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ULTRASTRUCTURE OF THE LARVAL ORGAN OF METACESTODE LATERIPORUS GEOGRAPHICUS COOPER, 1921 (CESTODA: DILEPIDIDAE)

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Abstract. The ultrastructure of the larval organ of strobilocyst, one of the two varieties of metacestodes of the family Dilepididae, is described. This larva differs from monocercus of Dilepididae in the absence of exocyst, structure of superficial tegument syncytium and outer fibrous layer, distribution of muscle elements, and presence of a layer of cytoplasmic processes bordering the cyst cavity. In the structure of the cyst wall the larvae of *Lateriporus* cestodes are more closely related to cysticercoids of Hymenolepididae than to monocerci of Dilepididae. The tail of the strobilocyst differs from that of other metacestodes of Cyclophyllidea in the presence of monocellular glands associated with the tegument. These glands were observed for the first time in the cercomer of cysticercoids. It is assumed that the larval organ of the two types (monocercus and strobilocyst) of Dilepididae larvae evoluted independently and that it originates from ancestors common with Hymenolepididae.

The Cyclophyllidea metacestodes are notable for a great diversity in the structures of the larval organ (a complex of preventive formations, including cyst and tail). In Hymenolepidata cysticercoids this organ serves for the adaptation to the development and survival in the intermediate host and transition to the definitive host (Krasnoshchekov 1980). The studies on the peculiarities in the larval organ morphology contribute to a better knowledge of the phylogeny and establishment of the systematic position of Cyclophyllidea (Freeman 1973). For this purpose, in addition to the anatomy of larvae also the ultrastructure of their elements should be studied. Especially the electron microscopical examinations reveal essential differences in the structures of tegument, cyst wall and tail and its homologues, which cannot be detected by other methods (Krasnoshchekov 1978). We have therefore studied the ultrastructure of cysticercoids of various species and modifications. The present paper deals with the ultrastructure of strobilocyst (Spassky 1954) (strobilo-precysticercus) (Freeman 1973) of cestodes of the genus *Lateriporus*, one of the two known types of Dilepididae larvae. While the ultrastructure of larvae of monocercus type has been studied sufficiently (Crowe et al. 1974, Gabrion and Gabrion 1976, Gabrion and Jordane 1979, Krasnoshchekov and Nikishin 1979a), no data on the ultrastructure of strobilocyst are available. We assume that it would be interesting to compare it with monocerci of Dilepididae and other larvae of the suborder Hymenolepidata.

MATERIAL AND METHODS

Strobilocysts of *Lateriporus geographicus* Cooper, 1921 were obtained from naturally infected Gammaridae caught in water reservoirs of North-Western Chukotka. A total of 5 larvae were recovered from the intermediate hosts, put in 6.5 % solution of glutaraldehyde in phosphate buffer (pH 7.2) and fixed in the same solution. After fixation the larvae were washed in sucrose solution

and again fixed in 2 % solution of OSO_4 in acetate-veronal buffer after Caulfield. The material was then dehydrated and embedded in Epon-Araldit. Sections were cut with LKB ultramicrotome, stained by uranyl acetate and lead citrate after Reynolds and examined in a BS-500 (Tesla) microscope at accelerating voltage of 90 kV.

RESULTS

The cyst wall of strobilocyst consists of the following layers: glycocalyx, superficial syncytium of tegument, external fibrous layer, parenchyma and layer of myeline-like fibres (Fig. 1).

The glycocalyx is about 8 μm thick. It consists mainly of a radially orientated fibrillar material, including numerous coiled tubules and vesicles representing mostly sections of tubules. In the outer parts of glycocalyx, they are often widened and bead-like, or they disintegrate into large fragments; some of the tubules are filled with a homogeneous matter of moderate density (Plate I, Fig. 1). The widened tips of tubules and vesicles are most numerous at the border with the superficial layer of glycocalyx, which is about 1 μm thick and is characterized by a more dense and regular arrangement of fibrils (Plate I, Fig. 1a).

The folded superficial syncytium of tegument is 1.5—2.5 μm thick. It is covered with regularly arranged finger-like evaginations conically tapering at the tip and passing to the coiled tubules. The evaginations contain neither microfilaments, typical of microvilli, nor membrane complex characteristic of homologues of microtriches of cyst tegument in cysticercoids (Krasnoshchekov and Nikishin 1979a). The matrix of the distal parts of evaginations is of higher density. Electron-dense material appears in the lumen of the initial parts of tubules (Plate I, Fig. 1). The superficial syncytium is filled with coiled bundles of homogeneous matter of moderate density with a small amount of matrix between them. In the inner third of tegument, the bundles are orientated parallelly to the cyst surface and mainly radially in the outer parts. The orientation of the bundles seems to be made by fibrils, a large number of which were found in the loci with a small concentration of bundles (Plate I, Fig. 2). Large globules of a more dense matter than that forming bundles are situated at some sites of tegument base. They are localized near the openings of cytoplasmic bridges between the superficial syncytium of tegument and its cytons in the parenchymatous layer. The basal plate is well visible in form of linearly arranged dense granules.

