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THE COMPARATIVE MORPHOLOGY OF THE CENTRAL NERVOUS SYSTEM OF THE LARVA, PUPA, AND ADULT OF *EPILACHNIA corrupta*

by

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INTRODUCTION

The nervous system of insects has been the subject of much study and research. By far the greatest part of this work has been on the orders Orthoptera, Lepidoptera, Hymenoptera, Diptera, and Coleoptera. This has been limited, in most cases, to a particular stage in the life history of the insect.

Since the changes in the larva, pupa, and adult nervous system of Passalus cornutus (Cody & Gray '38) and Oryctes nasicornis (Michels 1880), from the family Scarabeidae, had been well described, it seemed desirable to study the changes as they were found in the family Coccinellidae. It was then possible to make a comparison between the different species and also between two different families of the same order.

Epilachna corrupta Mul., the economically important Mexican bean beetle, was chosen for study. Only two morphological studies have been undertaken on this insect and these were on the alimentary tract (Potts '27) and the external morphology (Sweetman '30). So far as the author is aware no study on the nervous system of E. corrupta has ever been attempted before.

REVIEW OF THE LITERATURE

The review of the literature available on the nervous system of insects will begin with a discussion of general and miscellaneous literature. A survey of the literature on the different orders in phylogenetic arrangement, with the exception of Coleoptera, will follow the general discussion. This lends some order to the discussion and shows any phylogenetic trend in cephalization of the nervous system if it exists.

Dujardin (1850) was one of the early workers in the morphology of the insect nervous system. He was probably the first to observe the so-called "mushroom bodies" and named them corpora pedunculata. His conclusion that these structures were the seat of insect "intelligence," and offered an explanation for their seemingly intelligent acts, must have stimulated much of the later work which was done on these structures. It is interesting that the work which was done on these structures by Dujardin was completed with only whole mounts of the brains of Hymenoptera and Orthoptera (Kenyon 1896).

Binet (1892) did a somewhat comparable work on the internal structure of a thoracic ganglion of an insect. Additional information was given in a later paper which was concerned with the entire ventral ganglionic chain (Binet 1894). More information on the "mushroom bodies" was given by Kenyon (1896). Some additional knowledge was contributed by Hilton ('11a) who wrote on the motor and sensory tracts in insects with notes on the nerve connections. This was followed with a paper on the functional divisions of the insect nervous system (Hilton '25).

A comprehensive study of the stomodeal nervous system of insects was given by Bickley ('42). This was the only recent published paper which dealt exclusively with the much neglected stomodeal nervous system. This system has been most often described as an incidental item in an overall study of the central nervous system (Bickley '42).

Knowledge of the histology of the insect nervous system was contributed by Dornesco ('34) who made a cytological study. Other writers who have written articles of a general nature are Jawlowski

('48), Blanchard (1858) and Zawarain ('24).

The primitive order Collembola was best studied by Hilton. He studied three genera of this group, Aphorura (Hilton '13), Xenylla ('14b), and Neanura gigantea Tulb ('14b). These articles were reviewed and incorporated by Saylor ('36) in a paper on Collembola. One of the early studies on the order was that of Philiplschenko ('07). The connection of the frontal ganglion with the central nervous system of Anurida maritima Guer was discussed only by Denis ('26). In this primitive order we have the first indication that the degree of phylogenetic advancement of an organism is not necessarily correlated with the degree of cephalization of the central nervous system. The head and thoracic ganglia were present as in the typical insect but the abdominal ganglia have fused into a single ganglionic mass (Hilton '13 & 14a).

The nervous system of four genera of Thysanura was studied by Hilton ('17). A similar paper which included much of the same material was published by Aphlin ('36). The Thysanura were a primitive order in respect to their body structure and also in the organization of the nervous system which consists of a supra-esophageal ganglion, sub-esophageal ganglion, three thoracic ganglia and eight abdominal ganglia. The only cephalization which had taken place in this order was a consolidation of the last three embryonic abdominal ganglia into one terminal abdominal ganglion in the adult.

There were only two papers which discussed the central nervous system of Ephermerida. In his book "Biology of the Mayflies," Needham ('35) gave a general discussion of the nervous system. A brief discussion was given by Berry ('38) on the nervous system of this order. The head ganglia were found to be the same as those of Thysanura but some cephalization had occurred with a fusion of the first abdominal with the third thoracic and a consequent reduction of the abdominal ganglia from eight to seven.

The one published article on Odonata showed the head and thoracic ganglia to be the same as found in Ephermerida, but cephalization had occurred in the abdomen, where only six abdominal ganglia were found (Hilton '39b).

Orthoptera was one of the most widely studied orders and its central nervous system was most often given as the one which was generally typical of insects. One of the early studies on this order was on Periplaneta orientalis and also contained a good review of the early literature on the nervous system of insects (Koestler 1885). The brain of Blatta orientalis was studied by Newton (1879). Vialannes worked out the anatomy of the brain of Oedipoda caerulescens and Caloptenus italicus (1838). One of the very good early studies on the histology, fiber tracts, and the gross morphology of the brain of the locust was that of Packard (1880). Bordas (1900) and Hilton ('37a) discussed the nervous system of Orthoptera in general. The best recent review of the nervous system of the order was the work of Nesbitt ('41) who discussed and compared several families in regard to the shape, size, cephalization, etc., of the various ganglia of the central nervous system. There was only one study of the peripheral nerves and that was on the innervation of the pre-genital abdominal ganglia of the grasshopper (Schmitt '54). From these studies we find that in Orthoptera there may be a consolidation of one, two, or three abdominal ganglia with the third thoracic. In other respects the head and thoracic ganglia were like those found in a typical insect. There were from four to six abdominal ganglia (Nesbitt '41).

The genus Anisolalius was the only Dermapteran which had been studied in regard to the nervous system and this only as part of a more extensive study on Orthoptera (Nesbitt '41). The supra-esophageal ganglion, sub-esophageal ganglion, and first two thoracic ganglia were separate. The third thoracic ganglion was compound as a result of fusion with the first three abdominal ganglia. There were five separate abdominal ganglia.

Berry ('38) indicated that the head and thoracic ganglia of Plecoptera followed the general pattern of insects. He also indicated that there were only five abdominal ganglia.

From the one paper on Zoraptera (Scott '37) we know that the head and thoracic ganglia were not different from the typical insect and there were only two abdominal ganglia.

Embioptera resembled most insects in the head and thoracic ganglia and showed slight cephalization in the abdominal ganglia, the number being reduced to seven (Crazier '37). In the same paper the author indicated that the same ganglia were present in the head and thorax of Corrodentia but with a marked increase in cephalization of the abdominal ganglia, only three being found. In Mallophaga further consolidation of the abdominal ganglia was shown by fusion of all ganglia with the third thoracic (Crazier '37). Thysanoptera was one of the few orders of insects which had the first thoracic ganglion fused with the sub-esophageal ganglion, and additional cephalization was evidenced by a fusion of all abdominal ganglia into one mass of nervous tissue (Saylor '37). Anoplura possessed a typical nervous system except for the fusion of all abdominal ganglia into one mass (Crazier '37).

Hemiptera had the supra-esophageal and sub-esophageal ganglia as separate entities but the thoracic and abdominal ganglia were consolidated into one unit (Brandt 1879d and Hilton/ 396 '46). Graichen ('36) has also written on Hemiptera. In contrast to Hemiptera, Neuroptera had separate head, thoracic ganglia and nine abdominal ganglia (Hilton '39).

There were no reports on the adult Megaloptera but the larva of <u>Corydalis cornuta</u> had received attention from Kraus (1894), Hammar ('08), and Hilton ('11b). The variation in Mecoptera was in the abdominal ganglia with the first one fused with the third thoracic and only six remained as distinct entities (Berry '38).

