Ultrastructure of Glial Cells in the Nervous System of *Grillotia erinaceus*

N. M. Biserova

Moscow State University, Moscow, Russia

Papanin Institute of Inland Waters, Russian Academy of Sciences, Borok, Yaroslavl oblast, Russia

e-mail: nbiserova@yandex.ru

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Abstract—Until now, there has been no answer to the question of whether specialized glial cells exist in the nervous system of platyhelminths. The identification of these cells in parasitic flatworms is difficult due to their organization as parenchymal animals. The goal of this study was to reveal and describe structural elements corresponding to the term glia in the CNS of the parasitic flatworm *Grillotia erinaceus* (Cestoda: Trypanorhyncha). Three types of glial cells are revealed. The first type consists of fibroblast-like cells located in the cerebral ganglia that contain fibrils and excrete onto the surface fibrillar material and possess desmosomes; the presumable function of fibroblast-like glial cells is the isolation and support of ganglionar neurons. Glial cells of the second type form a myelin-like envelope of giant axons and bulbar nerves of the scolex and have laminar cytoplasm; they are numerous and exceed the number of neurons in the composition of nerves. Glial cells of the third type form multilayer envelopes in the main nerve cords and make contacts with the excretory epithelium; however, specialized junctions with neurons were not found. The existence of glia in other free living and parasitic flatworms is discussed.

Key words: nervous system, flatworms, glia, giant axons, ultrastructure, *Grillotia erinaceus*, Cestoda, Trypanorhyncha.

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INTRODUCTION

Glial cells are obligatory satellites of the nervous systems of higher animals. They perform important functions in the trophics and metabolism of neurons and supporting and barrier functions, as well as speed up impulse conduction in the nervous system. Information about the stage of evolutionary development of the nervous system at which the structural and functional differentiation of glial cells occur is insufficient. It is suggested that the phylogenetical foundation of differentiation and the development of the neuroglial relations originated from worms. The issue of the presence of glia in flatworms is rather disputed and poorly studied. The identification and description of the structure of glial cells in worms is quite problematic, as criteria of the true glia have been developed for vertebrates. At present, there is no answer to the question of whether there are specialized glial cells in the flatworm nervous system. Until recently, any special studies on the detection of glial elements and on the character of glia-neuronal relations in parasitic flatworms have been absent.

The absence of myelination of nerve fibers, as well as axonal enlargements and soma of neurons, has repeatedly been noted as a typical feature of the ultrastructural organization of the nervous system of free living flatworms (Golubev, 1982). The existence of glia in parasitic flatworms is studied even less, although the absence glial cells in parasitic platyhelminths have been postulated in many reviews (Halton and Gustafsson, 1996; Halton et al., 1997).

In connection with this, the identification in amphilinidae (*Amphilina foliacea*) of specialized glial cells and the existence of isolated nerve fibers seems to constitute a breakthrough in the process of understanding the structural evolution of the flatworm nervous system. Ultrastructural studies have shown the presence of myelin-like envelopes of cords and ganglia that contain specialized cellular and intercellular elements (Biserova, 2000a, 2000b).

The nervous systems and sensory organs of several cestodes from the order Trypanorhyncha were studied at the histological and ultrastructural levels (Biserova, 1987; 1991; 2002; Rees, 1988; Halton et al., 1994; Casado et al., 1999; Palm, 2000; Palm et al., 2000); however, information about the presence of glial cells or of cells accompanying neurons is lacking.

The task of the present study was to reveal and to describe structural elements corresponding to the term glia in the CNS of *Grillotia erinaceus* (Cestoda: Trypanorhyncha).

MATERIALS AND METHODS

Materials for study were adult mature tapeworms *Grillotia erinaceus* (Trypanorhyncha, family Lacistorhynchidae) from the spiral valve of the ray *Raja clavata* caught in the coastal waters of the Black Sea.

For ultrastructural studies, the objects were fixed in 2% glutaraldehyde (SERVA, GmbH, Germany) in 0.2 M phosphate buffer with an addition of 0.1 M sucrose with subsequent postfixation in 2% osmium tetroxide (Moscow Khimzavod, Russia) in the same buffer. Dehydration was performed in alcohols and acetone; objects were embedded in Araldite (Merck & Co., Inc., USA) and polymerized at 37 and 60°C. Anatomy of the nervous system was studied in semithin sections stained with 1% methylene blue. Ultrathin sections were obtained using an LKB-III ultramicrotome and contrasted in 4% aqueous solution of uranyl acetate at 37°C and lead citrate. The preparations were examined in a JEM-100C (JEOL) electron microscope.

RESULTS

Central nervous system (CNS) of *Grillotia erinaceus* is represented by paired bilobed cerebral ganglia (CG) connected by a median commissure. Running from the ganglia forward to the parietal area are four proboscis nerves and several bothridial nerves; running to the posterior end are four bulbar nerves and main nerve cord (MNC) located laterally in the strobile (Fig. 1). Ultrastructural studies of the CNS in the scolex and strobile of *G. erinaceus* have shown that, apart from neurons, the cerebral ganglia, nerves, and main cords contain satellite cells that form the envelopes of the nervous system.

Cerebral ganglia. Distribution of neuronal bodies and processes in CG is rather loose and intercellular space contains rough fibrils; they are directly adjacent to neurilemma and often fill invaginations by forming an additional support to neurons. The ganglionar neurons are surrounded by processes of fibroblast-like cells (Fig. 2). Processes of these cells contain various fibrils and are connected with each other by numerous dense contacts for protection and isolation of the neurons (Fig. 2b). The fibroblast-like cells do not contain vesicles in perikaryon and are characterized by a blade-shaped nucleus and the cytoplasm filled with filaments, fibrils, and microtubules. It is possible to observe complex interrelations of neurons with fibroblast-like cells that penetrate inside the neurilemma invaginations and form short desmosome-like contacts (Fig. 2a). The main function of the fibroblast-like glial cells is the isolation and support of ganglionar neurons.