The outer fibrous layer is about 15—20 μm thick and consists of three parts with different orientation of fibres. The outermost part is 1—1 5 μm thick, consists of longitudinally orientated fibrils and contains isolated muscle fibres (Plate II, Fig. 1) The middle part is 6—8 μm thick and consists of circularly arranged fibrils and numerous bundles of muscle fibres orientated in the same direction and localized near its border with superficial part. The muscle fibres are connected by processes with myofibroblasts of the parenchymatous layer. A large amount of glycogen is contained in the muscle fibres and processes only in the anterior part of larvae. In addition to the cytoplasmic processes of muscles, the fibrous layer is penetrated by thin coiled processes of tegument cytons projecting towards the superficial syncytium. Osmiophilic globules, identical with that found in the base of superficial syncytium of tegument, are rarely situated in the lumen of cytons. The inner portion of the fibrous layer is 6—10 μm thick. It is separated from the middle layer by circular muscle fibres embedded, like the longitudinal fibres, in the fibrous tissue. The cytoplasmic processes of cytons in this zone are more numerous, orientated in various directions and often uniting in distal parts.

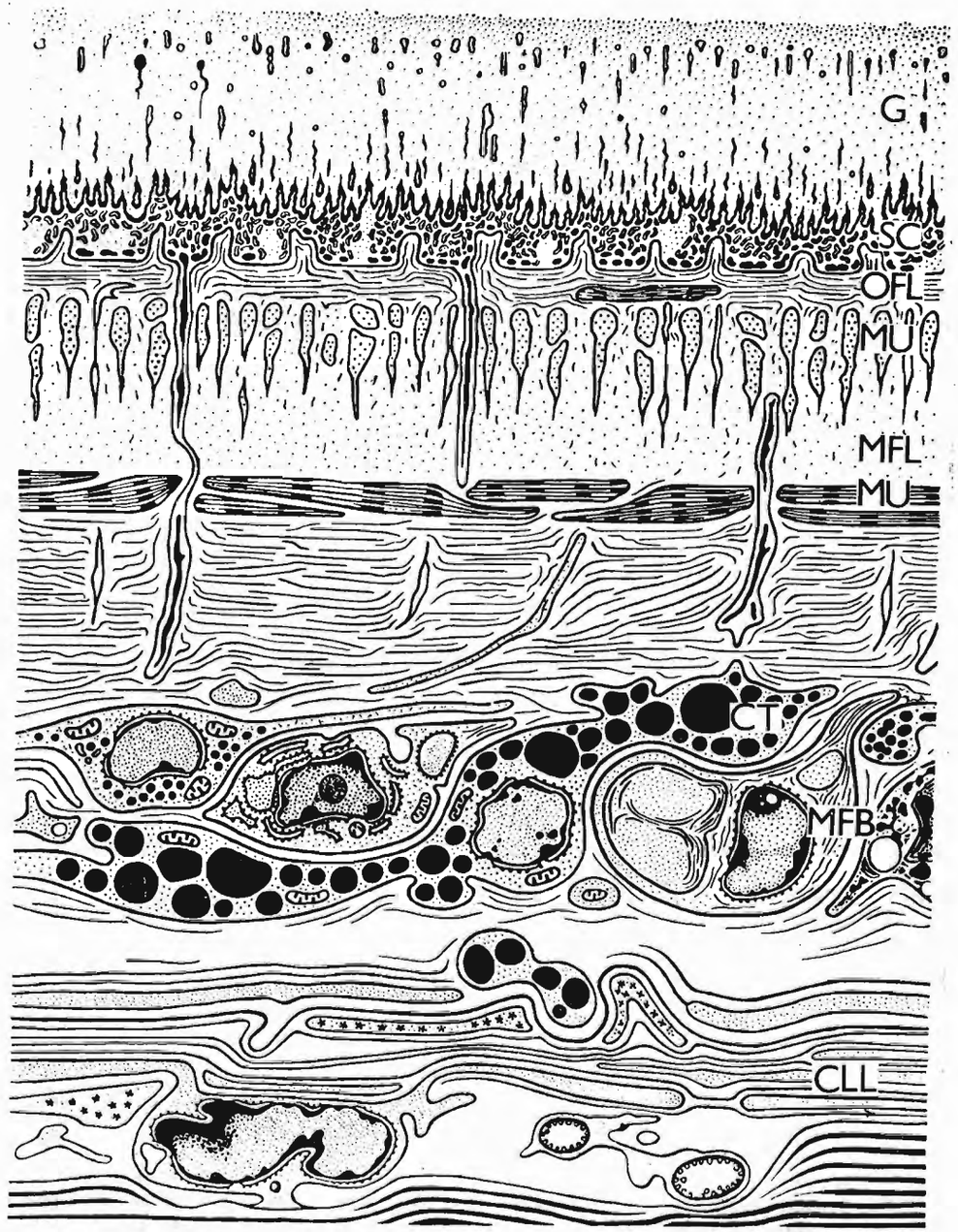

Fig. 1. Scheme of the structure of the cyst wall in *Lateriporus geographicus* metacestodes.

The parenchymatous layer is 5—11 μm thick and consists of several types of cells and their processes situated in the connective tissue. Large cells containing osmiophilic globules of various shapes and sizes predominate (Plate II, Figs. 2, 3). The globules are formed in the zone of Golgi complex as spherical, membrane-bordered granules, which then enlarge, probably by fusion. The perikaryons of these cells contain a large number of ribosomes. The mitochondria are light, large and localized near Golgi complex in some cells, and small, dense and with isolated cristae in others. Numerous processes containing globules project from the perikaryon. These cells are regarded as tegument cytons, though their cytoplasmic bonds with the superficial, syncytium were not found.

