ANATOMY AND HISTOLOGY OF THE NERVOUS SYSTEM OF EPHEMERA VULGATA L. (EPHEMEROPTERA)

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Present day views on the anatomical and histological structure of the insect nervous system are based on a large number of works by various authors. Almost all the main insect orders have been anatomically investigated in considerable detail, and the Odonata, Dictyoptera, Acridoidea, Apidae, Diptera and some other groups have been histologically investigated. There has been hardly any research on the Ephemeroptera. The world literature contains only the most general information on the anatomical structure of the nervous system of adult stage of these insects (Needham et al., 1935). The topography of the larval central nervous system has been examined in greater detail (Landa, 1969).

The inadequacy of the information on the anatomy of the nervous system in the Ephemeroptera and the complete lack of data on its histological structure prompted the present study.

METHODS

The anatomical structure of the ventral nerve cord of the mayfly Ephemera vulgata L. was investigated in fresh material and material preserved in alcohol. The fresh material was stained with methylene blue solution (0.01%) in sodium chloride solution (2.25%). The anatomy of the ventral nerve cord was also investigated in permanent total methylene preparations obtained by supravital staining with methylene blue. In the case of these preparations were used to study the histological structure of the nervous system. The object is difficult to stain; more than 1000 mayflies were used but only a few tens of stained preparations were obtained.

In order to study the nature of the motor innervation of the muscles, certain muscles were dissected along with the ventral nerve cord and permanent methylene preparations were made. The anatomy of the

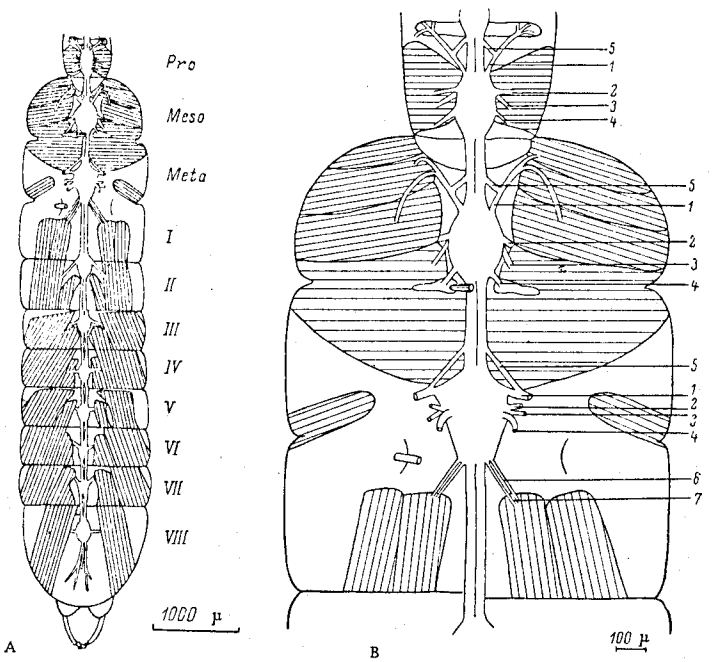

Fig. 1. General appearance of the ventral nerve cord of Ephemera vulgata L.

A) thoracic and abdominal divisions (Pro, Meso, Meta - prothorax, mesothorax and metathorax; I-VIII) abdominal segments); B) thorax (1) 1st pair of nerves; 2, 3) radicles of 2nd pair of nerves; 4) 3rd pair of nerves; 5) 4th pair of nerves; 6, 7) nerves of abdominal neuromeres).

aired nerve was also investigated in preparations ained with methylene blue.