The social habits of various Hymenoptera coupled with their acts of "intelligence" was a motivating force in stimulating interest in this group of insects. General works on this group were those of Brandt 1879c (1876), Alton ('10), Hilton ('40a), Keim ('15), and Viallanes (1888). Probably because of its economic importance and availability for study there was a great deal of information on the honey bee. Snodgrass ('25) has written a book on its anatomy and physiology. An excellent understanding of the brain of the bee may be gained from the works of Kenyon (1896), Jonescu ('09), and Miller ('38). The ants have also been the subject of a good deal of study by such authors as Rabl-Ruckhard (1875), Janet ('05), Pietschker ('11), Thompson ('13), all of whom studied the brain of the ant. Wheeler ('26), in his book "Ants," breifly discussed the nervous system. From these sources of information it was found that Hymenoptera have the usual ganglia in the head, two to three thoracic ganglia and two to seven abdominal centers (Hilton '40b).

Branch ('22) contributed knowledge of the central nervous system of Trichoptera as part of a study of the internal anatomy of Limnophilus indivisus Walker. The adults were said to have the usual head ganglia, three thoracic ganglia and seven abdominal ganglia (Hilton '38a).

The larval forms of Lepidoptera have probably received more attention and been studied more thoroughly as regards the nervous system than any other order. There was some research on the adults but much less than on the larval forms. One of the earliest investigations of the nervous system was carried out on the larva pupa, and adult of Sphinx lingustri L. (Newport 1832 & 1834). The structures innervated by the chief nerves from each of the ganglia were indicated as well as parts of the stomodeal nervous system. A comparative study of Mormo maura larva, Combyx larva and Sphinx pupa was completed by Anderson ('37). Packard (1893) wrote on the anatomy and transformations of Lagoa crispata in a general way. Peterson ('08) investigated the anatomy of the larva of Protoparce carolina and gave the nervous system an unusual amount of attention for a study of this type. The nervous system of the larva of Sphida obliqua Walker was studied by Du Porte ('15). A rather extensive study of the nervous system of the larva of Sthenopis thule Strecker was contributed by Swaine ('20 & '21). A comparative study of the brain of the caterpillar and the imago of Pieris brassicae was published by Hanstrom ('25). A developmental study of the nervous system of

Aglais antiopa was carried out by Ingles ('28). Another larval study was that of Hillemann ('33) on the mature larva of Papilio polyxenes Fab. Hilton ('40a) published a paper on the nervous system of Lepidoptera but it was generally inferior to those of the workers already mentioned. Brandt wrote many papers on the nervous system of insects and Lepidoptera were the subject of many of them (1877a, 1879e, 1879h). The Supra-esophogeal and sub-esophogeal were not fused with other ganglia but in some species there was a consolidation of the thoracic ganglia. There were four to five abdominal ganglia in insects of this order.

The morphology of the nervous system of Diptera has been subject of a fair amount of attention. Most of this, however, has been limited to one species namely Drosophila melanogastra. The importance of this species to genetics was one of the factors contributing to the great amount of study which it had received. Power ('43) said that his study of the brain of Drosophila was undertaken for the insight which it would give into the genetics and other investigations with the insect. The research papers of Power ('43, '46, '48) on the brain, the thoracic-abdominal ganglia and their connections were among the better papers of recent time. The developmental anatomy of the nervous system of Drosophila was treated rather extensively by Demerec ('50) as part of his book on "The Biology of Drosophila." The anatomy and variation of the nervous system of the insect has also been studied by Hertweck ('31). Other authors who worked with Diptera were Kurckel (1879), Cuccati (1887) Brandt (1879i), (1882), Escherich ('17), Hewitt ('10) and Turlock (1891?). The embryology of the central nervous system of Phormia regina Meigen was studied by Schaefer ('38). The metamorphosis of the nervous system of *Aedes dorsalis* was investigated by Wooley ('43). As a part of a paper on the internal morphology of Diptera, Owsley ('46) gave some information on the nervous system. The amount of cephalization in this order was subject to a great deal of variation. It ranged from separate supra-esophageal, sub-esophageal, separate thoracic ganglia and eight abdominal ganglia to a consolidation of all thoracic and abdominal ganglia into a thoracic mass, which also involved the sub-esophageal and to a lesser extent the supra-esophageal.

The Coleoptera have received as much study on the central nervous system as Hymenoptera, Lepidoptera, and Diptera. Beier ('27) made a very good study of the central nervous system of numerous larvae of Coleoptera. Goaszen ('49) studied the body size, the head and brains of thirty-two species of beetles. Brandt (1879a, 1879b, 1879g, 1881) published papers on members of several families in this order. The outstanding article from a comparative point of view was the work with *Orycetes nasicornis* in the larval, pupal, and adult stages (Michels 1880). The brain of *Dytiscus* was first studied by Faivre (1892). A good study of the adult form of *Dytiscus marginalis* was that of Holste ('10 & '23). The most recent comparative study of the larva, pupa, and adult forms of a Coleopteran was the paper by Cody & Gray ('38) on *Passalus cornutus* Fabricious. Hilton ('39d) gave a review of the articles by Beier ('27), Holste ('10), and Michels ('80). The anatomy of the nervous system of the adult of *Phyllophaga ephlida* has recently been worked out by the author (in manuscript). The Coleoptera are subject to a great deal of variation in their nervous system. In general the abdominal ganglia were fused into one mass with the thorax and head containing the usual ganglia. In some there may be an almost complete fusion of the three thoracic and abdominal ganglia into a thoracic mass.

REVIEW OF LITERATURE ON EPILACHNA corrupta

Epilachna corrupta Mulsant, commonly known as the Mexican bean beetle, was described in 1850 (Thomas '24). It was reported in New Mexico and Colorado in 1865 (Douglas '32, Chittenden '19). It was retained in these areas by natural barriers until approximately 1919 by the surrounding hot and dry territories which extended too great a distance for the beetle to cross by its own power of flight. In 1918 some investigators reported it in Bibb County, Alabama, but it was not positively identified in that state until 1920 (Thomas '24, Howard '24). It was thought to have crossed from Colorado in shipments of alfalfa hay which mining companies in Alabama imported for their cattle. (Howard '24). From this point it began to spread over the eastern section of the United States. Its advance was unchecked since there were no natural barriers such as those which had restrained it in Colorado. It appeared in Virginia in 1922 (Friend '31), South Carolina and Kentucky in 1922, Tennessee and Georgia in 1925, New York in 1927 (Cecil '28), in Delaware in 1928 (Dozier '29), in Canada in 1927 (Cecil '28), Connecticut in 1929 (Friend '31), in Ohio in 1923, and Michigan in 1927 (Pettit '27).

Following its introduction into the Eastern United States it became a serious pest and much research was done in an effort to control it and prevent damage to the commercially valuable bean crops. Most of this work was completed during the years 1920-1930 and gave valuable information on the life cycle, control measures, and occurance of the beetle. Only two morphological studies of importance were made, one on the external morphology (Sweetman '30) and another on the alimentary canal (Potts '27).

The life cycle varied in length depending upon the temperature but in general followed a regular pattern. The larva hatched from the eggs in 5-14 days and fed during a larval period of 16-20 days before it entered the pupa stage which lasted for 6-8 days. The adult lived from 25 days in the summer heat up to 58 days in the cooler spring (Howard '24).

The eggs were light yellow and deposited in clusters of 40-60 on the lower surface of the bean leaf (Howard '24, Hamilton '29). They were 1.25 mm x .6mm (Thomas '24). The eggs hatched in ten days to two weeks into small first stage larva. The larva increased progressively in size through four larval stages and fed voraciously during this period of 16-20 days. Each larval stage had spines covering the entire body and were a bright yellow. The first stage larva was 1-1.5mm, the fourth stage 5.4-10 mm (Thomas '24). The larva attached itself to a leaf by the posterior end before molting and entering the pupa stage.