The cells of the second type are myofibroblastic cells with widened cisterns of granular endoplasmic reticulum (GER). These cells are usually smaller than those containing globules. The perikaryon is dense and contains a large number of long and branched canals of GER. Some of them are widened and contain a microgranular homogeneous material (Plate II, Fig. 3). The mitochondria are not numerous, they are minute, with dense matrix and reduced cristae.

Besides these most numerous forms there are myofibroblasts containing one or two large cavities, representing widened cisterns of GER and containing a granular and rarely fibrillar matter (Plate III, Fig. 1). The presence of this matter shows that the myofibroblasts are associated with the production of fibrous tissue. The nuclei are usually of irregular shape, angular and with increased content of heterochromatin. The number of GER canals is decreased, but it remains still higher than in other cells. Inclusions of lamellar bodies often occur there.

In addition to the described cells, the parenchymatous layer contains protonephridia, excretory canals of various diamaters (Plate III, Fig. 2), cells similar to neurosecretory ones, containing granules measuring 120—200 nm in diameter, glycogen-depositing cells, localized mainly in the anterior part of cyst (Plate III, Fig. 3), and degenerating cells at different stages of cytolysis (Plate III, Fig. 4).

The innermost cyst layer consists of thin cytoplasmic processes, which are homologous to the myeline-like layer in Hymenolepididae larvae. At some sites the processes are connected with one another and their cytoplasmic membranes fuse in a single, more thick and dense membrane (Plate IV, Fig. 1). This layer of membranes contains strongly elongated cells with large, irregular nuclei and a narrow rim of cytoplasm turning into long cytoplasmic processes. These cells are localized mainly at the poles of larvae.

Previously, the absence of tail was regarded as a characteristic feature of strobilocysts of *Lateriporus* (Shapkin and Gulyaev 1973). It was not detected at autopsy of hosts containing mature larvae of *L. geographicus*. However, one of the authors who studied the development of *L. clerci* larvae found that the strobilocysts have a typical tail separating from the cyst during maturation of the larva and kept for a long time inside the hemocoel of the intermediate host (Gulyaev 1982). The electron microscopic observations revealed that the tail of strobilocercoids has the same structure as that of Hymenolepididae cysticercoids (Krasnoshchekov et al. 1979, 1981). Its outer surface is bordered by a thin cytoplasmic layer of superficial syncytium of tegument with numerous microvilli (Plate IV, Fig. 2). Its surface has a typical lining of microvilli. Below the tegument, there is the basal plate and a layer of connective tissue including bundles of circularly orientated muscle fibres. The central part of the tail is a wide cavity containing granular material and cell detritus.

The parenchyma of the tail consists of cytons, single cells of myofibroblast type, protonephridia. A peculiarity of the strobilocyst tail is the presence of unicellular glands. The perikaryon of gland cells contains accumulations of spherical and ovoid

electron-dense bodies measuring 200—250 nm, the largest being 300 nm long (Plate IV. Fig. 3). These bodies are formed in the zone of Golgi complex and they pass on the cytoplasmic processes into tegument where they concentrate near their openings. Some of the bodies are in a close contact with the outer cytoplasmic membrane of tegument and, evidently, secret their contents onto its surface. Cells at various stages of destruction usually occur in the central parts of the tail (Plate IV. Fig. 4).

DISCUSSION

The studies on the ultrastructure of the larval organ of *L. geographicus* strobilocyst revealed principal differences between it and that of monocercus, another type of Dilepididae larvae. The monocerci were found in the representatives of 11 genera of this family (Tomilovskaya 1979) and the ultrastructure was studied in 6 species: *Paricterotaenia paradoxa* (Crowe et al. 1974), *Anomotaenia constricta* (Gabrion and Gabrion 1976), *A. brevis* (Gabrion et al. 1976), *Choanotaenia crassiscolex* (Gabrion and Jourdane 1979), *Dichoanotaenia tundra*, *Paricterotaenia porosa*, *Platyscolex ciliata*, *Sacciuterina stellifera* and *Trichocephaloides megalocephala* (Krashoshchekov et al. 1983).

According to our results, the larval organ of the monocerci has the following common characters (Krasnoshchekov et al. 1983). The larva is surrounded by a cell-free envelope of exocyst, which is derived from the cystogenic glands of oncospheres and serves for the integration of the homologue of tail with the remaining parts of larva. The tail consists of the tegument tissue and separates from the endocyst when the larva matures. Then it disintegrates into individual follicles secreting a flake-like matter into the exocyst cavity. The superficial syncytium of endocyst tegument is filled with disk-shaped bodies similar to that contained in the tegument of mature cestodes. The microvilli on the endocyst tegument in mature larvae are replaced by nodular homologues of microtriches. The pores-canals typical of tegument in Hymenolepididae cysticercoids are lacking in the tegument of the endocyst. The tegument is connected with the deeper-lying tissue by hemidesmosomes which were not found in other types of larvae. Fibrous and muscular elements of the endocyst wall are separated and form independent layers. The myeline-like layer bordering the cyst cavity in cysticercoids of the cestode family Hymenolepididae is absent. The data completely correspond to the descriptions of Dilepididae monocerci published by other authors (Gabrion et al. 1976, Gabrion and Gabrion 1976, Gabrion and Jordane 1979). Crowe et al. (1974), who studied the cysticerci of *P. paradoxa*, found residues of degenerating tissue, which they considered to be remnants of mother cyst, at the site of the exocyst. However, the illustrations published by these authors show that they took follicles of the tail homologue for elements of mother cyst.