Proboscis nerves. The proboscis nerves involving neuronal bodies run from cerebral ganglia forwards to the parietal area along proboscis sheaths. The neurons form synaptic contacts between processes, although less than in cerebral ganglia neuropils. The intercellular space between neuronal bodies or processes in proboscis nerves is filled with thin filaments of the extracellular matrix. Outside, the proboscis nerves are covered with processes of the envelope cells, which contain electron-dense cytoplasm. The external plasma membrane of the envelope cells bears numerous rough fibrils. Cell processes form a rather loose envelope without tight interrelations with neurons and contacts between processes are rare; in their ultrastructure, they are similar to cells that form the glial envelopes of the main lateral cords as described below.

Bulbar nerves. Large bulbar nerves run from cerebral ganglia to the posterior end of the body along the median surface of the proboscis sheath and muscular bulbs (Fig. 3). These nerves are located in the central parenchyma zone. Ultrastructural analysis has shown that nerves are composed of large nerve fibers, are wrapped in glial cells, and lack perikarya of neurons. Each of the 4 bulbar nerves contains 2 giant axons of up to 12.5 μm and one middle-sized axon neighbor to the giant ones. Thinner fibers are arranged in lobes and glomerules and are tightly adjacent to each other (Biserova, 2002).

Giant axons have radially directed invaginations of axolemma and contain microtubules oriented strictly along the fiber, as well as a small number if neurofilaments and cisterns of smooth endoplasmic reticulum. Organization of the neuropil of bulbar nerves is characterized by high differentiation. Synaptic glomerules are revealed; unlike amphilinids (Biserova, 2000a), they often are composed only of two neurites (Fig. 3a, arrow). The glomerule is wrapped by a glial cell thin process containing electron-dense cytoplasm and the internal surface of adjacent membranes of neurites forms a long synapse (Fig. 3a, arrow). Most often, the synaptic membranes are curved as a zigzag line and form mixed-type junctions, including zones of chemical and electric synapses. In the chemical synapse zone, clear ovoid vesicles are revealed, while in the electrical synapse zone, a desmosome-like contact is observed; mitochondria are adjacent to one of the areas of contacting membranes. Most small neuritis are combined in compact groups (Fig. 3b), or lobes; synaptic clefts between them are enlarged and contain intercellular substance. The differentiation of neuropil into zones—giant axons, glomerules, groups of neurites—seems to be correlated with functional peculiarities of bulbar nerves innervating muscular proboscis bulbs.

Each bulbar nerve is wrapped by a common glial envelope; each giant axon is surrounded by its own envelope, unlike smaller processes whose membranes are directly in contact with each other. Nuclei of envelope cells are located symmetrically at the periphery of the nerve (Fig. 3b).

The glial envelope on the surface of bulbar nerves has a different ultrastructure than in CG (Fig. 3). Nuclei
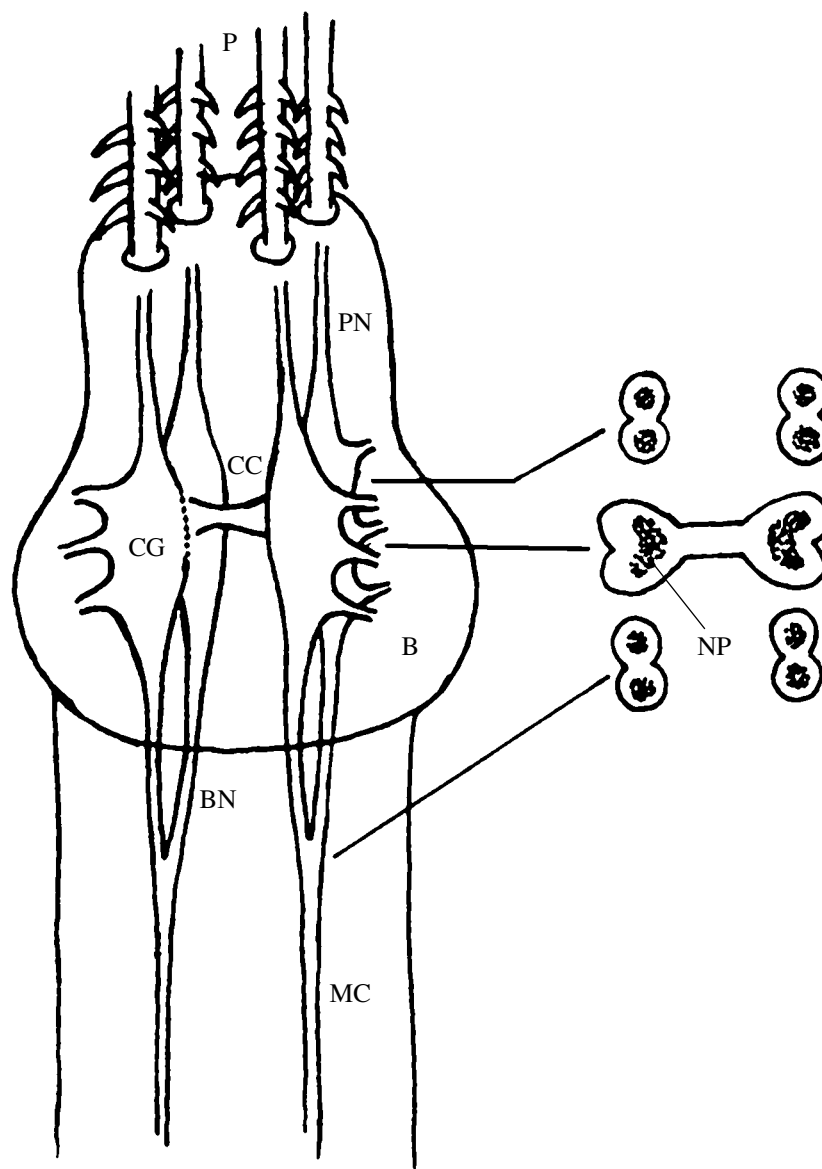
Fig. 1. Anatomical scheme of the CNS in scolex of *Grillotia erinaceus* (Trypanorhyncha). B, bothria; BN, bulbar nerves; MC, main nerve cord; NP, neuropil; CG, cerebral ganglion; CC, cerebral commissural; P, proboscis; PN, proboscis nerve.

of glial cells are smaller and elongated in shape, and are located on the nerve surface near giant axons. The cytoplasm contains thin filaments, lipid droplets, and numerous stretched membrane structures, which leads to the layered structure of the cell cytoplasm (Figs. 3b–3d). The membrane layers are parallel to the external plasmalemma and smoothly surround the nuclei, mitochondria, lipid droplets; the zone of the Golgi complex has not yet been revealed. Processes of glial cells wrapped each giant axon. A portion of slim axons form glomerules covered by the common layer of the glial envelope. Glial cell processes do not come to the synaptic contact zone inside the glomerule, but they do penetrate into the folds of axolemma. Most bulbar nerve axons are characterized by radial folds of the axolemma and a deep penetration of glial cell processes inside the invaginations. Desmosome-like densities in the invagination zones were not observed.

