planes and orientated at various angles before adhesion, especially for study of the brain and its associated nerves. Dissection tools were jeweler's forceps, knives made of razor blade edges, and needles made of electrolytically sharpened tungsten wire (Hubel, 1957).

The most satisfactory staining of nerves was obtained from topical application of a 0.0625 % solution of Luxol Fast Blue (Solvent Blue 38) in acidified alcohol (stock solution I of Lockard and Reers, 1962). After reaching the desired stage of dissection, the distilled water was drained and 1-3 drops of the stain was applied directly to the specimen with a Pasteur pipette. Staining time varied from 1-4 minutes, depending on the intensity of staining desired. When necessary, the same technique was repeated for different stages of dissection. In general, nerves stained more readily than surrounding muscles or organs, but ganglia were

not stained at all by this method. For the brain, retrocerebral endocrine glands, and ventral nerve cord, Luxol Fast Blue staining was alternated with topical application of a 0.2 % solution of methylene blue for 1-3 minutes. Where fine differentiation between nerves and muscles was needed, Luxol Fast Blue staining was followed by a counterstain of 0.5 % Eosin B in distilled water.

Dissections were carried out for the most part with a Leitz stereoscopic microscope with magnifications up to 250x. For study of finer differentiation, as in the structures of the heart, a Zeiss microscope adapted for phase contrast was used. Drawings were made to scale with the aid of an ocular reticle.

Dissected specimens were preserved in a 1:1 mixture of U.S.P. glycerol and distilled water, and refrigerated at 7°C.

RESULTS AND DISCUSSION

Imms (1957) divides the insect nervous system anatomically into three systems: (1) The Central Nervous System, composed of the Supraesophageal Ganglion, Subesophageal Ganglion, and Ventral Nerve Cord; (2) The Peripheral Nervous System, comprised of the nerves radiating out from the Central Nervous System, including both sensory and motor nerves to the periphery of the body; (3) The Visceral (Sympathetic) Nervous System, consisting of a stomodeal portion which innervates the foregut, a proctodeal portion which arises from the Terminal Abdominal Ganglion and which innervates the hindgut and reproductive organs, and a ventral portion which innervates the spiracles. Willey (1961) cites a fourth system, the Autonomic Nervous System, which had been considered part of the Peripheral Nervous System by Imms (1957). The Autonomic Nervous System consists of the intrinsic neurons of the gut, dorsal blood vessel, and Malpighian tubules. The distal processes of these cells ramify over the surfaces which they innervate, and the proximal connections unite with the ganglia of the Central Nervous System.

The present study is concerned with the Central and Visceral Nervous Systems of H. aeneus. The Peripheral Nervous System is discussed only concerning its gross anatomical association with the Central Nervous System. The Autonomic Nervous System is referred to only to supplement a review of the innervation of specific organs by the Central or Visceral Nervous Systems.

THE CENTRAL NERVOUS SYSTEM

The Central Nervous System of the superfamily Curculionoidea was found by Aslam (1961) to show a strong but somewhat varying degree of concentration of the ganglia. H. aeneus is considered to be among the more primitive, with six separate ganglionic masses: Supraesophageal, Subesophageal, and Prothoracic Ganglia; a fused Meso-Metathoracic-First Abdominal Ganglion, a fused Second-Third Abdominal Ganglion, and a composite Terminal Abdominal Ganglion (Fig. 1). The Terminal Abdominal Ganglion of H. aeneus is positioned in the ventral metathoracic cavity, and the large proctodeal nerves which exit from it posteriorly bear markedly to the right of the abdominal cavity (Fig. 1), at the same time raising the terminal portion of the ganglion and nerve trunk slightly above the ventral body wall (Fig. 2). This consistent position is possibly due to the large size of the anterior ventriculus of the midgut which lies in the left portion of the body cavity, and to the coiling of the posterior ventriculus, forcing the terminal nerve branches above its coils in order to reach the hindgut and reproductive organs.

Murray and Tiegs (1935) show the same degree of fusion in the Ventral Nerve Cord of Calandra oryzae (L.) (Curculionidae). They make no mention of an off-center location of the Terminal Nerve Trunk, but their description of the alimentary canal shows the large anterior ventriculus to be in the metathorax rather than the abdomen.

The nomenclature used here to designate parts of the Central Nervous System and related peripheral nerves is based on the Latin forms

of the name of the organ or tissue innervated. Similar terminology is found in Donges (1954) and Willey (1961) for cephalic nerves, and in Schmitt (1962) for thoracic and abdominal nerves.

The Supraesophageal Ganglion

The Supraesophageal Ganglion, or brain, is situated in the head closely connected to the Subesophageal Ganglion (SEG) by thick Circum-esophageal Connectives (CEC) around a greatly narrowed esophagus (ESO) (Fig. 3). The protocerebrum (PC) appears much larger than the deutocerebrum (DC) or tritocerebrum (TC), giving off optic lobes (LO) anterolaterally and forming a pointed apex posteriorly as it meets the dorsal boundary of the aortal sinus (SA). From a dorsal view, the optic lobes give the protocerebrum a heart-shaped appearance, allowing the deutocerebrum to be identified only by the large, paired antennal nerves (N Ant) proceeding from it anteriorly. The tritocerebrum is quite small, and not visible dorsally. A tritocerebral commissure (CTC) connects the two lobes ventral to the esophagus.

Doges (1954) attributes the similar forward position of the optic lobes and the slightly backward position of the protocerebrum in Cionis scrophulariae (L.) to the frontal rather than lateral position of the eyes and to the economy of space in the basicranium.

The Supraesophageal Ganglion gives rise to four major pairs of nerves:

(1) Antennal nerves (N Ant) (Fig. 3). In H. aeneus these large nerves extend anteriorly from the Deutocerebrum and run dorsolaterally

along the pharynx to the base of the antennae, which are positioned mid-way down the length of the rostrum. Youssef (1971) described the same nerve in Apis mellifera (L.) as an extension of a small antennal lobe of the deutocerebrum, and states that the roots of the antennal nerve come in part from the deutocerebrum proper and in part from the antennal lobe.

(2) Frontal connectives (CF) (Fig. 7). These short, thick nerves arise from the medial side of the tritocerebral lobes, just posterior to the exit of the antennal nerve from the deutocerebrum. They meet in the frontal ganglion (GF) on the dorsal surface of the esophagus. The terminology for both the frontal connectives and the frontal ganglion is fairly standard, although Youssef (1971) in Apis mellifera (L.) refers to the "inner nerve of the Nervus Pharyngeo-labralis" which meets in the "Ganglion Pharyngeale". Youssef contends that the nerves of this ganglion innervate muscles of the pharynx and anterior cibarial wall, rather than the frons. In P. americana (L.), as described by Willey (1961), and in a number of other insects, the frontal connective and the labral nerve run together initially for a short distance, forming a large "Fronto-labral Nerve".

(3) Labral nerves (N Lbr) (Figs. 3 and 7). Each exits anteriorly from the tritocerebrum and runs slightly medial to the antennal nerve. A short distance anterior to the tritocerebrum each labral nerve in H. aeneus is joined by either the procurrent nerve (N Proc) from the frontal ganglion, or by a ramus of it (RN Proc). The labral-procurrent nerves (N Lbr Proc) then continue anteriorly on the dorsal surface of the gut, coursing through the pharyngeal and cibarial muscles.

In Cionis scrophulariae (L.) Donges (1954) charts a similar bifurcation of the procurrent nerve, but shows that in cross section the Nervus Labralis-procurrens is composed of two separate nerves. This close association of the procurrent nerve with the labral nerve is also seen in Dytiscus marginalis (L.) by Holste (1910). In the Hymenopterans Apis mellifera (L.) and Vespula maculata, however, Youssef (1971) describes a branching of the procurrent nerve but does not state that it travels with the labral nerve.

(4) Tritocerebral commissure (CTC) (Figs. 3 and 7). This is a small thin band which connects the two lobes of the tritocerebrum, ventral to the esophagus. It is thought by some authors to be the equivalent to the deutocerebral and protocerebral "bridges" connecting the hemispheres of the brain. Youssef (1971) argues that the frontal connectives serve this function, and that with the frontal connectives, the tritocerebral commissure forms a complete neural ring around the esophagus.

The Subesophageal Ganglion

The Subesophageal Ganglion (SEG) is a large, egg-shaped nerve mass lying posteriorly and ventrally in the head. It is bound laterally and ventrally by a thin cuticle associated with the tentorial armature, and dorsally by the esophagus. In H. aeneus, five main nerves arise from the Subesophageal Ganglion.

(1) Mandibular nerve (N Md) (Fig. 3). This large nerve comes off the Subesophageal Ganglion anteriorly and runs forward in close as-

sociation with the uncoiled portion of the salivary gland and the tendon of the mandibular muscles, lateral to the pharynx. Numerous small branches are given off fairly close to the brain which go to the salivary glands and to the well-developed mandibular muscles. The main mandibular nerve continues forward to the conspicuous "saw-toothed" mandibles at the tip of the rostrum.

Holste (1910) showed the mandibular nerve in Dytiscus marginalis (L.) as branching twice to the mandibular flexor and extensor muscles, then continuing on to the mandibles. Donges (1954) describes a "mandibular-maxillary nerve" in Cionis scrophulariae (L.) which sends branches to both the mandibular and maxillary muscles of the head proper, then continues anteriorly beneath the pharynx as a fused nerve to a point midway between the antennae and the mandibles, where the maxillary nerves separate and the mandibular nerves bend lateral to the mandibles. In cross section, these nerves were shown to be definitely fused, in contrast to the loose association seen between the labral and procurrent nerves of the same weevil.

In numerous Hymenoptera Youssef (1971) charted a branch of the mandibular nerve innervating "mandibular glands" and notes that the innervation of the mandibular muscles, glands, and mandible itself by the mandibular nerve appears to be fairly constant in most insects, with the exception of those cases where the mandibular muscles or gland is poorly developed.

(2) Maxillary nerve (N Mx) (figs. 3 and 8). In H. aeneus each nerve arises slightly ventral to the mandibular nerve and runs forward

closely associated with the tendon of the maxillary muscle and a tracheal branch. Numerous small nerves are given off proximally to the surrounding muscle, and a nerve from the corpus cardiacum anastomoses with the maxillary nerve immediately anterior to its exit from the Subesophageal Ganglion.

(3) Labial nerve (N Lab) (Figs. 3 and 8). These relatively small nerves arise separately from the anteroventral portion of the Subesophageal Ganglion, but in some specimens run together sporadically as they course anteriorly on the ventral floor of the rostrum. According to Donges (1954) these nerves fuse in Cionis scrophulariae (L.) at the point of exit from the Subesophageal Ganglion and remain fused to the level of the antennae. Youssef (1971) found the labial nerves in Apis mellifera (L.) to be paired, and traced their fine branches to the muscles of the ventral basicranium and, posteriorly, to the "thoracic glands". Anteriorly, Youssef traced the labial nerves through the maxillary palps and into the labial palps.

(4) Tegumentary nerve (N Teg) (Fig. 3). Each nerve arises from the dorso-lateral portion of the Subesophageal Ganglion of H. aeneus and runs dorsally, immediately sending off an anterior branch to run forward around the tritocerebrum to the region of the labral nerve, and a posterior branch which runs around the brain posteriorly, over the corpus cardiacum and the anterior edge of the aortal sinus to the head capsule. The main tegumentary nerve continues dorsally along the side of the brain, eventually branching to the lateral and posterior head capsule.

A similar nerve was described in Dytiscus marginalis (L.) by Holste

(1910) and in various Hymenoptera (Apidae) by Youssef (1971). Snodgrass (1935) cites the tegumentary nerve as arising from the tritocerebrum in *Dissosteira carolina* (L.). It has been charted in numerous other insects as well, but disagreement exists as to its exact origin and sensory or motor nature.

(5) Jugular nerve (N Jug) (Figs. 3 and 4). In *H. aeneus* this small, branched nerve runs from the posterolateral portions of the Subesophageal Ganglion posteriorly, sending a few small branches to the tubular salivary gland, and then proceeding into the anteroventral portion of the prothorax in the hemocoel. This is the only innervation of the salivary gland noted in *H. aeneus*, in addition to the small branches to the uncoiled portion from the mandibular nerve, mentioned earlier.

Schmitt (1962) reviews various designations for this nerve, and describes the overall pattern as an innervation of the protergal muscles of the head, sometimes first fusing with the Dorsal Nerve Root from the prothorax. Holste (1910) in *Dytiscus marginalis* (L.) and Donges (1954) in *Cionis scrophulariae* (L.) found no fusion of the jugular nerve with the prothoracic Dorsal Nerve Root, and mentions only its innervation of the muscles of the cervical sclerite.

The salivary gland of *H. aeneus* is a highly coiled tube, situated mainly in the prothorax and lying dorsal and lateral to the esophagus and aorta (Fig. 4). It is composed of large, densely staining cells surrounding a narrow tube of thin intima. Externally, the salivary glands of *H. aeneus* appear similar throughout, including the uncoiled portion which courses through the head and rostrum, and so it was not

possible in this study to label a salivary duct. However, Murray and Tiegs (1935) describe long, narrow salivary ducts in Calandra oryzae (L.) which open on the first maxilla at the tip of the rostrum, and a simple, tubular pair of salivary glands, very long and narrow, which extend in a highly coiled position as far posterior as the crop. In both H. aeneus and Calandra oryzae (L.) the salivary glands themselves appear to end blindly in the thorax. Tissot (1938) describes the salivary glands in Naupactus leucoloma (Boheman) as "long, delicate threadlike tubes that loop about in the side of the head, lying above the powerful mandibular muscles" and cites their opening into the mouth cavity at a point near the base of the maxilla. Donges (1954) describes "mandibular glands" in Cionis scrophulariae (L.) which fit the same general description as seen in H. aeneus, Calandra oryzae (L.), and Naupactus leucoloma (Boheman), and labels the entire uncoiled portion as the "mandibular duct".

Numerous connections exist between the ganglia of the head and the stomodeal nervous system of H. aeneus, and will be discussed with the visceral (sympathetic) nervous system.

The Thoracic Ganglia

The positions of the thoracic ganglia of H. aeneus, relative to each other, are shown in Figs. 5 and 6. Schmitt (1962) gives a thorough comparison of the nomenclature used in the major works on thoracic innervation, and concludes that if nerves to the various muscles are grouped as "innervation fields" or nerve "roots", a basis for comparison of thoracic innervation is much easier to establish. Schmitt's general terminology

is sufficient for gross neuroanatomical descriptions, and will be used in the present study.

