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THE STRUCTURE OF THE CENTRAL NERVOUS SYSTEM OF CORYDALIS LARVA.

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Concerning the insects, many extensive works have been published upon the nervous system from early times down to quite recently. The work of Dujardin, '50, may be said to be a starting point. Numerous papers by Villanes from '87 to '93 give general accounts of the structure, but nothing very definite as to the distribution of individual nerve termination and origin within the ganglia. The extensive work by Saint-Remy, '90, is also a somewhat fragmentary account of numerous forms of tracheate head ganglia. Other earlier papers dealing with cephalic ganglia in particular are those of Newton, '79, and Packard, '80, and in more recent times we have the valuable works of Kenyon, '96, and Haller, '04. In connection with the structure and relationships of abdominal ganglia, the investigations of Binet, '94, and Benedicenti, '95, should be mentioned; and for a summary of the form and structure of the insect nervous system, the general work of Berlese, '97, is invaluable.

Although there are numerous and extensive papers dealing with the structure of insects, very few give a very complete account of the whole nervous system of a single species and practically no single work treats of the larval centers in much detail, although numerous papers take up the development and some as Bauer, '04, consider the transformations of larval into the adult conditions.

The external anatomy and general distribution of ganglia and nerves of Corydalis have been studied by Krauss, '84, and by Hammar, '08. The relations of the trachea to the nervous system and their distribution within it by Hilton, '09. The

present paper is a continuation of the study of the nervous system in the larval form and, although not as complete as might be wished, it is at least a start in the direction of a clearer comprehension of the insect central nervous system, undertaken for the purpose of preparing for a study of the finer structure of the nerve cells, and for experiments upon their metabolism and function.

The methods employed were various. For obtaining the best idea of the general distribution of nerve cells and fibers, and the tracts of which they are parts, intra vitam methylene blue injections were used. Beautiful results were obtained at times, but it was only after hundreds of specimens were gone over that much was learned as to the organization of the ganglia. Sectioning methods with the usual fixers and stains gave fair results and the methods of Golgi and Cajal were tried, also those of Villanes and Kenyon. All of these gave good preparations except the Golgi method which I hope to try again at another time. There were difficulties in the way of fixing and staining because the ganglia are inclosed in chitin and because of the numerous tracheal vessels, and in the larger ones it was not possible to get perfect whole mounts. Sketches were made from the methylene blue preparations both before and after fixation and in the first stages of the work peripheral nerves were traced by means of gross dissections.

ABDOMINAL GANGLIA.

The abdominal ganglia, eight in number are quite uniform in appearance and general structure with the exception of the eighth or most caudal. The first abdominal is separated by only short connectives from the third thoracic, and the seventh is even closer to the eighth. The seven first abdominal ganglia have quite uniformly on each side, two large nerve trunks connected with them, a cephalic lateral and a ventral more caudal branch. The eighth ganglion has four pairs of branches leading into it from the caudal end of the animal.

Specimens were injected with methylene blue and nerves traced to the periphery and from here followed into the ganglia as nerve tracts as far as possible. In an earlier study on the nervous system of larval insects I found that in some cases some of the more cephalic branches connected with the ganglia were in large part if not totally sensory, that is arising from

bipolar nerve cells and nerve plexuses, from tactile hairs and from the surface of the hypodermis. In Corydalis at various times during several years I have tried to determine the motor and sensory parts of each peripheral trunk for the purpose of following them into the central nervous system. To some degree methylene blue stain is of a differential value in determining the nature of nerve trunks, for very often the first neurons to take the stain are sensory, while motor fibers and cells are often slower to turn blue. But this method is not absolutely sure, for there is great variability in the staining reactions of different individuals. The only sure way of telling whether a given branch is motor or sensory is by tracing the nerves to their endings in muscle fibers or from their origin in bipolar sense cells at the periphery. The tracing of a motor or a sensory nerve or tract is not possible in a large number of cases because the stain is incomplete or too dense, but occasional selectively stained preparations enable one to make positive if not complete statements in regard to nerve trunks; that is to say, one can determine surely from a specimen that a large number of branches of a certain nerve are all motor or all sensory, but it would be impossible to say with *perfect* assurance that the nerve was pure motor or pure sensory because some fine terminations might remain uncolored, especially in the case of a stain which was good for sensory terminations, for there would be a strong probability that some at least of the fine motor ends would not show.

The work of Hammar, '08, on the nervous system of Corydalis has been very helpful, and the general description of the nervous system given by him is so complete that I shall not need to spend time on the gross anatomy of the various ganglia, and in speaking of the several branches of the ganglia I shall follow his terminology.

There are three chief branches breaking from the *Lateral* trunk of each of the first seven abdominal ganglia, their method of branching from this trunk and from each other is somewhat variable, but these three main parts are easily recognized. Branch 2 is large and comes off quite near the base of the lateral trunk, runs caudally a short distance and then disappears between muscle fibers in a ventral direction. I could not determine it to be anything but a motor branch although some of the fibers from it are among the first to stain and some of them pass not into the ganglion connected with the nerve

trunk, but run directly up to the next ganglion by the way of the connectives, in a tract which from its other connections in other species and in this form, and from its staining reactions, I took to be sensory. Branch 3 is long, it runs up to the dorsal side of the animal and is without doubt mixed motor and sensory, containing fibers which supply dorsal muscles and fibers which come from the hypodermis. Branch 4 runs into the lateral appendage and seems to be sensory, for the most part at least. Besides these, there are two minute branches, 1 and 5, running out to the trachea, according to Hammar, '08.

The ventral trunk runs caudally and ventrally, branches 1, 2 and 3 run to more and more caudal portions of the ventral side of the animal and seem to be entirely sensory, branch 3 runs to some extent also into the lateral appendage, while branch 4 runs into the tracheal gill and was the only one traced into it. So this whole ventral trunk seems to be for the most part sensory.

The eighth abdominal ganglion seems to be made up of at least two centers fused, there are four main trunks entering it on each side below and all of these so far as could be determined are both motor and sensory. Trunk (a) is most lateral, (b) a ventral trunk corresponding to the ventral one of other abdominal ganglia, (d) a more median one supplying lower dorsal and ventral portions of the body and (c) median, with a large branch which runs back up the intestine.

NERVE CELLS.

(Fig. 5.)

The nerve cells of the periphery have already been figured in an earlier article, Hilton '02. The functional cells of the ganglia both thoracic and abdominal appear to be much of the same type in methylene blue preparations, uni- or bipolar nerve cells, one of the processes or branches of which may run out quite a long distance before they break up into a number of terminations, the other portion usually breaks up into branches near the cell body. Indications of multipolar cells were seen in some specimens but with these usually all of the processes but one were very small and hard to trace very far. In addition to the functional neurones of both large and small size, there were in all of the ganglia, numerous neuroblasts, or smaller cells with slight protoplasm about the nucleus, and neuroglia networks.

NERVE TRACTS IN ABDOMINAL GANGLIA.

(Figs. 1 and 2.)

By means of methylene blue preparations it was possible in some more deeply stained specimens to trace the main tracts of fibers within the ganglia and within the connectives and in lighter stained specimens the distribution of special tracts and even individual fibers. At times the cells stained as well as the fibers at other times only fibers were colored.

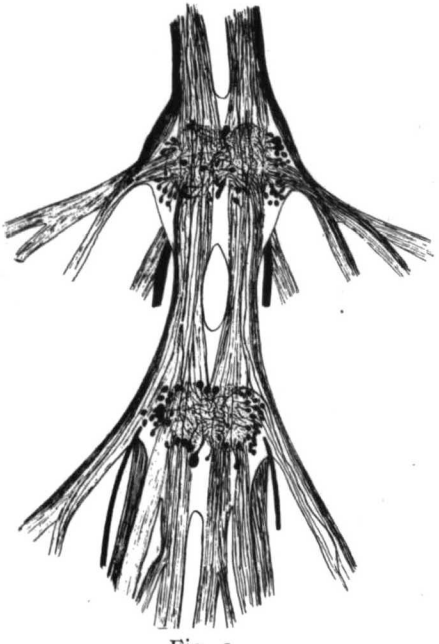

Fig. 1.

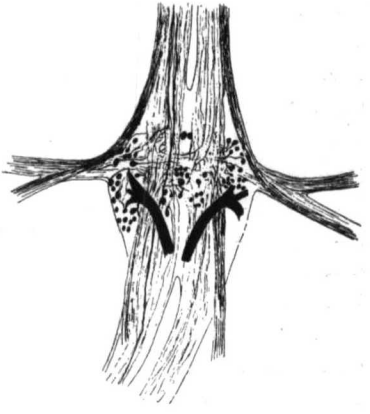

Fig. 2.

FIG. 1. Figure of the 7th and 8th abdominal ganglia from methylene blue preparation. Dorsal side. A few nerve cells are shown in black. The chief nerve trunks show with their fibers. The central "Punktsubstanz" of the ganglia dotted. Some of the larger tracheal tubes shown as thick solid black lines.
The caudal end is down in this and the following figures. x30.

FIG. 2. Sixth abdominal ganglion from ventral side. Methylene blue. x30.