The main nerve cords. The MCs run along the body cortically from the excretion channels. In their level of muscular bulbi, MCs do not exceed or are thinner than bulbar nerves. In the transverse section of the plerocercoid scolex, MCs are seen to be shifted from the central position to one side of the body towards one of the bothria.

Neuronal bodies in this area are extremely rare. Neurites are grouped in lobes containing tens of pro-
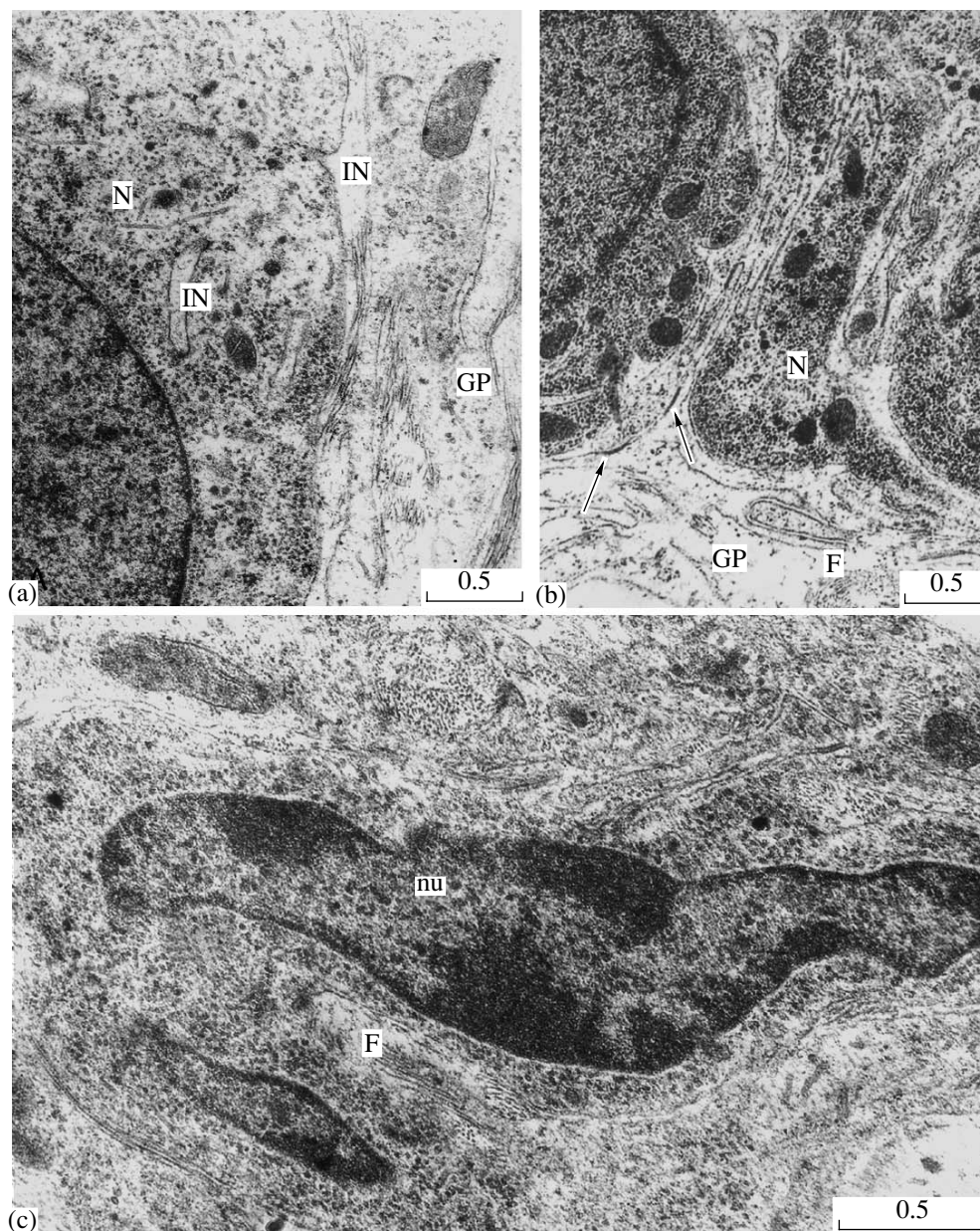
Fig. 2. Fibroblast-like glial cells (type 1) are located in the cerebral ganglion. (a) The ganglionar neuron is surrounded by processes containing supporting fibrils that are inserted into matrix and surround neurilemma and its invaginations; (b) fibroblast-like cell processes encircle cerebral ganglion neurons and permeate into neuropil; arrow indicate specialized contacts between glial processes; (c) the nucleus and an area of the cytoplasm of the fibroblast-like glial cell. F, extracellular fibers; GP, glial cell process; IN, invagination of the neurilemma; N, neuron and nerve process; nu, glial cell nucleus.

cesses of different sizes; each lobe is surrounded by its own very thin, electron-dense glial envelope.

In the posterior part of the scolex, MCs occupy a lateral position and are represented by the main and accompanying bands composed of light and darker processes of different sizes. The central part of the cord is surrounded by the multilayer electron dense envelope (Figs. 4a, 5a, 6). Bodies of nerve and muscle cells are located at the periphery in the external layer. It is interesting to note the presence of large (giant) axons in the

MC (Fig. 6a), the membranes of which form deep invaginations with mitochondria located near them. The giant axon cytoplasm contains many neurotubules. The presence of numerous neurotubules in general is characteristic of light axons. Neuronal processes are combined into isolated groups and wrapped with an envelope; series of synaptic contacts are formed inside the groups between neighboring nerve processes.