The prothoracic ganglion (Gng 1) lies on the ventral floor of the prothorax, just anterior to the prothoracic spina and between the first pair of legs. It is separated from the Subesophageal Ganglion by long, thick connectives, and from the mesothoracic ganglionic mass (Gng 2+3+1A) by short, thick connectives. The ventral side of the ganglion is very convex and the dorsal side flat, a characteristic shown by the entire Ventral Nerve Cord (Figs. 2 and 6).

The prothoracic ganglion of H. aeneus gives rise to one large pair of nerves, which immediately divides, sending a large branch dorso-laterally (I DN) to dorsal longitudinal and lateral muscles of the prothorax, and a second large branch ventrolaterally (II) to ventral and lateral prothoracic musculature and to the muscles of the first pair of legs. In addition, a small pair of cervical nerves (Cv N) comes off the prothoracic ganglion anteriorly, just lateral to the interganglionic connectives, and extends anteroventrally to the neck muscles.

The mesothoracic, metathoracic, and first abdominal ganglia form a single nerve mass (Gng 2+3+1A) which lies entirely within the reduced mesothorax. The individual ganglia are discernible due to slight lateral and ventral constrictions between them, as well as to the destination of the nerves emanating from them. The entire ganglionic mass is held in place by the ventral apodemal structures of the mesosternum, and is separated from the fused second and third abdominal ganglia (2+3A) by relatively short, thin connectives (Figs. 5 and 6).

The mesothoracic ganglion itself has two main nerves branching off the ganglion. The first leaves anterodorsally, then immediately branches again sending one nerve (2 DN) dorsolaterally to the dorsal mesothoracic musculature, including the muscles of the forewing. The other branch (II) innervates the lateral and ventral mesothoracic musculature. The third major nerve root leaves the ganglion posteroventrally (III) and innervates the mesothoracic legs and associated musculature.

The metathoracic ganglion has three large paired branches. The first leaves the dorsal rim of the ganglion (3 DN) and runs in a dorso-lateral direction, towards the base of the hindwings. The second branch leaves the lateral margin of the ganglion (II) and runs lateroventrally, its many branches innervating the well-developed ventral and lateral muscles associated with the metathoracic coxal cavities. The third branch (III) leaves the ganglion as a swollen lobe on the posteroventral side, soon narrows, and continues ventrally and posteriorly into the metathorax where it innervates the metathoracic legs and associated musculature.

This peripheral innervation of the thoracic segments of H. aeneus follows the same basic plan as that described by Snodgrass (1935) and that reviewed by Schmitt (1962). Detailed topographical studies in this area have been performed mostly on Orthopterans, with an attempt to establish homology between nerves and muscles of different insects based on the mesothoracic segment. Mitchell and Seabrook (1973) compared the mesothoracic nerves of representative insects of five pterygote orders, and describes homologies in terms of dorsal, anterior, ventral, and leg "roots".

Mitchell and Seabrook's study is based on that of Schmitt (1962) which was used in the present study. This system of nomenclature greatly simplifies comparisons between insects, as well as between ganglia, and appears necessary in order to overcome the problems of terminology and homology presented by the high degree of variation found.

The Abdominal Ganglia

Stone, Herman and Brady (1971) describe the abdomen of most Curculionoidea as normally consisting of seven segments, of which the seventh is complex and includes the seventh through tenth. In H. aeneus these seven abdominal segments are innervated individually by lateral segmental nerves from the Ventral Nerve Cord.

The first abdominal ganglion (1A) (Figs. 5 and 6) has fused with the meso- and metathoracic ganglionic mass, and is discernible by the single pair of nerves extending from it ventrolaterally to the spiracular mechanisms of the first abdominal segment.

The second and third abdominal ganglia are fused (2+3A) and form a small, spherical mass which lies in the anterior metathorax. Two pairs of small nerves radiate from it posteriorly, and extend to the second and third pairs of abdominal spiracles.

The terminal abdominal ganglion (TA) is a composite neural mass formed from the ganglia of the remaining segments. It is connected to the preceding ganglion by short, thin connectives, and lies within the metathorax. Its anterior portion follows the curvature of the ventral body wall closely, and so appears "wavy" from a lateral view (Fig. 2). Three pairs of small nerves come off the ventral surface and extend posteriorly

to innervate abdominal segments 4 through 7.

The terminal abdominal ganglion narrows posteriorly into a thick nerve trunk which sends nerves to the hindgut, the reproductive organs and genital muscles, as well as to the intersegmental musculature of the seventh and eighth segments.

These abdominal nerves comprise the Proctodeal Nervous System and will be discussed in more detail with the Visceral Nervous System.

Due to the apparent overlapping nature of the functions of the transverse nerves of the Ventral Sympathetic Nervous System, and the abdominal segmental nerves of the Central Nervous System, the peripheral abdominal innervation will be considered with the Ventral Sympathetic Nervous System.

THE VISCERAL NERVOUS SYSTEM

The Visceral (Sympathetic) Nervous System is composed of the ganglia and nerves of the Stomodeal, Proctodeal, and Ventral "Unpaired" Nervous Systems, and is closely allied with the neurosecretory mechanisms of the insect.

Neurosecretion has been briefly defined by Gabe (1966) as the connecting link between the nervous system and the endocrine glands. Various neurosecretory pathways involving the brain, ventral ganglia, retrocerebral endocrine glands, and heart have been elucidated, and all have in common the fact that most neurosecretory material (NSM) must somehow arrive at an efficient dispersing point, usually associated with the circulation of hemolymph. Various such "neurohaemal organs" have been identified: the lateral cardiac nerves in *P. americana* (L.) by Miller and Thomson (1968); the axons of NCC I or II in the dorsal blood vessel wall, near the head in various Heteroptera by Dogra (1967) and Srivastava (1970); the aortal wall itself in *Metochus uniguttatus* (Thunb.) (Hemiptera: Lygaeidae) by Awasthi (1972); and the corpora allata in all insects, releasing neurosecretory material directly into the hemocoel (Wigglesworth, 1970).

The Stomodeal Nervous System

Snodgrass (1935) first referred to the ganglia of the foregut as comprising the Stomodeal Nervous System because these ganglia arose from the embryonic stomodeum. The terms "stomatogastric", "retrocerebral",

and "sympathetic" have all been applied to this portion of the Visceral Nervous System, resulting in a misleading conception in much of the literature concerning the actual relationship of the Stomodeal Nervous System with the Central Nervous System. Willey (1961) considers the Stomodeal Nervous System to be composed of two functional parts: (1) the "unpaired", or stomatogastric, which consists of the frontal and hypocerebral ganglia and associated nerves, and which innervates the foregut and, in some insects, the salivary glands; (2) the "paired", which consists of the corpus cardiacum and corpus allatum and associated neurosecretory tracts, and which are mainly neuroendocrine in function. This corpus cardiacum-corporis allatum complex, due to its position posterior to the brain, comprises the "retrocerebral complex". It is intimately linked, morphologically and physiologically, with the brain and Subesophageal Ganglion.

The gross morphology of the Stomodeal Nervous System of H. aeneus is shown in Figs. 3 and 7. Both Willey (1961) and Youssef (1971) have published a historical comparison of terminology for the Stomodeal Nervous System. Willey's work on P. americana (L.) has served to standardize stomodeal nervous system nomenclature, and his designations will be used in the present description of H. aeneus.

(1) The Stomatogastric Nervous System (Fig. 7).

The frontal ganglion (GF) lies on the dorsal surface of the gut just anterior to the brain. It is relatively large, and is joined to the tritocerebral lobes laterally by two short, thick frontal connectives (CF).

The frontal ganglion narrows anteriorly into the procurrent nerve (N Proc) then bifurcates, each segment running obliquely to join the labral nerve (N Lbr). These "fused" labral-procurrent nerves then continue anteriorly the length of the rostrum.

The position of the frontal ganglion is surprisingly variable in the Curculionoidea in which it has been described, and has been used by some workers as a morphological landmark in demarcating the clypeus from the frons. Panji and Chhibba (1972) describe the frontal ganglion in Calandra oryzae (L.) as lying roughly in the middle of the rostrum on the dorsal wall of the elongated pharynx. Murray and Tiegs (1935), however, state that the frontal ganglion of the same weevil lies at the tip of the rostrum. Dennell (1942) describes paired frontal ganglia in Calandra granaria (L.), which lie near the anterior end of the pharynx on each side. Sundman and King (1963) use the position of the frontal ganglion to indicate the true beginning of the foregut, and describe it in Anthonomus grandis (Boheman) as lying ventral to the frontal fovea, which is located between the eyes. Other Curculionidae referred to by Sundman and King as having the frontal ganglion located in the head capsule proper are Mononychus yulpeculus (Germar) and Pantomorus godmani (Crotch). Donges (1954) states that in Gionis scrophulariae (L.) the frontal ganglion lies in front of the brain, closely connected to the tritocerebral lobes, as is seen in H. aeneus. Atkins and Chapman (1957) describe the frontal ganglion in Dendroctonus pseudotsugae (Hopk.) as being posterior to the brain, with very short frontal connectives which are not closely associated with the labral nerves. Casal (1948) found a large frontal ganglion situated slightly anterior to the brain to be the

general plan in the Coleoptera he studied.

Posteriorly, the frontal ganglion narrows sharply into the recurrent nerve (NR) and runs dorsally on the esophagus between the hemispheres of the brain. It passes between the corpora cardiaca, and above the corpora cardiacal commissure (CCC). Posteriorly to the corpora cardiaca, it slants sharply to the insect's left, where it swells into the small, elongate hypocerebral ganglion (GH).

The hypocerebral ganglion continues posteriorly as the esophageal nerve (N Oe), still winding toward the left side of the foregut and giving off numerous small branches to the wall of the gut. At approximately the level of the anterior mesothorax, midway between the brain and the midgut, the esophageal nerve forms a small but distinct triangular shaped ganglion, the ingluvial ganglion (G In). Two ingluvial nerves (N In) continue posteriorly, giving off many small, ramifying branches during its course (Fig. 11). The main ingluvial nerves undergo a slight, flat swelling at the posterior end of the proventriculus to form diffuse proventricular ganglia (GP) from which nerves radiate in all directions, some extending posteriorly into the anterior portion of the midgut. Casal (1948) uses the term "diffuse ganglion" to refer to a group of neurons loosely concentrated in one area of a nerve, causing a characteristic flattened lateral enlargement. Willey (1961) also uses this term in reference to the proventricular ganglia of P. americana (L.).

Donges (1954) stated that Cionis scrophulariae (L.) has no hypocerebral ganglion (he called it Occipital Ganglion), but that the recurrent nerve beneath the brain was swollen with ganglionic cells. Donges further describes the recurrent nerve in C. scrophulariae as running

under the fused corpus cardiacum, then sending nerves back to connect with the caudal side of the corpus cardiacum "crossbridge".

As was seen in H. aeneus, Donges also noted that the recurrent nerve runs to the left of the esophagus in C. scrophulariae; he mentions no proventricular ganglia at the end of the ingluvial nerves on the posterior proventriculus, however.

Murray and Tiegs (1935) describe the hypocerebral ganglion in Calandra oryzae (L.) as lying anterior to the brain and forming a definite connection with the tritocerebrum. The ingluvial ganglion of C. oryzae is described to be in its usual position on the proventriculus. It bifurcates into two individual nerves, but no proventricular ganglia are described. Cazal (1948) found no Hypocerebral Ganglion in Dytiscus marginalis (L.) but notes a very slight enlargement of the recurrent nerve which sends a pair of nerves to the corpora cardiaca. Atkins and Chapman (1957) found no hypocerebral ganglion in Dendroctonus pseudotsugae (Hopk.) but suggest that the nerve cells which constitute that ganglion in other insects, are located within the frontal ganglion, due to its unusually posterior position in D. pseudotsugae. Gabe (1966) states that in general, the frontal ganglion of Coleoptera is more highly developed than the hypocerebral ganglion.

(2) The Retrocerebral Complex (Fig. 7).

The corpus cardiacum (CC) of H. aeneus is a paired, saddle-shaped structure which lies dorso-laterally on the esophagus, immediately posterior to and partially underneath the Supraesophageal Ganglion.

Distally, each corpus cardiacum is attached to a smaller, spheroidal corpus allatum by a very short connective (NCA). The dorsal aorta (Ao) runs dorsally on the esophagus, and dilates in the region of the corpora cardiaca to form an aortal sinus (SA) and as a result, is in very close association with the corpora cardiaca. Two short cerebral-cardiacal nerves (NCC I and II) connect the protocerebrum posteriorly with the corpora cardiaca. A third, very fine pair of nerves (NCM) leaves the corpora cardiaca anteriorly, travels above the esophagus on the inner sides of the cerebral hemispheres, and connects with the maxillary nerves. The precise course of this nerve, however, is quite variable, and is sometimes found running external to the tritocerebral lobes rather than internal. Donges (1954) described for Cionis scrophulariae (L.) an even more pronounced variation in the path of this nerve, which he referred to as Nervus Collateralis. Joly (1942) identifies this nerve in Dytiscus marginalis (L.) as the Nervus Cardiomaxillaris, and Casal (1948) uses the same terminology. Willey (1961) described no such nerve in P. americana (L.).

Lateroventrally, each corpus cardiacum narrows to a thin band of tissue which connects with the anterodorsal surface of the Subesophageal Ganglion (NCSOe). This connection of the corpus cardiacum with the Subesophageal Ganglion has previously been described in very few insects.

Dorsally, each corpus cardiacum of H. aeneus gives off an aortal nerve (NA) to the lateroventral sides of the dorsal aorta, and a cardiostomatogastric nerve (NCS) which runs posteriorly to connect with the hypocerebral ganglion. The corpora cardiaca unite with each other by a wide commissure (CCC) which runs dorsal to the esophagus and lies immed-

ately beneath the recurrent nerve.

Tombes (1972) described the corpus cardiacum-corpora allata complex of Hypera punctata (Fab.) as being very similar in position to that of H. aeneus. In addition, his scanning electron micrographs illustrate many small connections between the corpora cardiaca and both the brain and the gut. Although Tombes describes no hypocerebral ganglion in H. punctata (Fab.), he does cite a relatively large pair of nerves connecting the corpora cardiaca caudally with the recurrent nerve. Tombes also notes that several untraced nerves extend ventrally from the corpora cardiaca, and possibly connect with the tritocerebrum, subesophageal connectives, or another organ.