Stained or unstained, the central region of each ganglion is more opaque or darker, due to the nerve fibers crossing and terminating in this region. This forms on each side a central body made up of two oval masses more or less fused into one at the middle line, the "Punktsubstanz" of some authors. The

nerve fibers of the connectives when stained in a mass form deep lines apparently running straight through the center of the ganglia, these longitudinal bundles of nerve fibers seem to be a little broader before entering and after leaving the central mass. The nerve trunks in deeply stained specimens send masses of fibers into the ganglia and in the case of most of the fibers, the region where they seem to terminate is in the central part of each ganglion. This is true of all the ventral fibers and of most of those from the lateral trunk, but a few of the latter, and some fibers from the second branch of the lateral, run up into the edge of the ganglion only, and then straight up the connective to the next ganglion above. In the case of the eighth adbominal the four nerve trunks enter the fibrous central mass from below, those most medially placed seem to be continued up through to the connectives and to be largely continuous with them in deeply stained specimens, while the more lateral trunks are lost sight of as they enter the central portion of the ganglion, although *some* of the fibers from the more laterally placed nerve trunks pass through the edge of the ganglion without communication with its cells and pass up the outer side of the connectives on either side to the next ganglion above. There are then two masses of fibers entering each center but the last, those of the connectives and those of the nerve trunks. I will first take up those of the connectives.

Beginning with the seventh abdominal ganglion great masses of fibers enter, and it is possible to distinguish; (a) Fibers which run straight through without terminating. There seem to be great numbers of these, but this is due *in part* to the fact that when fibers *do* terminate in a ganglion they end at various levels. These fibers can however individually in a number of cases be traced through a ganglion without endings of any sort within it, just how far some of these may run without termination is a question, but there was no difficulty in tracing them through three ganglia and there is no reason to doubt that they may be longer than this. Those most easily followed were usually of larger size than the rest. (b) Fibers from below, terminating within the ganglion. Of these there are several sorts: (1) Those ending in the lower part of the "punktsubstanz" on the same side. (2) Those ending on the same side above. (3) Those crossing over towards the opposite side from below. (4) Those crossing over to the opposite side above.

In those entering from below some run straight in and end in the caudal region of the central fibrous mass, while in many specimens fibers from the outer side of the connectives sweep sharply in towards the center of the lower part of the ganglion to end near the middle line, either on the same side or just over it. (c) Fibers from above. In general there are similar bundles of fibers to those traced from below: (1) Those ending in the lower part of the ganglion on the same side. (2) Those ending on the same side but in the cephalic portion of the ganglion. (3) Those crossing to end in the lower part. (4) Those crossing to end in the upper part.

In the case of fibers ending in the ganglion from the cephalic direction, none were seen forming such a dense sweep into each center from the sides of the connectives, although there were a few fine ones of this sort. Most of the fibers leave the "punktsubstanz" to run in the connectives without great deviation from a straight course. (d) Fibers passing into the connectives from cells within the ganglion. There may be distinguished in many of the preparations cells with their fibers well stained, the more central of these may be more clearly seen in some cases. Some of the larger more central cells seem to be merely for association within the ganglion, with all of their processes ending within it. Others send one main process up one connective and another down into one of the other great masses of fibers. Other cells of medium or small size, located chiefly at the sides of the ganglion send one long process into one of the nerve trunks while the other shorter process may run for a short distance in the connective trunk or be lost in the central mass of the ganglion.

THE FIBERS OF NERVE TRUNKS.

These have already been spoken of to some degree. Most fibers of both cephalic and ventral nerves seem to enter the central part of the ganglion and are lost track of in the "Punktsubstanz," but both the lateral and ventral trunk-fibers are continued into the connectives in the cephalic direction at least, and possibly to some extent in the caudal, although this was not determined. In the case of the lateral trunks of all the abdominal ganglia, there is a possible sensory tract entering the cephalic edge of the nerve center without coming to the central "punktsubstanz" or having any communication with

nerve fibers, running along the outer side of the connective and for the most part ending in the basal portion of the ganglion next above, near or across the middle line. A similar tract to this has been described coming from the two most lateral trunks in the last ganglion.

These fibers which enter from cephalic lateral trunks seem to stain among the first and in the case of some other insects were found to come from bipolar sensory cells at the periphery, and I still think that they are to some extent sensory, but these tracts which have no communication with the cells of the ganglia with which they are connected are not *all* of the sensory fibers of each nerve center, for the ventral branches have many sensory fibers and these do not follow exactly the same path, and in the case of the first seven abdominal ganglia many of the fibers could be traced from the branch 2, which so far as could be determined was a decidedly motor trunk.

Fibers other than those coming from cells on the opposite side to run into the branches as motor axones, are directly supplied by cells on the same side, long branches from certain cells run into the various motor trunks while the other terminations are in the "punktsubstanz."

Fibers from the periphery or from sensory cells enter the ganglion from both main trunks and are of the following groups: (a) Those ending within the ganglion to which the trunks are connected, the exact termination of these I could not make out, but some at least ended near the central part of the ganglion, although very often arborizations of the terminations could be traced both on the same side and on the opposite side. Fibers entering straight from below in the last abdominal broke up into branches near the middle line with arborizations in the central margin of the ganglion.

(b) Those passing from one ganglion to the next without sending branches to the center to which the nerve trunks are connected, some of these fibers may run past one or more ganglion, but the most of them form a definite tract from the periphery by way of lateral trunks, running on the outside of the connectives, and turning sharply in towards the middle line in the caudal portion of the central mass of fibers, to end here or a little higher up, or to cross over and end in the "punktsubstanz" of the opposite side not far from the middle line.

(c) Those passing from the periphery into the nerve trunks and having extensive arborizations in the ganglia to which they are connected and then passing on to another ganglion with arborizations in it. Only a few of such fibers were distinguished one in connection with the 8th ganglion was the clearest case. A nerve fiber from the periphery was easily traced into the 1st. lateral trunk, a branch from this fiber was given off in the cephalic and lateral region of the ganglion, this fiber could be traced into the "punktsubstanz" of the nerve center, some of its arborizations ending on the same side and one branch was traced to the cephalic region of the other side, while the main fibers passed up the connective and ended by arborizations in the "punktsubstanz" of the ganglion next above chiefly on the same side in the caudal region.

ABDOMINAL GANGLIA STUDIED IN SECTION.

Individual cells and fibers were not so easily traced by this method, but general masses of fibers and the location of cell groups were determined.

All of the ganglia, connectives and nerve trunks are inclosed in a chitinous envelope which in many cases is very close to the nervous tissue but usually separated by neuroglia cells. This envelope is especially thick about the connectives just before and just after they enter a ganglion, it appears as a uniform mass in section with large and smaller openings where trachea penetrate it.

In places under the chitin of the ganglia, especially on the dorsal side, there are large spaces with little or nothing in them but delicate neuroglia networks. The trachea radiating in the chitin covering the connectives and ganglia have already been referred to; as stated in a previous paper large branches and fine tracheoles run to the nervous system and are distributed to all centers and their branches. These are superficial or run in the chitinous sheath, and the deep, supplied in part by the superficial twigs but chiefly by larger special branches and enter the ganglion and connectives. In these connectives it is easy to see numerous openings, large and minute between the masses of nerve fibers, and in cross section the air tubes are shown to be fully as numerous as one would expect from a study of surface views where all the trachea were made to show. Tracheal tubes within the ganglia are particularly noticeable

in the centers of bundles of fibers and most easily seen in these traced from the connectives. The exact place and method of termination was not determined. Injections of fluids into the ganglia by way of trachea failed to penetrate any of the finer branches.

All of the abdominal ganglia seem to be of practically the same type, but individual variations occur.

In all of the nerve centers the cells are grouped for the most part on ventral and lateral portions of the ganglion and towards the caudal end, a few cells occur on the dorsal side especially near the middle line and these are often quite large.

Description of 4th abdominal ganglion traced by sections beginning at the caudal end:

The connectives entering from the ventral side are easily followed as distinct longitudinal masses of fibers well up into the ganglion, these connectives as well as others in other parts of the nervous system are composed of numerous closely packed longitudinal fibers, scattered between these are the openings of trachea, when the ganglion is reached the chitin for each of the connectives becomes fused into one mass and farther in the central portion of chitin between them disappears and the two bundles of fibers are more or less crowded against each other. Farther up into the ganglion the fiber bundles do not occupy all of the area under the chitin because large spaces on all sides occur and then soon cells in a single layer are found close to the wall of the ventral side, and then on the dorsal side a very large cell is found wedged in between the two bundles of fibers. Some of the cells of the ventral side may be seen at this level sending fibers into the two longitudinal bundles. The single layer of cells on the ventral side becomes a double row of medium and small, and the large cell of the dorsal side gives way to a group of small ones and there comes to be on the ventral side two groups of fibers running more transversely, probably made up in part from fibers connected with the cells appearing on the ventral side.

Farther up these ventral nerve cells extend out laterally so that numbers of them might be seen from the dorsal side. No cells are left for a distance on the mid-ventral line, and they disappear from the mid-dorsal line also to some extent, but before they are gone fibers can be traced about the connective bundles and to the cell region of the ventral side. At this

level there are nerve fibers seen between the cells on the ventro-lateral margins of the ganglion and fibers connected with these regions of the nerve center join the bundle from the cells on the dorsal side, on the ventral median side of the ganglion, while a third runs in from these cells into the central part of the longitudinal fibers. We have then at this level three transverse bundles of fibers crossing from the lateral cell groups, a dorsal, a ventral and median and a little farther along we have also a bundle of fibers running across the section but from the dorsal to the ventral side and uniting to some degree with the three right and left commissures. Other little branches from these main ones and other tracts from the lateral cell groups also invade the longitudinal bands from the connectives.

