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Acta Biologica Szeged. 23 (1—4), pp. 89—95 (1977)

ANATOMY OF THE NERVOUS SYSTEM OF MAYFLY LARVAE (PALINGENIA LONGICAUDA OLIV)

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(Received October 8, 1976)

Abstract

The nervous system of the mayfly larva is a modified ventral nervous cord, the ancient traits of which are the double connectives providing segmentation and the partial fusion inside segments. Its characteristic, pointing to the development, is the formation of complexes of the third thoracal and seventh abdominal ganglia. Comparison of the results with other literature data indicates that the mayfly is one of the most ancient species of the Ephemeroptera.

Introduction

In recent years, research into the life, organizational construction, and occurrence of the Arthropoda has become more and more comprehensive. It is understandable therefore, that such knowledge relating to the Ephemeroptera is being completed with an ever increasing number of data.

The mayflies, that representing one of the most ancient groups of the present-day Arthropoda, may afford a reliable starting-point for the solution of a number of problematical questions (mainly with respect to evolution, but often morphology or anatomy, as well).

The peculiar, hidden life, long development, and restricted geographical occurrence of the mayfly (*Palingenia longicauda*) larva are all factors explaining why we know comparatively little about the constructions of their organisms and organs (LANDA, 1969; SWAMMERDAM, 1675).

In the present paper, our aim was an exact anatomical study of the central nervous system of the larva. This work will serve as the basis for further of our results a waiting publication.

Materials and Methods

The larvae used in our investigations were collected from the rivers Tisza and Maros. Studies were carried out on larvae in different stages of development, but our findings and photographs all refer to the larvae in the last year of their life. (It is to be noted that the localization of the ganglia and the course of the nerves are similar in the younger larvae the only differences observed related to their sizes.)

The larvae collected were fixed partly in 70 per cent alcohol, and partly in 10 per cent neutral formalin. To facilitate study of the localization of the ganglia and the courses of the nerves, STEINMANN'S (1960a) negative staining technique was applied.

Results and discussion

The nervous system of the larva is a double ventral nerve cord. It has preserved the ancient features (double connectives, segmentation) in many respects, but, at the same time, in the case of the ganglia of the nerve cord, we could observe further fusions.

Similarly to other Arthropoda, three main parts may be distinguished in its nervous system: the oesophageal nerve ring, the thoracic and the abdominal ganglia (DUPORTE, 1915; HANSTRÖM, 1928; PETERSON, 1912; WEBER, 1966).

