Architectonics of the Central Nervous System of Acoela, Platyhelminthes, and Rotifera

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Abstract—Based on the literature and own data, consecutive stages of development of the central nervous system (CNS) in the lower Bilateria are considered—separation of brain from parenchyma, formation of its own envelopes, and development of the trunk and orthogonal nervous system. Results of histochemical (cholinergic and catecholaminergic) and immunocytochemical (5-HT- and FMRF-amid immunoreactive) studies of the CNS in representatives of Acoela, free living and parasitizing Platyhelminthes and Rotifera are considered. The comparative analysis makes it possible to describe development and complication of the initially primitive Bilateria plexus nervous system. A special attention will be paid to the Acoela phylogenesis, based on molecular-biology data and results of study of their nervous system.

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INTRODUCTION

Phylogeny of lower Bilateria has been essentially revised for the last few years due to results of molecular–biological studies. The basic state of Acoela (acoelic turbellaria) among Bilateria was accepted by outstanding zoologists, particularly by our teacher Academician A.V. Ivanov. However, until recently, this group was placed among Platyhelminthes (flatworms) and thereby the entire group of flatworms turned out to be in the base of the Bilateria tree. The current molecular phylogeny indicates that Acoela is the most ancient branch of the Bilateria tree, which is independent of Platyhelminthes [1–3]. Nowadays, Platyhelminthes are ascribed to the Lophotrochozoa group combining animals with trochofore-like larva (annelids, molluscs, etc.) or with a lophophore [4]. Rotifera are also ascribed to this group [5]. Recently, Platyhelminthes have been subdivided into two groups: Catenulida and Rhabditophora [6]. The latter includes both the major part of free-living and all parasitic flatworms. Until now, no clear synapomorphies combining these two groups have been found. Rhabditophora apart from macrostomids form the Trepaxonemata group with a certain type of spermatozoid axoneme (the spiral central cylinder) [6], which characterizes it as the monophyletic group.

For the last quarter of the XX century, histochemical and immunocytochemical (ICC) methods have become predominant for study of the invertebrate nervous system by using fluorescent and confocal laser scanning microscopes. These techniques have made it possible to reveal parts of the nervous system with a certain ergity and immunoreactivity (IR), which expanded significantly the results obtained using classic histological methods.

Due to the recent revision of the Bilateria mac-
system, it seems essential to analyze the extensive material on the nervous system structure and to evaluate morphologic data on the central nervous system (CNS) including brain, longitudinal trunks, and their connecting commissures. CNS appeared in the flatworms. It is to trace the initial stages of improvement not only of all elements of this system separately, but also of the system as a whole, and to analyze pathways of its evolution in Acoela, Rhabditophora, and Rotifera. For performance of the phylogenetic analysis, 150 species of Bilateria belonging to Acoela (24 species), Platyhelminthes—Rhabditophora, including free-living turbellaria (64 species), cestodes (22 species), trematodes (16 species), monogeneic flukes (9 species), and rotifers (15 species) were studied. Cholinergic (ACh-ergic), catecholaminergic (CA-ergic) and 5-HT- and FMRF-amide or GYRF-amide-immunoreactive (IR) parts of the nervous system were examined. Peculiarities of exposure of all parts of the nervous system and their interaction are an index of their developmental level, while the level is determined by analysis of the obtained data.

**ACOELA**

Nervous apparatus of the acoelic turbellaria is characterized by unusual diversity and gives examples of incomplete state that is usually interpreted as initial for all Bilateria [7]. We called the acoelic nervous system the trunk nervous system [8] and the brain—the commissural brain [9]. Histochemical and ICC studies showed that Acoela brain looks like a ring, arch, or several commissural rings connected with longitudinal connectives [9–11]. It has no its own membrane and is penetrated by muscle fibers and ducts of frontal glands [12, 13]. Some longitudinal ACh-ergic trunks run from the brain; they lose strong longitudinal orientation at the posterior end of the body and fuse with the submuscular nervous plexus twining round the whole body of acoelic turbellaria [14]. The dorsal part of the Acoela nervous system is always developed better than the ventral one regardless of the brain shape and the umber of trunks (Fig. 1a). In Platyhelminthes Rhabditophora and most Spiralia, the dorsal nervous trunks are never dominating (Fig. 1b).

Both brain and the nervous trunks demonstrate selective localization of 5-HT- and FMRF(GYIRF)-amid IR without colocalization of polypeptides and monoamines in the same cell. In the brain area, many small and several pairs of large 5-HT-IR neurons are found (Fig. 2a), mainly in the sites of intersection of connectives and commissures. The FMRF(GYIRF)-amid IR reveals symmetric clusters or 1–2 symmetric pairs of large peptidergic neurons (Fig. 2b) [11].

Our studies have confirmed the dual (orthogonal + endon) nature of the brain [15]. The 5-HT- and FMRF-amide IR elements correspond to the brain “orthogonal” part (Figs. 1a, 1b). However, these IR elements were not found in the other, endonal,

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1 *Abbreviations for figures.* AA—Anterior arch; AC—anterior commissure; C—commissure; CC—circular commissure; DC—dorsal connective; DLT—dorsolateral trunk; DLS—dorsolateral neuron; DN—dorsal neuron; DS—dorsal trunk; E—eyes; ES—elliptical structure; B—brain; BN—brain neuron; LC—lateral connective; LS—lateral trunk; N—neuron; Ne—neuropil; PC—posterior commissure; S—statocyst; VLN—ventrolateral neuron; VLT—ventrolateral trunk; VN—ventral neuron; VT—ventral trunk.