RESULTS AND DISCUSSION

The ventral nerve cord of E. vulgata consists of ganglia: 3 thoracic and 7 abdominal (Fig. 1). It located on the ventral side of the body between the mentary canal and the ventral muscles. The racic ganglia are appreciably larger than the dominal ganglia. The prothoracic and mesothoracic glia are simple, while the metathoracic ganglion a ganglionic center. Three pairs of nerves extend m the first 2 thoracic ganglia; the nerve of the 2nd r emerges as 2 radicles, since it divides within ganglionic membrane. One of the radicles (sen- ry) runs from the ventral surface of the ganglion, other (motor) from the dorsal surface. The 3rd ve is the thickest; it runs caudad and is traceable far as the leg, which it also innervates. To judge the emergence of nerve stems from the metathorac- ganglion, it consists of a single thoracic neuro- re and two abdominal neuromeres merged with it he course of embryogeny. Three pairs of nerves from the thoracic neuromere of the metathoracic glion as they do from the first 2 thoracic ganglia. nature of their departure from the ganglion is the e. The remaining 2 pairs of nerves of the meta- acic ganglion are the nerves of the 2 abdominal romeres incorporated in this ganglionic center.

All three thoracic ganglia are typified by the pre- e of a nerve stem connecting the anterior con- ive with the 1st nerve running from the ganglion. g the stem nerve fibers from the preceding glion extending along the connective directly enter lst nerve of the following ganglion. This nerve corresponds to the 4th pair of nerves of the tho- ic ganglia.

The first 6 ganglia in the abdomen are of approxi- ly the same size and each bears a single pair of es. The last abdominal ganglion is considerably r and gives rise to 2 pairs of nerves, which sug- s, on its comparison with the other abdominal lia, that it contains 2 neuromeres.

Consequently, the metathoracic ganglion and the abdominal ganglion are ganglionic centers, or nglia, consisting of several ganglia that have d in the course of embryogeny, i.e. there are enters of fusion in the ventral nerve cord of E. ta.

The system of the unpaired nerve which, accord- Zavarzin (1924a), corresponds in insects to the sthetic division of the vertebrate nervous sys- has not previously been described in mayflies. btain permanent total methylene preparations of ntral nerve cord in which the system of the un- nerve was stained. A segment of the unpaired runs from the dorsal surface of each ganglion in horax (Fig. 2). This comparatively short nerve ded into 2 branches (left and right). In addition, in the thorax and in the abdomen, what is known median nerve extends along the ventral nerve from ganglion to ganglion between the connectives. en ganglia it gives rise peripherally to a pair nsverse nerves. Their point of origin is shifted ically or caudally depending on the location of the racles in the segment concerned.

We were able to detect neurohemal organs in lene preparations of the ventral nerve cords of

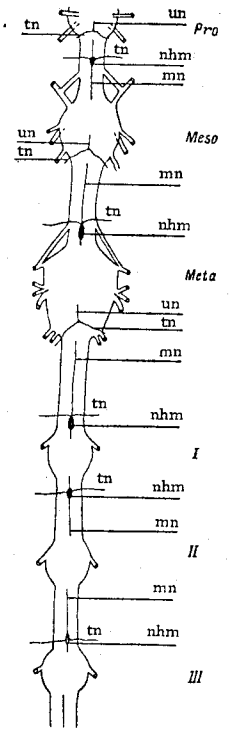

Fig. 2. Structural diagram of the system of unpaired nerves and the location of the neurohemal organs in Ephemera vulgata L.

mn) median nerve; nhm) neurohemal organ; un) unpaired nerve; tn) transverse nerves; Pro, Meso, Meta) thoracic ganglia; I, II, III) abdominal ganglia; the emergence of a nerve radicle from the ventral side of the ganglion is indicated by a dashed line.

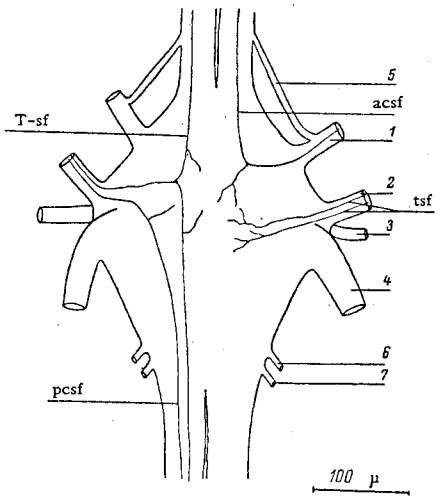

Fig. 3. Sensory fibers of the metathoracic ganglion of Ephemera vulgata L.

pcsf) posteroconnective sensory fibers; acsf) anteroconnective sensory fibers; tsf) terminal sensory fibers; T-sf) T-shaped sensory fibers. Otherwise as in Fig. 1.

mayflies (Fig. 2). The neurohemal organ in each segment lies on the median nerve where the transverse nerves originate from it.