The MC envelope is formed by thin processes of glial cells that have dark, dense cytoplasm and is asso-
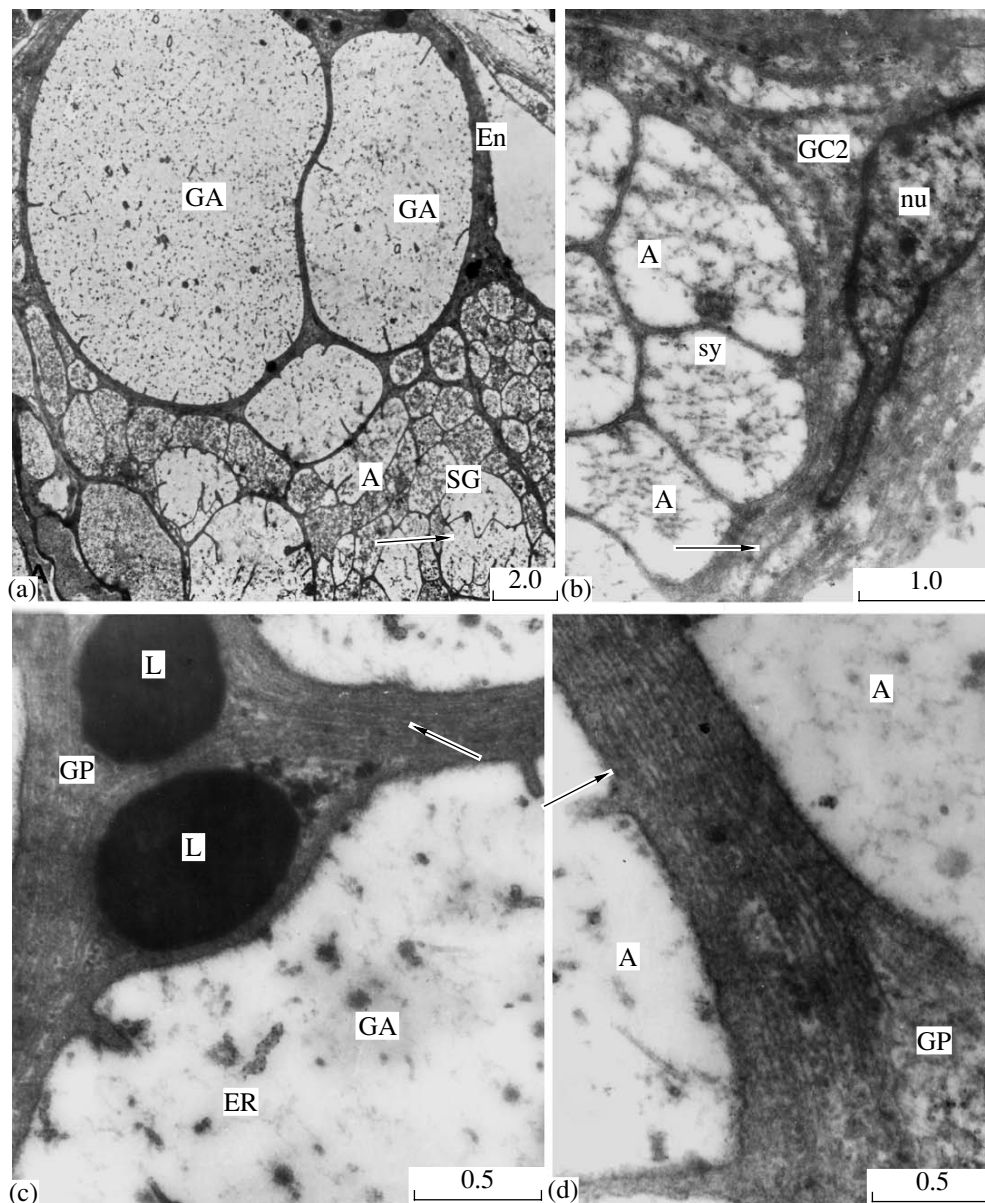
Fig. 3. Structure of the glial cells (type 2) located in the bulbar nerves of *Grillotia erinaceus.* (a) The bulbar nerve with giant axons and bundles of fine neurites; it is surrounding by electron dense envelope formed by peripheral glial cells; neurites in the synaptic glomerule form a synapse (arrow); (b) nucleus of the glial cell, the cytoplasm contains lamella membrane structures (arrow); (c) lipoprotein granules and stretched membrane layers (arrow) in the cytoplasm of the glial cell; (d) cytoplasm in the glial cell process; contains filaments and lamellas of membranes, forming thin layers (arrow). A, axon; GA, giant axon; GC2, gline cell type 2; En, envelope of the nerve cord; ER, endoplasmic reticulum; L, lipid droplets; SG, synaptic glomerule with stretched synaptic contact (arrow); sy, synaptic contact. Other designations are as in previous figures.

