

THE CENTRAL NERVOUS SYSTEM OF SIMPLE CRUSTACEA

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THIRTEEN FIGURES

Although the general form of the nervous system of branchiopod Crustacea is well known, there has been very little recent work. Most papers deal with the general form and arrangement of the ganglia and not at all with the structure and arrangement of cells. Zaddach, '41, wrote on *Apus*. Leydig, '51 and '60, considered *Artemia*. In 1853 there is the paper of Grube on *Limnetis*. The work of Claus on *Branchipus*, *Daphnea*, *Estheria* and *Apus* appeared in 1873, 1876, and 1876, and that of Weismann on *Leptodora* in 1874. Spangenberg's publication on *Limnadia* was in 1878. Packard has something of the general anatomy of *Estheria* and *Branchipus* in 1883. The well known and often copied work of Lancaster on *Apus*, '81, was followed by that of Pelseneer on the nervous system of the same genus in 1884. Spencer in 1902 discusses and figures the anterior nerves of the brains of *Artemia* and *Branchipus*.

From the various observations the general ladder-like type of nervous system has been described and figured in this group of Crustacea. There is the supraesophageal ganglion with its marked region of optic nerves, while the two other pairs of nerves to the antennae and antennules are less marked and come from more caudal portions of the brain or on or near the esophageal connectives. From the cephalic margin of the brain are the median eye branch and the two small pairs of nerves lateral to it, at least in *Branchipus* and *Artemia*, as described by Spencer, '02. Each segment of the body below the brain is ordinarily represented by a pair of ganglia connected across the middle line

by two commissures. The number of pairs of ganglia depends largely upon the degree of segmentation of the body of the crustacean.

The fortunate opportunity to obtain a large number of living Crustacea gave much of the material for this study. Methylen blue was tried without success as long as the animals could be obtained alive, afterwards dissections and sections were made from preserved material. Mercuric chloride fixation seemed most advantageous. The whole nervous system was dissected out and lightly stained with a carmine solution or a clear alcoholic hematoxylin. Later the specimens were mounted in balsam. This method had many advantages because all parts of the simple nervous system could be seen at once. The cells and fibers were not numerous enough to greatly interfere with the clearness of the preparations. Especially was it noted that the cells were not distorted as is usually the result after sectioning methods. Some serial sections of whole animals or parts were prepared for comparison.

GENERAL FORM OF THE GANGLIA

In the forms studied, in general no new features of external morphology were noted. *Artemia* and *Branchipus* were practically the same except for the larger size of the nervous system in *Branchipus*. In these the brain has connected with it laterally the two large optic nerves which expand into the optic ganglia (not shown in figures). The antennular nerves come off from the brain where it joins the esophageal connectives and the larger antennal nerves come off a little farther down. From the cephalic side of the brain a median nerve is connected to the median eye and two pairs of nerves lateral to this supply upper parts of the head.

The first three pairs of ventral ganglia supplying the head, mouth parts and upper portions of the body are much smaller than the more caudal ganglia. The last ganglion or pair of nearly fused ganglia change somewhat as they terminate in abdominal branches (figs. 1 and 2).