The corpus allatum does not arise from the embryological stomodeum, and hence, although endocrine in function, is considered by Wigglesworth (1970) to be a non-neural addendum to the Stomodeal Nervous System. Under the scanning electron microscope, Tombes (1972) found the corpora allata of Hypera punctata (Fab.) to be trilobed, and connected to the Subesophageal Ganglion by two pairs of very fine nerves. The corpus cardiacal-corpora allatal nerve of H. punctata (Fab.) was found to be similar but somewhat longer than that of H. aeneus. Tombes studied a gravid specimen, however, which, according to Wigglesworth (1970), may have a bearing on the size and appearance of the corpora allata.

The corpus cardiacum-corpora allata complex cited by Donges (1954) for Cionis scrophulariae (L.) varies considerably from the pattern seen in H. aeneus and Hypera punctata (Fab.). Donges (1954) illustrates a dorsal fusion of the two saddle-shaped corpora cardiaca, forming a "cross-bridge" which runs over the recurrent nerve. The paired, spherical cor-

pora allata of C. scrophulariae (L.) lie in the prothorax, connected to the corpora cardiaca by extremely long posterior extensions from the corpora cardiaca. Donges also cites no connection between either the corpora cardiaca or the corpora allata and the Subesophageal Ganglion.

According to Gabe (1966), the general position of the corpora cardiaca in Coleoptera is on the lateral sides of the esophagus, not closely associated with the aortal wall as is seen in many other orders. The corpora allata of Coleoptera generally lie on the same plane as the corpora cardiaca, slightly posterior to the latter, on the lateral wall of the esophagus in the head.

Nabert (1913) studied the corpora cardiaca-corpora allata complex of four members of Coleoptera. He found that in Tenebrio molitor (L.) (Tenebrionidae) the corpora cardiaca were closely associated with each other and with the aortal wall, and that the corpora allata attached to the "lower extremities" of the corpora cardiaca. In Angelastica alni (L.) (Chrysomelidae) the corpora cardiaca are not closely associated with the dorsal vessel, and the corpora cardiaca-corpora allata complex occurs in the head. In Lampyris splendidula (L.) (Lampyridae) the corpora allata are found alone at the junction of the head and the thorax, whereas in Rhagonycha melanura (Fab.) (Cantharidae) both the corpora cardiaca and the corpora allata are located together in the thorax. Casal (1948) describes a similar arrangement for the corpus cardiacum-corpora allata complex of Rhagonycha fulva (Scop.).

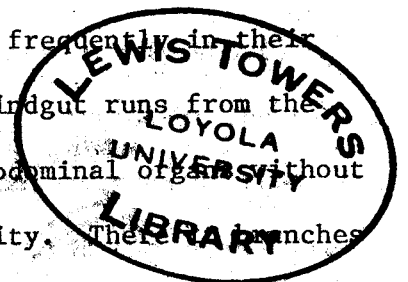
Bickley (1942) describes a fused corpus cardiacum-hypocerebral ganglion in both the larva and adult of Passalus cornutus (Fab.) (Scarabaeidae), with two esophageal nerves and no ingluvial ganglion.

Cazal (1948) summarizes his view of the evolutionary trend of the morphology of the Stomodeal Nervous System, based on the representation of insects he reviewed: (1) a regression towards the presence of a frontal ganglion, a hypocerebral ganglion, and only one esophageal nerve; (2) total extracerebral fusion of the NCC I and II; (3) lateralization of the corpora cardiaca; and (4) fusion of the corpora allata, either above or below the aorta.

Davey (1964) postulates that impulses can travel from the sensory nerves of the frontal ganglion sending information about pressure, viscosity, and amount of ingested food along the motor (recurrent) nerve to the posterior portion of the foregut to effect the opening of the stomodeal valve. Thus, the Stomodeal Nervous System would be acting independent of the Central Nervous System.

The Proctodeal Nervous System

The hindgut of H. aeneus is innervated by two branches of the terminal abdominal ganglion. One nerve runs to the anterior part of the hindgut which lies in the abdominal cavity in very close association with the reproductive glands and ducts (fig. 11). There it divides again, sending one branch in the direction of the origin of the Malpighian tubules, and the other branch to the more posterior ileum (IL) and colon (CO) of the hindgut. The nerves branch and anastomose frequently in their course of innervation. The second nerve to the hindgut runs from the nerve trunk directly through the spaces between abdominal organs without branching until it reaches the posterior body cavity. There it branches twice, the first branch going to the dorsal longitudinal muscles of the



reduced eighth tergite, the second branch dividing again and then attaching to the wall of the rectum (REC) and branching highly around it.

Davey (1964) postulates a chain reaction for the contraction of the hindgut: (a) the corpora cardiaca produce NSM and liberate it into the hemolymph; (b) the NSM activates a secretion of "special" cells in the lower colon; (c) the secretion produced by the colon and activated by the NSM now stimulates the proctodeal nerve of the hindgut, resulting in contraction. Davey also cites a similar activation chemical in the secretion of the accessory gland of males in copulation. This secretion would activate the proctodeal nerves of the oviduct of the female to cause contraction, allowing the semen to progress into the spermatheca.

It must be emphasized that the degree of branching and the order of the innervation of the various organs of the hindgut and reproductive systems in H. aeneus is extremely variable. The two branches of the terminal ganglion which innervate the hindgut may arise separately or as a single nerve; they may come from the ventral side of the large nerve trunk which extends posteriorly from the terminal ganglion, or from numerous other branches. In addition, the nerve trunk itself is quite variable in structure: it may be quite long, extending through two or three abdominal segments without branching, then divide at one time into a fan-like array of eight branches; it may send off individual branches periodically, or two or more at a time; or, it may be extremely short, giving off from two to eight branches at the posterior portion of the terminal ganglion itself. The manner of the actual innervation of the organs and tissues themselves, however, was consistent in that the nerves, regardless of the nature of the previous branching, appeared to enter the

same general area of the organs. Other than the differences in individual arrangement of organs, this variation of branching was seen equally in both sexes.

The female reproductive system of H. aeneus is shown in Fig. 12. The ovaries contain five ovarioles each, the two being most posterior usually containing the largest eggs. The ovarioles (OVL) are connected anteriorly to the dorsal body wall of the prothorax via a suspensory ligament. Posteriorly the ovarioles enter a wide, short calyx (CAL) which narrows into a lateral oviduct (L Ovid). The lateral oviducts fuse into a large common oviduct (C Ovid) which runs anteriorly a short distance then bends posteriorly upon itself, forming a blind pouch anteriorly. The vagina (VAG) is a large, muscular tube which narrows slightly at its posterior end to form the ovipositor. A copulatory pouch is not distinguishable externally in H. aeneus. The spermatheca (Spt) lies in the right side of the body cavity. Its blunt end is connected to the dorsal base of the common oviduct by a thin, coiled spermathecal duct (Spt Dt). A lobular spermathecal gland (Spt Gl) connects also to the blunt end of the spermathecal capsule.

Six nerves run from the terminal abdominal ganglion to the female reproductive organs and musculature (Fig. 12). Two of these nerves, usually the outermost lateral branches, run directly to the lateral oviducts (N Ovid). These nerves then branch highly in two directions, running around the lateral oviducts medially towards the common oviduct, and laterally towards the ovarioles. A nerve also runs to the long, thin band of muscle which connects the ventral side of the calyx with the longitudinal muscles of the eighth tergum (8T), but this nerve does not

always arise from the nerve branch to the lateral oviducts.

A common pattern seen for the remaining branches of the terminal nerve trunk consists of the nerve trunk itself dividing into two major nerves, which divide again before they near the vagina. The major nerve on the right side sends one branch to the base of the spermathecal duct (N Spt Dt), and the other branch down the dorsal right side of the vagina to innervate its muscular wall (N Vag DR). The major nerve on the left side travels intact under the common oviduct, then divides at the apex of the vagina, sending one branch to the ventral vaginal wall (N Vag V) and the other around and down the left dorsal side (N Vag DL).

The male reproductive system of H. aeneus is shown in Fig. 13. The testes are paired and bilobed, and each lies in the abdomen at the level of the third, fourth, and fifth true sternites. (According to Burke (1959) the first two sterna of Curculionoidea are incorporated into the posterior portion of the metacoxal cavities, and hence are not visible as sterna). Each testis lobe sends off a short vas efferens (VE) which unites with the other to form a long, coiled vas deferens (VD), which looks very similar to a Malpighian tubule. The vas deferens dilates towards its posterior end to form a small, opaque lobed seminal vesicle (SV). A pair of accessory glands (Acc Gl) enters the seminal vesicle anteriorly with the vas deferens. In H. aeneus these accessory glands consist of three cylindrical, relatively thick pouches of unequal length on each side, although it is not uncommon to find only two on one side or the other. Similar accessory glands were found in Anthonomus grandis (Boheman) by Burke (1959), and in other weevils, including Rhynchites pauxillus (Germ.) by Aslam (1961).

The two seminal vesicles are close together in the body cavity; the vas deferens of each emerges and runs only a short distance posteriorly before uniting to form the ejaculatory duct (Ej Dt). The ejaculatory duct of H. aeneus extends posteriorly and dorsally, over the endophallic sac (End S), which is folded back upon itself, before entering the sac at its anterior end. The aedeagus (Aed) and associated sclerotized structures extends from the posterior end of the endophallic sac, opening beneath the eighth tergite (8T). There is no muscular sheath present, as Burke (1959) describes in Anthonomus grandis (Boheman).

As in the female, six large nerves from the terminal abdominal ganglion innervate the male reproductive organs and genital musculature. A common pattern seen involves two lateral branches innervating the vas deferens near the accessory gland (N VD), then branching along the vas deferens in both directions, to the testes and to the accessory glands. Two more main branches coil loosely around the seminal vesicles, then continue posteriorly. The right branch divides into a dorsal nerve which courses around the endophallic sac and into the upper musculature of the aedeagus (N Aed DR), and a ventral branch which runs along the ventral right side of the aedeagus (N Aed VR). The large left branch divides on the left ventral side of the aedeagus, sending a dorsal branch to the dorsal aedeagal muscles (N Aed DL) and a ventral branch to the ventral aedeagal wall and to the muscles of the eighth tergite (N Aed VL).

Accounts of innervation of the reproductive organs and hindgut of many other insects are not available, hence it is possible to make

only a limited comparison of the high degree of variation seen in H. aeneus with that of other insects. Murray and Tiegs (1935), in describing the metamorphosis of the nerves of Calandra oryzae (L.) state only that "the nerves, though they enlarge, retain their individuality, except in the last compound ganglion, where they unite loosely to form a pair of large nerve trunks supplying the abdomen." Atkins and Chapman (1957) studied the innervation of the reproductive systems of Dendroctonus pseudotsugae (Hopk.) (Coleoptera: Scolytidae) and found the same striking degree of variation in the branching of the terminal abdominal ganglion.

The Ventral Sympathetic Nervous System

By definition, the Ventral Sympathetic Nervous System is composed of an unpaired median nerve originating from the ventral surface of each ganglion of the Ventral Nerve Cord, and dividing into two transverse nerves which innervate the segmental spiracular mechanism. No such nerves were found in H. aeneus. However, innervation of the abdominal spiracles and associated segmental musculature was traced to the lateral segmental nerves which come off the abdominal ganglia medially on the ventral side, their origin compensating for the off-center location of the terminal abdominal ganglion (Fig. 8).

Plotnikova (1968) studied in detail the cellular structure of the unpaired nerve centers of the metathoracic ganglionic mass of Locusta migratoria migratoria (L.), which has both a median unpaired nerve and paired lateral segmental nerves for each of the four neuromeres it con-

tains. Judging by synapses of the medial and lateral neurons, Plotnikova concludes that the symmetrical lateral nerves which go to the periphery are part of the unpaired nerve elements. For this reason I am treating the segmental abdominal nerves of H. aeneus as part of its Ventral Sympathetic Nervous System, using the terminology of Schmitt (1962) to designate the major nerve branches.

The ventral sympathetic innervation of the abdominal segmentation of H. aeneus is shown in Fig. 9. The same basic plan of innervation is followed by each of the segmental nerves, with a few minor exceptions. Midway down its length, each nerve branches. The dorsal, main nerve (DN) continues to the lateral periphery and the small, ventral branch (VN) innervates the ventral longitudinal muscles of the ventral body wall. Close to the lateral edge of the sternites, the Dorsal Nerve divides again, sending a battery of branches towards the spiracle and another group of tiny branches to the lateral (tergosternal) muscles of that segment.

A nerve of the posterior branch of the Dorsal Nerve continues dorsally around the body, through the dorsal longitudinal muscles of the tergum, to unite with the lateral cardiac nerves in the wall of the heart.

An exception to this pattern is found in the first and second lateral nerves from the terminal abdominal ganglion. The anterior branch of the Dorsal Nerve innervates the fourth spiracle and tergosternal muscles, and the posterior branch of the Dorsal Nerve innervates the fifth spiracle. The second segmental nerve from this terminal ganglion innervates only the lateral muscles of the fifth abdominal segment, and gives

off two branches to the ventral body wall, rather than the usual one.

The sixth pair of segmental nerves innervates the sixth spiracle with the anterior branch of the Dorsal Nerve, but the posterior nerve branches to three destinations: the tergosternal muscles of the sixth segment, the spiracle of the seventh segment, and the tergosternal and ventral longitudinal muscles of the seventh segment.

The abdominal innervation described in H. aeneus closely follows that found in other insects. Schmitt (1962) describes the Dorsal Nerve in various Orthoptera as "curving upwards to the abdominal musculature and dorsal organ" and the Ventral Nerve as "curving posteriorly to the ventral muscles and cuticular epithelium". However, Schmitt also cites variations from this general plan, such as a branch of the Dorsal Nerve innervating some ventral muscles in Dossosteira carolina (L.), and a branch of the Ventral Nerve innervating some dorsal longitudinal muscles in Acheta spp.