The pupae resembled the adult in body structure but still retained the yellow color of the larva. They remained in this state for 6-8 days. When the adult emerged from the pupa state it was a bright lemon yellow without the characteristic black spots. In a week to 10 days the color deepened and the spots began to appear. The entire beetle darkened and became copper colored with age.

The adult beetle was a copper colored hemispherical insect with markedly arched wing covers with, characteristically, eight black spots on each. They were approximately ¼ inch in length and slightly less in width. The females fed about fourteen days and then began to lay eggs which totaled as many as 1600 in a single season. The fertility was fairly high with 46-52% of the total hatching (Howard '24). The males differed from the female only in being a little smaller and possessing a notch in the posterior abdominal segment.

The primary food for all stages was the bean family. It had been known to feed on <u>Phaseolus</u> (bush, pole, lima, navy, and kidney beans) <u>Glycine</u> (soybean), <u>Medicago</u> (alfalfa), and <u>Trifolium</u> (sweet clover) (Cecil '28, Rodney '28). When the food supply diminished and the temperatures dropped the adult females went into hibernation (Cecil '28, Chittenden '19). They preferred wooded areas where they dug down to the moist leaf mold and were protected from freezing temperatures.

MATERIAL & METHODS

The specimens for dissection were collected during the months of August, September, and October, from gardens in Eastern Henrico County, Va. There was no way of knowing precisely the age of a particular larva, pupa, or adult. Some indication was given in the larva by the size but was not exact because of overlap in the size between the four stages. A relative age of the pupa was determined by the degree of pigamentation in the eyes. Pupae without any eye pigamentation were very young and probably no more than one day old. This was based on the presence of the larval form of abdominal ganglia of the central nervous system in this stage. Pupae with a light brown or brown eye color were intermediate between those without any color and those with very black eyes. Those with the black eyes were nearly mature with the adult form of nervous system and soon emerged as adults.

Approximately 100 specimens, each of larva, pupa, and adult, were collected. Fifty of each stage were cut in half before fixation in Bouin's fixative; the remaining fifty were fixed intact. The Bouin's was heated to 70° C. before using. The insects were left in the fixative for 24 hours. At the end of this time they were removed and stored in 70% alcohol. This was changed two to three times in order to remove some of the picric acid but no effort was made to remove all of it since the stains used were not affected by the picric acid. Some additional specimens were fixed in 10% formalin, others in FAA, and some were frozen at -10° C. Preservation was found to be best and most satisfactory in the Bouin's. Those specimens which were fixed by other methods were fair but not nearly so well preserved. There was no apparent difference between those cut and those left intact for the purpose of dissection. The frozen specimens were well preserved but were in general more difficult to dissect.

Dissection was done manually under the high power (60x) of a steroscopic dissecting microscope. The light source was a 100 watt bulb focused by a Florence flask of copper sulfate solution and further intensified by focusing with a magnifying lens. Dissecting forceps were made by grinding an ordinary pair of forceps down to a fine point. Scapels were made of razor blades which were broken in such a manner as to give small chips. These were mounted on wooden handles and ground to fine points. At first attempts were made to fasten the insect with "minute natleen" to paraffin but these were too large for holding the head. The most satisfactory method was to melt the paraffin and stick the insect into it. It was then possible to do most of the dissection without too much difficulty. Dorsal, ventral, and lateral approaches were tried on all stages. The dorsal was found to be the most satisfactory for the adult and pupae; the ventral was best for the larva.

In each dissection an effort was made to follow each nerve of the head and thorax from its origin on a ganglion to the structure which it innervated. Nerves from the abdominal ganglia were traced only to the segment in which they terminated. The nerves, with the ganglia and connections were removed as intact as possible, stained, and mounted as whole mounts in balsam. Eosin, Delafield's haematoxylin, congorred, and aceto-orcein were stains which were tried. Delafield's haematoxylin alone was generally best for both whole mounts and sections.

The findings of gross dissection were confirmed by serial histological sections. Specimens were dehydrated in alcohol or cellosolve and cleared in xylene, cedar oil, or carbo-xyol and embedded in tissuemat for sectioning. The ten micron sections were mounted on slides, stained and mounted in balsam. In addition to the above named stains picrocarmine was tried, but was not as satisfactory as Delafield's haematoxylin alone or Delafield's counterstained with eosin.

DESCRIPTION OF THE NERVOUS SYSTEM OF E. corrupta

The nervous system of the larva of Epilachna corrupta had in its first instar the approximate shape which it maintained throughout its larval development (fig. 1-2). There were no major changes in either the central nervous system or stomodeal nervous system except for an increase in size up to the pupa stage. Therefore, the following description of the nervous system of a larva may be applied to any of the four larval stages (figs. 1-8).

The supra-esophageal ganglion (1Br, 2Br, 3Br) (figs. 1, 3, 6, 8) was located in the head dorsal to the esophageus. The shape might be compared to two inverted teardrops which have fused by the sides of the bulbous lobes. This shape was most apparent from a lateral or posterio-ventral view. Projecting from the morphologically anterior surface of each lobe were four nerves. The most lateral and dorsal area of each lobe was the protocerebrum (1Br) (figs. 2, 3, 6, 8). It was from the protocerebrum that the optic nerve (OpNv) (figs. 3, 4, 5, 6, 7) originated. Each nerve took an anterio-lateral course to the side of the head where it divided into three fasciles and these in turn innervated three pigamented ocelli which were in the position that corresponded with the compound eyes of the adult. Ventral and medial to the protocerebrum near the base of the optic nerve was the antennal nerve (AntNv) (figs. 3,4,5) which began in the deutocerebrum (2Br) (figs. 3, 4, 6). The much reduced tritocerebrum (3Br) (figs. 3,4,6,8) was ventral and medial to the deutocerebrum. From the tritocerebrum there was a nerve trunk which extended anteriorly and divided immediately into the labral nerve (LmNv) (figs. 1,3,5) and the frontal ganglionic connective (FrCon) (figs. 1,2,3,5). At the point of division the frontal ganglionic connective turned medially to join the frontal ganglion (FrGng) (figs. 1,3,5,7,8). From the posterio-ventral surface the circumesophageal connectives (CoeCon) (figs. 1,2,7,8) originated and extended around the esophageus to the sub-esophageal ganglion (SoeGng) (figs. 1,3,4,5,7). Approximately 2/3 of the distance between the origin of the circumesophageal connective and its junction with the sub-esophageal ganglion there was a nerve tract between the two connectives which was the tritocerebral commissure (Com) (figs. 1,3,5). (This was called the sub-esophageal commissure by some authors.) Midway between the tritocerebral commissure and the junction of the circumesophageal connectives with the sub-esophageal ganglion, the mandibular nerve (MdNv) (figs. 1-6, 8) originated and extended anteriorly. In sections it was possible to see that the nerve had its true origin in the fibers of the sub-esophageal ganglion.

The sub-esophageal ganglion was in general oval but comparatively flat dorsally and more rounded ventrally. There were three pairs of nerves which arose from the sub-esophageal ganglion. The mandibular has already been mentioned. Slightly posterio-lateral to the mandibular were the maxillary nerves (MxNv) (figs. 1,3,5,7,8). The labial nerves (LbNv) (figs. 1,2,3,5,7,8) began still more laterally and about midway of the ganglion. The sub-esophageal was joined posteriorly to the first thoracic (T1) (figs. 1-8) by a relatively short connective.

The thoracic ganglia (T1-T3) (figs. 1-12) were somewhat shield-shaped in appearance from a dorsal or ventral view and were slightly elongated ovals from a lateral view. There were two major pairs of nerves from the second (T2) and third (T3) thoracic ganglia but only one pair from the first thoracic ganglion (T1). The anterio-dorsal pair led to the lateral and dorsal body muscles, and the posterio-ventral pair (TLNv2) (figs. 1,3,5,7) led to the leg muscles. The connectives between the first and second, also between the second and third ganglia, were quite long. In the larva each thoracic ganglion was located in its respective segment.