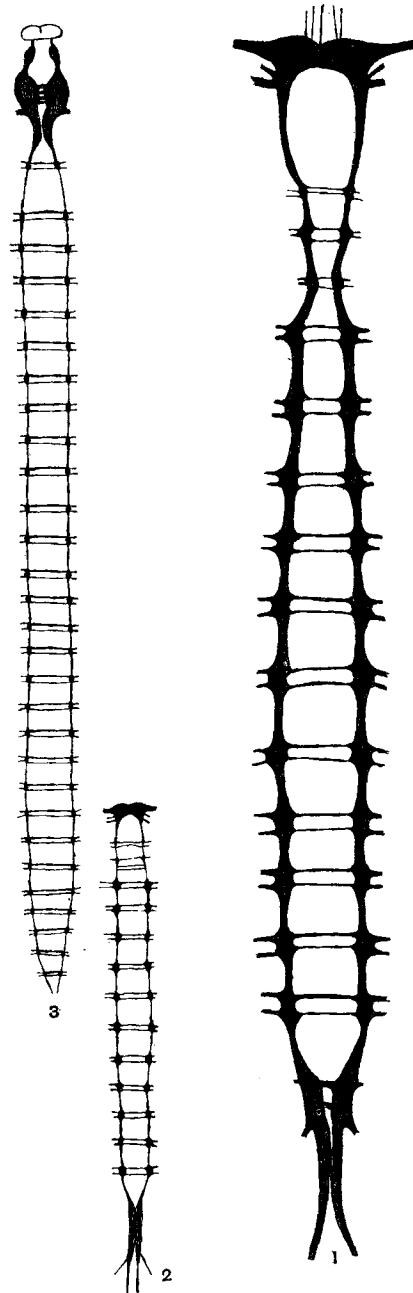
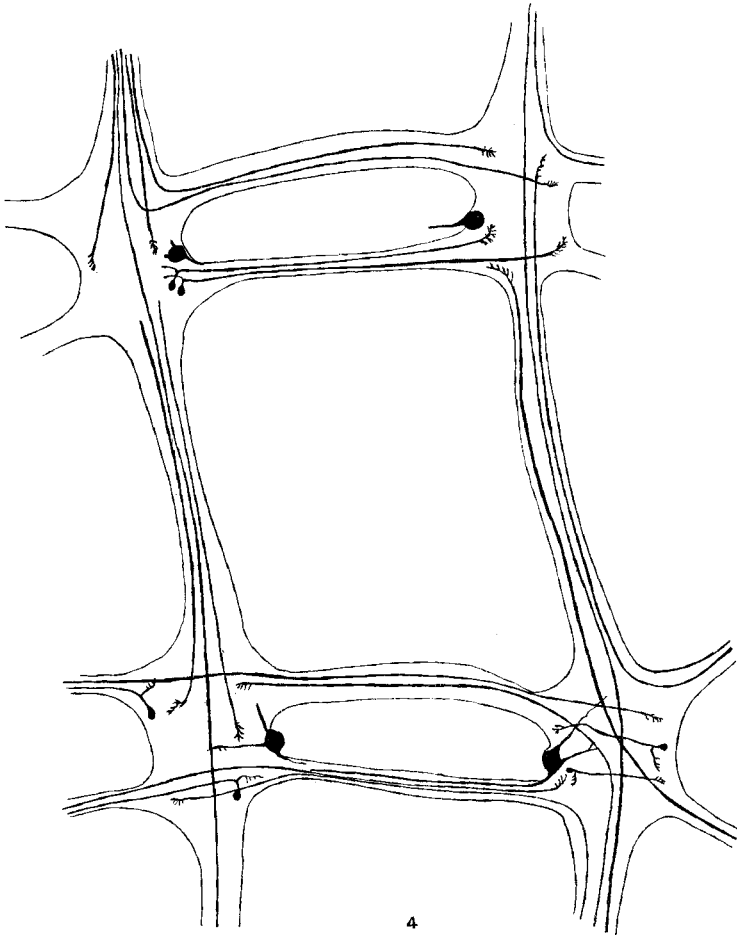


Fig. 1 The central nervous system of *Branchipus venalis*. $\times 10$.
 Fig. 2 The central nervous system of *Artemia* sp. $\times 10$.
 Fig. 3 The central nervous system of *Estheria californica*. $\times 10$.

In *Estheria* it was very difficult to remove the ganglia intact, so the sketch given is from the nervous system *in situ* for the most part. The brain is of quite a different shape, the optic ganglia are shown in the drawing connected with the compound eyes, which nearly touch each other. Only one pair of antennal nerves is shown in the drawing. The brain is more decidedly



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Fig. 4 Diagrammatic plan of cell arrangement in the ventral ganglia of *Branchipus*. $\times 75$.