A little above this level again on the ventral side a single layer of cells appears in the middle line and no cells are seen on the dorsal side except laterally.

A little above this, the large ventral trachea enter passing through the cell layer and breaking up into numerous branches. The central fibrous mass of the ganglion is largely made up of longitudinal strands in all levels so far and besides the commissures mentioned there are usually a number of fibers crossing irregularly both dorso-ventrally, laterally and obliquely especially at about this last level. None of them are large and the great mass of fibers remains longitudinal. It is at about this level that the ventral nerve trunks come off from the lateral and ventral sides of the ganglion from the central part of the latero-ventral cell mass, just before the tracheal trunks are reached. Fibers from this trunk may mingle with the cells of this region and are also continued into the central mass of fibers of the ganglion.

Beyond this point the cells become thin again especially ventrally and also laterally, the central thickest part of the ganglion is now reached and the fibers form a rather large dense mass. Longitudinal ones may still be seen mixed in with numerous lateral and transverse strands all bound up together into a dense fibrous mass with no very marked special tracts or strands except for quite a well marked short broad median commissure of fibers connecting more intimately the two already well fused masses of each lateral half of "punktsubstanz."

Slightly beyond this, the cells have about disappeared, only a few remaining at the dorso-lateral edges of the ganglion.

Beyond this something of the central commissure remains, many of the other crossed fibers in the central part of the ganglion have disappeared. A bundle of fibers partly transverse and partly fused with the central longitudinal bands begins to be seen on either side of the ganglion ventrally, these are partly mixed with the main longitudinal tracts. They are endings of the bundles of the lateral nerves to be followed later and might be called lateral nerve tracts. At this level a few scattering cells on the ventral side and two small dorso-lateral groups, one on each side of the ganglion indicate about all of the cell masses seen lower down, while in the mid-dorsal line a new group of dorsal cells makes its appearance and sends fibers *through* the central part of the ganglion as a central tract which breaks up laterally and can be traced to various parts of the central fiber mass of the ganglion. For several sections these fibers become quite prominent and the central commissure seems to be lacking, then as this central tract disappears higher up, another and a better marked commissure comes to view running transversely through the center of the ganglion from side to side. At this level cells again come into view laterally. The ventral tracts of the lateral nerves become more prominent and there is a dorsal band of fibers close to the edge of the "punktsubstanz" on the dorsal side. This last is parallel with the median.

Slightly beyond this a few cells are seen on the ventral side laterally, two of the same commissures, a dorsal and a median may be seen, but the lateral cells have disappeared to give place to the entrance of the fibers of the large lateral nerves. These fibers for the most part run directly into the lateral nerve tract noted above when it was seen more caudally. Beyond this and beyond the entrance of the lateral nerve, a few cells are seen laterally, one or so in the mid-dorsal line, and the dorsal and median connectives disappear and only a few tangled fibers replace them, although for a few sections the great sweep of transverse fibers is continued from side to side, from the lateral nerve tract.

Above this no commissure or cross fiber of any sort connects the lateral halves of the ganglion and a small group of nerve cells comes to lie on the middle line and dorsal and ventral to it. At the line of separation of the lateral halves, the tracts of the lateral nerves can be distinguished as a dense mass on either

side of the longitudinal fibers which are continued out into the connectives.

Above this as the cells disappear and we come clearly into the region where there are only longitudinal tracts, these may be followed and they are indistinguishable from other fibers of the connectives. The reason why the lateral tracts could be told from the longitudinal for such a distance was because they seemed denser and stained more deeply. The fibers in the cephalic connectives have about the same arrangement as the caudal ones.

In other abdominal ganglia, ventral and lateral groups of nerve cells were more clearly seen contributing to the commissures and the central tracts. Some of the fibers of the lateral trunks end in the central portion of the ganglion, probably in cells.

The tract of the lateral trunk needs a word of additional comment. In preparations made by a method that removes the cells and all but the denser fibers so that little more than a skeleton of the fibrous framework is left, it is found that a transverse portion connecting the two sides of the ganglion is *much* denser than other parts of the fibrous mass and under the highest powers of the microscope, this seems to be very finely granular as well as fibrous and is continuous from side to side between the nerve trunks. This same fine granular substance with fibrils in it was traced up into the connectives a short distance, and as many fibers are seen to end in this region it may be due to a dense grouping of their endings that there is a deeper color at such a place. Similar substances to this only in more isolated portions is found in other parts of the ganglion and in other nerve centers. In specimens stained with ordinary hematoxylin there is no differentiation between this substance and the general fibrillar mass.

The eighth abdominal ganglion is similar to the others except that the connective fibers begin *within* the ganglion and there are more commissures developed. The first lateral branch can be easily traced out into the connective on the outside, fibers also deeper in go on up the connective, while still others enter the ganglion and are distributed to all parts of one side and probably also across to some extent, as there are numerous cross connections, by means of at least three of four well marked commissures, besides irregular fibers. Other

branches also send fibers to the central mass, some of these run straight through, while others seem to cross in commissures or end.

In general then, there are in each abdominal ganglion, cells on the ventral caudal region, on the lateral sides, and a few on the median dorsal side. These cells surround a central fibrous mass made up of strands running longitudinally through the ganglion from the connectives and best marked in the cephalic and caudal parts; fibers running across from side to side, these run in about three commissures, a dorsal, a ventral and a median and at various cephalic and caudal levels these commissures are interrupted. The lateral nerve trunks may be seen to contribute largely to the formation of the large ventral commissure. The other cross connections seem to be more exclusively from cells on the sides of the ganglia and from these cells also other cross or diagonal fibers may be followed.

The dorsal group of cells which seems to be to a large degree for association, sends fibers through the ganglion to the cells of the lateral and ventral groups, so that these fiber tracts may be found above or below the commissures penetrating to the opposite side, or part way through when the median commissure is present.

THORACIC GANGLIA.

Methylene blue method. (Fig. 3).

The three thoracic ganglia are quite a little larger than the abdominal and the branches come off differently.

There are on each side three main trunks the most cephalic of these has its most cephalic branches pure sensory, but No. 2 was not determined, also No. 1 of trunk B or the middle trunk seems sensory while other branches of the middle trunk are more or less mixed and the last which goes into the leg is also mixed. So then the more cephalic nerves are sensory while the rest seem to be mixed. The exact nature of the two parts of the last or leg branch was not determined, but there was no reason from the staining reactions to indicate that they were of greatly different composition.

In the thoracic region as in the abdominal, the main trunks easily took up the stain, but here greater difficulty was encountered in surface studies because of the larger opaque mass of the ganglion. Cells and fibers were however made out and found

to be in a general way similar to the conditions found more caudally. The main tracts of the connectives and of the nerve trunks enter the central portion of each center as in the abdominal region, but their distribution within was harder to make out. There were tracts entering the last thoracic ganglion from below, leaving it again as in the abdominal centers.

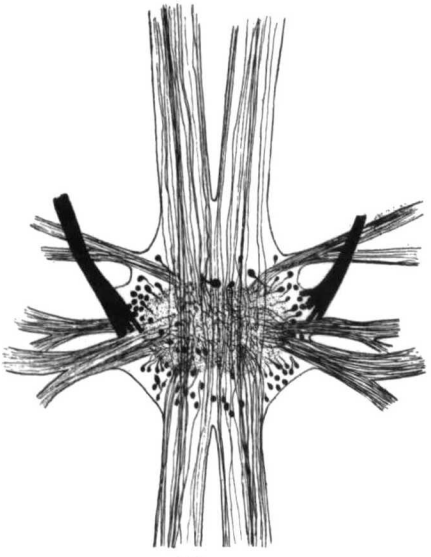

Fig. 3.

Fig. 4.

FIG. 3. Third thoracic ganglion from below. Methylene blue. x30.

FIG. 4. Connective branch leading off between the 2d and 3d thoracic ganglia, nerve fibers from above and below enter the nerve trunk from the connective. Also large and small nerve fibers shown. Methylene blue. x45.

Tracts from the first abdominal pass up the outside of the connective and cross over into the middle line, but from the third thoracic to the second, and from the connectives of the second to the first no such tract was clearly recognized. Fibers entering laterally both from motor and sensory nerves all pass in towards the central part of the ganglion. In other words there was no indication of a tract passing from cephalic branches into the edge of the ganglion to run without termination up the outside of the connective to the next center. But there was an indication of fibers passing through or into one ganglion from the one below it.

In the cephalic part of the thoracic ganglia fibers coming from above may some of them be traced as a fine tract ending

in the cephalic portion of the ganglion. Other than these differences, there were no essential ones between these nerve centers and those of the abdominal region.

In regard to the arrangement of cells as shown by methylene blue, it was found that the lower ventral and lateral regions had the greatest number, great masses of them, with many more cells than in the smaller ganglia. For the most part similar arrangements of individual fibers were seen. Nerve cells sending fibers directly into motor trunks, cells of medium or rather small size, were observed, but these were few in number. Most of the cells seen had their processes running into the "punktsubstanz" of the ganglion. Large and smaller association cells were found as in the lower regions and of various sorts such as already described for them, some at the surface of the ganglion other at the edges of the "punktsubstanz."