ciated with the main excretory vessel (Figs. 4 and 5). The glial cell processes penetrate between axons into the central part of the cord and are sometimes revealed near the nerve cell bodies. These processes wrap the cord in several layers, the intercellular space between the which contains collagen-like fibrils about 170 Å in diameter (Figs. 5c, 5d). Sometimes, cross striation can be identified in the fibril bundle. Lipid droplets are present in the cytoplasm of glial cell processes; membranes of processes sometimes are closely adjacent and form junction contacts. Cleft between the contacting membranes is around 13 nm wide and is blackened; in the center, electron dense material is observed in the form of a broken line. The processal glial cells have nuclei of irregular shapes; the perinuclear cytoplasm forms numerous processes and is filled with ribosomes, β-glycogen granules, and lipid droplets. Glial cell perikarya are located at some distance from the cord,
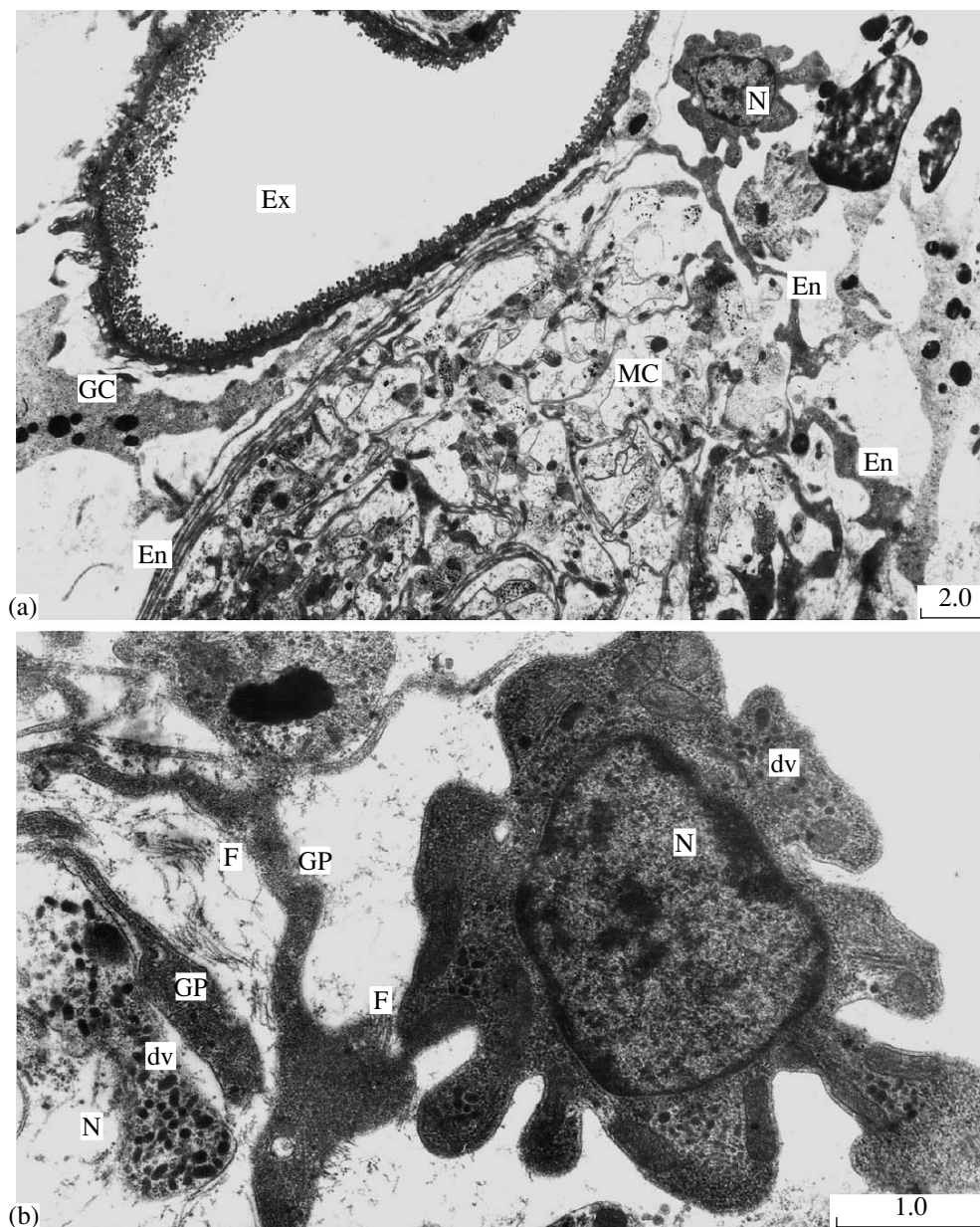
Fig. 4. Main nerve cord with multilayer envelope. (a) Transverse section of the scolex posterior; the main nerve cord going parallel to the main excretory vessel; an area of glial cell and its processes forming a multilayer envelope; neuron located outside of the main cord envelope; (b) perikaryon of the multipolar neuron with its processes containing dense vesicles and forming a part of the main cord, penetrating beneath the loose envelope. dv, electron dense vesicles in the neuron; Ex, excretory vessel. Other designations are as in previous figures.

near the epithelial walls of the excretory vessel; membranes of excretory and glial cells form a gab-like junction (Figs. 4a, 5a, 5b). Glial cell processes penetrate deeply inside the conducting part of the cord wrap individual groups of axons.