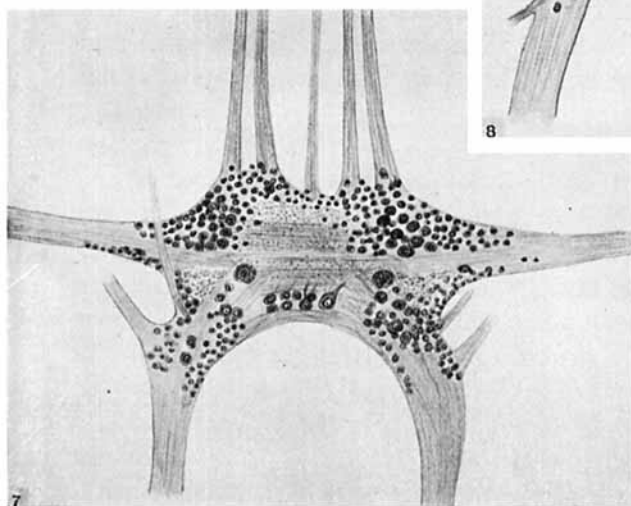
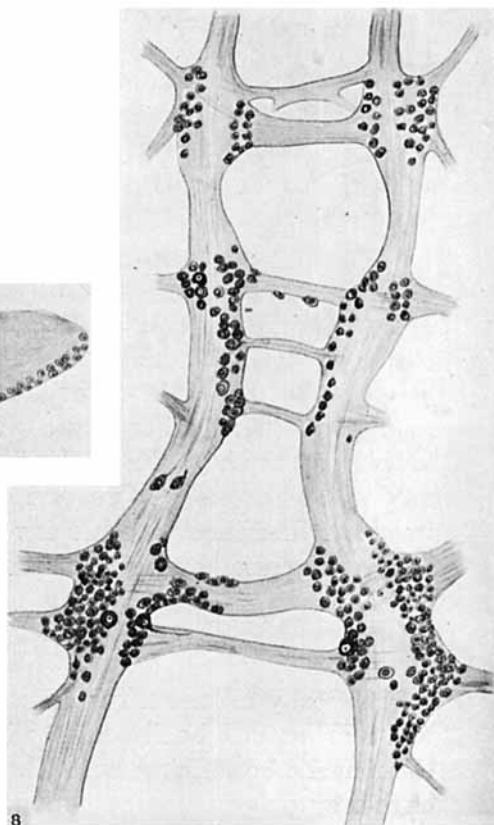
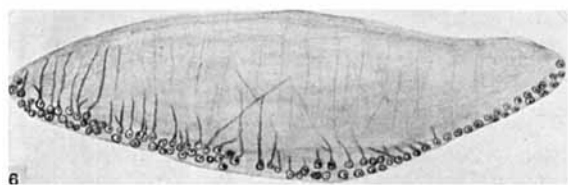
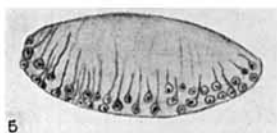
made up of two lateral masses than in the other genera studied. Four commissures may be clearly seen connecting the two lateral parts. Four were also seen in *Artemia* and *Branchipus* but not so clearly. The ventral ganglia of *Estheria* begin with the mandibular and extend to the end of the body with a pair of ganglia to each segment and with two commissures connecting each pair (fig. 3).

Cells of a number of types were found. In *Branchipus* they are from 0.01 mm. to 0.05 mm. in diameter. The much smaller but similar *Artemia* has smaller cells, the largest being about 0.02 mm. and the smallest about 0.005 mm. Two divisions of cells may be made, the neuroglia cells and the nerve cells. The neuroglia cells, small or large, were not so deeply stained in the fibrillar area; they usually have granular nuclei. From whole mounts and sections it was evident that the neuroglia nets are much as described in other invertebrates. It is possible that some of the small cells which seem to be nerve cells are neuroglia cells.

CELLS

Practically all the nerve cells, especially of *Branchipus*, have well-marked cell bodies filled with dark staining material and clear nuclei containing nucleoli. A few nerve cells have much clearer cytoplasm than the others. In the large cells especially, tigroid substance may be seen even in surface views. In the larger cells also the fibrillae are quite evident. The general shape of the cells is spherical, but some are elongate. Most cells are unipolar or bipolar, but a few are multipolar (figs. 5 to 13).