The abdominal ganglia (A1-A8) (figs. 1-8) were all similar in size and appearance except for the terminal ganglion which was the largest. The connectives between all the ganglia were short especially in the early stages. In the third and fourth larval stages the connectives were often somewhat elongated in contrast to those in the first two stages. There was one pair of nerves from each ganglion that innervated the segment from which the ganglion arose. In the first stage larva there was already a fusion of embryonic abdominal ganglia eight to ten into one ganglion and a migration of the ganglia forward into the anterior segments. In the first stage the first abdominal ganglion was in the third thoracic segment which was also true of all other larval stages. The second abdominal and usually the third or part of the third were in the first abdominal segment. The second abdominal segment occasionally contained parts of the third ganglion and always the entire fourth and generally part or all of the fifth ganglion. The third segment contained the remainder of the fifth and ganglia six to eight in the last three larval stages but in the first larval stage the eighth or terminal ganglion was found in the fourth abdominal segment. The terminal ganglion, was the result of fusion of several ganglia and as such was the only abdominal ganglion with more than one pair of nerves. There were two pair of nerves on the terminal ganglion; an anterior pair which were comparatively small innervated the eighth abdominal segment, and a larger posterior pair which innervated the terminal segments. In some well stained whole mounts it was possible to make out the dual nature of this large pair. This indicated that remnants of the eighth, nineth, and tenth ganglia were still present and had fused instead of disappearing.

The shield-shaped frontal ganglion of the stomodeal nervous system lay in the mid-line dorsal to the esophageus, and anterio-ventral to the supra-esophageal ganglion. It was joined to the central nervous system by the frontal ganglionic connectives from the tritocerebrum. There were two nerves which arose from the ganglion, the frontal nerve (FrNv) (figs. 1-5,7) which extended forward to the clypeus and the recurrent nerve (RNv) (figs. 1,3,5) which extended posteriorly to the occipital ganglion (OcGng) (figs. 1,3,5,7). The occipital ganglion was located on the dorsum of the esophageus just at the posterior margin of the supra-esophageal ganglion. It sent two nerves posteriorly, one on each side of the digestive tract.

It was in the transition from the larval stage to the pupa that the most marked changes occurred in the morphology of the nervous system. The protocerebrum (1Br) (fig. 9) had increased in diameter and in length so that the supra-esophageal ganglion (1Br, 2Br, & 3Br) (fig. 9) was a great deal wider than in the larva. The number of fasicles or optic nerves (OpNv) (fig. 9) had increased from three to many which entered the compound eye.

An interesting feature of the supra-esophageal ganglia of the pupa was the presence, on the lateral posterio-dorsal aspect, of three black spots (PiSp) (fig. 9) which gave a gross and microscope appearance of an area of degeneration.

The most lateral lobe of the brain was the optic lobe and contained the optic glomeruli and the chiasmata between the glomeruli. The antennal nerves originated near the base of the optic lobes on the deutocerebrum. Medial to the antennal nerves the labral nerves and frontal ganglionic connectives began from a common trunk (AntNv, 2Br, LbNv, FrCon) (fig. 9). The labral extended anteriorly much the same as it did in the larva. The frontal connective, however, was not nearly so long and arched but turned more directly medially to the frontal ganglion than it did in the larval stage. Janet ('05), according to Thompson ('13), placed the frontal connective in the protocerebrum because it originated more anteriorly. Janet also believed that the tritocerebrum was represented by the nerve to the interior dilator muscle of the pharynx. The frontal and labral nerves did arise close to the protocerebrum but in the early larva all of the nerves from the brain were close to each other.

The supra-esophageal was joined to the sub-esophageal by the circumesophageal connectives (CoeCon) (fig. 9) which circled the esophageus. The tritocerebral commissure (3Com) (fig. 9) in the pupa was located very close to the sub-esophageal ganglion, leaving in many cases only a small opening between itself and the ganglion. There was some dispute as to whether it was actually a commissure between the tritocerebrum or i~~f~~t if was a fusion of two lateral nerves which arose from the connective. This idea was prompted by the observation that the distance from the tritocerebrum to the commissure in the adult was fairly great. Wheeler ('26), however, stated that in the formation of the brain in ants only the protocerebrum was pre-oral at first, and the rest of the brain was post-oral. The deutocerebrum and tritocerebrum moved anteriorly prior to hatching.

The mandibular nerves originated near the base of the subesophageal connectives and in some cases were parallel to the connectives for a short distance. In such instances it was possible by saggital sections to see the line of fusion between the nerve and the connective. The maxillary nerves had not changed position markedly from the larva and were posterio-lateral to the mandibular nerves. The labial nerves were still about midway of the ganglion and on the ventro-lateral margins of the ganglion(MdNv, MxNv, and LbNv) (fig. 9).

The thoracic ganglia of the pupa were more varied in size and shape than those of the larva. The first thoracic ganglion was located in the anterior portion of the first thoracic segment and the smallest of the thoracic ganglia. The major nerve from this ganglion innervated the leg muscles while a smaller one extended dorsally and anteriorly to the dorsal muscles of the first thoracic segment. The second thoracic ganglion was slightly larger and a large nerve extended from the posterior portion of the ganglion to the legs of the second thoracic segment. A nerve from the anterior region of the ganglion innervated the elytra muscles (TWNv2) (fig. 9). The third thoracic ganglion, like the first and second, was located in the anterior portion of the segment which it innervated. Two pairs of nerves from the anterior region of the ganglia innervated the wing muscles, and a large nerve from the posterior end of the ganglion innervated the third pair of legs. Just posterior to this nerve were two pair of smaller nerves which represented the first and second abdominal ganglia fused with the third thoracic ganglia. Near the third thoracic ganglion but not fused with it, or with the other abdominal ganglia, was the third abdominal ganglion. It still innervated the third abdominal segment even though it was now located in the third thoracic segment. Immediately posterior to this ganglion was a mass of nerve tissue which may be called a "ganglionic mass" (Cody & Gray '38). This mass represented a fusion of segments 4-10 of the abdominal ganglia. The mass as described by Cody & Gray included all of the abdominal ganglia.

The stomodeal nervous system in the pupa was very similar to that found in the larva. The frontal ganglion (FrGng) (fig. 9) remained shield-shaped and sent the frontal nerve (FrNv) (fig. 9) anteriorly and a recurrent nerve (RNv) (fig. 9) posteriorly to the occipital ganglion (OcGng) (fig. 9), which again sent a nerve posteriorly along each side of the intestinal tract. From the posterior aspect of the brain a very minute, posterio-lateral nerve joined the Corpus Alatum (CA) (fig. 10,12) to the supra-esophageal ganglion. These two bodies of glandular appearance, which lie bilaterally on each side of the digestive tract, may have been present in the larva but were not observed.

There were no significant changes in the nervous system of the adult over that of the late pupa. This may be seen by comparing the pupa (figs. 9, 10) with the adult (figs. 11, 12). The description of the pupa can also be applied to the adult.

There was found in the early pupa or the late larva a transition stage in the transformation of the larval nervous system in the adult system. This stage had characteristics of both the larva and the adult. The larval characteristic was the retention of the eight abdominal ganglia which had not yet fused. The adult characteristic was the broadening of the optic lobes into the adult form. It seemed, therefore, that the changes occurred first in the head region and progressed posteriorly in the transformation from the larva to the adult.

DISCUSSION

A review of the literature on the nervous systems of the larvae of Passalus cornutus (Cody & Gray '38) and Orycetes nasicornis (Michels '80) of the family Scarabaeidae revealed that there was little variation from that found in Epilachna corrupta, a Coccinellid. O. nasicornis varied from both P. cornutus and E. corrupta in the location of the sub-esophageal in the first thoracic segment instead of in the head and in the fusion of the first abdominal ganglion with the third thoracic ganglion (leaving seven separated abdominal ganglia).