Holste (1910) describes the lateral segmental nerves of Dytiscus marginalis (L.) as leaving each side of the ganglion singly, then bifurcating into a Dorsal Nerve to the ventral and dorsal longitudinal muscles, and a Ventral Nerve to the "transverse abdominal muscles". According to Snodgrass (1935), transverse abdominal muscles comprise the dorsal and ventral diaphragms, and Holste does not describe a ventral diaphragm in Dytiscus marginalis (L.), nor has a ventral diaphragm been described in any Coleoptera to date. Richards (1963) describes and illustrates various transverse abdominal muscles which could appear similar to a ventral diaphragm, but according to the illustrations indicated by Holste the Ventral Nerve most probably innervates a lateral muscle in D. margin-

alis (L.).

As in H. aeneus, Holste (1910) described no transverse nerves in D. marginalis (L.). Schmitt (1962) describes Dorsal and Ventral Nerves of various members of Phasmidae as being fused for a considerable distance, but after bifurcation, the Dorsal Nerve fuses with the Transverse Nerve, leaving the Ventral Nerve to innervate the ventral longitudinal muscles as well as some lateral muscles.

Youssef (1968) refers to "Anterior" and "Posterior" segmental nerves in Nomia melanderi (Ckll.) and notes that the two nerves exit the abdominal ganglion separately. However, there are frequent interconnectives between the Anterior and Posterior branches, as well as a connective between the Posterior nerves of opposite sides of the same segment. Youssef also cited nerves going from the Anterior branch to the dorsal diaphragm.

Shankland (1965) labelled the lateral segmental nerves of P. americana (L.) by letter designations of "A", "B", or "C", corresponding by description with the anterior Dorsal, posterior Dorsal, and Ventral Nerves.

As in the abdomen, separate nerves to the spiracular mechanism in the thorax of H. aeneus are not present. Although a detailed description of the peripheral nerves of H. aeneus is not part of the present study, it can be postulated that the basic plan of thoracic spiracular innervation seen in other insects is followed here. Pipa and Cook (1959) describe the thoracic transverse nerves of P. americana (L.) as arising separately or via a median nerve from the ganglion, then fus-

ing with the Dorsal Nerve Root from the next posterior ganglion, and eventually innervating the spiracular muscles of that segment. Schmitt (1962) reviews a similar pattern of thoracic innervation for a number of insects, and adds that in most, the transverse nerves from the metathoracic ganglion join with the Dorsal Nerves of the first abdominal ganglion.

Interaction between the "sympathetic" and "somatic" nervous systems is little understood. Plotnikova (1968) links the Ventral Sympathetic, Stomodaeal, and Central Nervous Systems through the functioning of the tritocerebrum. Impulses would travel from the heart and spiracles to the unpaired nuclei of the Ventral Nerve Cord, then to the tritocerebrum and on to the protocerebrum or the frontal ganglion, hence incorporating either the Stomatogastric or Central Nervous System. Davey (1964) speculates that the midgut is controlled by neurohormones possibly produced in the ganglia of the Ventral Nerve Cord, thus adding a neuroendocrine function to the Ventral Nerve Cord.

The heart of H. aeneus begins at the anterior boundary of the abdomen. It is lined on each side laterally with 1-2 layers of large, binucleate pericardial cells, numbering on the average 6 cells per side per segment. Examination with phase microscopy reveals that some of the connective tissue strands from the alary muscles unite to the pericardial cells themselves, while others appear to go through these cells or around them and into the loosely woven mesh of the heart wall itself (Fig. 14). The ostia appear as V-shaped notches in the wall of the heart, slightly anterior to each group of alary muscles. In the undissected heart, the pericardial cells obscure the ostia and must be care-

fully teased away.

At most, five pairs of segmental nerves are seen innervating the heart of H. aeneus, following the general plan of innervation of the spiracles. These segmental nerves can be seen attaching to the lateral cardiac nerves of the blood vessel, usually between two fan-like arrays of alary muscle. Under the phase-contrast microscope, small nerve fibers were found branching among the alary muscles themselves and appeared to connect to the heart wall. Their precise origin was obscured by the pericardial cells, however.

In addition to the segmental innervation by the Dorsal Nerves from the Ventral Nerve Cord, the anterior portion of the dorsal aorta appears to be innervated by the aortal nerve (NA) (Figs. 3 and 7) which leaves the dorsal rim of the corpus cardiacum posteriorly. The paired aortal nerve runs along both sides of the dorsal vessel, as the lateral cardiac nerve, and ends blindly with the heart in the seventh abdominal segment.

The innervation of the heart has been studied in few insects. Most of those studied are members of Orthoptera or Dictyoptera, and thus a great deal of the present knowledge concerning the mechanism of innervation of an insect heart is based on a large insect with a primitive plan of innervation.

In H. aeneus the heart is innervated by the Dorsal Nerve of the segmental ganglia, and by the aortal nerve from the corpus cardiacum. In addition, the alary muscles appear to be innervated but the source of these nerves is not confirmed.

Alexandrowicz (1926) describes the lateral cardiac nerves in Periplaneta orientalis, but does not trace them anteriorly. He does observe the termination of the Dorsal Nerves of the abdominal ganglia in the lateral cardiac nerves. Bullock and Horridge (1965) describe the cardiac nerve as being composed of its own cardiac nerve cell bodies in addition to axons from the segmental nerves. However, Bullock and Horridge as well as Jones (1964) also note that the hearts of some insects are not innervated at all; that the lateral cardiac nerves of insects have been traced to the corpora cardiaca, recurrent nerve, tritocerebrum and protocerebrum; and that identifiable cell bodies are not always present in the lateral cardiac nerves. Bullock and Horridge (1965) attribute the innervation of the alary muscles in general to the lateral cardiac nerves, but do not specify further whether they are innervated by cardiac neurons or by other axons running in association with these lateral nerves. Jones (1964) describes in some insects a small branch of the Dorsal Nerve of the segmental abdominal nerves as innervating the alary muscles directly. Holste (1910) claims that the lateral cardiac nerves of Dytiscus marginalis (L.) send fine nerve branches directly to the spiracles.

The segmental nerves usually attach to the lateral cardiac nerves near the ostia, as noted by Alexandrowicz (1926), Bullock and Horridge (1965), and McCann (1970). Miller and Thomson (1968) found a similar relationship in P. americana (L.) and also described two neurosecretory pathways associated with the heart: (1) Neurosecretory material (NSM) is synthesized in the ventral ganglia, then enters the

heart via the segmental nerves. (2) NSM is elaborated in the cardiac neurons themselves. Johnson (1966) had studied heart innervation of the same insect, and had previously hypothesized that the NSM from the Ventral Nerve Cord may originate in the retrocerebral complex. Neither Miller and Thomson (1968) nor Johnson (1966) mention the anterior origin of the lateral cardiac nerves.

The exact function of the NSM on the heart is not known. Jones (1964) states that there is an evolutionary tendency for either or both of the lateral cardiac and segmental nerves of the heart to be reduced or suppressed. McCann (1970) gives a schematic proposal for heart-alary muscle functional relationship, and attributes a function of frequency-amplitude modulator to the alary muscles. McCann describes the heart-alary muscle association as having a myogenic cycle of its own, the heart being activated by a combination of nervous and humoral stimuli via the corpora cardiaca and, possibly, the pericardial cells, and the segmental nerves completing the cycle via the Ventral Nerve Cord to the neural center of the insect.

List of Abbreviations

A (1,2,3).....	abdominal ganglion 1,2,3
Acc Gl.....	accessory gland
Aed.....	aedeagus
Al M.....	alary muscles of heart
Ao.....	aorta
CA.....	Corpus Allatum
Cal.....	calyx
CC.....	Corpus Cardiacum
CCC.....	Commissurus Corporis Cardiaci
CEC.....	Circumesophageal Connective
CF.....	Connectivus Frontalis
C Ovid.....	common oviduct
CTC.....	Commissurus Tritocerebralis
CvN.....	cervical nerve
DN (1,2,3).....	Dorsal Nerve root of Gng 1,2,3 and SN
Ej Dt.....	ejaculatory duct
End S.....	endophallic sac
ESO.....	esophagus
GF.....	Ganglion Frontale
GH.....	Ganglion Hypocerebrale
G IN.....	Ganglion Ingluviale
Gng (1,2,3).....	ganglia of thoracic segments
GP.....	Ganglion Proventriculare

IL.....ileum
 LCN.....lateral cardiac nerve
 LO.....Lobus Opticus
 L Ovid.....lateral oviduct
 MT.....Malpighian tubules
 NA.....Nervus Aorticus
 N Aed D (R,L).....Nervus Aedeagus Dorsalis (right, left)
 N Aed V (R,L).....Nervus Aedeagus Ventralis (right, left)
 N Ant.....Nervus Antennalis
 NCC I, II.....Nervus Cardiocerebralis I, II
 NCM.....Nervus Cardiomaxillaris
 NCS.....Nervus Cardiostomatogastricus
 NCSOe.....Nervus Cardiosubesophagealis
 NSM.....neurosecretory material
 N In.....Nervus Ingluvies
 N Jug.....Nervus Jugularis
 N Lbm.....Nervus Labialis
 N Lbr.....Nervus Labrualis
 N Lbr Proc.....Nervus LabroProcurrens
 N Md.....Nervus Mandibularis
 N Mx.....Nervus Mavillaris
 N Oe.....Nervus Oesophageus
 N Proc.....Nervus Procurrens
 NR.....Nervus Recurrens
 N Ovid (R,L).....Nervus Oviductis (right, left)
 N Teg.....Nervus Tegumentarius
 N Vag D (R,L).....Nervus Vaginalis Dorsalis (right, left)

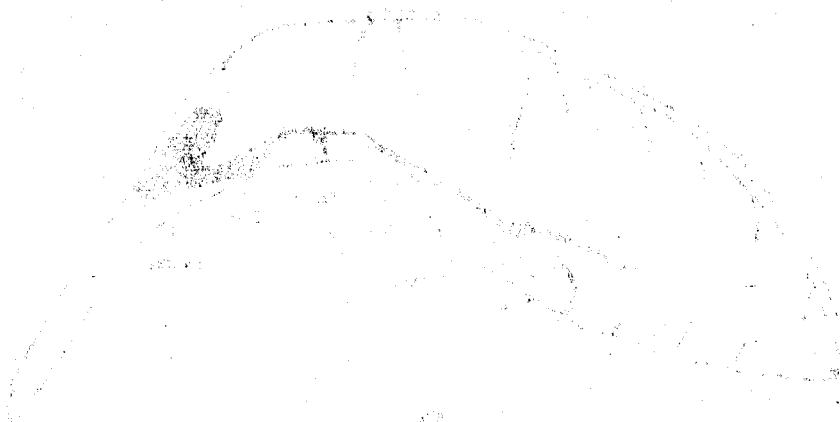
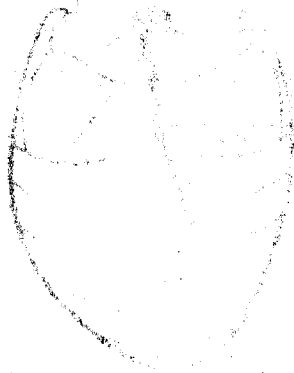
N Vag V.....Nervus Vaginalis Ventralis
 N VD (R,L).....Nervus Vas Deferens (right, left)
 Ovl.....ovariole
 PC.....Protocerebrum
 Per C.....pericardial cell
 PHAR.....pharynx
 PROV.....proventriculus
 REC.....rectum
 SA.....Sinus Aorticus
 Sal Dt.....salivary duct (unverified)
 Sal Gl.....salivary gland
 SEG.....Subesophageal Ganglion
 SN (1-7).....segmental nerves to abdominal segments
 sp (1A-7A).....abdominal spiracles
 Spt.....spermatheca
 Spt Dt.....spermathecal duct
 Spt Gl.....spermathecal gland
 SV.....seminal vesicle
 TA.....Terminal Abdominal Ganglion
 TC.....Tritocerebrum
 Vag.....vagina
 VD.....vas deferens
 VE.....vas efferens
 VENT.....ventriculus of midgut
 VN.....Ventral Nerve of SN
 8T.....eighth tergum

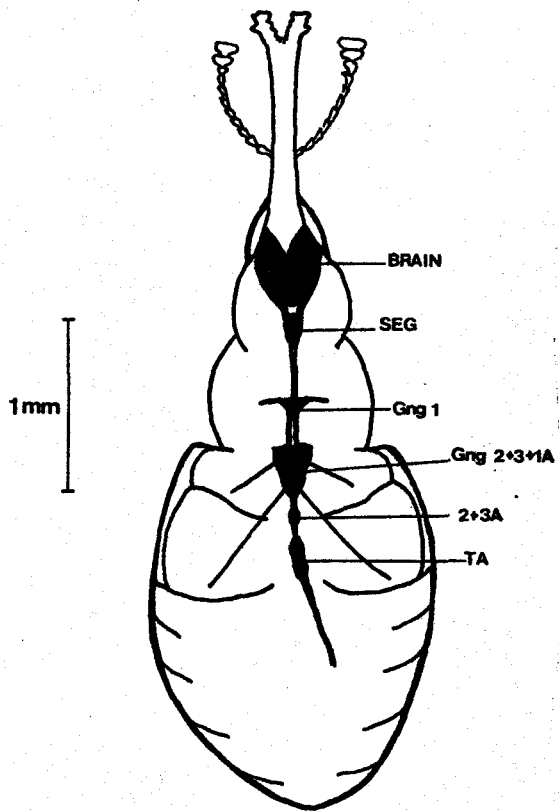
II.....second nerve root of Gng 1,2,3

III.....third nerve root of Gng 2,3

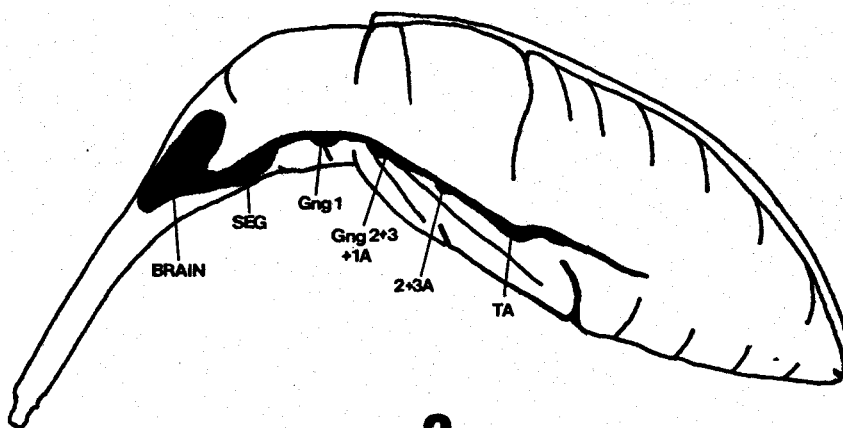
EXPLANATION OF FIGURES 1-2

1. Haplorhynchites acneus (Boheman). Position of Central Nervous System in body outline. Dorsal view.
2. H. acneus. Position of Central Nervous System in body outline. Lateral view.