Between the third and second and the second and first thoracic ganglion, there are branches off from the connectives, a pair between each of these, and between the subesophageal and the first thoracic there are two pairs. The upper of these last were not so well stained in any of the preparations but all of the others were quite well colored and found to be motor. These branches when studied as to their composition did not differ much from each other and in each one, fibers could be seen descending to run out the nerve trunk from the ganglion next above and also from the ganglion below. These two tracts of fibers entering the lateral trunks were clear and distinct from each other for quite a distance into the nerve trunk. (Fig. 4).

THORACIC GANGLION IN SECTION.

(Plate XV, Figs. 1–4.)

The internal structure of the thoracic ganglia is much more complicated than the abdominal, due to the fact that the larger branches from the more numerous nerve cells are more intimately woven together, and it was practically impossible to follow commissures or tracts very far except in a very general way. However, a general description as detailed as seems necessary will be given of one of the thoracic ganglia, the first.

From above the connectives which enter as in the abdominal ganglia are in every way similar. Not many cells are seen scattered in the upper part of the ganglion, then two large

groups appear one on each side laterally and a small ventral group. (Fig. 1-3, Plate I). These masses at the sides of both large and small cells are at least three deep. The three groups a little farther along become united by a single row of cells which farther up becomes double layered and all the cell groups are not distinguishable in the single mass. There are also at about this level as a part of this mass a few cells in the mid-ventral line between the bundles of fibres of the connectives.

Farther up, the connective tracts are less clearly *all* longitudinal fibers and the lateral part of the nerve cell mass gives way for the entrance of the first or most cephalic of the three nerve trunks, the fibers of which pass into and mingle as transverse and dorso-ventral fibers in the connective tracts. The fibers of this nerve are very extensive and may be followed into the center of the ganglion, both dorsally and ventrally. Fibers from the ventral cells on either side of the ganglion enter the center of each lateral half from below and are there lost and partly pass into the nerve trunk. Fibers from the cells in the mid-ventral line, which cells form a wedge shaped mass at higher levels between the connective masses, run to the dorsal side of each of these masses of longitudinal fibers, and from here circle about to become associated with the fibers of the nerve trunks and with other more median strands on each side of the ganglion and with the strands described above which come from the ventral mass. Slightly beyond this part and nearer the center of the ganglion the two central masses of fibers or connective masses become fused together, the cells disappear and commissures, a dorsal, a ventral and a median, connect to some degree the sweeps of fibers already described. (Fig. 4, Plate XV, just above this level.)

Farther down, two commissures, a median and a dorsal are seen but numerous fibers cross the middle line at many levels and angles. Farther on but one commissure can be noted, a ventral, but many other fibers cross at different angles and the whole lateral portion of the ganglion is a dense system of complicated interlacing fibers having a dense meshwork. On the lateral part of each ventral half the fibers stain darker, probably due to more numerous fine branches in this region and on the dorsal median line a little wedge shaped group of cells makes its appearance, the only cells of this region. These send their fibers through the center of the ganglion to the ven-

tral side, while a central commissure crosses these to end in the tangled mass of fibers on either side of the ganglion. Farther along, these dorso-ventral bands a little one side of the middle line do not cross the now larger central commissure, but run in to it as do the other fibers from the ventral side, running from the more deeply stained ventral mass already spoken of.

Farther along and at the level of the next nerve, three commissures, a ventral, a dorsal and a median may be again recognized while the fibers of the middle nerve both end in the lateral portions of the fibrous mass and contribute to the three commissures. In this level only a few scattering nerve cells were seen. Beyond this a ventral, almost a lateral group appears again on each side and fibers from these form a little arch about the now smaller mass of darker staining fibers. On the mid-dorsal line fibers from this arch and others from these cells also ramify into all parts of the ventral portion of the ganglion. Along from this the dorsal part comes to be separated into two separate masses of longitudinal fibers of the connectives again. Farther along the arch becomes in its dorsal portion fused into a median commissure which soon disappears as the cleft between the connectives becomes deeper and reaches way down to the now small area of deeply staining substance which now forms a ventral commissure. The ventral cell group has become more lateral at this level and another large group has come in just dorsal to it, but still only on the side. In the mid-ventral line also, there has come in a small new group of cells.

The last nerve trunk comes to be associated with this commissure of deeply staining fibers on the ventral side and farther along fibers also pass freely into it from the lateral group of cells which has been spoken of as coming in more dorsally, this for a time remains distinct from the other more ventral groups.

Along farther these cell groups unite to form a large thick single lateral mass and from them more fibers run into the commissure of deeply staining fibers and "Punktsubstanz."

Soon after this the commissure breaks through as the two connective bundles separate, each with a little of the darkened mass which soon disappears as do the cells of the ganglion.

Although the above description is only a very general one, it will be seen that the ganglion is more complicated than the abdominal, but the general plan of arrangement and structure is as in the abdominal region. The nerve cells as in the abdomi-

nal ganglia are chiefly grouped in the caudal, cephalic and ventral regions and may be seen to take direct part in the formation of commissures as well as diagonal strands. While dorsal cells on the median line and ventral median cells, send fibers through the ganglion dorso-ventrally, as well as association fibers to different tracts and lateral groups. In both thoracic and abdominal ganglia dark staining masses made up of very minute fibers fused together are chiefly found on the ventral side and associated with a ventral commissure.

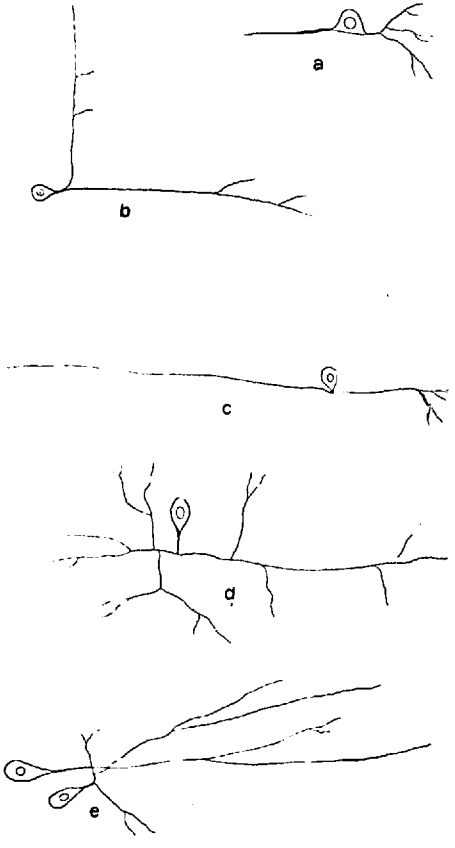

Fig. 5.

FIG. 5. Nerve cells from the central nervous system. (a) Motor nerve cell from the 3d thoracic ganglion. (b, c and d) Association cells from the same. (e) Cells from the brain. x100.

THE SUBESOPHAGEAL GANGLION.

(Figs. 6 and 7, Plate XVI, Fig. 5.)

This ganglion is larger than the others described, and is less flattened and less easy to study from the surface. The branches have already been traced quite well to the periphery and I will only mention them briefly.

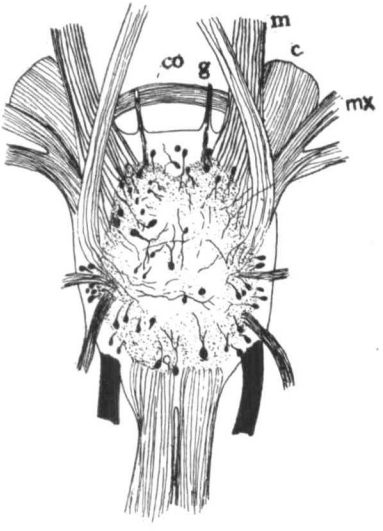

Fig. 6.

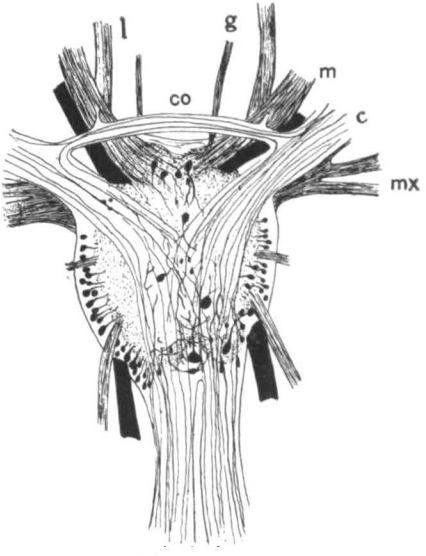

Fig. 7.

FIG. 6. Subesophageal ganglion from the ventral side. Methylene blue. x30.

c.....connective with brain.
co.....commissure
mx.....maxillary
m.....mandibular
l.....labial
g.....gustatory

FIG. 7. Subesophageal from the dorsal side. x30.

The caudal portion of the ganglion becomes thick soon after the connectives have entered. The cephalic lateral portion of the ganglion is connected with the supraesophageal above by two large connectives, but smaller than those from the 1st thoracic ganglion. These cephalic connectives or crura cerebri are connected together a short distance away from the ganglion by a cross branch or commissure.

From the cephalic end there are three pairs of large nerve trunks, the *mandibular*, the *maxillary* and the *labial.* The mandibular is the largest the labial the smallest and most ventral. All appear to be mixed nerves, both sensory and motor.

Either side of the middle line on the cephalic border are two small nerves, the *gustatory*, which are motor in part at least. On either side of the ganglion not far from its central portion is a small *ventral* nerve and not far from the connectives near the entrance of the caudal tracheal tubes are the small *salivary* nerves. I know nothing of the composition of these two last pairs.