The outer cyst, characteristic of Dilepididae monocerci, is absent in *L. geographicus* strobilocysts and the glycocalyx of its tegument is in a direct contact with the host. The glycocalyx layer on the cyst surface is well developed and no resorption was observed, in contrast to some cercocysts of Hymenolepididae (Krasnoshchekov et al. 1981). This may be explained by peculiarities in the host reaction or presence of a more dense superficial layer of glycocalyx. The latter prevents the elimination of fragments of disintegrating microvilli into the hemocoele cavity of host and in this respect it may be considered to be an analogue of the acellular envelope of exocyst in monocerci. However, its function as a filter (or partly permeable membrane) is realized less effectively and products of microvilli degradation are partly discharged onto the glycocalyx surface.

The microvilli on the surface of cyst tegument in mature cysticercoids lose the matrix and turn into coiled tubules. This is typical of most of the studied cysticercoids of Hymenolepidata (Baron 1971, Crowe et al. 1974, Gabrion and Gabrion 1976, Krasnoshchekov and Nikishin 1979a), except for H. *diminuta*, the cyst tegument of which keeps the lining of microvilli (Krasnoshchekov et al. 1979).

The transformation of microvilli into coiled tubules occurs also in *L. geographicus*. In contrast to monocerci, however, there are no nodular homologues of microtriches the membrane complex of which separates the matrix of tegument from the lumen of coiled tubules. Consequently, the material filling the endocyst tegument penetrates into the coiled microtubules and can be excreted into the body cavity of the intermediate host. An analogous phenomenon was described by us in the larvae of *Hymenolepis* sp. (Krasnoshchekov et al. 1981).

The structure of superficial cyst tegument is different in different types of metacestodes of Cyclophyllidea. Several modifications are known in larvae of Hymenolepididae, which differ in the character of the material filling the superficial tegument syncytium. The cytoplasmic structure of cyst tegument was described in *H. diminuta* larvae. The tegument is hypertrophied and contains a large number of microtubules and flake-like material (Krasnoshchekov et al. 1979). In other members of Hymenolepididae, the matrix of cyst tegument is substituted by a homogeneous electron-dense substance (Gabrion and Verdier 1978, Krasnoshchekov and Nikishin 1979a, b, Krasnoshchekov et al. 1981).

In all studied Dilepididae monocerci, the superficial cyst tegument is filled with disk-shaped (rod-shaped) bodies with electron-dense contents (Crowe et al. 1974, Gabrion and Gabrion 1976, Gabrion et al. 1976, Gabrion and Jourdane 1979, Krasnoshchekov et al. 1983). Although such tegument structure was found in the cyst of Hymenolepididae larvae (in *H. microstomata* by Caley 1974), it may be regarded as typical of Dilepididae monocerci. The tegument of *L. geographicus* strobilocysts, containing bundles of moderately osmiophilic substance, is another modification of the cyst tegument found in Dilepididae metacestodes and first recorded in the larvae of Cyclophyllidea.

According to our observations, the cyst tegument of Hymenolepididae larvae, the superficial syncytium of which is filled with a homogeneous electron-dense matter, contains pores-canals serving for the transport of substances from cyton perikaryons to tegument surface (Krasnoshchekov and Nikishin 1979b). The pores-canals are lacking in the cyst tegument of *H. diminuta* and in Dilepididae monocerci (Krasnoshchekov et al. 1979, 1983). This may be explained by the fact that after the matrix of the superficial syncytium of tegument has been substituted by an electron-dense material, the transporting function of tegument is excluded. In other structures of superficial syncytium of cyst tegument it is realized by a way common for cestode tegument and the pores-canals are lacking. This completely concerns also the *L. geographicus* larvae, in which the possibility of secretion (excretion) through the superficial syncytium and reduced microvilli is preserved even in mature larvae.

The structure of deeper parts of the cyst wall in *L. geographicus* larvae is identical with that in Hymenolepididae. The fibrous layer and muscle elements in it are well developed, but not divided into separate layers; muscle fibres are embedded in the connective tissue and their orientation coincides with that of the fibres.

Cytons and myofibroblastic cells form the major part of the cyst parenchyma in cysticercoids. The myofibroblastic cells, which are muscle cells, provide also the secretion of fibrillar substance of the outer fibrous layer and basal plate (Ubelaker et al. 1970, Caley 1974, 1976). Two varieties were marked among the myofibroblasts of *L. geographicus:* cells with slightly widened cisterns of GER and minute dense

mitochondria, and cells with isolated strongly widened cisterns, substituting the larger part of perikaryon. Both varieties are related to myofibroblasts with reduced functional activity. The transformation of the contents of widened canals into the fibrillar material confirms the earlier indirect evidence of the fibroblastic function of the cells with widened GER cisterns.

The muscle cells in cestodes are characterized by the presence of a large amount of glycogen. It was not found in the perikaryon of myofibroblastic cells and only small groups of alpha-granules of glycogen were found in their cytoplasmic processes. Cells filled with glycogen were found around the excystation pore. These cells seem to represent muscular elements differing from the myofibroblasts. This supposes a certain functional autonomy of the muscle system serving for the opening of the excystation pore of the endocyst during excystation.