Large, medium sized and small cells are found in the cellular areas with no apparent special order, but the largest cells are found at certain places at the margins of the ganglia. At least one, sometimes two or three of the largest cells are located on each side near the more caudal commissures of each ventral ganglion. These in many cases send or receive processes to or from the connectives. Perhaps they are cells in most cases with long commissural fibers.



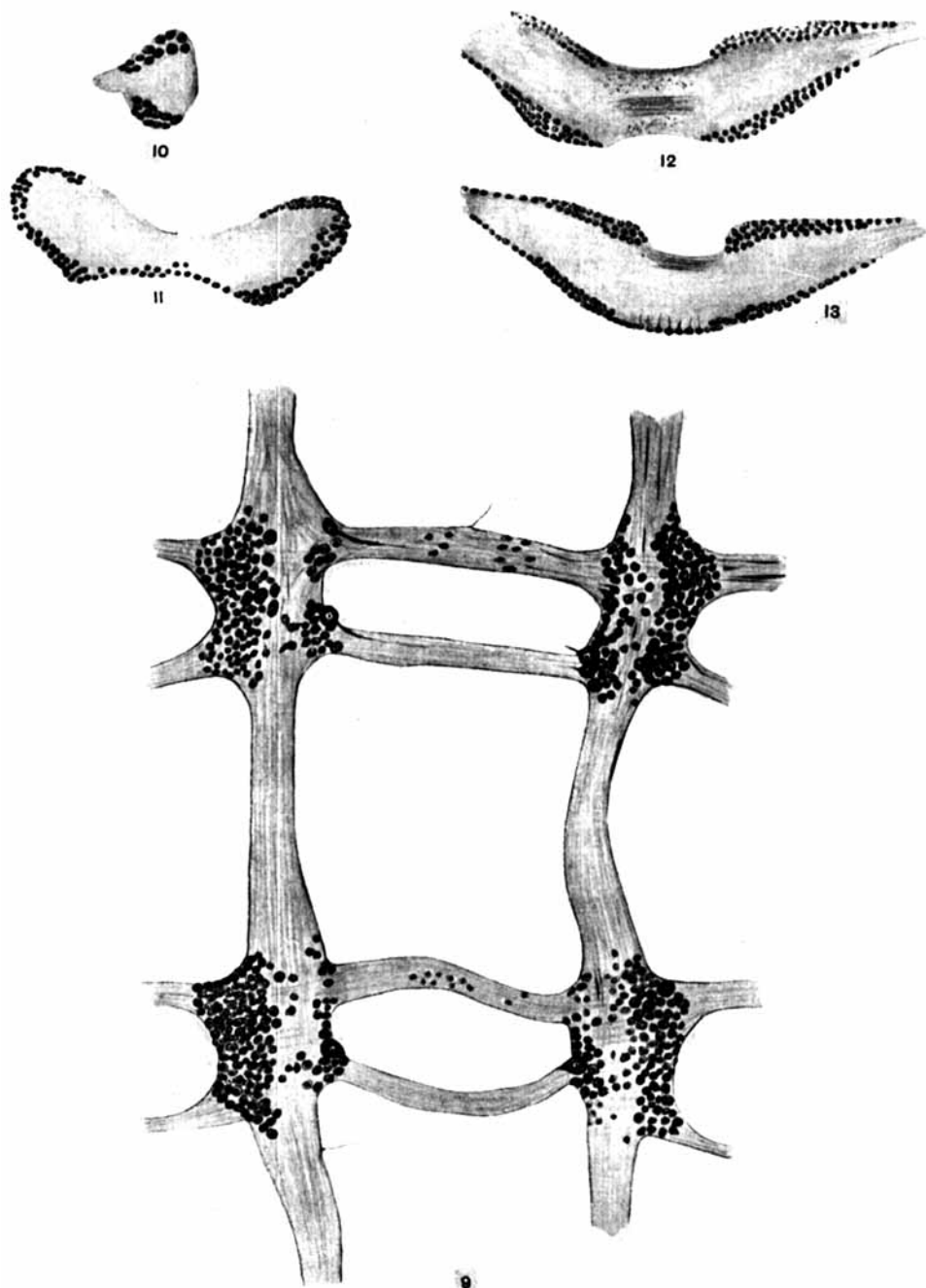
In each ganglion of each side the cells are arranged in a characteristic manner. In all the middle body ganglia the ventromesal cell group is less marked than the ventro-lateral. The outer portion of the ventral-lateral group often has a number of large cells similar to those in the other group. The larger cells in most cases represent those that send their fibers longer distances, but they often have more than one branch and the external and internal mass of fibrillae connected to them seems more complex than on smaller cells. In some cases the larger cells seemed to have their cytoplasm fused, but most of the cells, although near each other, had their cell bodies distinct. Nerve fibrillae are evident between and in cells, although some of the largest cells have one or two large fibers which leave or enter the cells. Some cells of apparently the same type seem to have no very large branch, but fibrillae enter and leave the cell. Many large cells seem to be penetrated on all sides by numerous fibrillae, or if fibrillae do not all penetrate they are closely related to all the peripheral parts of the cell body.