The pigment spots which were associated with the supra-esophageal ganglia of the pupa and adult of E. corrupta are comparable to the ones mentioned by Newport ('32 & '34) as being present in the pupa of Sphinx lingustri L. He thought that they might be pigment spots which became part of the choroid. In another genus Papilo he showed five similar spots in the pupa and located in a corresponding area. There were six optic fasicles in the larva of this species. It was not likely that these spots became part of the choriod in E. corrupta since they were present in the same area on the supra-esophageal ganglion of the adult form (PiSp) (fig. 11). It was observed that this pigment in practically every case, was organized into three distinct masses. It will be recalled that in the larva there were three pigmented spots or ocelli joined to the brain by the optic nerve. These spots in the pupa and adult must represent pigment which remained from the larval ocelli and was not absorbed or excreted during metamorphosis.

A comparison of *E. corrupta* adult with three adult Scarabeidae (*O. nasicornis*, *P. cornutus*, and *Phyllophaga ephlida* (Moore, in manuscript) showed more differences than occurred in the larva. *P. cornutus* was not unusual except for a complete fusion of all abdominal ganglia into one unit. The adult of *O. nasicornis* differed from this only in the location of the sub-esophageal ganglion in the first thoracic segment instead of the head. *P. ephlida* presented the most variation and the most marked consolidation of nerve tissue with a fusion of all thoracic and abdominal ganglia into one mass. In *P. ephlida* as in *O. nasicornis* the sub-esophageal was located in the first thoracic segment. In *E. corrupta* the first two abdominal ganglia were fused with the third thoracic ganglion, the third abdominal ganglion remained separate and the fourth to eighth larval ganglia fused into one mass in the adult.

If reference is made to Table 1 certain conclusions may be drawn about the cephalization of the insect nervous system. The supra-esophageal, with the exception of Diptera, is well stabilized both in regard to location and fusion with other ganglia. The sub-esophageal, with two exceptions, is subject to few variations. In the thorax there is an increase in occurrence of fusion between ganglia. The cephalization of abdominal ganglia presents an interesting and variable pattern. In general the terminal three to four embryonic ganglia fuse into one ganglion by the time the larval stage is reached. In some larva there may be a fusion of all the ventral ganglia into one mass (Cody & Gray '38). In the adults there may be a further reduction in number of abdominal ganglia with the fusion of one, two, or three ganglia to the third thoracic and in some species there may be a fusion of all abdominal ganglia into one mass,

Insect	Brain	Sub-esophageal	Thorax	Abdomen	Remarks
Collembola	X	X	2-3	Fused	Abdominal ganglia fused to T-3
Thysanura	X	X	3	8	Terminal Gng.large
Ephemeroptera	X	X	3	7	First abdominal fused with T-3
Odonata	X	X	3	6	First abdominal fused with T-3
Orthoptera	X	X	3	4-6	1, 2, 3, ganglia fused with T-3
Dermaptera	X	X	3	6	First abdominal fused with T-3
Plecoptera	X	X	3	5	
Isoptera	X	X	3	6	First abdominal fused with T-3
Zoraptera	X	X	3	2-3	Abdominal ganglia fused with T-3
Embioptera	X	X	3	7	
Corrodentia	X	X	3	?	
Mallophaga	X	X	3	1	One mass fused with T-3
Thysanoptera	X	Fused with T-1	2-3	Fused	Not fused with T-3
Anoplura	X	X	Closely joined	Fused	
Hemiptera	X	X	1	Fused	
Neuroptera	X	X	3	9	
Mecoptera	X	X	3	6	
Hymenoptera	X	X	2-3	2-7	
Coleoptera	X	May be in Segment T-1	3	1-2	Thoracic Gng.may be fused and A.joined to them
Trichoptera	X	X	3	7	
Lepidoptera	X	X	2-3	4-5	
Diptera	X	X	3	1-8	All ganglia may be fused into one unit
Siphonaptera	X	X	3	7	

TABLE 1

consolidation of thoracic and abdominal, and in Diptera a cephalization of all the ventral ganglia.

It has been said, that, "Usually in insects, concentration (of nervous tissue) progresses with the development of the insect, both ontogenetically and phylogenetically." (Cody & Gray '38). From the above discussion and Table 1 we may say that there is a slight trend toward cephalization in the more advanced orders of insects, however, this cephalization of the nervous system does not parallel the advancement or specialization of the insect. It would seem more accurate to say that variability in the form of the nervous system increases with the phylogenetic advancement of the insect, because examples of cephalization found in the advanced insects may also be found in the more primitive types.

SUMMARY

1. The literature available on the morphology of the nervous system in insects is reviewed.

2. A description of the nervous system of the larva, pupa, and adult of *E. corrupta* is given.

3. An explanation of pigmented spots on the optic lobes of the pupa and adult of *E. corrupta* is given.

4. The significant differences in the nervous system of the larvae of *E. corrupta*, *P. cornutus*, and *O. nasicornis* are discussed. *P. ephlida* in addition to those mentioned above are the adults which are compared.

5. From the literature available it is not possible to say that there is any dominent tendency toward cephalization of the nervous system in insects with phylogenetic advancement. It is rather an increase in the variability of the morphology of the nervous system.

Appendix I

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Appendix II

KEY TO ABBREVIATIONS*

A	Abdominal ganglion
Ant Nv	Antennal Nerve
1Br.	Protocerebrum
2Br.	Deutocerebrum
3Br.	Tritocerebrum
CA	Corpus Allatum
CoeCon.	Circum-esophageal connective
3 Com	Tritocerebral commissure
FrCon	Frontal ganglion
FrNv	Frontal nerve
LbNv	Labial nerve
LmNv	Labral nerve
MdNv	Mandibular nerve
MxNv	Maxillary nerve
OcGng	Occipital ganglion
OpNv	Optic Nerve
PiSp	Pigment spot
RNv	Recurrent nerve
SoeGng.	Sub-esophageal ganglion
T	Thoracic ganglion
TLNv	Nerve to Thoracic leg
TWNv	Nerve to wings

*The above key follows Snodgrass ('35) where terms are applicable.

Appendix III

Plate I-The Nervous System of the first and second stage larvae

Explanation of figures 1-4

Figure 1 - Ventral view of a first stage larva.

Figure 2 - Lateral view of a first stage larva.

Figure 3 - Ventral view of a second stage larva.

Figure 4 - Lateral view of a second stage larva.