As in all other insects, the ventral nerve cord of mayflies has a connective tissue sheath. We obtained preparations in which the outer noncellular layer of the sheath stained well. It invests both the ganglia and the peripheral nerves. This layer incorporates many collagen fibers, which run mutually parallel and do not branch. They extend all along the nerve cord, without interruption. In addition, there are collagen fibers in the sheath investing the unpaired nerve. The ventral nerve cord is supported in the body cavity by connective tissue tendons that extend, branching profusely, not only to the ganglia, but also to the nerves running from them.

We obtained some information on the structure of the ganglia in the ventral nerve cord. As in other insects, the bodies of the motor and associated neurons of mayflies lie on the periphery of the ganglia of the ventral nerve cord. The bodies of the sensory neurons lie outside the ganglia in the tissues of the organ that is innervated. The central processes of these sensory cells, the sensory fibers, extend from the periphery to the ventral part of the ganglion and branch in the sensory neuropil. A cell process extending from the body of the motor neuron lying on the periphery of the ganglion extends all across the neuropil and joins on the dorsal surface of the ganglion with a branch of the nerve cord from which there originate dendrites and an axon extending into the lateral nerve. The zone of the principal neuropil lies between the motor and sensory zones. The long conducting fibers that form the ventral and dorsal regions of the connective fibers occupy the most ventral and dorsal position in the ganglion. Consequently, the neuropil of mayfly ganglia consists of the same principal zones as have been described by Zavarzin (1924b) in a larva of the genus Aeschna (Odonata).

We succeeded in staining the sensory elements of the metathoracic ganglion and some of the abdominal ganglia. The pattern was practically the same in both instances, but since it was more complete in the metathoracic ganglion we shall describe the sensory elements that were discovered on the basis of the last thoracic ganglion (Fig. 3). Here we found sensory fibers extending through the first pair of nerves and the sensory radicle of the second pair of nerves, branching and terminating on their side of the ganglion as terminal fibers. In addition, we stained fibers that gave rise to collaterals dividing into several small branches and running along the connective to the mesothoracic ganglion. Tsvileneva (1953) has referred to such fibers in a larva of the genus Aeschna as anteroconnective. The posteroconnective fibers give rise to a collateral on their side and extend to the posterior connective. In addition, there are fibers here that divide into two branches immediately after entering the ganglion, each of which gives rise to short smaller branches. One branch extends to the anterior connective, the other to the posterior connective. These are T-shaped fibers. Consequently, the neuropil of mayflies consists of the same sensory elements as have been described in other insects.

We discovered motor neurons in the abdominal ganglia of Ephemera vulgata typified by emergence of the axons into the posterior connective. The axons of ordinary motor neurons extend to the lateral nerve of the ganglion itself, while emergence of the axons into the connective is typical of associative neurons. However, we confidently classify the neurons discovered as motor neurons, since their branches in the ventral nerve cord are not in the principal neuropil, as in