The identification of tegument cytons in mature larvae, if the cytoplasmic bonds between them and superficial syncytium are reduced, is difficult because of the absence of specific inclusions common for the perikaryon and distal cytoplasm. In the cyst of the studied larvae, cells containing osmiophilic globules are assigned to tegument cytons. The globules were found also in the cytoplasmic processes of cytons in the outer fibrous layer and in the base of tegument. They are formed in the zone of Golgi complex as granules; the formation of large globules in the perikaryon of cytons seems to be associated with the deposition of secretion resulting from its decreased transport to the superficial syncytium after differentiation of the outer fibrous layer.

The formation of bundles of moderately osmiophilic material filling the superficial syncytium of cyst tegument was not observed in the perikaryon. They are probably formed in the superficial syncytium from the globules coming from cytons.

The innermost layer bordering the cyst cavity of *L. geographicus* consists of thin cytoplasmic processes and myeline-like membranes. This layer is typical of metacestodes of the family Hymenolepididae, but it is absent in the monocerci of Dilepididae (Krasnoshchekov 1978).

The tail of *Lateriporus* larvae resembles more that of Hymenolepididae metacestodes than of Dilepididae monocercus in the form and ultrastructure. In contrast to the follicles of monocerci, it has a layer of connective tissue and muscle elements (Krasnoshchekov 1978). The principal difference from the tail of all earlier studied larvae of Cyclophyllidea is the presence of unicellular glands associated with the tegument. These glands are similar to that occurring in the tegument of Pseudophyllidea (Arme and Threadgold 1976, Hayunga 1979, Davydov and Kuperman 1979) and their functional significance is interpreted in different ways. One of the possible functions is the participance of their secretion in the protective responses of the parasite, which corresponds to our supposition on the function of the tail in Cyclophyllidea metacestodes. Their presence in the tail suggests its progressive functional specialization in higher cestodes. Another character separating the tail of *L. geographicus* metacestode is the presence of a large number of protonephridia. This contradicts the assumption on the formation of tail in parts situated more distally from the opening of excretory canals (Gulyaev 1982).

An analysis of the peculiarities in the ultractructure of larval organ in metacestodes of the genus *Lateriporus* shows that these larvae are more similar to the metacestodes of the family Hymenolepididae than to larvae of monocercus type, typical of other genera of Dilepididae. This supposes differences in the historical evolution of Dilepididae metacestodes. Most probably the cestodes of this family separated from the ancestral forms of Hymenolepidata at earlier stages of phylogenesis and their evolution was accompanied by a marked divergence of morphological characters of the larval organ. The larval organ in the strobilocysts developed in the way typical of the

metacestodes of Hymenolepididae, but, with regard to the presence of glands in the tegument of tail, it became more advanced in the course of evolution than that in the larvae of this family.

УЛЬТРАСТРУКТУРА ЛИЧИНОЧНОГО ОРГАНА МЕТАЦЕСТОД *LATERIPORUS GEOGRAPHICUS* COOPER, 1921 (CESTODA: DILEPIDIDAE)

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Резюме. Описана ультраструктура личиночного органа стробилоцисты — одного из двух типов метацестод семейства Dilepididae. От моноцерков Dilepididae эти личинки отличаются отсутствием экзоцисты, организацией поверхностного синцития тегумента и наружного фиброзного слоя, распределением мышечных элементов, наличием ограничивающего полость цисты слоя цитоплазматических отростков. По строению стенки цисты личинки цестод рода *Lateriporus* ближе к цистицеркоидам Hymenolepididae, чем к моноцеркам Dilepididae. Хвостовой отросток стробилоцист отличается от такового других метацестод циклофиллидей наличием одноклеточных, ассоциированных с тегументом желез, впервые отмечаемых в церкомере цистицеркоидов. Предполагается независимое формирование личиночного органа двух типов (моноцерка и стробилоцист) личинок Dilepididae в эволюции и происхождение его от общих с Hymenolepididae предковых форм.

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KEY TO LETTERING OF FIGURES

AT — areolar tissue, CLL — cyst-lining layer, CT — cyton of tegument, G — glycocalyx, GER — granular endoplasmatic reticulum, Gl — glycogen, E — excretory cell, EC — excretory canal, MFB — myofibroblast, MFL — middle fibrous layer, MU — muscle fibre, MV — microvilli, OFL — outer fibrous layer, SC — superficial cytoplasmic layer of tegument.