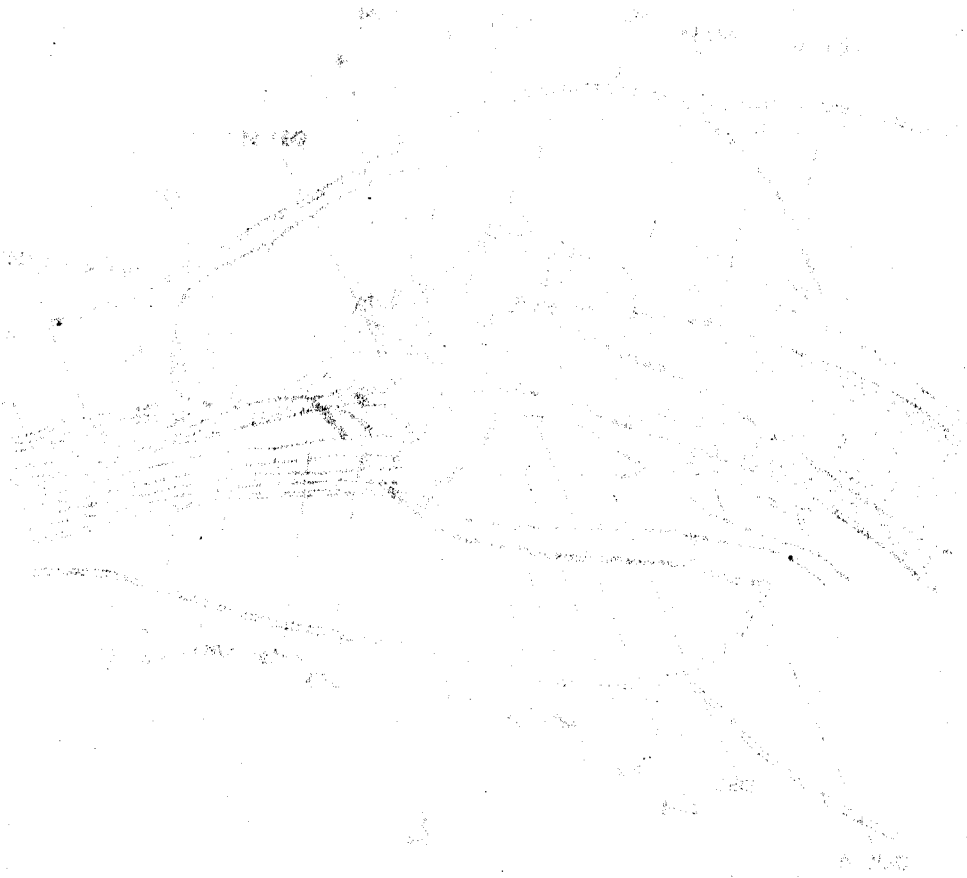
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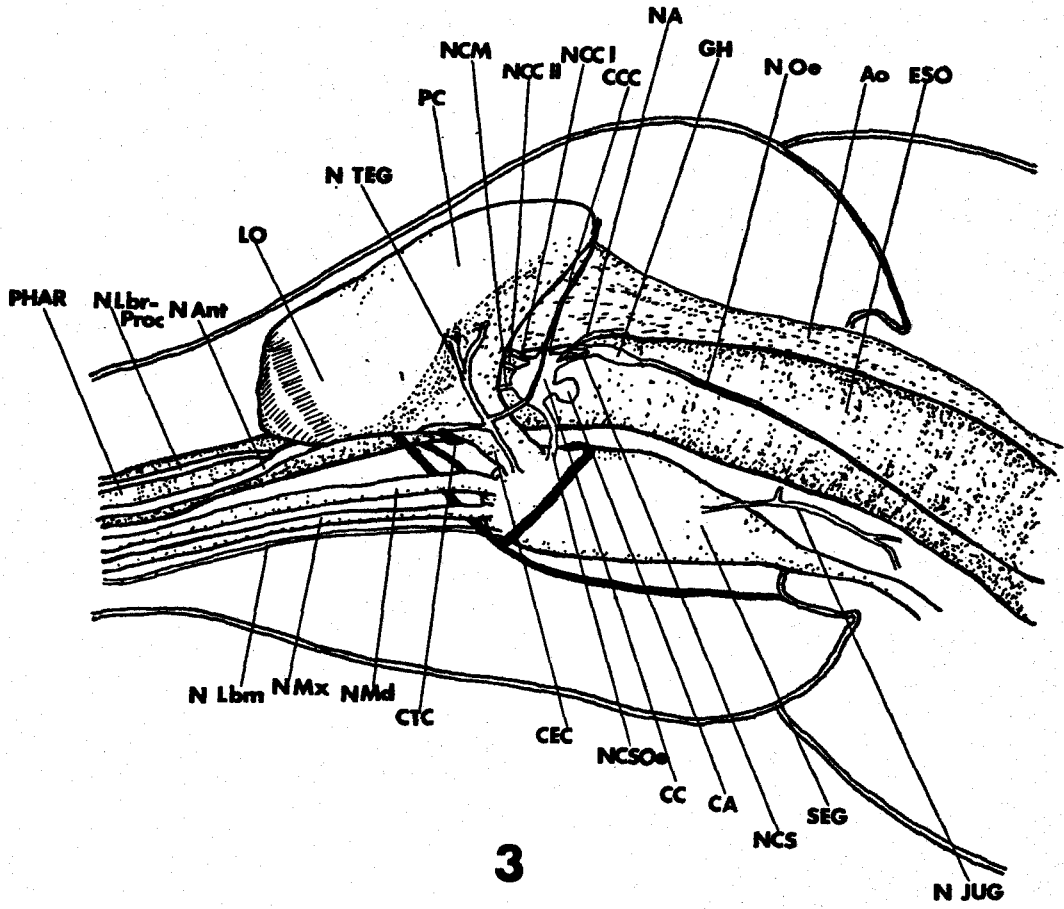
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EXPLANATION OF FIGURE 3

3. H. aeneus (Boheman). Brain and cephalic nerves, showing association with retrocerebral complex. Lateral view.



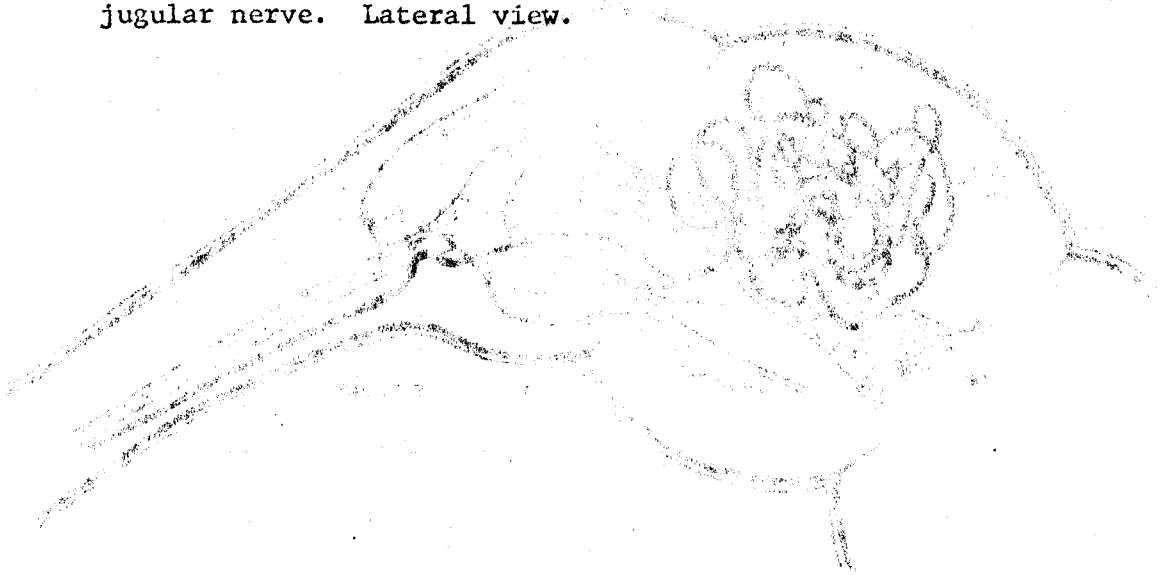
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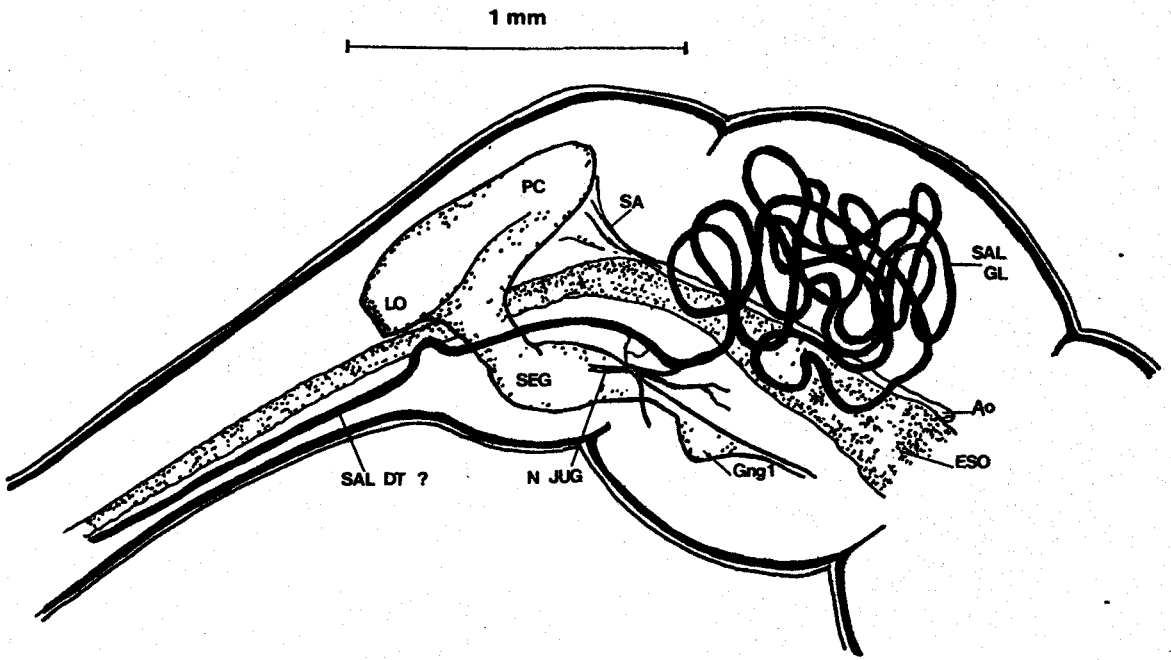


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EXPLANATION OF FIGURE 4

4. H. aeneus (Boheman). Position of salivary glands with respect to brain and Subesophageal Ganglion, showing innervation by jugular nerve. Lateral view.