The dense central mass of the ganglion prevents one from tracing nerve fibers very deeply in surface preparations, but a few more fortunate specimens gave now and then a fiber or a tract which could be easily followed. In general with the nerve trunks and connectives of other ganglia, these bundles of fibers entered the central portions and like them, too, the nerve cells were chiefly grouped on the sides with scattering cells on the dorsal and a denser mass on the ventral and caudal portions, but in this the dorsal side has more cells than was usual with the other ganglia. The same arrangement of cells and fibers was noticed as in others, that is, most of the peripheral cells could be seen to send their processes into the central portion. Fibers from the connectives above and below could be traced through the ganglion, but there were such masses of them that it was difficult to tell whether they were branched or not.

Fibers from the lower connectives were seen to end in the caudal portion of the "punktsubstanz": (a) On the same side, (b) Crossing over the middle line. These were both superficial fibers and resembled those in the bases of the abdominal ganglia. Probably deeper fibers end higher up.

Fibers running *down* the upper connectives run: (a) Down the connective to end in the central portion of the ganglion; (b) Down the connective to end in the caudal region of the ganglion.

Probably among both of these groups of fibers there are some which cross over into the opposite side of the ganglion.

Fibers running down the connectives and crossing over to the opposite side through the commissure connecting the crura cerebri: (a) Cross over in the commissure to the opposite side and run down to end in the upper or lower portions of the ganglion.

Two other sorts may be given although no *complete* fibers were traced through such a course;

(b) It seems probable from the specimens that fibers cross to the opposite side in the commissure and run over to the opposite side of the ganglion:

(c) Probably some fibers cross in the commissure and run back to the brain.

Fibers running straight through the ganglion from above and from below were not traced but it is very possible that such are present as in other ganglia.

THE NERVE TRUNKS.

The mandibular branch sends its fibers into the cephalic dorsal border of the "punktsubstanz." Some of its fibers seem to end here, others pass in deeper.

The maxillary sends its fibers into the very center of the upper half of the ganglion and here some of them seem to end or cannot be traced farther in surface views. This is true of the more cephalic branch of the maxillary in part at least, while the rest of the fibers of this and those of the caudal branch are traced in laterally a little farther down.

The fibers of the labial nerve; some of them run in deeply about where the branch enters the ganglion, others go down farther and may be traced as far as the place where those of the ventral nerve trunk enter the mid-lateral portion of the central fibrous mass.

The salivary nerve fibers run in and can be traced to near the point where the ventral nerves were.

The small gustatory nerves run some distance down into the ganglion from the point where they take their exit and a motor nerve cell was found sending out its axon directly into this tract.

SUBESOPHAGEAL GANGLION STUDIED IN SECTION, BEGINNING AT THE CAUDAL END.

The connectives which run up to the subesophageal ganglion are much like the others described. As the caudal portion of the ganglion is reached these two longitudinal tracts of fibers become fused although they may be distinguished from each other. A group of nerve cells appears on the lateral sides, and a group of large ones on the median side dorsally, some of these

penetrate in between the tracts and a few cells appear ventrally on the median line, while the cells become more numerous laterally. The salivary nerves enter latero-ventrally and unite with the mass of longitudinal fibers. The cells disappear dorsally, but some are between the mass of fibers of each connective and the lateral cell group has become more ventral. There is at this level a transverse commissure on the dorsal side and fibers running down ventrally in the ventral line. Farther along the fibers do not so many of them run from dorsal to the ventral side and a median commissure comes to be formed. More cells come in laterally and ventrally and these sending their fibers into the central mass contribute to its complexity. These cells also run into the large but ill-defined median commissure.

Two little spots of darker more dense fibers come in on the ventral side and fibers from the ventral cells form an arch about them.

Farther cephalad the median commissure becomes less well defined. The dorsal is lost and a median group of cells comes in dorsally again. Fibers from the ventral and dorsal cells, especially the former go in curved sweeps to the dorsal and ventral sides of the fiber mass, fibers also run in laterally from the lateral cell groups. Farther along no clear commissure can be seen, but sweeps of fibers cross from both sides, those of opposite sides interdigitating to some degree. The ventral darker mass of fibers mentioned a short time ago has now become a transverse mass and is larger, being joined by fibers from the labial and ventral nerves. At the level of this entrance only a few scattering groups of cells are seen.

The dark fiber mass becomes expanded to the center of the "Punktsubstanz."

The broad cerebral cruri are reached. From the central to the dorsal side laterally four small groups of nerve cells mostly small, with now and then a large one are seen. Fibers from the cerebral crus can be traced to the center of the fiber mass and into one or more of the several irregular masses of dark fibers. Dorsally and ventrally fibers cross from side to side and run diagonally from the dorsal to the ventral side. Farther along a ventral commissure of dark fibers is present, some of its strands reaching up into the dark fibers in the direction of the commissure and farther along breaking through it. A short dis-

tance cephalad of this point the ventral mass disappears and the lateral halves of the general mass of fibers becomes distinguishable once more as the upper region of the ganglion is reached. At this upper region, lateral cells are no longer seen, there is however, a small group ventrally placed, either side of the middle line and a small dorso-median mass. Fibers sent in from these curve up to run into the crus which may also at this level be seen to receive fibers from the middle and opposite parts of the ganglion by the way of a group of fibers just one side of the middle line and a group running from the center of the lateral central mass.

Just beyond this last level at the place where the maxillary branch enters, a little group of nerve cells comes in between it and the crus. Fibers from this large maxillary nerve run into the crus, into the central and ventral portion of the ganglion and apparently across to the other side, while many of its fibers are lost in the deeper staining central masses.

Farther along the ventral cells become much more abundant, a wedge shaped group 6–7 layers thick with a few large cells. A few cells come in on the mid-dorsal line and some come in latero-ventrally just above where the maxillary nerve joins the ganglion, and some of these cells seem to contribute directly to the nerve.

The large mandibular nerve joins the ganglion on its upper border, fibers come to it from ventral and dorsal sides of the ganglion and connections with the darker fiber masses in the center can be traced. Cells are now in masses both dorsally and ventrally as the cephalic end of the ganglion is approached and some of these at least seem to contribute directly to the nerve.

The above description is a very general one, only the main features of structure and arrangement were spoken of. The complexity of the ganglion is such that a general summary of it follows:

(a) *Cells*

The cells at various levels differ greatly. Beginning at the caudal end and passing forward there might be recognized about three main dorsal cell groups one after another which fuse and separate from each other at various levels. The median ventral cells are at first also separated from the other groups

but farther up they grow out laterally to become continuous with the lateral and dorsal cells at various levels while they become absent from the mid-ventral line, then become united again on the cephalic region where all the cell groups are joined together. In intervals where these groups are not in distinct masses a few scattered cells are often found.

(b) *Connectives*

Ventral connectives. Fibers from these run straight into the ganglion for a short distance until the central tangled mass is reached. Only a few of the fibers in the central part of the ganglion can be seen to take a straight course through it. Many others run straight or nearly so for a short distance and then turn off sharply to one side. Fibers from the connectives seem to end at all levels and in practically all parts of the central fibrous mass and to be contributed to by cell masses especially on the ventral side, but also clearly on the dorsal. These fibers coming in from both sides of the ganglion at different levels and as single fibers or groups add considerably to the complexity of the ganglion as does the fact that many of the fibers from the connectives which run through to the crura cerebri and nerves do not always take a straight course or run to the same parts of the nerve trunks. Sweeps of fibers for instance, can be traced quite straight up on the ventral side of the ganglion and then may be seen to turn over to the dorsal side.

Crura cerebri. These have fibers from the caudal connectives but not nearly all from them can be traced into the crura, for they are smaller and have their own special fibers which come from almost every part of the ganglion. The cells in various parts seem to furnish many of these, some of which come from the same side, but single strands were followed running in the direction of the crura which were from the opposite side. Fibers may also be seen to sweep back into it, probably from the mandibular trunk.

(c) *Nerve trunks.*

Mandibular. Many of the fibers of this end in the first part of the fiber mass. A few apparently run into the crura. Some fibers could be traced from near the median central part of the ganglion in a line with the lower connectives. Some came to it from cephalic median cells.

Maxillary. Fibers were followed into this from the lower connectives and from the upper parts of the ganglion. From this nerve trunk some fibers seem to end near the junction of the nerve with the central "punkstubstanz."

Labial. This is made up from fibers which enter the ventral central portions of the ganglion, just above the entrance of the small ventral nerves. They may be traced from the connectives up and from the upper portion of the ganglion down into these trunks and ventral caudal cells evidently contribute fibers to the mingled mass which is connected with these branches.

(d) *Commissures.*

The commissures connecting the crura cerebri have fibers which cross from one side to the other in the case of descending or ascending strands. No other kinds were recognized although I think there is a strong probability that some fibers merely cross and do not descend at all.

Within the ganglion there are a number of commissures connecting the lateral halves. Some of these are of straight fibers, others are closely woven deep staining masses. Dorsal, ventral or median commissures are found at almost every level, especially ventral ones, although not always clearly marked. A longitudinal section through the whole ganglion shows from three to four main commissures, a cephalic, a caudal and two median ones.

THE SUPRAESOPHAGEAL GANGLION.

(Figs. 8, 9, and Pl. XVI, Figs. 1–4.)