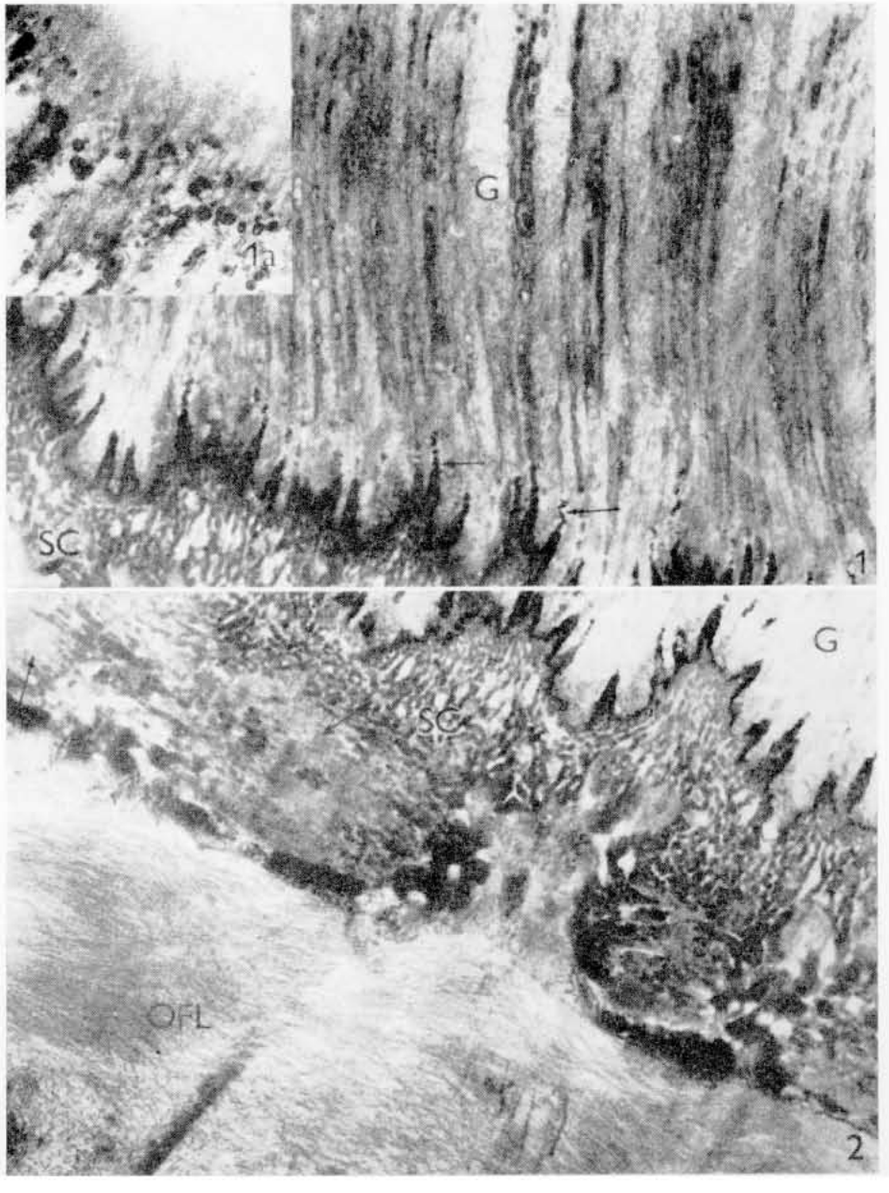

Fig. 1. Outer part of the superficial syncytium of cyst tegument with glycocalyx, reduced microvilli in glycocalyx (arrow) and elimination of electron-dense material from the top of tegument protrusions into lumen of tubules (double arrow) (× 16 000).
Fig. 1a. Accumulation of inclusions near the border of outer layer of glycocalyx (× 12 800).
Fig. 2. Superficial syncytium of cyst tegument filled with bundles of moderately dense material of various orientations. Microfibrils in the loci with a small number of inclusions (arrow). Electron-dense bodies near inner cytoplasmic membrane (double arrow) (× 16 000).