The cerebral ganglia forming the oesophageal nerve ring (ggl. supraoesopha-

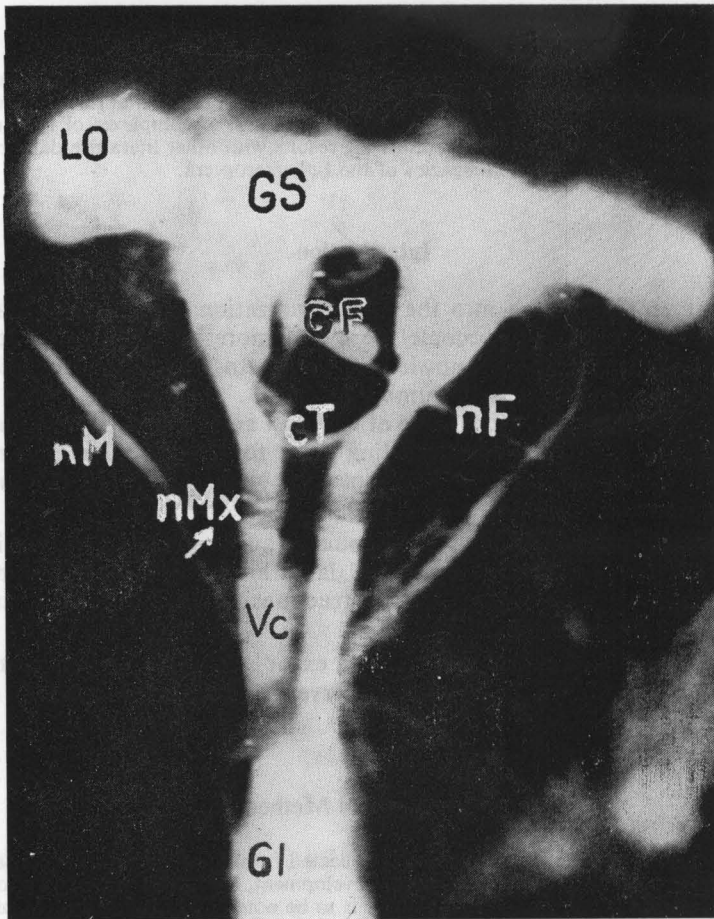


Plate 1. Oesophageal nerve ring of the *Palingenia longicauda* larva ($\times 45$).

(CT=commissura tritocerebralis, GF=ganglion frontale, GI=ganglion infraoesophageum, GS=ganglion supraoesophageum, LO=lobus opticus, nF=nervus frontalis, nM=nervus mandibularis, nMx=nervus maxillaris, Vc=connectivum ventrale).

geum), the suboesophageal ganglion (ggl. infraoesophageum), and the connectives between them can be well differentiated (Plate 1).

The cerebral ganglion (with the largest dimensions) has grown together out of three paired ganglia, and consequently it can be divided into three cerebral sections (HANSTRÖM, 1928; PETERSON, 1912; STEINMANN, 1966b; WEBER, 1966). Its anterior part is the protocerebrum, divided into two parts by the intercerebral fossa. At its lateral part the lobus opticus (of similarly large extent) appears with the strongly pigmented eyes. Somewhat laterally from the intercerebral fossa, symmetrically, the nerves of the point (simple) eyes may be observed.

The deutocerebrum, occupying the central site, grows more narrow as it proceeds backwards. The sensory and motor fibres of the nerves of the antenna, as well as the frontal nerves, are localized dorso-laterally. The former leave the brain in a common nerve, but the sensory and motor fibres soon branch off.

The tritocerebrum turns backwards in the ventral direction, grows quite narrow, and runs close to the pharynx. Its biggest nerve, the upper nervus labralis, starts out of the ventral side of the brain. On the medial side of the third brain section the only cerebral commissure, the tritocerebral commissure, is to be seen. In the beginning, the first ventral connective runs parallel with this, joining the brain to the suboesophageal ganglion (ggl. infraoesophageum). The nerves leaving the suboesophageal ganglion are vigorous. These are the nervus mandibularis, the nervus maxillaris and the nervus labialis. In the mayfly larvae (just as in the chewing insects) these nerves are powerfully developed (KÜKENTHAL et al., 1930; STEINMANN, 1960b; 1962; VAJON, 1970; WEBER, 1966).

From a comparison of the nervous systems of the larvae and imagos it was possible to establish that these nerves were poorly developed in the imagos, and progressively degenerated in time before development into the imago.

The ggl. frontale is to be found in the oesophageal nerve ring. It is joined to the tritocerebrum by a very thin small nerve. Starting from the ganglion, the nerve runs backwards to the dorsal part of the alimentary canal.

The suboesophageal ganglion is joined by ventral connective II to thoracic ganglion I (Plate 2). In the area of the thorax three dorso-ventrally flattened paired ganglia can be found, corresponding to the three thoracic segments. The ganglia are joined together by paired connectives. A big nerve, the nervus ventralis, emerges laterally from every ganglion. This soon divides into several branches, bringing about a plexus (Plate 3, Fig. 2). The branches innervate the longitudinal muscles of the ventral side.

The nerves (nervus lateralis) originating in the anterior-lateral part of the ganglia innervate the dorsal longitudinal muscles and those lying orbicularly in the segments (CAMPBELL, 1961; EWER, 1954; GREGORY, 1974). An unpaired nerve, the nervus medialis, originates from the ventral side of the ganglia. For a while this runs parallel with the longitudinal connectives linking the two ganglia. It then divides into two branches, the transversal nerves. The nervus medialis and nervus transversalis are also parts of the sympathetic nervous system (PETERSON, 1912, SRIVASTAVA, 1972; VAJON, 1962). In thoracic ganglion III, there originate other nerves, apart from those mentioned above, from the posterior-lateral part of the ganglion (Plate 2, Plate 3, Fig. 1). These go over from the third thoracic segment into the first abdominal segment. There they divide into two branches, innervating the dorsal, and ventral