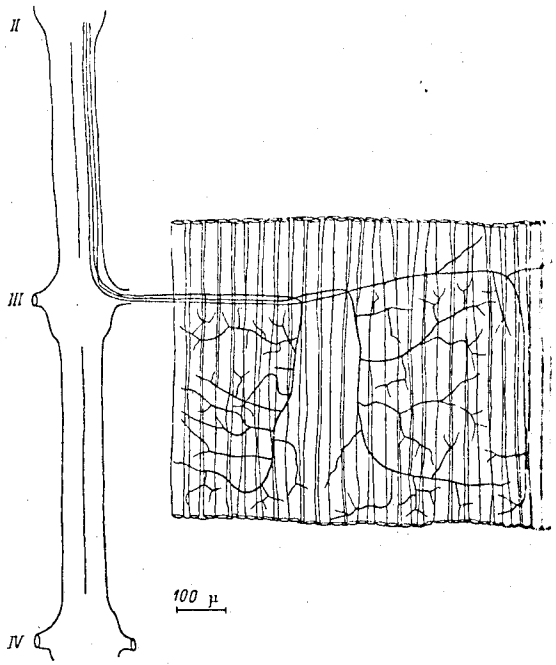

Fig. 4. Motor innervation of ventral abdominal muscle of Ephemera vulgata L.

II, III, IV) 2nd, 3rd and 4th abdominal ganglia.

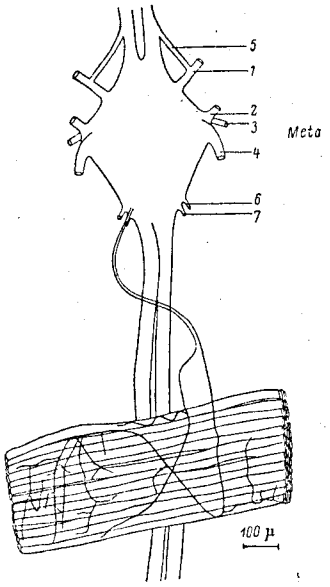

Fig. 5. Motor innervation of part of ventral muscle of Ephemera vulgata L.

Meta) metathoracic ganglion. Otherwise as in Fig. 1

associative neurons, but in the zone of the motor neuropil. We traced the axons of motor neurons extending caudad along the connectives to the next abdominal ganglion (Fig. 4). The axons enter this ganglion along the anterior connective and emerge on the periphery as part of its single lateral nerve. We observed the course of the axons along the nerve to the ventral abdominal muscle which they innervate.

Such motor neurons, which send out axons through the posterior connective to the next ganglion and innervate the muscles of the following segment were found in the first 5 abdominal ganglia with 3 pairs of symmetrical neurons in each. Neurons of this type have been described by Tsvileneva (1970) in the 3rd thoracic ganglion of a larva of the genus Aeschna (Odonata). Here they send out an axon into the short posterior connective, are traceable along it to the accessory abdominal ganglion and emerge onto the periphery with its lateral nerve. These axons were not traced to the muscles. Plotnikova (1973) has described motor neurons in the abdominal and thoracic divisions of the thoracic nerve cord of Locusta migratoria, the axons of which extend to the posterior connective. However, owing to the length of the connective she was not able to trace them to the following ganglion. It is interesting that these motor neurons of L. migratoria are very similar, in the nature of the branches in the nerve cord and in the arrangement of the dendrites, to the effector neurons described by the present authors in Ephemera vulgata.

In addition to this type of motor innervation of the muscles, there is also innervation of the muscles in E. vulgata by motor neurons, the axons of which do not extend to the posterior connective, but to the lateral nerve of their ganglion. We give the example of the motor innervation of a part of the ventral muscle by two motor neurons of the metathoracic ganglion, the axons of which emerge through the lateral nerve of the final abdominal neuromere of this ganglionic center (Fig. 5). Consequently, the motor neuropil of mayflies also contains the same motor elements as have been discovered in other insects investigated.

SUMMARY

It has been demonstrated on the basis of an anatomical study of the ventral nerve cord of the mayfly Ephemera vulgata that it consists of 3 thoracic and 7 abdominal ganglia and their connectives. There are 5 synganglia in the ventral cord of this species: the metathoracic ganglion incorporates the ganglion of the 3rd thoracic segment and 2 abdominal neuromeres, while the last abdominal ganglion incorporates at least 2 neuromeres.

An account is given of the structure of the system of the unpaired nerve and the location of the neurohemal organs.

The neuropil of mayflies is typified by the presence of the same sensory and motor elements as for the other insects investigated. The motor innervation of the muscles in the abdominal division has been found to be effected by the axons of neurons whose bodies lie in the ganglion of the previous segment.

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