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ULSTRASTRUCTURE OF THE METACERCARIA AND SPOROCYST SAC OF LEUCOCHLORIDIUM PERTURBATUM POJMAŃSKA, 1969

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Abstract. The metacercaria and sporocyst sac of *L. perturbatum* were studied by transmission electron microscopy. The body of metacercaria is covered with a thick layer of glycocalyx, which is in the peripheral part incrusted by numerous calcium particles clustered in conglomerates of various sizes. Crystalline inclusions and oblong, compact, strongly electron-dense structures occur sporadically among the filaments. The glycocalyx is firmly connected with the tegument containing a large number of rod-shaped and oval granules, spines and two types of aciliated sensory receptors. Two types of gland cells occur in the body of metacercaria. Ducts of frontal gland cells with longitudinal microtubules open at the surface of tegument in anterior part of metacercaria body. The ducts are fixed by circular septate desmosomes to the plasmalemma of tegument. Both the bodies and ducts of these cells are filled with secretory granules of irregular shape. The praepharyngeal gland cells have the same structure. The digestive system is lined with two different coverings — tegument with characteristic lacunae in the posterior part of oral sucker, and pharynx and cells with well-developed microvillous zone in caecal branches. The surface of the sporocyst wall is covered with the microvillous zone of tegument. Circular muscles and pigment cells are accumulated in pigmented bands of sacs. The cavity of sporocyst is bordered with cells with a large number of lipid vacuoles and lamellar processes.

This paper is a continuation of previous studies (Žďárská et al. 1984) dealing with the histochemistry and morphology of larval stages of *L. perturbatum.* It is a part of complex investigations of adaptation of larvae of the superfamily Brachylaimoidea to the existence in terrestrial environment.

MATERIAL AND METHODS

Sporocysts and metacercariae of *L. perturbatum* were obtained from naturally infected snails, *Succinea altaica evoluta*, from the vicinity of Alma-Ata. The material was fixed with 3% glutaraldehyde in 0.1 M cacodylate buffer, pH 7.2, at 4 °C for 2 h and postfixed with 1% OsO_4 for 2 h, then dehydrated through an alcohol series and embedded through aceton into Epon or Araldit. Ultrathin sections were cut with Reichert's OM-U2 ultramicrotome, contrasted with 20% uranyl-acetate and Reynold's solution of lead acetate and examined with a JEM 100 B electron microscope.

RESULTS

A. Metacercaria

The body tegument of the metacercaria is firmly connected with a thick glycocalyx covering the cavities of oral and ventral suckers and pharynx. The glycocalyx is thinnest in the pharynx. The filaments of glycocalyx are connected with the outer lamina of the trilaminal unit membrane of tegument. The layer of glycocalyx near the tegument consists only of filaments, without any inclusions. Electron-dense concrements of variable size and shape (Plate I. Figs. 1, 2) are arranged in concentric bands and situated in the peripheral part of glycocalyx. The observations in TEM correspond to the results of histochemical studies — the bands with concrements conform to Kóssa-positive peripheral part of glycocalyx, the bands without concrements to Kóssa-negative layer of glycocalyx (Žďárská et al. 1984 — Plate I, Figs. 1, 2). Consequently, the concrements (Plate I, Fig. 1) represent the calcium salts in the glycocalyx of metacercaria. The size of these inclusions increases towards the periphery. The calcium particles are spherical and their centres and peripheral parts are more electron-dense. They are situated among the filaments of glycocalyx, either single or in conglomerates (Plate I, Fig. 2) of irregular shape consisting of 2—6 particles surrounded with electron-dense envelope. In addition to these concrements, the glycocalyx contains solitary crystals and large, oblong, strongly electron-dense structures (Plate I, Fig. 1).