Apart from the peripherally located glial cells, the central part of the MC has also been found to contain cells with electron-dense cytoplasm that have specific features. The cytoplasm of these cells looks like individual profiles of complex configurations that are not connected to each other (Fig. 6). Apart from numerous ribosomes and mitochondria with fine granular matrix of intermediate electron density, these cells contain microtubules organized in a bundle located at a distance from the nucleus (Fig. 6a). Long processes run from the perykarya of these cells (Figs. 6a, 6b) that form multilayer envelopes around large axons. In the area of contact of the nerve and glial processes, dense juxtaposition membranes are observed (Fig. 6a, arrows).
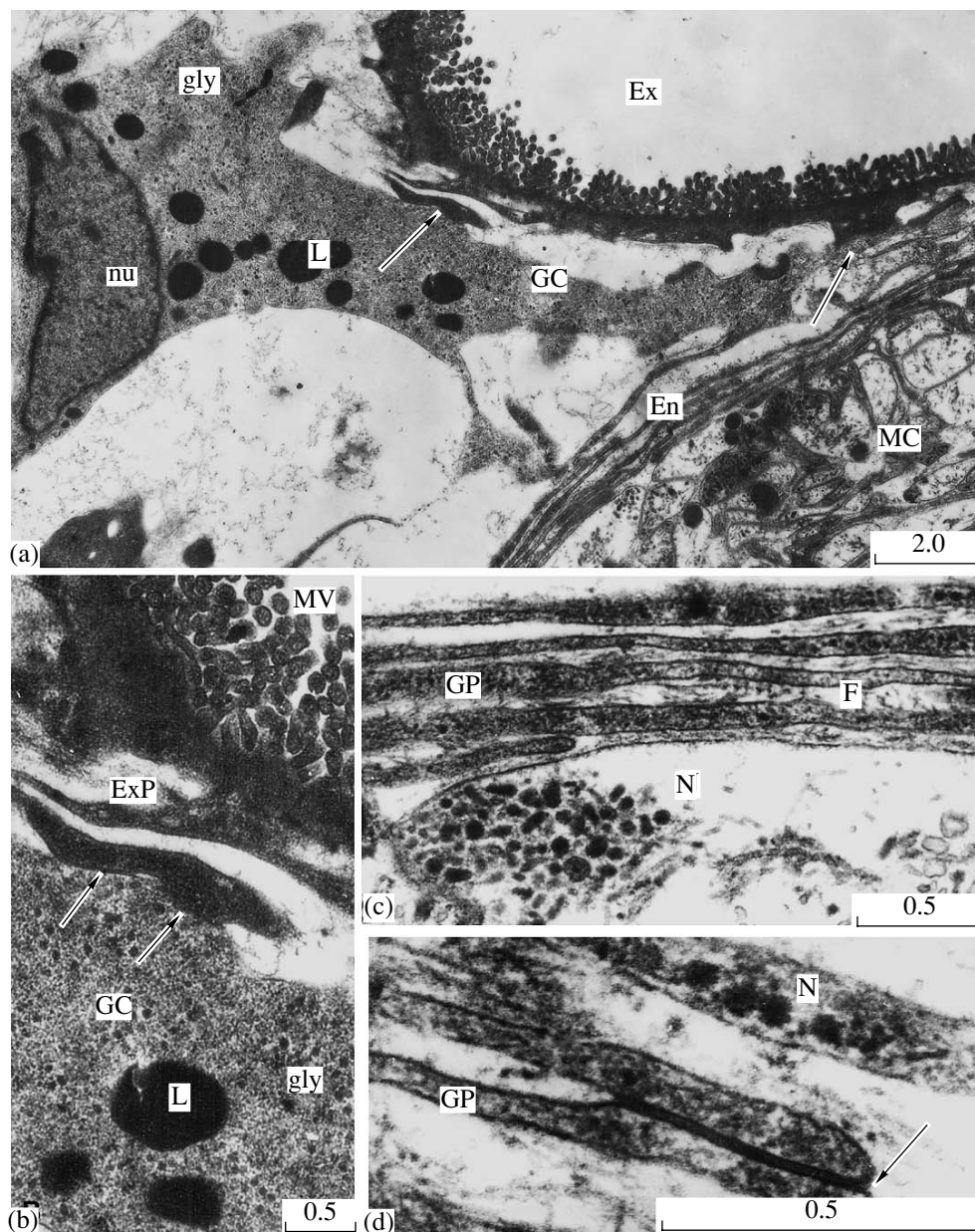
Fig. 5. Ultrastructure of glial cells in the main nerve cords of the scolex posterior area. (a, b) The contacts (arrow) between the glial cell and the excretory epithelium cell; (c) multilayered (4–5 layers) envelope around of the main cord; collagen-like fibers are situated between glial processes; (d) junction (arrow) between glial processes. gly, glycogen; ExP, excretory epithelium processes; MV, microvilli of the excretory channel wall epithelium. Other designations are as in previous figures.

DISCUSSION

The term *glia* was developed for the nervous system of vertebrate animals, on which the main types of glial cells and their functions were studied and described; therefore, description of the glia of the lower worms presents a terminological challenge.

For higher invertebrate CNSs, there is evidence that glial cells not only occupy up to half of their volume, but are also represented by very wide structural diversity and perform different functions, such as the formation of a permeable barrier, mechanical support, the protection and elimination of neurons, the wrapping of axons to speed up impulse conduction, and the guidance of migrating neurons (Pentreath, 1989). The cestode nervous system continues to grow constantly due to the supply of undifferentiated cells (Biserova and Salnikova, 2002); therefore, the guiding function of glial structures should be actual, not only at early stages of ontogenesis, but throughout the entire life cycle.
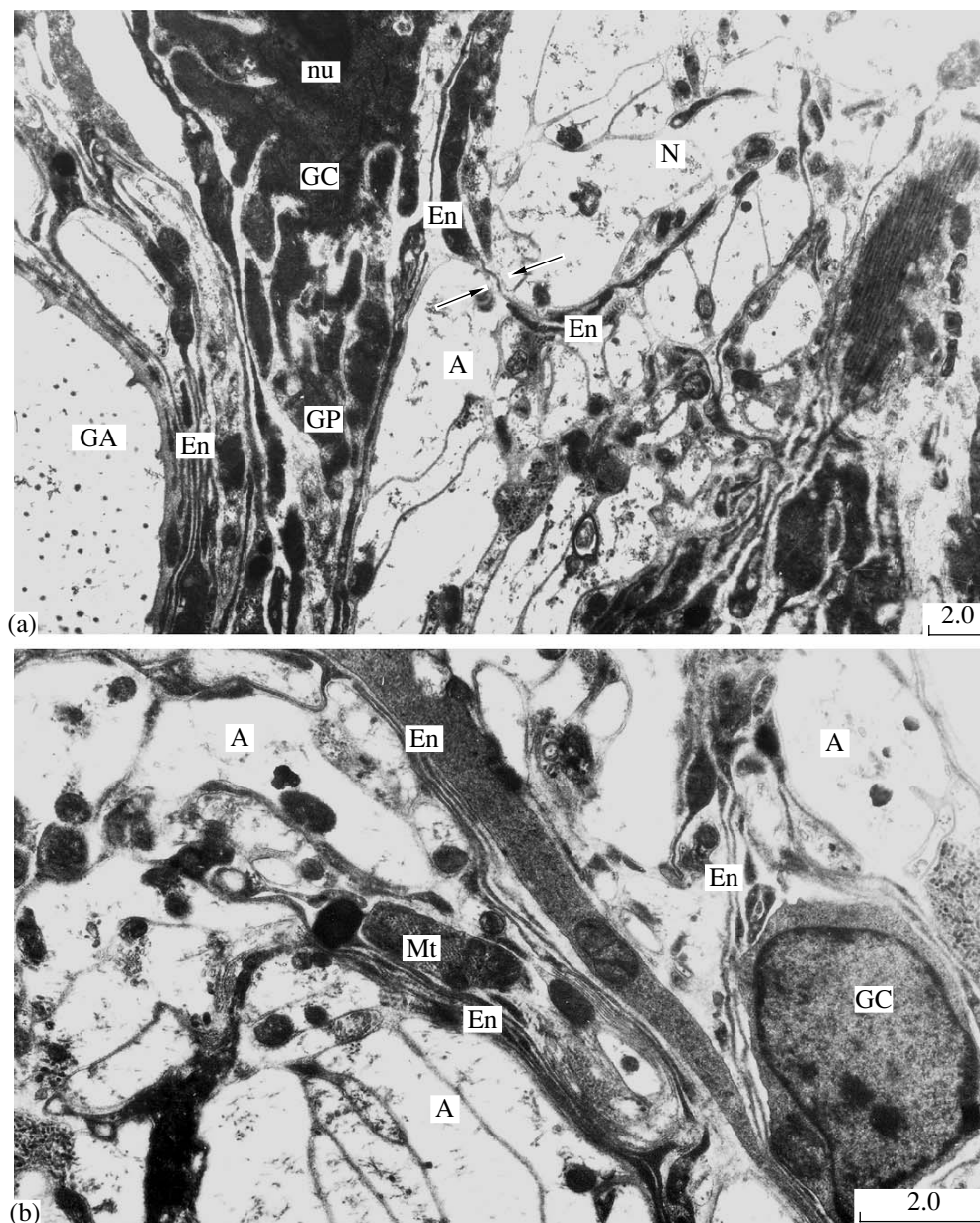
Fig. 6. Ultrastructure of glial cells in neuropils of the main nerve cords; strobila. (a) Transverse section of the cord; the glial cell perikaryon with numerous processes; arrow show zone of dense contacting membranes of nerve and glial processes; (b) glial processes penetrating into neuropil. Mt, compact bunch of microtubules in glial processes. Other designations are as in previous figures.