Cells of varying numbers are found in the commissures, these are chiefly medium or small cells and some at least are nerve cells. The number of cells in the ganglia was possible to determine quite well from surface preparations and some comparisons were made between *Artemia* and *Branchipus*. The larger species has not only the larger nerve cells, but the larger number of nerve cells. The number of cells in corresponding ganglia was found to be less in the smaller animals. The average number of cells in the middle ventral ganglia on each side ran from 130 to 204 in *Branchipus*, while *Artemia* had from 120 to 160 cells in each lateral ganglion. The number of cells in the intermediate ganglia of a number of specimens was counted and, although the count cannot be considered absolute because of

Figs. 5 and 6 Sections through the abdominal ganglia of *Branchipus*. The dorsal side is to the top of the page. $\times 75$.

Fig. 7 Brain of *Branchipus* from a surface preparation. The cephalic side is to the top. $\times 75$.

Fig. 8 Upper ventral ganglia of *Branchipus*, surface view. The cephalic end is at the top. $\times 75$.



difficulty in seeing all at one focus, difference in mounting and difference in staining, yet the following seems clear:

1. The cells often differ slightly in number in different similar ganglia of the same animal, both in the same segment on each side and in different segments at various levels.

2. The number of cells is also variable in the same parts of the same ganglia in different animals.

3. The peripheral parts supplied by each of these ganglia do not differ in any way that could be determined.

4. It was even more clear that the cells in the commissures differed widely. The next to the last cephalic commissure in one specimen had 38 cells, the next 20, then, 19, 7, 10, 12, 16, 10, etc. Similar variations were found in other specimens. The lower cephalic commissures as a rule had more cells, while the upper had less.

It was also noted that some of the large cells which have quite a characteristic position are in some places represented by one cell, in others by two. In a few cases noted the large cells have an independent peripheral distribution as compared with the usual indirect distribution through a commissure. It is as though a cell which ordinarily grew out to the periphery by way of a commissure missed it in some way and left the ganglion by a single fiber.

FIBER TRACTS

Branchipus was especially studied because the material was more favorable.

The brain so far as could be determined is united from side to side by four commissures, a dorsal, two medial and a ventral. The last is below a small group of medial cells. The commissure just above this group seems the largest. The ventral commissure is partly from near-by cells and from basal parts of the con-

Fig. 9 Sixth and fifth ventral ganglia of Branchipus. Surface view. Cephalic side at the top. $\times 75$.

Fig. 10 Section through one abdominal ganglion of Artemia. The dorsal side is above. $\times 75$.

Figs. 11, 12 and 13 Sections through various levels of the brain of Artemia, from the base to the region of the optic nerve. The dorsal side is up. $\times 75$.

nectives. Many of the medial fibers may be traced out to the optic lobes. Fibers from the largest median cephalic cells descend the connectives. Fibers from cephalic and lateral cell groups cross in the center of the brain and either run straight into commissures or cross somewhat diagonally. Fibers from the smaller cell groups on the connectives near antennal nerves descend the connectives and ascend into the central parts of the brain to the same side or the opposite side. The small cephalic branches of the brain send fibers for a short distance into the brain and cells near here supply them. The mass of the connective fibers runs straight in to the central parts of the brain. Fibers from cephalic lateral cells cross at angles to relate themselves to various cell groups, to run in the optic nerves and to run into the central part of the brain.