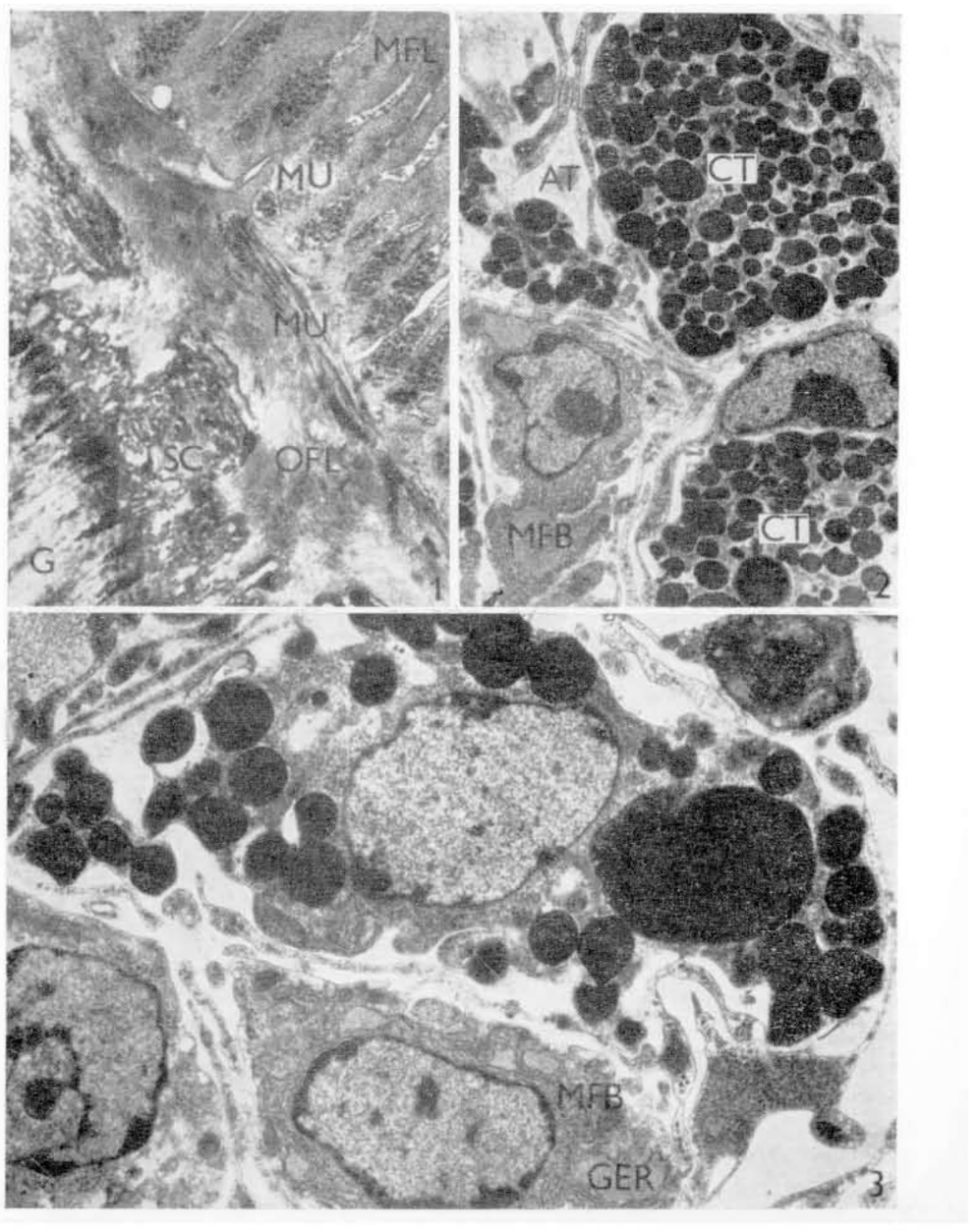

Fig. 1. Oouter fibrous layer (× 13 300). **Fig. 2.** Cytoplasmic processes of cytons filled with electron-dense bodies. Myofibroblasts with individual widened canals of granular endoplasmic reticulum (× 13 300). **Fig. 3.** Polymorphism of electron-dense bodies in cyton (18 300).