The brain is made up of two large ovoid masses distinctly marked from each other on the the middle line. It is connected on the ventral side to the subesophageal ganglion by means of the short, broad crura cerebri. All of the larger nerves come out laterally and of these there are three main trunks, the only ones to be considered at this time.

Three portions of the brain may be made out each connected with these trunks. The most dorsal is the *protocerebrum*, and it is also the largest and best marked and connected with the optic nerves which divide on each side into seven branches one for each ocellus.

The middle lobe of the brain or the *deutocerebrum* is the least marked of any and its nerve trunk the antennal, is the smallest of the three. It enervates muscles at the base of the antena as well as sense organs in it and so is mixed. This lobe is best seen on the cephalic and dorsal side and not at all on the cephalic ventral.

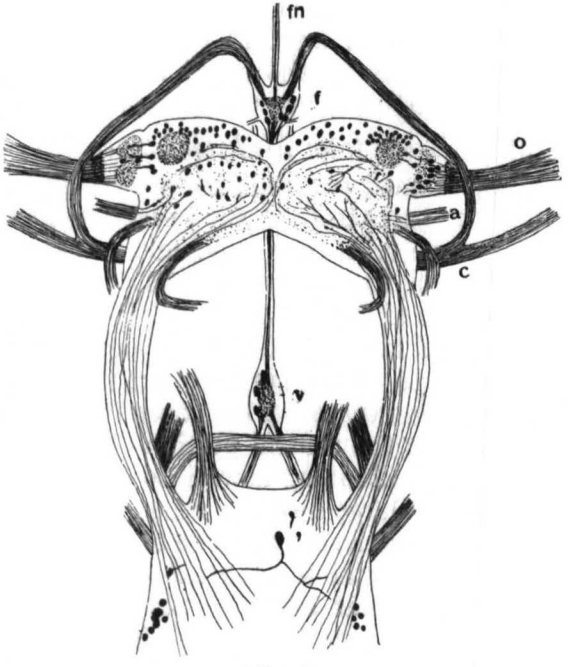

Fig. 8.

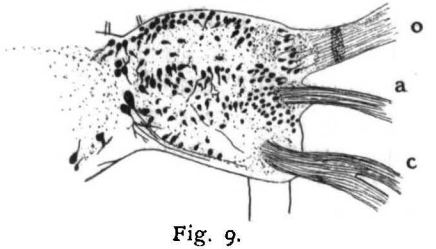

Fig. 9.

FIG. 8. Supra- and sub-esophageal ganglia with their attached nerves and ganglia. The brain is turned over cephalad. The sub-esophageal ganglion is dorsal. x30.

a.....antennal
c.....clypeolabral
f.....frontal ganglion
fn .....frontal nerve
v.....vagus ganglion
o.....optic

FIG. 9. Cephalic view of one half of the brain. Methylene blue. x30.

Finally the *tritocerebrum* is well marked as a little lobe just dorsal of the crus giving off the rather large clypeo-labial trunk which with the arched nerve comes off as one. From the distribution of this it seems probable that it is mixed.

This arched nerve runs ventrally and cephalad to unite at the middle line with the one of the opposite side in the *frontal* nerve ganglion. A branch from this small nerve center runs forward as the *frontal* nerve, another runs back on the dorsal surface of the esophagus to the small *vagus ganglion*, which sends two branches farther down the alimentary canal.

General form of the Brain from Methylene blue.

In successfully stained preparations almost all parts of the brain, especially the parts in from the nerve trunks are seen to be covered with nerve cells, both large and small. Those just under the chitin seem to quite completely incase the central dark staining portions of the ganglion. This central dark mass in each well separated lateral half of the ganglion is roughly of the same general shape as the surface. In the main part out from the median portion there is a lobe deep in and opposite the ocular nerve, this is in the central portion of the ganglion and connected with it, but extending down into the tritocerebrum is another lobe almost as large near the crus.

Partly separated from the central lobe of "punktsubstanz" is a spherical mass of dark staining substance and out from this a little distance in the ocular lobe and beyond its constriction from the main part of the protocerebrum is another little mass of deeply colored material. About each of these last little masses of "punktsubstanz" a special arrangement of cells is seen, while over the surface of the main portion of dark substance on every side the cells form a thick covering.

Fibers running up the crura may be traced into the ganglion in its dorso-caudal region. Some apparently run only to the lower portion of the "punktsubstanz," others may be followed farther up and are lost in the central area. Fibers can also be traced to the central portion of the ganglion, to the medial portions and probably freely ramify all through the central mass.

Near the middle line of the ganglion some large cells on the surface were found with long processes extending down long distances in the direction of the crura and probably were continued into it.

The great bulk of fibers connected with the crura seem to take origin or terminate in the central portion of the "punktsubstanz."

The ocular nerves enter the protocerebrum through large nerve trunks which form a decided lobe on the surface of the brain. At the junction of this *ocular* lobe with the ganglion there is a little area of deeply staining substance mentioned, before and back of this are nerve cells, and also a few cells on the eye side of the mass. These may be seen to send their processes into a dark mass and in towards the main part of the brain. Fibers run out the nerve from the ocular lobes' deep staining mass and into the spherical body before mentioned and into parts of the "punktsubstanz" near it, the former are processes from cells located near the ocular "punktsubstanz." About the spherical mass may be seen many nerve cells whose fibers are connected with it.

Nerve cells on all surfaces of the protocerebrum are very numerous and may be seen sending their processes into the central fibrous mass of the ganglion.

The deutocerebrum is less marked than the other two neuromeres and the fibers of its nerve, the *antennal*, come in closer to the clypeolabial segment of the brain than the ocular portion. The fibers of the antennal nerve can be traced as a distinct band for nearly one-half of the distance from its entrance to the middle line, where they seem to end in a mass of deep staining fibers of the clypeolabral trunk where it joins the main central portion and here at least some fibers can be seen to end well towards the caudo-ventral portion of the ganglion.

The tritocerebrum is best marked in the dorso-cephalic side of the ganglion where it lies over the crus. The fibers of its nerve seem to be of two sorts. The labral part is often stained while the arched nerve portion is clear. Both branches enter the ganglion and plunge at once into the mass of deeply staining fibers. Not quite so many cells were stained overlying this region in the specimens prepared. Some of these sent fibers more or less directly into the central mass while others as in other surfaces of the brain seemed to be association cells in a small area.

SMALL GANGLIA OF THE HEAD.

Connected with the arched nerves somewhat cephalad of the brain is the frontal ganglion. This in well stained preparations may be seen to have a central deep staining mass surrounded by nerve cells, the processes of some of which run into the central mass, while those of others run out from the cell, and down into the nerve which runs under the brain and connects this with the smaller so-called *vagus* ganglion. This last is like the former only smaller and fewer cells surround the central mass, some of the fibers run from this and probably also rather directly from the cells of the ganglion, down and out the two caudal branches. Occasionally the two lateral ganglia of the esophagus take the stain but their connections or structure was not especially studied. They seemed to differ from the other two ganglia, as they showed from the surface no nerve cells, the whole body taking on a uniform deep blue color. Sections showed them composed of very many cells closely massed together.

Sections of the frontal ganglion show a small mass of cells quite well filling the caudal end, a few larger, but mostly smaller cells of the same general sort found in other places. Of these there were about two large and eight smaller ones at a level where the ventral nerves come off on each side of the "Punktsubstanz," although farther cephalad than the place where these nerves are seen from the surface. Farther cephalad where there are only three or four large cells, fibers cross in various directions in the central portion of the ganglion. A large cell for instance was seen to send a process into the center of the ganglion where it broke up into a number of branches. Fibers cross in the various directions but most run longitudinally. At a level where a branch to the frontal ganglion arises, there are no nerve cells, the central part of the ganglion is divided into three masses of longitudinal fibers by trachea and cross fibers. This division is continued only for a short distance.

Farther along a dorsal and a few small ventral cells come in. The central mass of fibers is rather uniform, but made up of both cross and longitudinal strands. A little farther cephalad three cells come in dorsally at about the level where the arched nerves come off. Fibers running from side to side connect

these nerves through the center of the ganglion.

The so-called vagus ganglion has a central mass of fibers and at its central part a nearly double row of cells closely packed about this central fibrous mass, these cells are continued down from the center a short distance, especially on the dorsal side.

THE BRAIN STUDIED IN SECTION.

(Plate XVI, Figs. 1–4.)

Only the main features of the structure of this complicated organ will be given at this time. Many of the elements of the brain of the adult may be present in the larva but for the proper interpretation of these it will be necessary to follow up this work with studies on the ganglia of pupae and adults.

As in the other centers, a central fibrous mass forms the bulk of the organ and about this central "Punktsubstanz" nerve cells are grouped in great numbers on practically all sides but the ventral. As in the other ganglia, large and small nerve cells and small neuroblasts are found, the latter are especially abundant and occur in great masses. Besides these, filling in between and in places where there are no nerve cells is the neuroglia network, which is often continued to the layer of surface supporting cells just under the chitinous sheath of the ganglion.