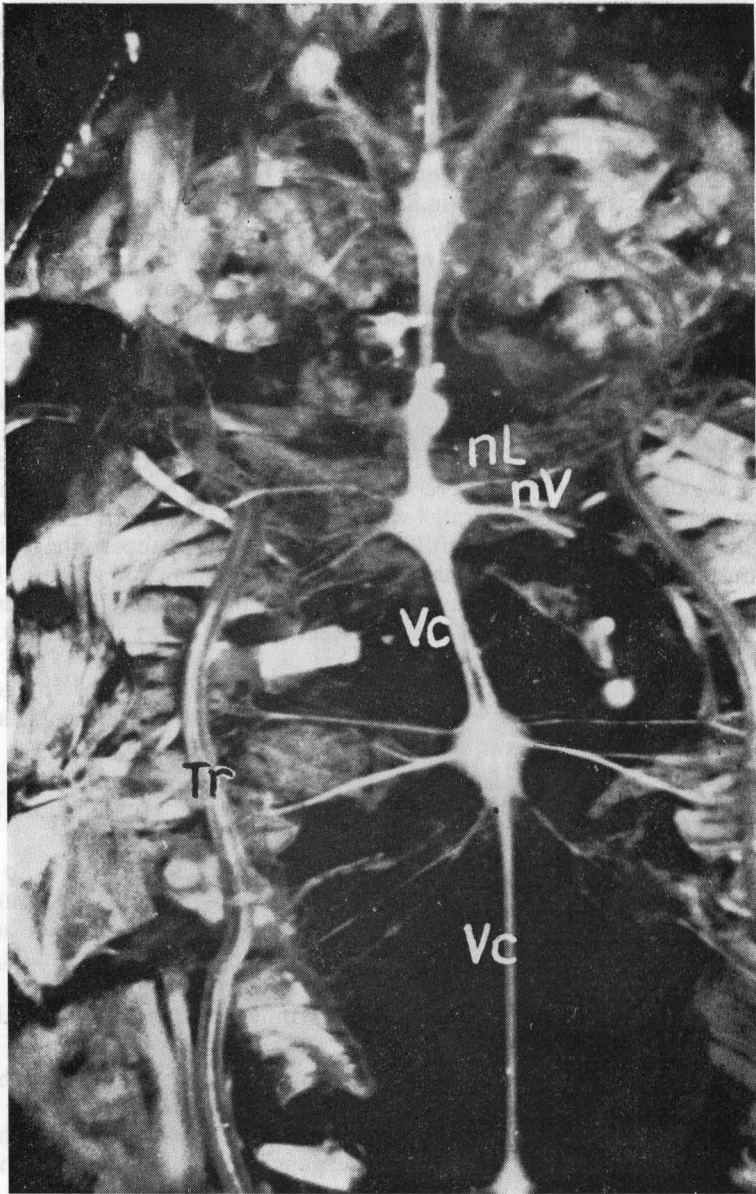


Plate 2. Thoracic ganglia of the larva ($\times 17$).

(nL=nervus lateralis, nV=nervus ventralis, Tr=trachea, Vc=connectivum ventrale).

muscles of the first abdominal segment (KÜKENTHAL et al., 1930). In the first abdominal segment no ganglion was found. We assume that in the course of the embryonal development this ganglion fused with the last thoracic ganglion (ggl. metathoracale).