Glial cells at different times were described in the CNSs of several worms; in nemertines, they form an envelope of the main cords that is also covered from the outside by a fibrillar layer or basal lamina (Golubev, 1982). In nematodes, both glial specialization of hypoderma and the presence of glial cells in the esophageal nerve ring are described; the latter cells are characterized by the zonal distribution of organoids inside the cytoplasm (Golubev, 1982). Glial cells have not been revealed in Acantocephala. In annelids, glia are well developed, differentiated, and represented by various types of cells closely connected with neurons and processes. In leeches, glial cells are present both in the CNS and in the peripheral nerves. Functional diapason of glia in annelids is diverse. The annelid level of organization of glia and of glia–neuron relations has been considered the morphofunctional ground of evolution of the nervous system in invertebrates and vertebrates (Sotnikov et al., 1994).

Ultrastructural studies of the brains of some turbellarians have shown the presence of organoid-poor cells ascribed to neuroglial cells, for instance, in *Dugesia*

dorotocephala (Morita and Best, 1966), *Policelis nigra* (Bocharova and Sveshnikov, 1975), and in Baikal endemic *Geocentrophora* (Prorhynchida) (Bockerman et al., 1994). Cells of elongated shapes with processes penetrating between neurons have been described in *Strongilostoma simplex* (Bedini and Lanfranchi, 1998), whereas in others, *Dugesia donocephala* (Oosaki and Ishii, 1965) or *Procotyla fluviatilis* (Lentz, 1967), glial cells have not been revealed. In triclads, unlike other turbellarians, glia-like cells have been reported by the majority of authors. In *Armilla livanovi* and *Rimacephalus pulvinar* (Sotnikov et al., 1994), these organoid-poor cells do not form a complete envelope; their processes pass between neuronal bodies and axons and, in the authors' opinion, perform a supporting function. Similar cells have also been noticed in the triclad *Procerodes littoraslis* (Mantyla et al., 1998). Glial cells are absent in rhabdocoela turbellarians (Sotnikov et al., 1994).

In contrast to the widespread opinion of the absence of glia in animals with parenchymatous organization, detailed studies of the nervous system of parasitic flatworms have shown the presence of cells performing isolating, supportive, and trophic functions in their CNSs, i.e., functions corresponding to the definition of glia. Thus, it has been demonstrated that all CNS compartments in *Amphilina foliacea* (Amphilinida) belong to structures isolated from the internal medium tissues and are wrapped by specialized glial cells that are immunoreactive to the marker of vertebrate glia S100b (Biserova, 2000a, 2000b, 2004). Glial cell bodies are located outside cords and commissures. Glial cell processes in amphilinids form multilayer envelopes around neurons, groups of neuritis, and synaptic glomerules and isolate nerve structures from each other and surrounding tissues. Glia–neuronal relations are fairly intimate. Small, short processes of glial cells enter invaginations of neurons and large axons in glomerules and tightly wrap zones of the central and lateral motor neuropils; thus, the input muscular processes have only penetrated neuropil in certain areas. Structural differentiation of glial cells has been noted in different compartments of CNS in *Amphilina foliacea* (Biserova, 2000a), which was previously shown only for annelids (Lagutenko, 1981; Golubev, 1982; Sotnikov et al., 1994).

Envelope cells of cestodes originate from different cytological source and isolate and support the CNS. Thus, in *Triaenophorus nodulosus* (Pseudophyllidea) and aberrant forms of cyclophillid cestodes, *Gastrotenia dogielli* cells of excretory epithelium form thin superficial processes that surround nerve cords and cerebral ganglia and form unique envelopes that perform the function of glia (Davydov and Biserova, 1988; Biserova, 1997a; Biserova and Salnikova, 2002). Besides, intercellular matrix fibrils take active part in the formation of the CNS envelope by forming in *T. nodulosus* a developed fibrillar layers first noted at the stage of early plerocercoid.