In sections we may recognize the dense staining parts seen in surface views to be masses of fibers more or less complexly arranged in the central and ventral portion, more or less paralleled by straight bands of the entering nerve trunks. Some of the special denser masses of fibers have already been described from surface views as that in the ocular lobe just as it joins the brain and in from the little spherical area just within and beyond this point. These two masses although quite separate from each other dorsally, ventrally and laterally are centrally connected by fibers and are also connected to each other to a less degree in the same way. The central fibers described in connection with the crura cerebri, are continued down into the labral lobe, but the deepest mass is in the central portion dorsally where it is somewhat lobed because of groups of cells on the surface and due to the processes of some of these cells passing down into the center. In this central "Punktsubstanz" either side of the middle line, is a well marked denser group of fibers, a rod of substance projecting from those on the

dorsal side of the brain. This runs down to the mid-ventral line and there branches into two parts, one ventral, the other dorso-lateral. Farther along each of these parts run caudally as a single piece, one ventrally, the other dorso-laterally and the middle portion of the rod and afterwards the dorsal part disappears in section because of the curve in it. Later the lateral part disappears and the mid-ventral portion extends in towards the middle line to meet, but not unite with its fellow of the opposite side, running caudally in this way some distance, just above a ventral fibrous commissure and below a broad central one. In other words this body is a long slightly curved rod standing up in the ganglion with its base divided into two portions of which the lateral is shorter, the median longer and extends in towards the middle line. These represent the *stalks* and *roots* of the "mushroom bodies," the cup, such as described by Kenyon and others is not present and the special cells if developed were not recognized. This stalk and root of fibrous substance seemed to have a lighter core, that is in sections it gave to some extent the appearance of a tube. The fibers which compose it are very densely massed together. Preparations in which the tissues were allowed to macerate showed them to be little affected.

On the cephalic margin of the brain as on the dorsal side, the central fibrous mass as a whole is lobed as already spoken of and masses of cells fill in over these. The cell groups are difficult to describe in detail. The whole dorsal and lateral portions of the ganglia are covered with them, both large and small and in places many cells deep. There are almost no cells on the ventral side of the brain.

Beginning laterally and dorsally we have about the spherical mass of fibers back from the ocular lobes, masses of cells, on the dorsal, ventral and mesal sides. A peculiar condition of some of the dorsal and ventral sides of this mass is the appraent epithelial character of some of the cells. Most of these are very small and are probably neuroblasts. The epithelial character is especially marked in two places on each side because there are little cavities one dorsal and one ventral in the outer portion of the circular mass of fibers. (Plate XV, Figs. 1, 2, 3.) There are some fibers from the two lateral groups of cells just described which run both to the mesal group and out the ocular nerve. This is also continued dorsally and forms all along

the dorsal part of the ganglion a thick layer, in the middle region of the brain.

A group of large cells occurs dorsally either side of the middle line, most of these point ventrally or centrally and send fibers to the crura cerebri, to the commissures and to the central portions of the fibrous mass; theirs are the longest fibers recognized from any cells in the brain.

Out laterally and ventral to the ocular lobes in the region of the antennal lobe and just above the crura is a small group of nerve cells, sending fibers into the crura and into the fibrous substance near that region of the brain.

In the cephalic region the cells surrounding the spherical mass may be seen divided into a dorsal, a ventral and a median group of small cells, already mentioned, while larger ones fill in on the dorsal side and are part of the general dorsal mass. These and the median masses run together and separate again at various levels, groups of smaller and larger cells often alternating, and these are continued on the cephalic and caudal sides of the ganglion. One of the most marked is a small group of cells surrounding a curved lobe of the central mass of the ganglion and continuous with cells on the cephalic side of the brain.

Fiber Tracts in the Brain.

(1) *The labial.* Fibers seem to end chiefly in the dense fibrous mass located in the labial lobe. A few fibers could be traced doubtfully into a dorso-lateral group of cells.

(2) *Antennal nerve.* Fibers from this end in cell groups either side of it. Fibers pass down ventrally into the lateral central part of the "punksubstanz" in large masses where some of them end, others cross to the ventral side and run in strands back in the main tract of the crura towards the other side. Others run towards the crus of the same side and apparently into it.

(3) *Ocular.* Fibers seem to end in the lateral mass of the ocular lobe, numbers of them connect this with the more median spherical "punktsubstanz." Fibers connect these two masses and fibers from the surrounding cell groups run into one or both of them.

Fibers connect the ventral epithelial-like cell region with the lateral dark mass, and also with an adjoining group of small cells more medially situated.

The more median ventral mass of epithelial-like cells lying ventral to and slightly out from the spherical fibrous area probably has connections with the larger more dorsal cells.

The more dorsal of epithelial-like cells which are one side of a small cavity, send fibers into the lateral optic "punktsubstanz" and are connected by fibers with the more central dorsal cells which adjoin it.

(4) The *Crura cerebri.* The main mass of fibers goes up to the central portion of the "punktsubstanz" on each side and receives branches from all parts of it and also especially from the median and lateral dorsal cell groups and probably also from lateral masses. A large part of the band runs ventrally and forms or is joined into a commissure with fibers from the other side. Fibers come into this last from all ventral parts of the ganglion from *both* directions, from ventral parts of the mushroom bodies, and from various lobes of the deep staining mass of the ganglion.

(5) *Commissures.* Two commissures have been mentioned, a ventral which was described above. The other more medial is found toward the caudal region. It is short and broad.

SUMMARY.

1. In the abdominal ganglia practically all the nerve trunks and branches are mixed motor and sensory.

In the thoracic ganglia, the three main trunks are mixed. Pure sensory divisions were found in connection with cephalic branches. The branches given off between the thoracic ganglia and between the 1st thoracic and the subespohageal seem to be motor. At least the more caudal ones were determined to be, with fibers ascending and descending from the ganglia below and above.

The three large nerve trunks connected with the subesophageal ganglion seem to be mixed motor and sensory. The other smaller ones were not determined, but the small gustatory nerves were motor at least.

The three main trunks connected with the supraesophageal ganglion were all mixed but the ocular.

2. Sensory tracts were recognized entering thoracic and abdominal ganglia and distributed to various parts of the ganglion to which they were connected. That is distributed to one or both sides either as individual fibers or as branches from

one. Some tracts were found distributed to the next center above as well as the nerve center to which their nerve trunks were connected. Others were found passing in to the ganglion to which the trunk was attached but giving no branches and passing on up to end in the next above or higher up.

A number of fibers apparently sensory were found passing through a number of ganglia without branches. These were often larger strands and although not traced as far as the head there was no reason to doubt that some of them were that long.

Sensory fibers and tracts were however traced into the large head ganglia and were found distributed to all portions of the fibrous mass. Sensory tracts were easily traced in connection with the ocular trunk, connecting it with the special lateral masses of fibrous substance.

3. Motor tracts could be traced as having their origin from cells in the ganglion to which the motor trunks were connected. Motor fibers could be traced out of the ganglia some distance but were not followed in as much detail as the sensory.

4. Association and descending tracts were recognized in all centers and at all levels of variable extent. Probably some of these were motor tracts.

5. Cells of many sizes were found in all centers. The largest and the smallest functional nerve cells seemed to be for association, those of the former sort having extensive aborizations, the second kind being much less extensively branched. Many of the medium sized cells were found to be motor. The general type was uni- or bipolar with one long branch which might run out for a considerable distance. Some association cells seemed to be bipolar with long processes running out in both directions. Some association cells seemed to be uni- or bipolar with all the branches coming off and branching again not far from the cell. A few multipolar forms were seen.

Neuroblasts were found to some extent in all ganglia, but great masses of them were especially noticeable in the brain.

Neuroglia networks filled in places under the chitin where there were no nerve cells and also formed more or less of a network in the regions where they were present.

6. Cells were grouped about the central fibrous mass in all of the ganglia. In the abdominal they were found to be especially abundant in the caudal and ventral regions, although the cell masses extended out laterally in all, and there were

often well marked mid-dorsal masses of large and smaller cells, as well as scattered cells in all parts. In the more cephalic ganglia, the cells are not quite the same in distribution. Cell groups and masses are found abundantly ventrally, but also on the dorsal and lateral sides and also great masses of them at the cephalic as well as the caudal end.

In the supra esophageal ganglion, cells are especially abundant dorsally and on the cephalic and caudal borders, less abundant laterally and ventrally. The cells are very numerous. Each side of the middle line a group was located with very long processes, the cells being mostly large.

Other groups were densely massed lateral to these, both cephalad and caudally, some of them were large, others small, and two groups of small cells on each side out near the optic nerves were found with a cavity near them.

Nerve cells were found partly surrounding two masses of fibers on each side near the optic nerves.

From the distribution of the cells and fibers there was no evidence of the dorsal cells being especially *motor* and of a ventral, particularly *sensory* region as Binet was led to think from experiments. I would rather incline to Kenyon's idea of ventral motor and dorsal sensory if I choose either of the two views, as undoubtedly most of the ventral cells in the thoracic and abdominal ganglia are motor cells, while many if not most of the fewer dorsal cells of these ganglia seem to be association cells, sending their fibers superficially over the surface or deeply into and *through* the fibrous mass to be associated with the cells and fibers of the ventral side.

7. In all of the ganglia the central mass into which many of the nerve cells send their processes has a very complex arrangement of fibers and nerve terminations. Certain portions of this mass in all are much denser than the rest.

In the brain this central "punktsubstanz" is somewhat more intricate in its texture on the dorsal side than on the ventral and is more or less lobed while off from the central mass there are two smaller groups of "punktsubstanz" in connection with the optic nerves on each side. In the central part of the brain is a *stalk* and *root* of a mushroom body on either side, but the *cup* is not present. The ventral portion of the ganglion is mostly made up of *straight fibers*.