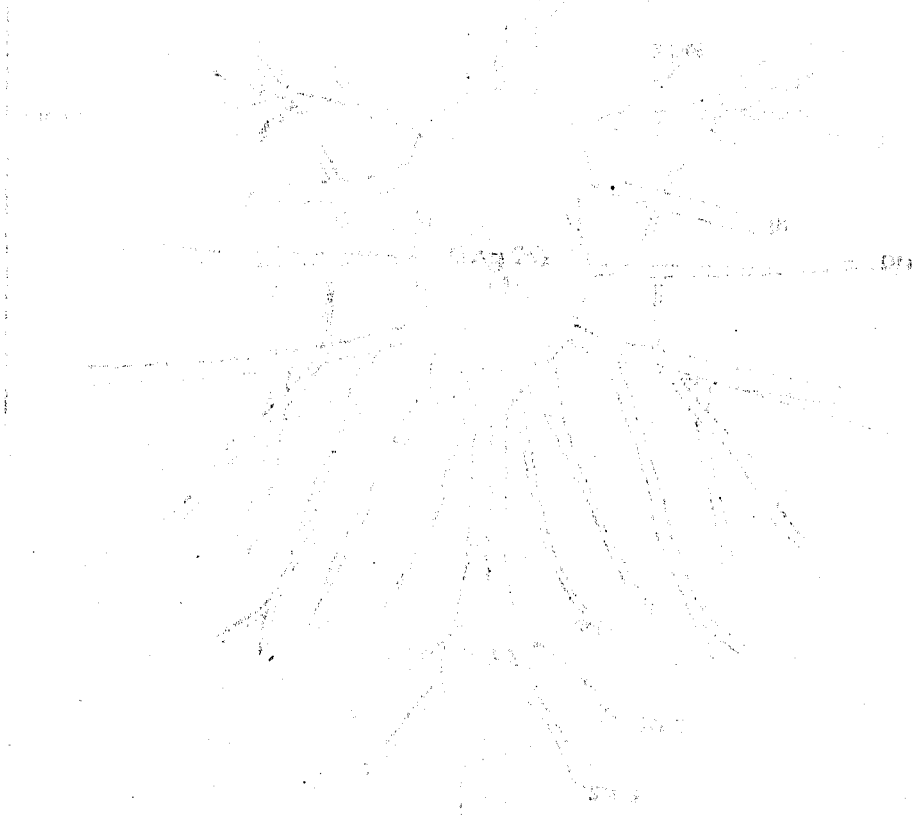


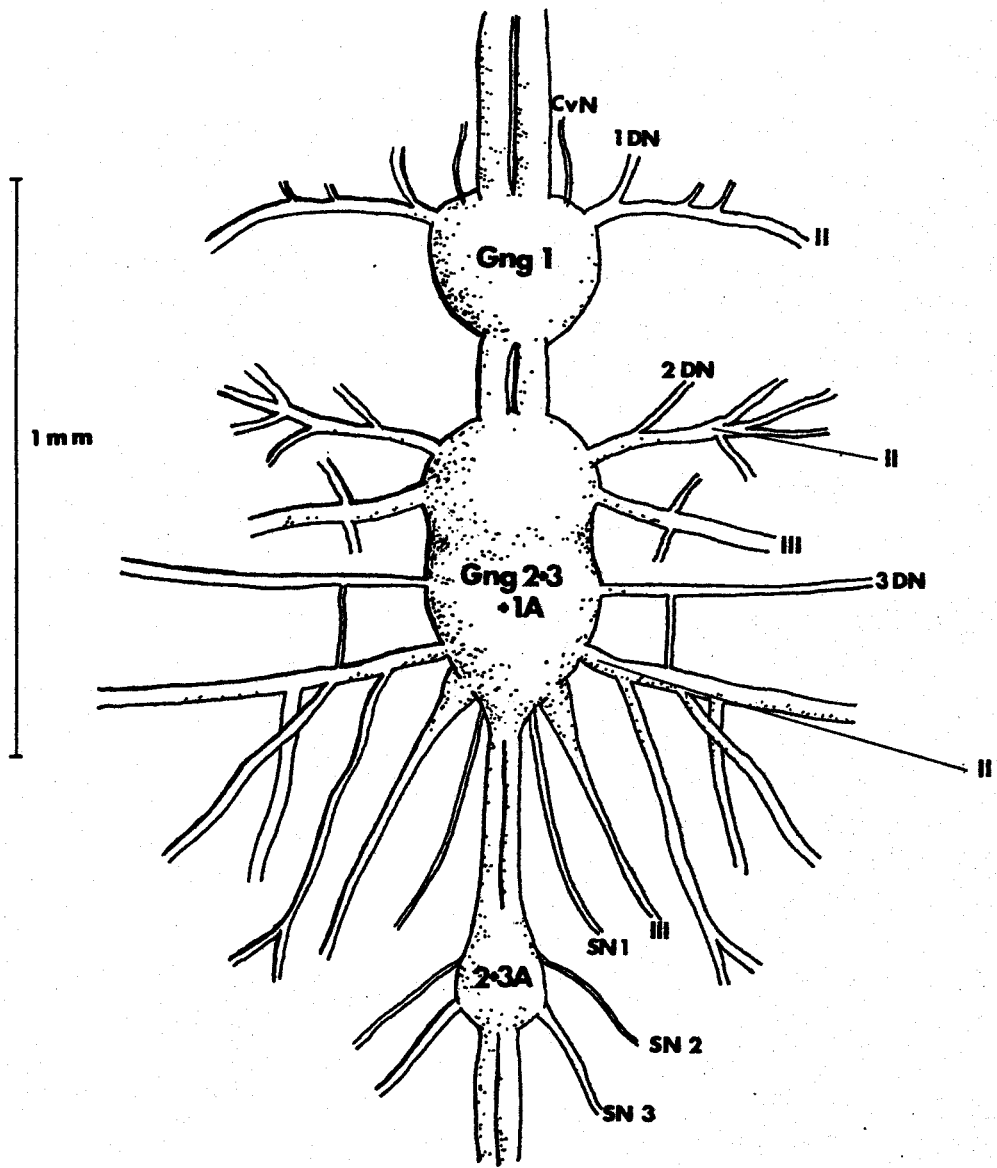


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EXPLANATION OF FIGURE 5

5. H. aeneus (Boheman). Thoracic ganglia and first three abdominal ganglia. Dorsal view.





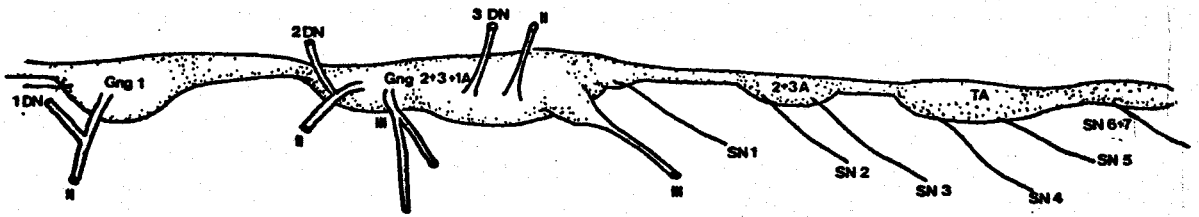
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EXPLANATION OF FIGURE 6

6. H. aeneus (Boheman). Thoracic and abdominal ganglia, showing direction of nerve exits. Lateral view.



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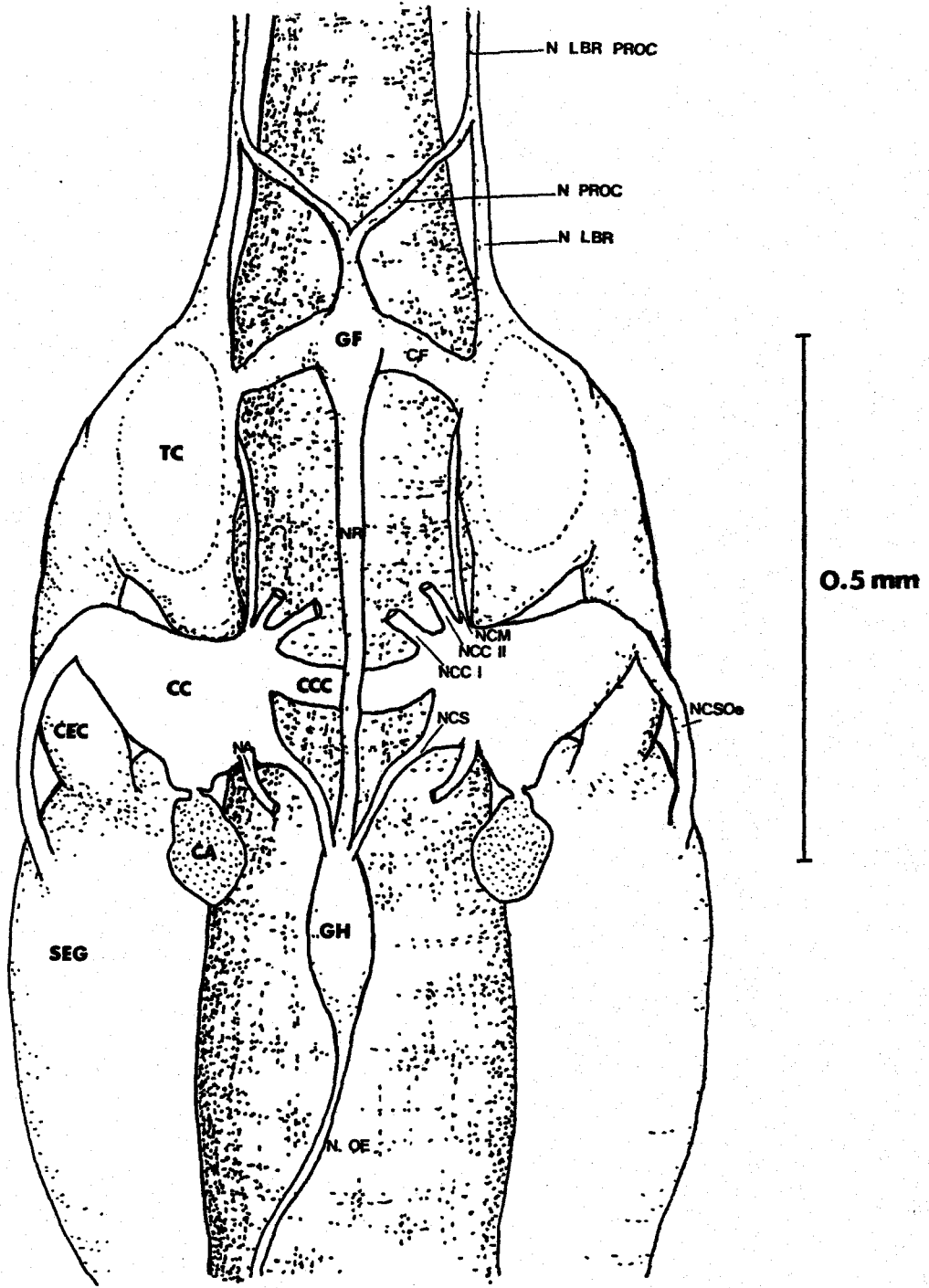


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EXPLANATION OF FIGURE 7

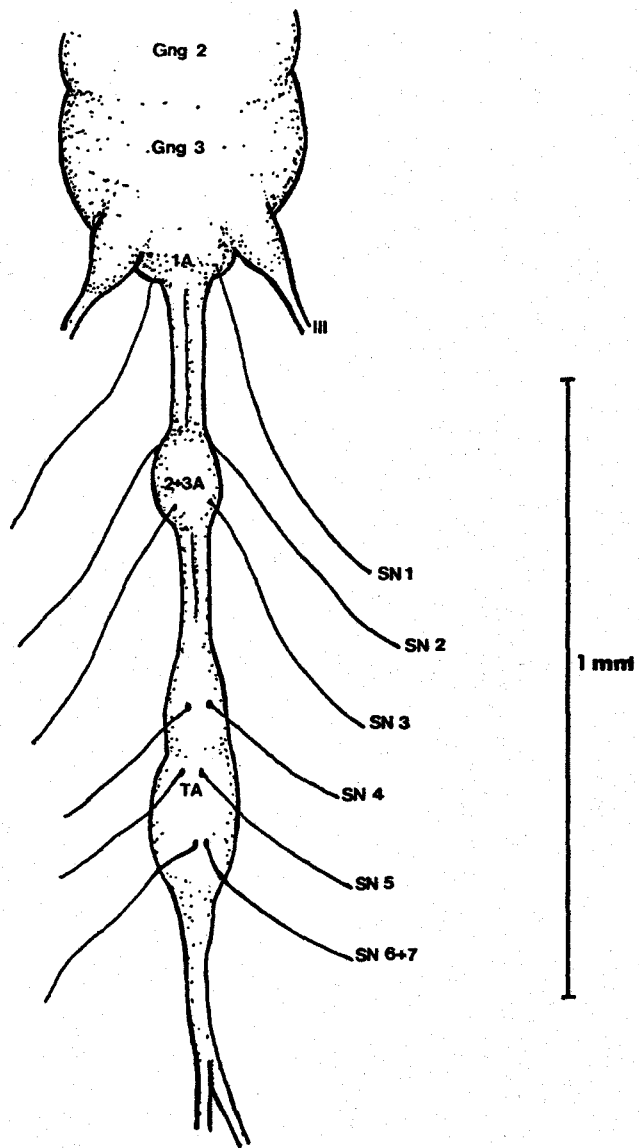
7. H. aeneus (Boheman). Stomodeal Nervous System with
Protocerebrum and Deutocerebrum removed. Dorsal view.





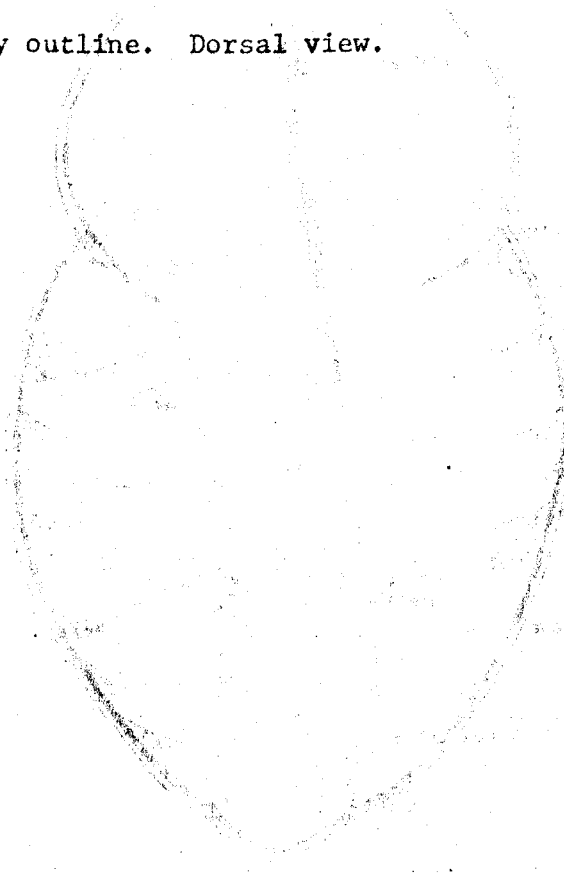
EXPLANATION OF FIGURE 8

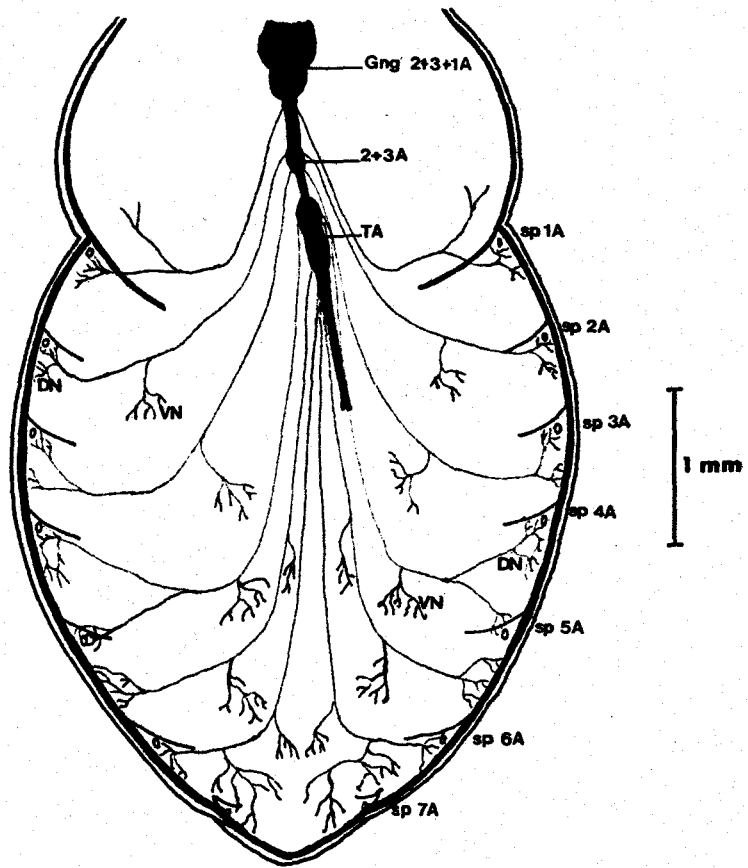
8. H. aeneus (Boheman). Position of segmental nerves as they exit from the abdominal ganglia, showing the off-center origin of SN 6+7. Ventral view.