Origin and development of envelopes in the nervous system of the cestode *T. nodulosus* were studied in ontogenesis at all development stages starting from oncosphere (Biserova and Korneva, 2006). In procercoids, a full-value CNS envelope has not yet been formed. At the stage of early plerocercoids, processes of excretory epithelium cells are located outside, separate nervous elements from other cell structures. On the surface of the envelope, rough fibrils of an intercellular matrix are formed. In the ripe plerocercoid *T. nodulosus*, the CNS envelope is completely formed. Functions of glia are performed by excretory epithelium cells forming thin superficial processes that are associated with nerve elements in procercoid and completely surround nerve cords and cerebral ganglia of plerocercoids and adult worms (Biserova and Korneva, 2006).

Close relations with excretory system have always been emphasized for the cestode nervous system (Webb and Davey, 1975; Golubev, 1982; Pospekhova et al., 1993; Biserova et al., 1996); they also are noted in amphilinids (Biserova, 1997b). However, the network-like exposed vessels come into contact with CNS irregularly and do not form obvious cytological structures. On the contrary, in cestodes, the main longitudinal excretory vessels always run parallel to the main nerve cords. Epithelium of excretory vessels participates in processes of the secondary absorption of nutrients (Webster, 1972; Lindroos and Gardberg, 1982; Vinogradov et al., 1982). The close interrelations of the nervous and excretory system can serve an evidence for evolutionary process, in which the excretory vascular wall epithelium, by forming envelopes of nerve cords and ganglia, performs supportive and trophic functions peculiar to the glia of higher animals.

In *Grillotia erinaceus* the CNS envelopes are more differentiated and are represented by different cell elements in different compartments. In the cerebral ganglia and proboscis nerves, the function of glia is performed by fibroblast-like cells. In their cytoplasm and on the cell surface, these cells contain dense fibrillar material and form invaginations and contacts close in their ultrastructure to those revealed in the proboscis ganglion of the acantocephalida *Echinorhynchus gadi* (Golubev and Salnikov, 1979). Acantocephala worms are not connected with cestodes by the direct phylogenetic relation, but have a functionally similar attaching apparatus. Cells of the cerebral ganglion that experiences constant deformations as a result of activity of proboscis muscles-retractors have been shown to contain specialized connections of nerve cells with intercellular substances in the form of neurilemma cleftlike invaginations performing supportive functions. A similar function is also performed by fibroblast-like cells in cerebral ganglia of *G. erinaceus*, the processes of which penetrate the neurolemma invaginations by anchoring and fixing neurons submitted to powerful deformation loads during the proboscis activity.

Giant axons of *G. erinaceus* revealed recently in cestodes (Biserova, 2002) are, as in the higher invertebrates, isolated structures. The presence of specialized envelopes undoubtedly promotes fast signal conduction. Glial cells in bulbar nerves of *G. erinaceus* form a tightly adjacent envelope around axons, are involved in intimate connections, and form invaginations into giant axons, which seems to indicate trophic function. The function of membrane lamellas in the glial cell cytoplasm is unclear. Based on their ultrastructure, these cells are similar to glial cells of caudal ganglia of *Amphilina foliacea* (Biserova, 2000a). Stretched membrane structures are reported in the glial cell cytoplasm of some insect representatives, including aphids (Kats, 1995, 1996) and locusts (Skiebe et al., 2006); however, their description and functional significance are not presented in these publications.

An important indicator of a high degree of differentiation of glia–neuronal relations is a large amount of glial cell nuclei in bulbar nerves, whereas neuronal bodies are absent.

Interrelations between giant axons of some invertebrates (leech, snail, crawfish) with their Schwann cells are physiologically complex and multivariant; the presence of an obvious signal is shown between them, the function of which has not fully been studied (Coles and Abbott, 1997).

In the strobile and posterior part of the scolex, certain process glial cells are associated with main lateral cords that form, on one hand, a multilayer envelope around nerve cords and, on the other hand, specialized contacts with cells of excretory channel walls. This fact indicates the participation of glial cells in the metabolic processes of the nervous system and, possibly, in the maintenance of tropics of neurons. These cells are characterized by the presence of numerous lipid droplets in the cytoplasm. Glial cell processes are connected to one another by gaplike junctions, which is characteristic of the high animal glia and confirms the participation of neurons in trophics. In the opinion of some authors (Pentreath, 1989; Coles and Abbott, 1997), the gap junctions participate in the formation a neuronal environment and, further, take part in the metabolism of the CNS. Unlike *T. nodulosus*, bodies of neurons in the MCs of *G. erinaceus* remain outside the multilayer envelope. Thus, as compared to cerebral ganglia, the glial–neuronal relations in the main cords are less close. Furthermore, only the conducting cord part is wrapped and glial cells do not form deep invaginations into the cytoplasm of axons or neurons; instead, numerous fibrils remain between the envelope layers. It is apparent that differentiation of glial elements in the strobile is lower than in the scolex.

CONCLUSIONS

Thus, in the nervous system of *G. erinaceus*, three types of glial cells differing in their locations and ultra-

structures have been revealed. The first type includes glial cells of cerebral ganglia, which are similar to fibroblasts, have specialization as supporting elements, synthesize fibrils, and participate in active transport. The second type of glial cells forms a myelin-like envelope of giant axons and bulbar nerves and is characterized by stretched membrane structure in the cytoplasm. The number of glial cells of the second type significantly exceeds the number of neurons in bulbar nerves. Belonging to the third type are glial cells of the main nerve cords, which form multilayer loose envelopes and are connected with gablike junctions with one another and with the epithelium of the excretory channel wall. Their relations with nerve elements are less intimate; they do not penetrate into invaginations of axolemma, do not form specialized contacts with neurons, and only wrap the central conducting cord part.

The origin of glial cells of higher animals in ontogenesis is not uniform. Our studies have shown that, among parasitic flatworms, many types of glia–neuronal relations and the development of specialized envelopes from different cytological sources are present. Cestodes and amphillinids have many features of the so-called "annelid" level of organization of glia. The fact that the nervous system of parenchymatous flatworms—cestodes and amphillinids—has specialized glial envelopes that are formed at different stages of ontogenesis and have different degrees of structural–functional differentiation is novel in principle.

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