In all of the lower ganglia there are at almost any level, from one to three commissures recognizable, a dorsal, a median

and a ventral. These are broken up at various levels so that there may be several, three or more, cephalic or caudal parts of these commissures. There are more in the 8th abdominal and in the subesophageal than in the others.

From dorsal to ventral sides also, fibers chiefly from dorsal cells connect the upper and lower surfaces.

In the brain there are two commissures a broad short median and a longer ventral. Many other cross and longitudinal fibers connect all levels.

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PLATE XV.

A series of four photographs of cross sections through the 1st thoracic ganglion of Corydalis through a caudal level. The last figure is through the more central portion of the ganglion. Nerve cells show at the sides. The central fibrous mass is shown in all, and longitudinal fibers can be traced. In the last three figures cross commissures may be seen. The dark mass at the left or ventral side is part of the surrounding tissues and not a part of the ganglion. x60.

PLATE XVI.

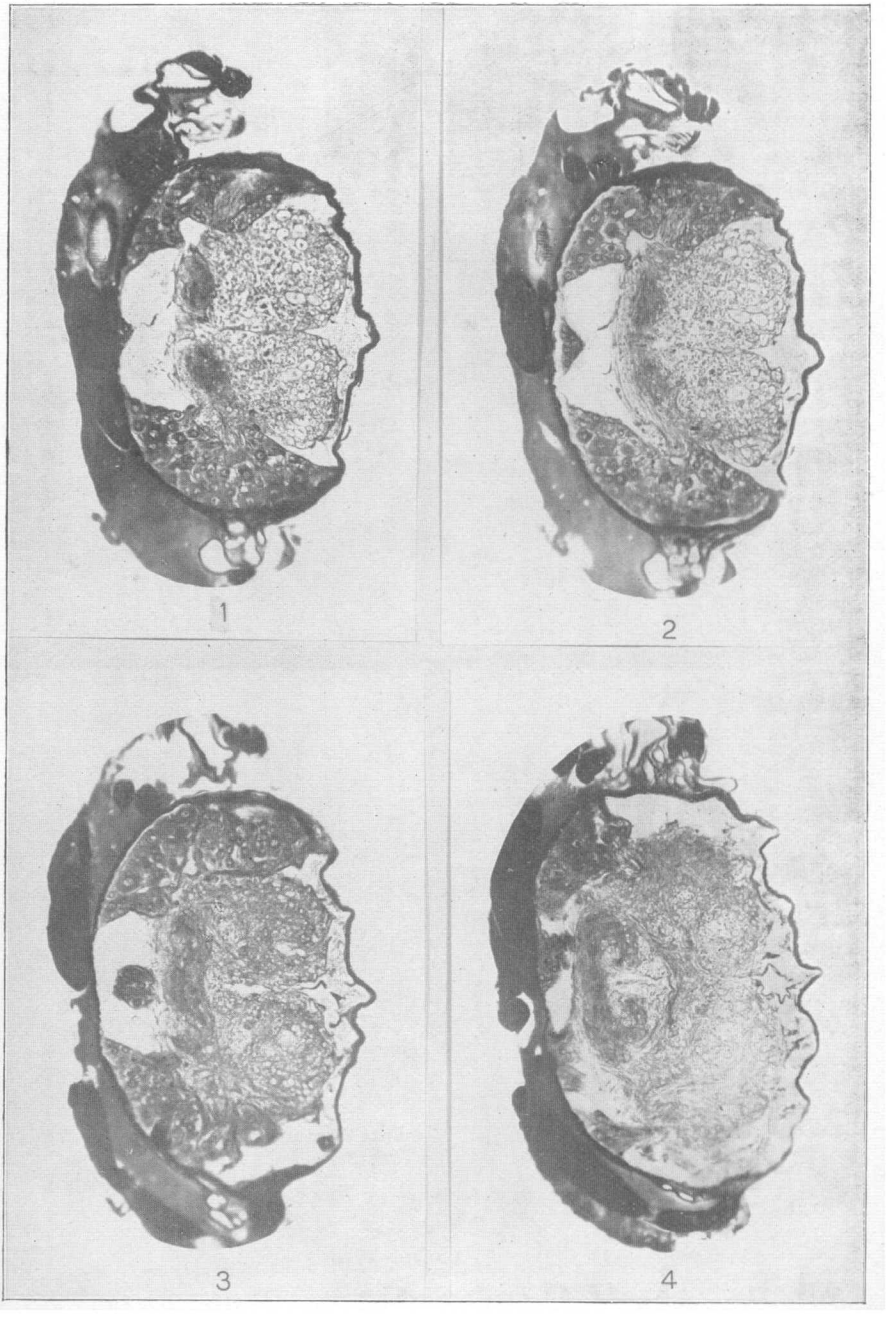
FIG. 1. Photograph of a cross section parallel with the long axis of the brain through its central region. One half only shown. The dorsal side is up. The optic nerve is the swelling off at the right above, while leading off below is the broad crus. The dorsal masses of cells show, also central fibers and the stalk and root of the mushroom body. x75.

FIG. 2. A similar photograph from the same series cut farther one side, cephalad. x75.

FIG. 3. Photographs of the larger cavity shown in Figs. 1 and 2. x250.

FIG. 4. Section of the brain cut in a similar way as Figs. 1 and 2, but farther cephalad. The ventral side is at the left. The dorsal to the right. x75.

FIG. 5. Longitudinal section of the sub-esophageal ganglion. Above the first branch to the left is one of the crura cerebri, the next it is the mandibular. Below the branch cut only through its edge is one of the ventral connectives. x75.



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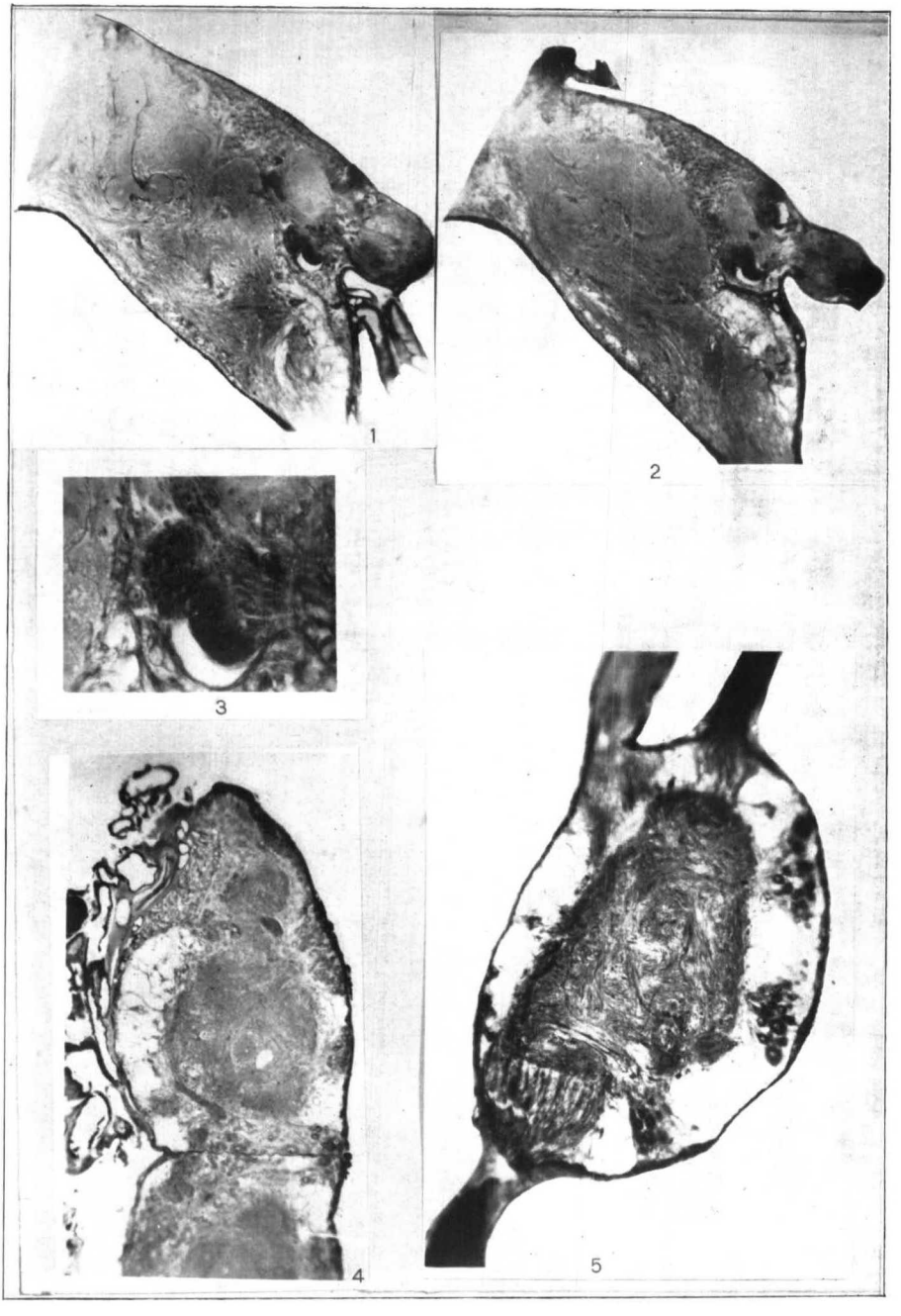

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