EXPLANATION OF FIGURE 9

9. H. acneus (Boheman). Position of Ventral Sympathetic Nervous System in body outline. Dorsal view.

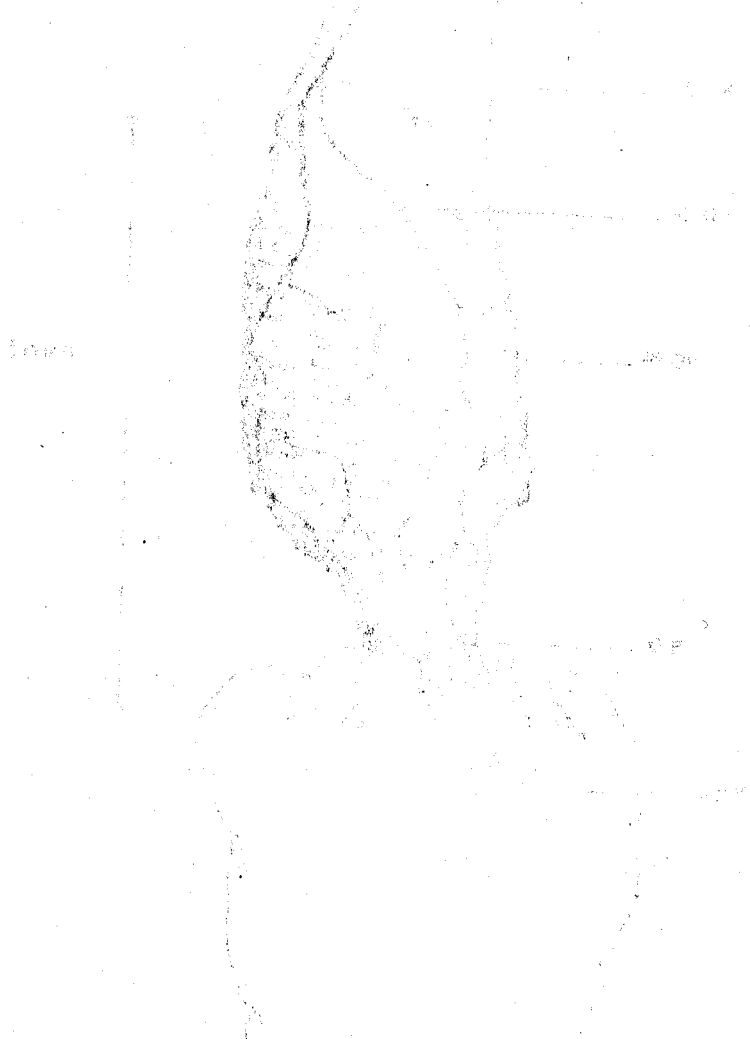


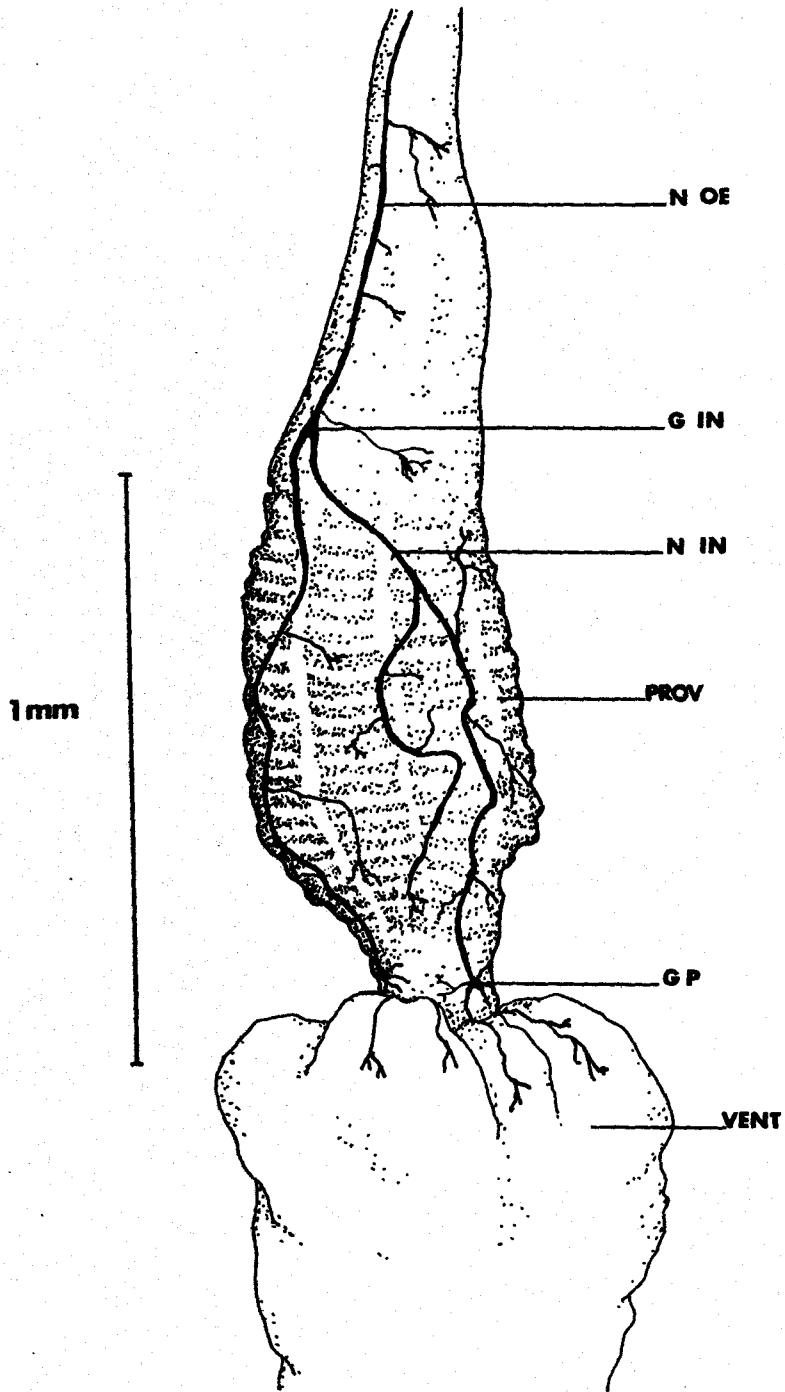


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EXPLANATION OF FIGURE 10

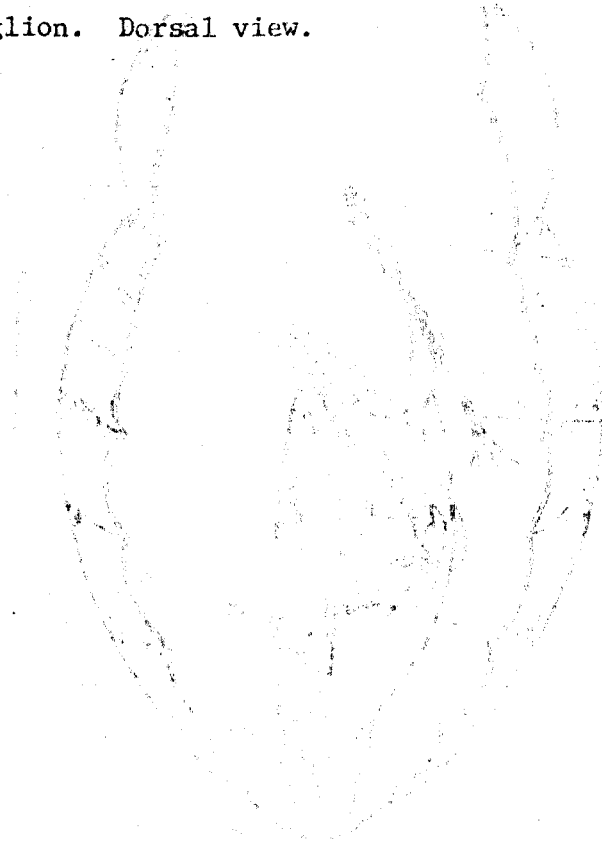
10. H. acneus (Boheman). Innervation of foregut from Stomatogastric Nervous System. Dorsal view.

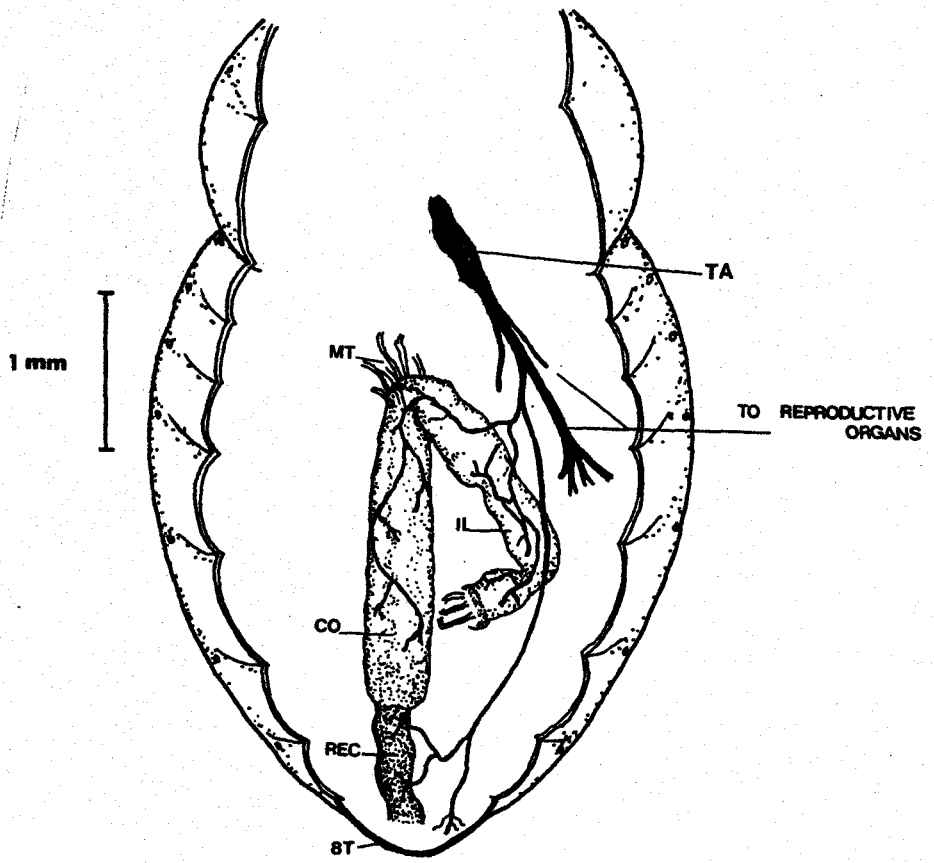




EXPLANATION OF FIGURE 11

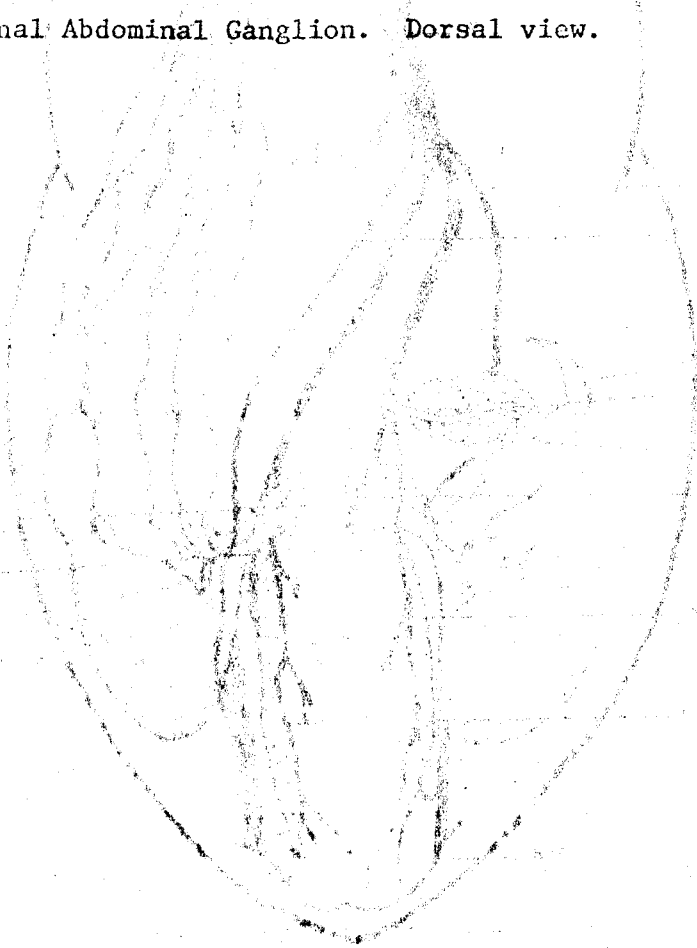
11. H. aeneus (Boheman). Innervation of hindgut from Terminal Abdominal Ganglion. Dorsal view.