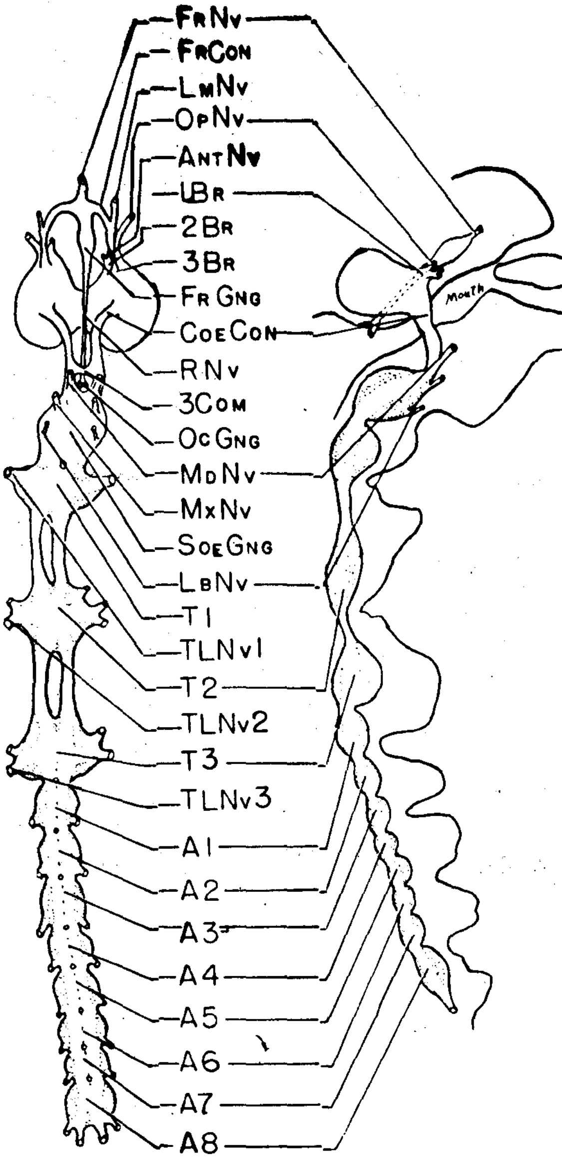


FIG. 1 FIG. 2

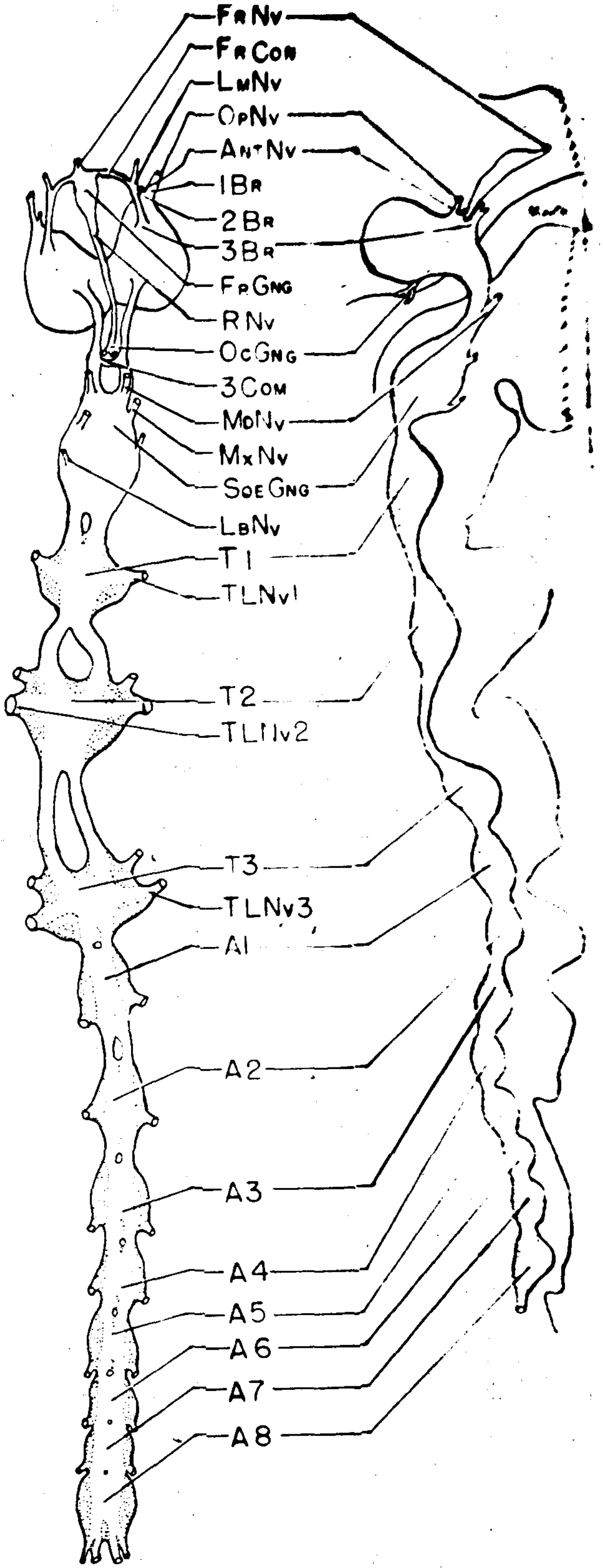


FIG. 3 FIG. 4

Plate II - The Nervous System of the third stage larva

Explanation of figures 5-6

Figure 5 . . . Ventral view

Figure 6 . . . Lateral view

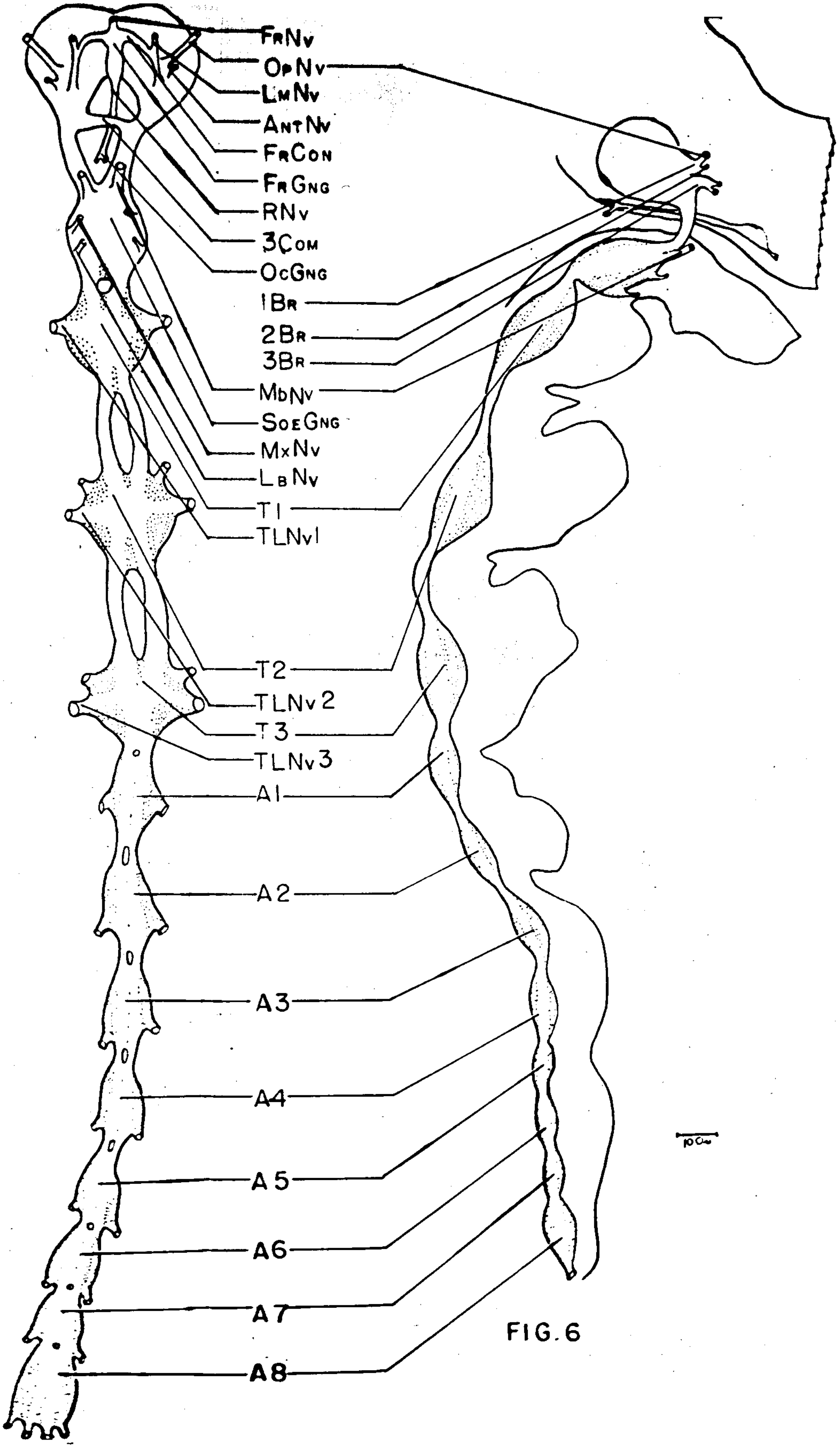

FrNv
OpNv
LmNv
AntNv
FrCon
FrGng
RNv
3Com
OcGng
1Br
2Br
3Br
MbNv
SoeGng
MxNv
LbNv
T1
TLNv1
T2
TLNv2
T3
TLNv3
A1
A2
A3
A4
A5
A6
A7
A8
10Cm