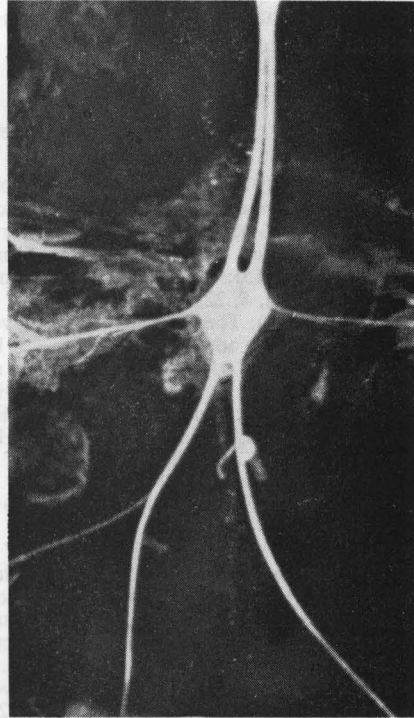
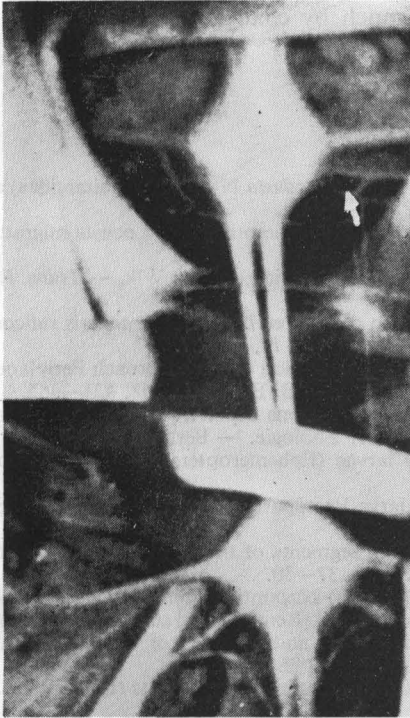
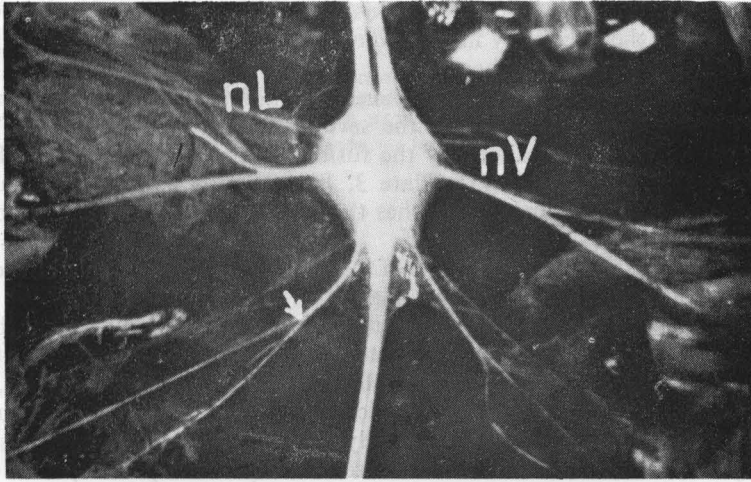


Plate 3. Fig. 1. Magnified picture of the third thoracic ganglion ($\times 24$). (nL=nervus lateralis, nV=nervus ventralis. The arrow indicates the nerves going over to the first abdominal segment).
 Fig. 2. A detail of the thoracic ganglia ($\times 25$). (The arrow indicates the plexus system of the nervus ventralis).
 Fig. 3. Ganglion abdominale VII ($\times 30$).

This seems to be verified by the extreme length of the connective lying between the third thoracic and the effectively first abdominal ganglia (in abdominal segment 2), being about twice as long as the others.

In the eleven segments of the abdomen seven abdominal ganglia can be found, lying in segments 2 to 9. The last of the seven ganglia (ggl. abdominale VII) is a ganglionic complex brought about by the fusion of three paired ganglia (BIRKET—SMITH, 1971). Ggl. abdominale VII (Plate 3, Fig. 3) ends in two powerful nerves, bringing about with their further branches the somatic nerves of the last abdominal segments.

Comparison of the nervous systems of the larva and imago revealed the considerable identity in the positions of the ganglia.

It can be said of the Arthropoda in general, including the mayfly, that the degree of development of the central nervous system is determined by the extent to which it is concentrated. This concentration is of low degree in the species studied, because it can be observed only at the third thoracic and seventh abdominal ganglia. Hence, ten paired ganglia may be found in the body of the mayfly. This confirms that the mayfly may be considered one of the most ancient Ephemeroptera species (KÜKENTHAL et al., 1930; LANDA, 1969). The degree of brain development, of course, must not be left out of consideration, either. However in our opinion, the latter may be characterized within the Arthropoda not so much by changes in dimension as by structural changes.

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