The connections of the optic ganglia were not studied. So far as there is a special center in the brain to which all fibers converge it would be the general region of median cephalic cells. It is from this region that the larger cells probably send their fibers long distances down the connectives to ventral ganglia.

In general the distribution of tracts in the ventral ganglia is as follows:

1. Fibers in the connectives ascending or descending.
2. Fibers from the branches or nerve trunks end, cross in commissures and ascend or descend in the connectives. Many end where they enter the ganglia or on the opposite side in the same ganglion or in the opposite ganglion.
3. Fibers in the commissures cross from cells of either group and end in relation to cells of either group of the opposite ganglion. Fibers in the commissures may also be seen to ascend or descend in the direction of the connectives.
4. Each cell area of each ganglion is probably connected as follows: a) Fibers to other cell areas of each side through the commissures. b) Fibers to cell areas of each side not from the other side through the commissures. c) Ascending fibers. d) Descending fibers.

The commissures are probably made up as follows: a) Fibers from cells in upper levels. b) Fibers from lower levels. c)

From the same level from both sides, especially from median cells. d) Probably fibers to and from lateral branches of ganglia, although this was not clearly demonstrated (fig. 4).

SOME GENERAL CONCLUSIONS

The study of these nervous systems shows certain advantages due to the nature of the material and the method. There is less distortion because with whole mounts no heat was used. There is also a more perfect picture presented than in most methylen blue preparations because all the cells show. When large ganglion cells were at the edge of the preparation quite a little could be seen of their finer structure and the fibers and fibrils were often presented with great clearness. I believe that, although the grosser processes are important, that the fibrillar connections are more important in determining the intimate relationships of cells to each other. It seems probable from these observations that any cell may have its cytoplasm penetrated by fibrils which are directly connected with other cells, while its one or two main branches carry out fibrils in larger masses, break up into fibrils and by usual methods are not followed farther.

The variation in the number of cells in similar segments suggests the probability that the nervous system acts not so much through individual innervation of special areas by special cells, as by a more general innervation by groups of cells. In the course of evolution in more specialized forms it may be that individual functions may more nearly be connected with individual cells or small groups.

BIBLIOGRAPHY

- CLAUS, C. 1873 Zur Kenntniss des Baues und der Entwicklung von *Branchipus stagnalis* und *Apus cancriformis*. Abh. k. Gesell. Wissens., Göttingen, Bd. 8.
- GRUBE, A. E. 1853 Bemerkungen über die Phyllopoden. Arch. f. Nat., Bd. 19, Berlin.
- LANKESTER, E. R. 1881 Observations and reflections on the nervous system of *Apus*. Quart. Jour. Mic. Sc., April.
- LEYDIG, FR. 1860 Naturgeschichte der Daphniden. Tübingen. 1851 Ueber *Artemia salina* und *Branchipus stagnalis*. Zeit. Wiss. Zool. Bd. 3.
- MÜLLER, P. E. 1868-9 Danmarks Cladocera. Kroyer's Tidssk. ser. 3, Bd. 5.
- PELSENEER, P. 1884 Observations on the nervous system of *Apus*. Quart. Jour. Mic. Sc., vol. 25.
- PACKARD, A. S., JR. 1883 Monograph of the phyllopod Crustacea of North America. Twelfth Ann. Rep. U. S. Geo. Surv. Terr.
- SPANGENBERG, FR. 1878 Bemerkungen zur Anatomie der *Limnadia hermanni*. Zeit. Wiss. Zool., Bd. 30.
- SPENCER, W. K. 1902 Zur Morphologie des Centralnervensystems der Phyllopoden. Zeit. wiss. Zool., Bd. 71.
- WEISMANN, A. 1874 Ueber Bau und Lebenserscheinungen von *Leptodora hyalina* Lill. Zeit. wiss. Zool., Bd. 24.
- ZADDACH, E. G. 1841 De *Apodis cancriformis*. Anat. et Hist. evolut. Bonnae.