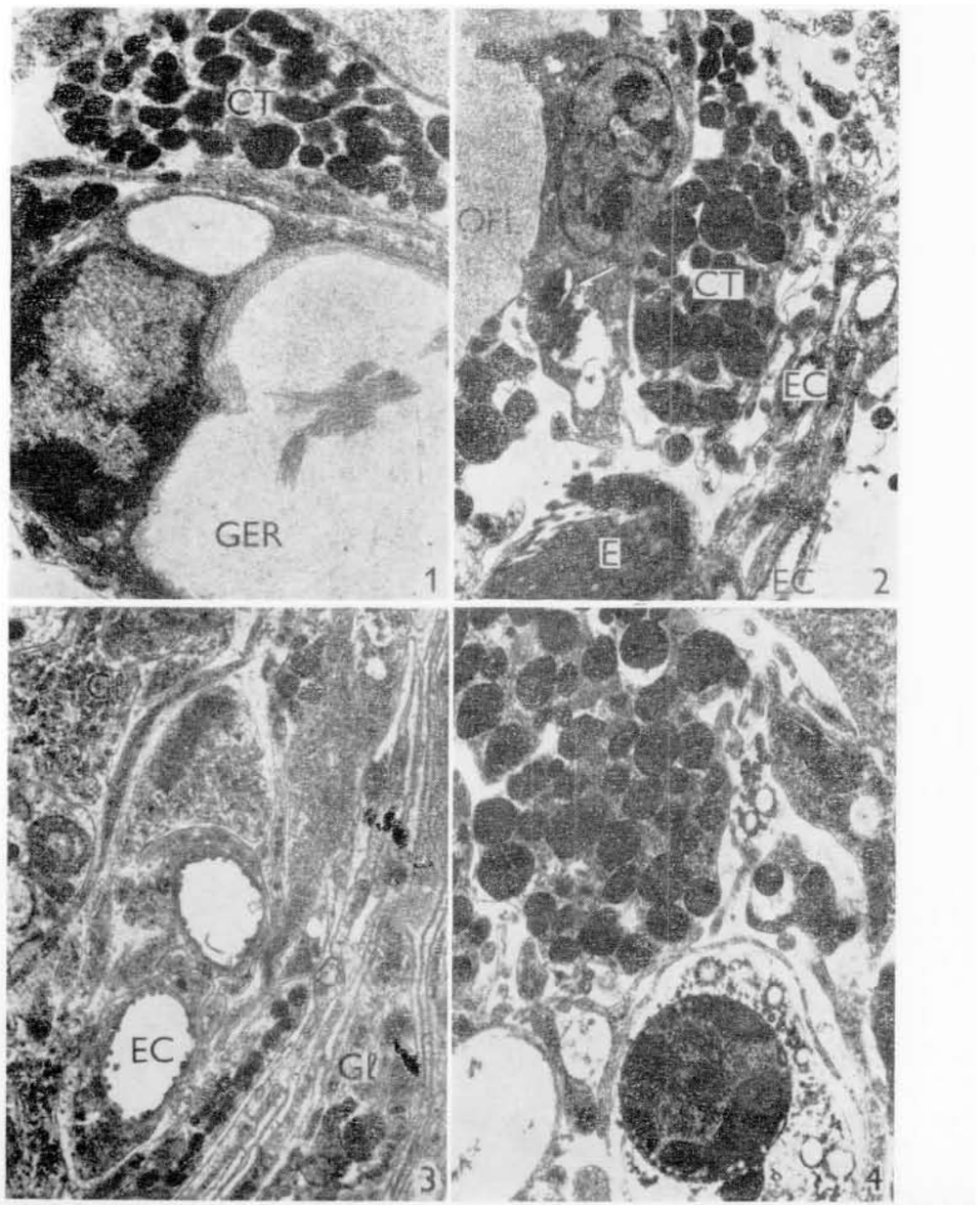

Fig. 1. Myofibroblasts with reduced cytoplasm; fibres identical with areolar tissue fibres in widened canals of granular endoplasmic reticulum (× 13 300). **Fig. 2.** Lamellar bodies (arrow) in cells of parenchymatous layer, excretory cell and canals (× 13 300). **Fig. 3.** Cytoplasmic processes of muscle cells with inclusions of granules of glycogen (× 13 300). **Fig. 4.** Degenerating cells with cytoplasm lysis and hyperchromic nucleus (× 18 300).

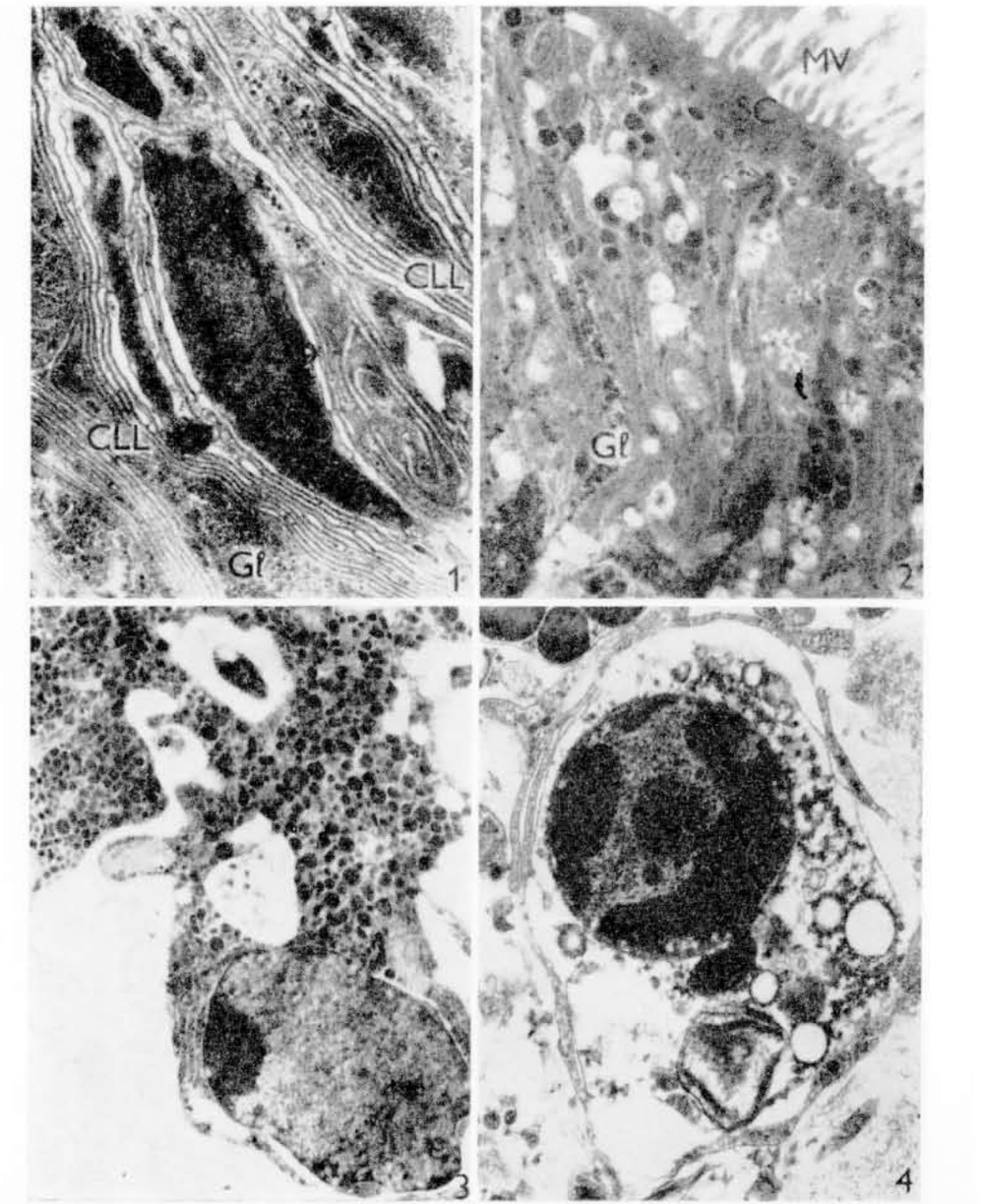

Fig. 1. Layer of myelinelike fibres bordering the cyst cavity (× 13 300). **Fig. 2.** Tail tegument. Secretory granules in cytoplasmic bonds of cytons with superficial syncytium (× 16 700). **Fig. 3.** Secretory cell of tail at the border with central cavity (× 13 300). **Fig. 4.** Degenerating cells, cell detritus in central cavity of tail (× 10 000).