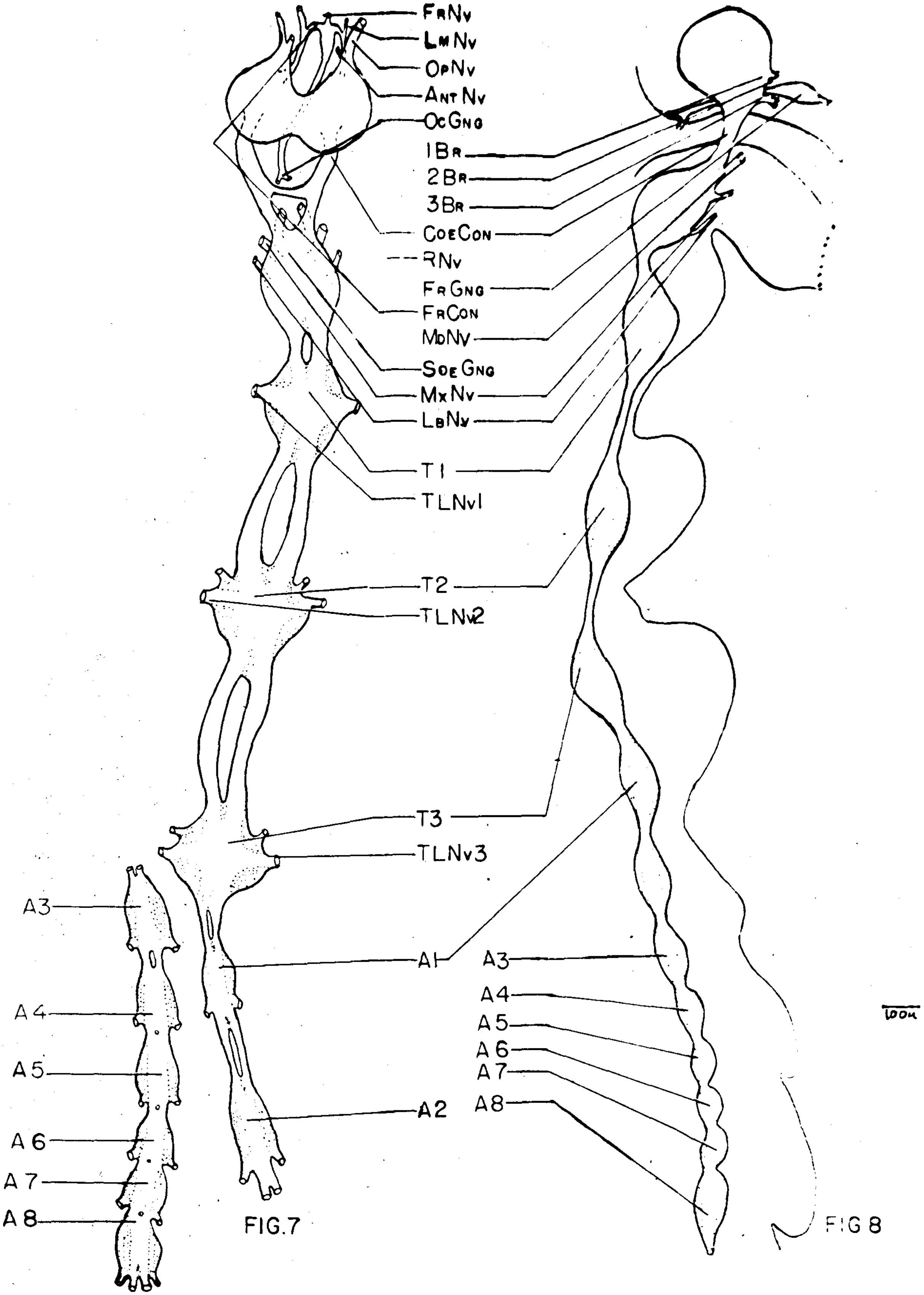
FIG.5

FIG.6

Plate III - The Nervous System of the fourth stage larva

Explanation of figures 7-8

Figure 7	Dorsal view
Figure 8	Lateral view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LmNv
OpNv
AntNv
OcGng
1Br
2Br
3Br
CoeCon
RNv
FrGng
FrCon
MdNv
SoeGng
MxNv
LbNv
T1
TLNv1
T2
TLNv2
T3
TLNv3
A1
A2
A3
A4
A5
A6
A7
A8
A3
A4
A5
A6
A7
A8
100μ

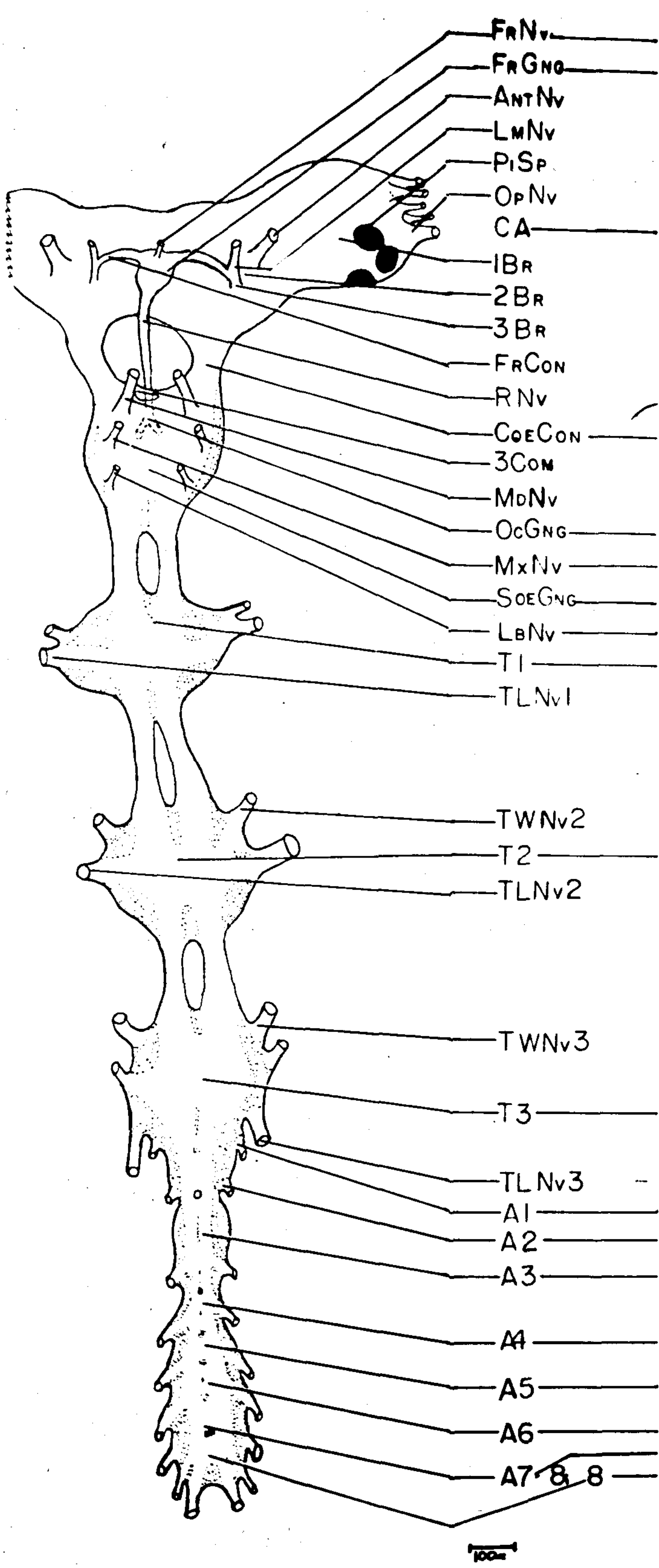
FIG.7

FIG 8

Plate IV - The Nervous System of the Pupa

Explanation of figures 9-10

Figure 9	Ventral view
Figure 10	Lateral view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FrGng
AntNv
LmNv
PiSp
OpNv
CA
1Br
2Br
3Br
FrCon
RNv
CoeCon
3Com
MdNv
OcGng
MxNv
SoeGng
LbNv
T1
TLNv1
TWNv2
T2
TLNv2
TWNv3
T3
TLNv3
A1
A2
A3
A4
A5
A6
A7·8
8
100µ

FIG. 9

FIG. 10

Plate V - The Nervous System of the Adult

Explanation of figures 11-12

Figure 11	Ventral view.
Figure 12	Lateral view.