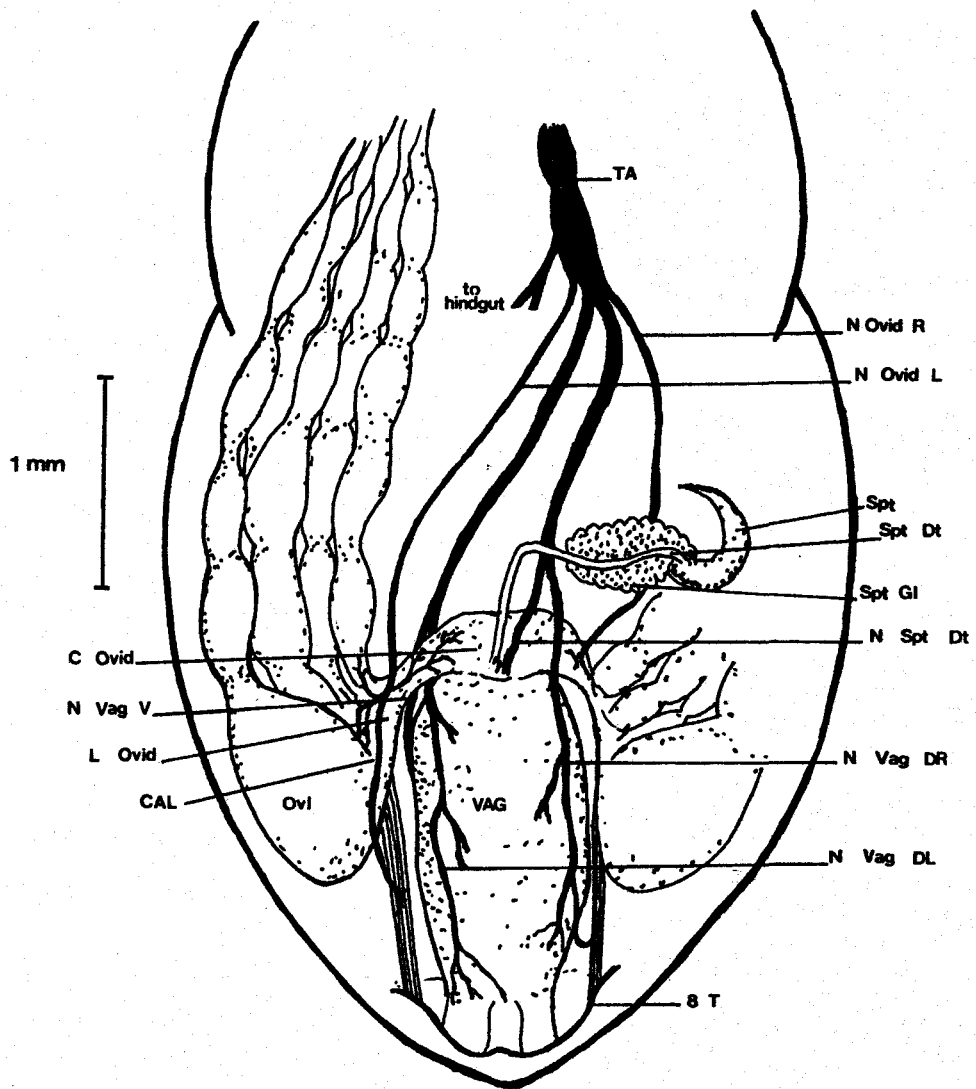




EXPLANATION OF FIGURE 12

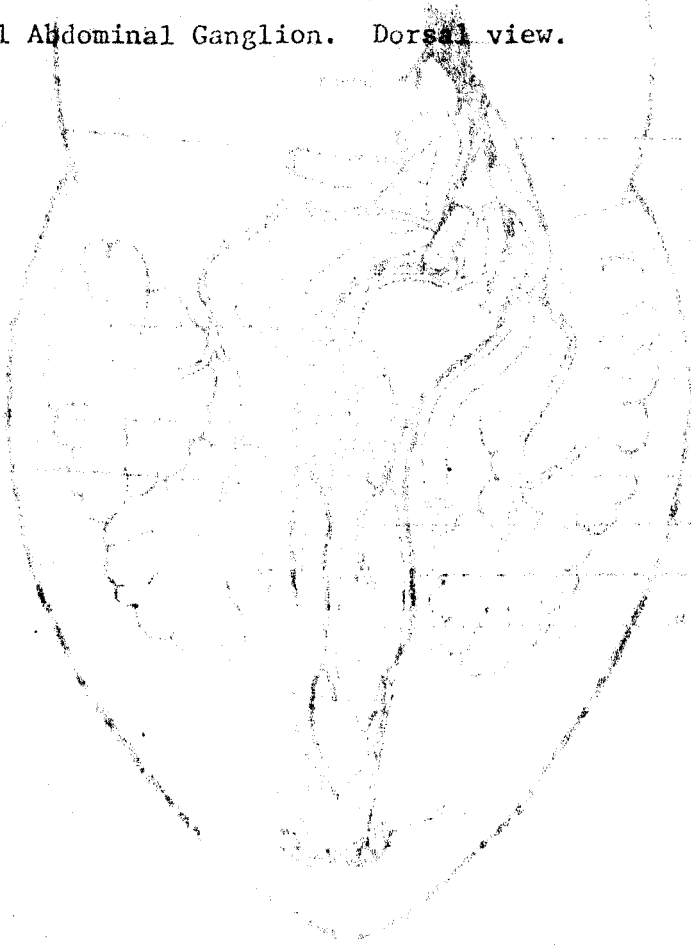
12. H. aeneus (Boheman). Innervation of female reproductive system from Terminal Abdominal Ganglion. Dorsal view.



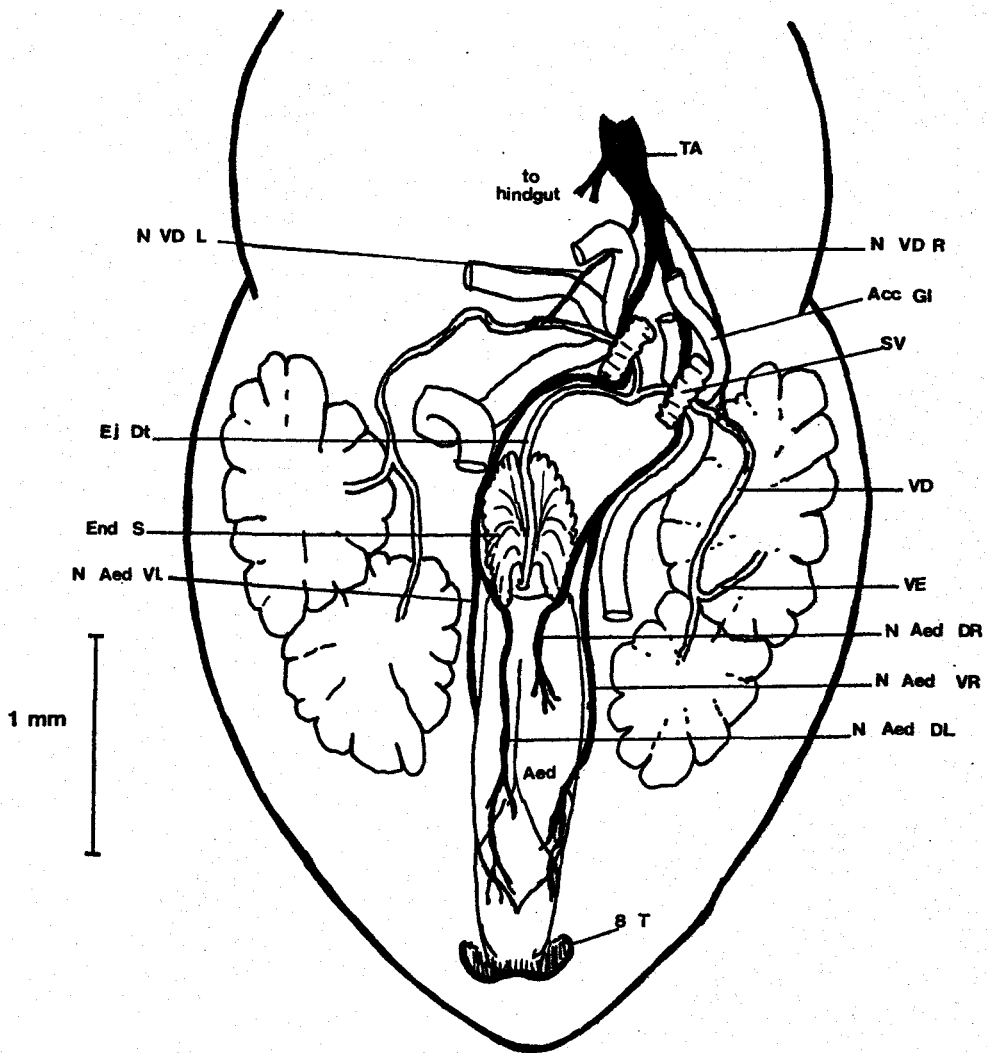


EXPLANATION OF FIGURE 13

13. H. aeneus (Boheman). Innervation of male reproductive system from Terminal Abdominal Ganglion. Dorsal view.

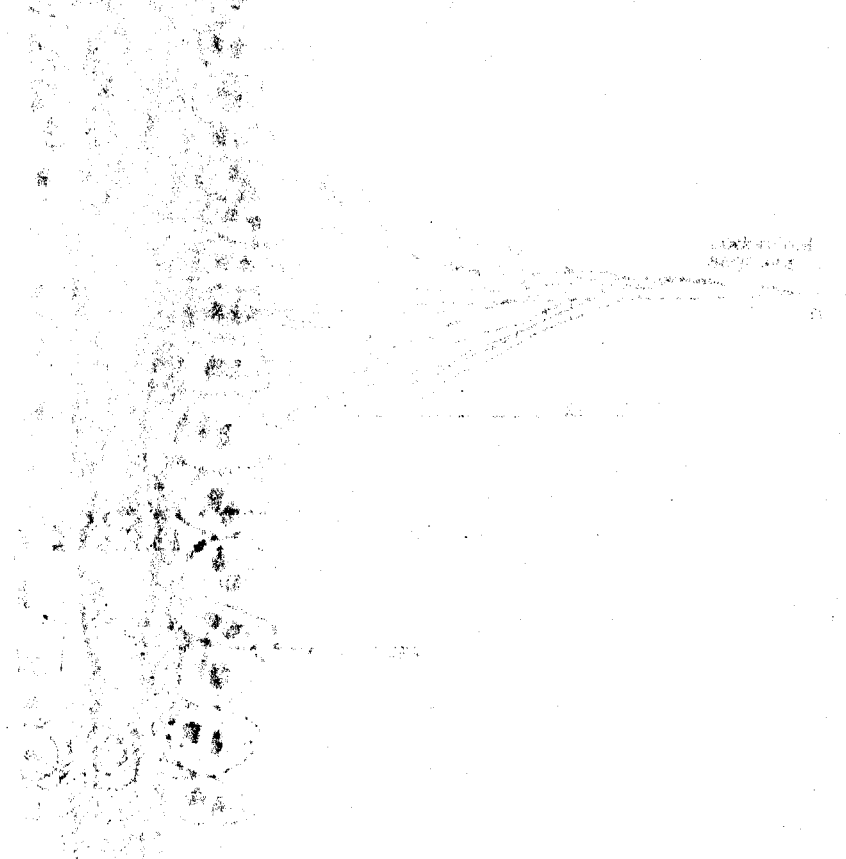


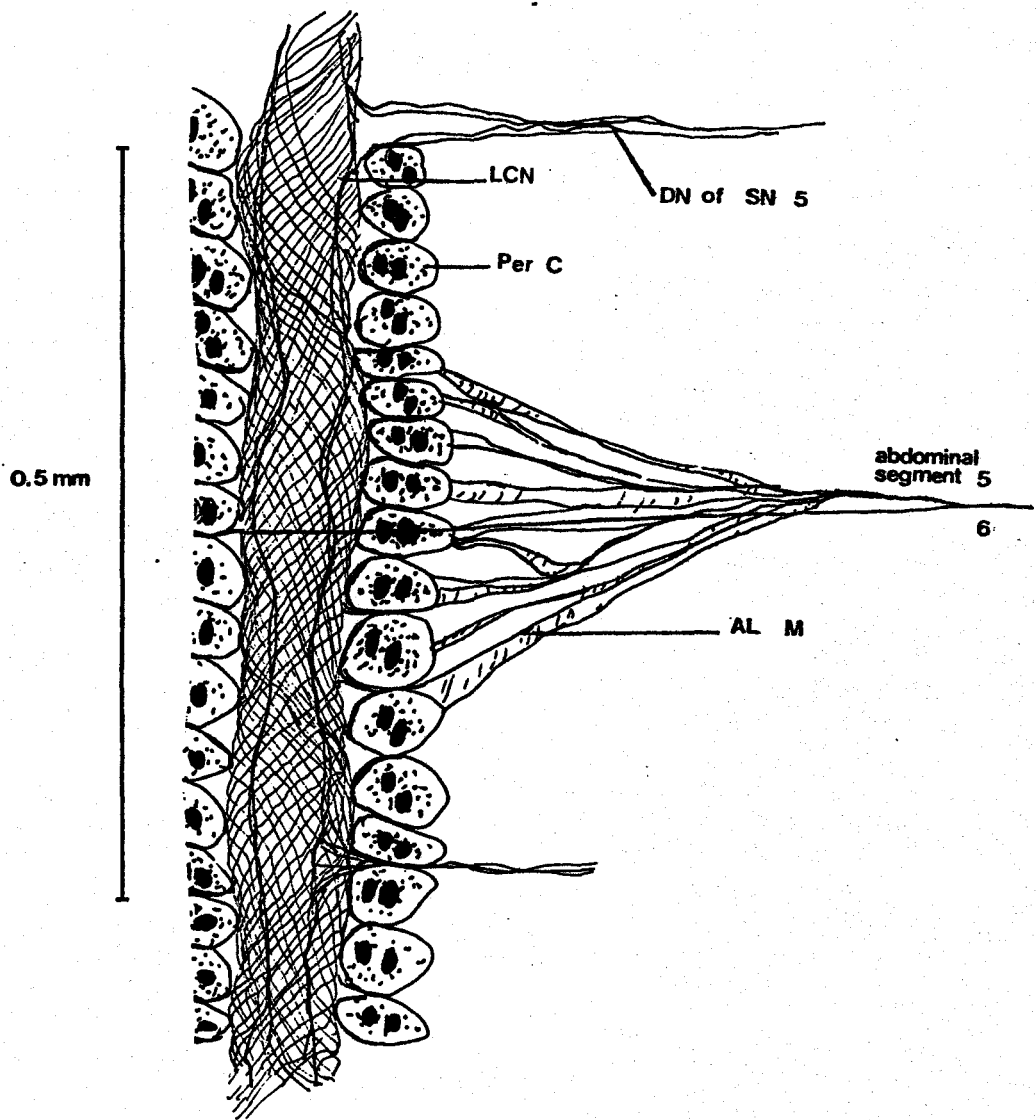
13



EXPLANATION OF FIGURE 14

14. H. aeneus (Boheman). Portion of heart showing innervation from Dorsal Segmental Nerves. Dorsal view.





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APPROVAL SHEET

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The final copies have been examined by the director of the thesis and the signature which appears below verifies the fact that any necessary changes have been incorporated and that the thesis is now given final by the Committee with reference to content and form.

The thesis is therefore accepted in partial fulfillment of the requirements for the degree of Master of Science in Biology.

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