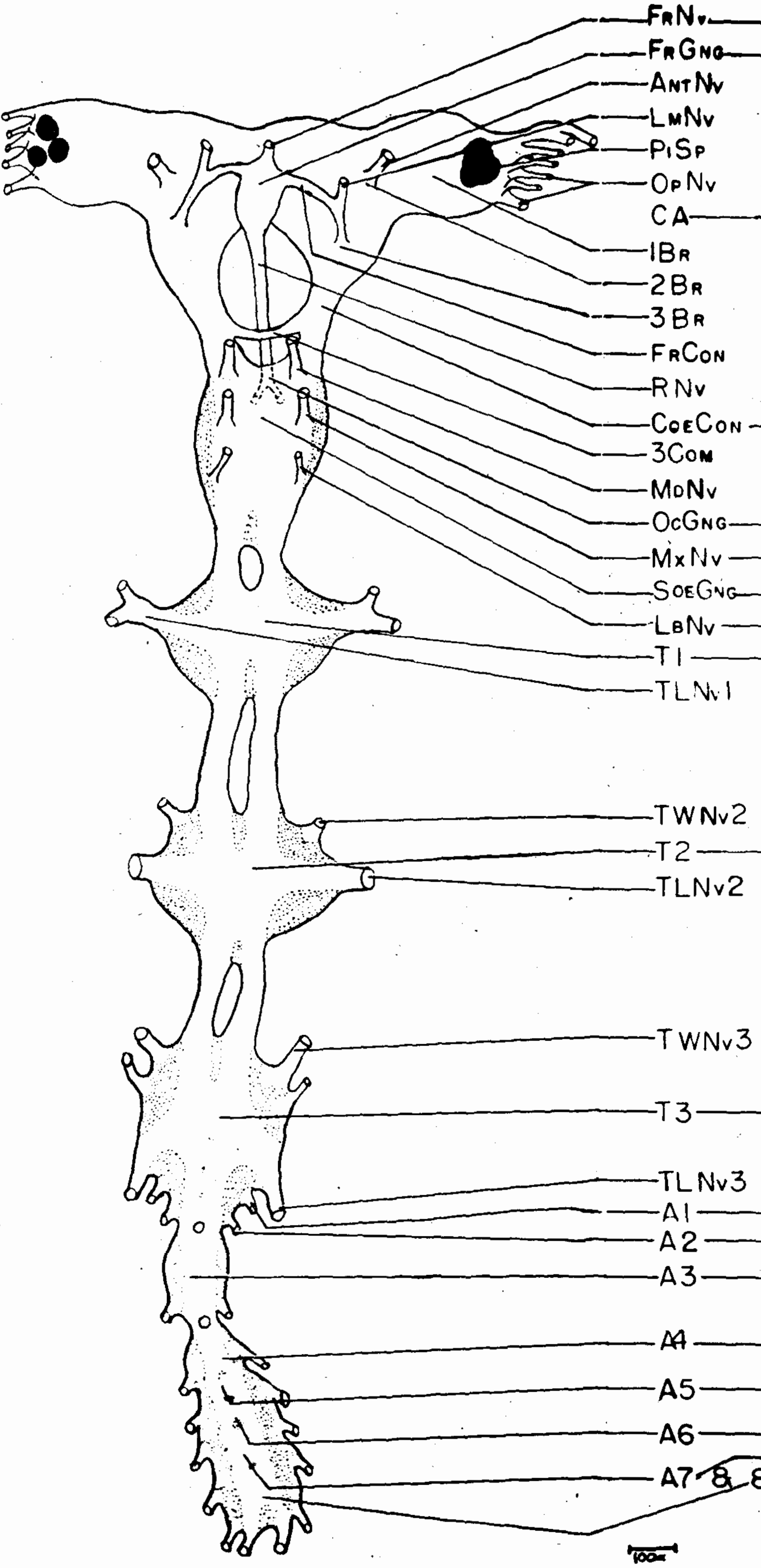
FrNv
FrGng
AntNv
LmNv
PiSp
OpNv
CA
1Br
2Br
3Br
FrCon
RNv
CoeCon
3Com
MdNv
OcGng
MxNv
SoeGng
LbNv
T1
TLNv1
TWNv2
T2
TLNv2
TWNv3
T3
TLNv3
A1
A2
A3
A4
A5
A6
A7
8
8
100μ

FIG. 11

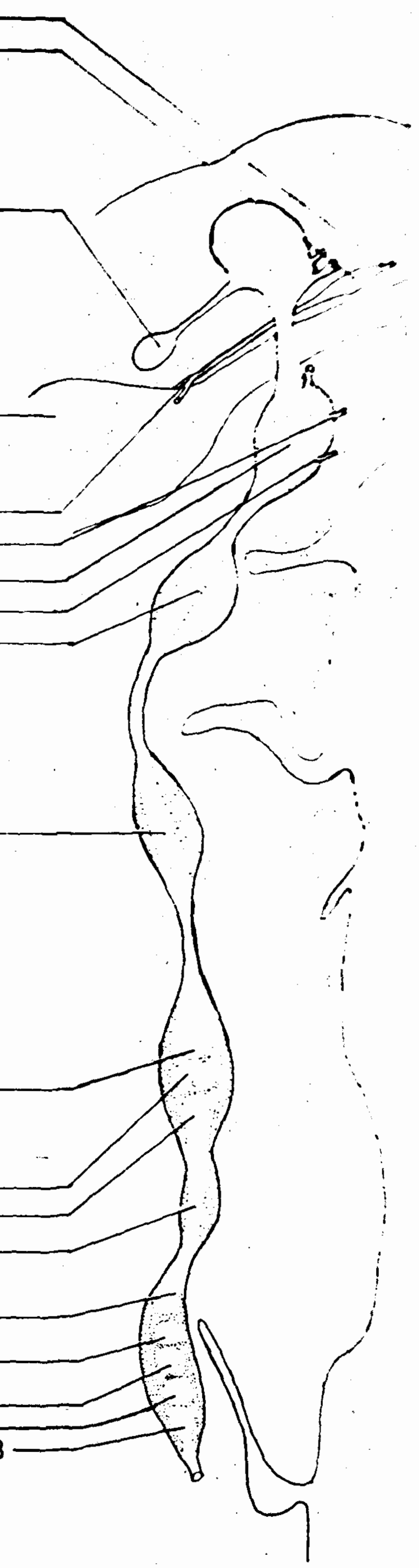

FIG. 12

Appendix IV

VITA

Raymond F. Moore, Jr., was born December 17, 1927, at Fishersville, Virginia. He was educated in the public schools of Augusta County, Virginia, and was graduated from New Hope High School, New Hope, Virginia in June 1945. He served two years in the U. S. Army after which he entered the University of Dubuque, Dubuque, Iowa, in 1948 and transferred to Bridgewater College, Bridgewater, Virginia, in September, 1949. He was graduated from Bridgewater in June, 1951, with the B. A. degree. In June, 1951, he was married to Verna Hess Caricofe. He attended the Medical College of Virginia from September, 1951, to June,1954. In September, 1954, he entered the Graduate School of the University of Richmond as a candidate for the degree of Master of Arts with major emphasis on Biology.