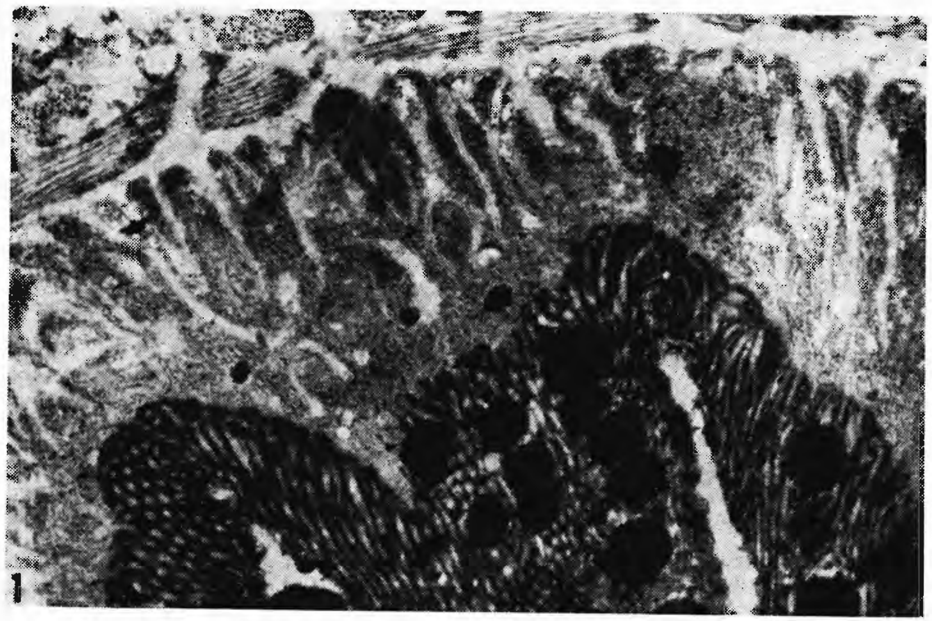

Fig. 1. Section through caecal wall of *L. perturbatum* metacercaria. Numerous invaginations of basal plasmalemma of caecal cells are visible under the layer of circular and longitudinal muscles (at the top). In the apical part of these cells, there are numerous microvilli (at the bottom) cemented by a dense substance. Note lipid vacuoles in the microvillous zone. (G, Os, UAc, Pb) (x 13 400).

The tegument of metacercaria is bordered with a unit membrane on the surface and at the base and its cytoplasm contains a large number of rod-shaped, strongly electron-dense granules, oval granules of medium electron-density and spines. The rod-shaped, electron-dense granules under the tegument surface are upright, whereas in the remaining part, they are oriented irregularly. Oval granules and mitochondria are localized mostly in the basal part of tegument. Long, flat spines elevate the outer unit membrane of tegument high above its surface (Plate II, Fig. 1). Their widened base adheres to lamina basalis and their substance has the character of a crystalline lattice (Plate III, Fig. 3). The basal plasmalemma forms numerous invaginations (Plate II, Fig. 1). A thick layer of connective tissue and of circular and longitudinal

muscles is situated under the lamina basalis. Bodies of subtegumental cells with large nuclei are under this layer. Their nuclei contain regularly distributed chromatin and a conspicuous compact nucleolus, and the cytoplasm is filled with rod-shaped and oval granules and mitochondria (Plate III, Fig. 2).

There are two types of sensory receptors in the tegument. They do not communicate with the tegument surface and most of them are localized in oral and ventral suckers. Sensory receptors of the first type are bulb-shaped and they are surrounded with plasmalemma connected in its proximal part by a septate desmosome to the plasmalemma of tegument. A strongly electron-dense, disc-shaped structure is situated near the top of sensory receptor, above transversely striated ciliary rootlet. The remaining space of the bulb is filled with electron-lucent vesicles, microtubules and mitochondria (Plate V, Fig. 2). No cilia have been found in any of these receptors.

The sensory receptors of the other type (Plate III, Fig. 1; Plate V, Fig. 3) differ from the previous ones only in the structure of bulb contents — instead of transversely striated ciliary rootlet there are one or two basal bodies.

The rim around the oral sucker contains frontal gland cells opening at the surface of tegument. Their lobular bodies (Plate V, Fig. 1) are localized in the subtegument and contain a large nucleus with evenly dispersed chromatin and compact nucleolus. The cytoplasm is filled with large, irregular, electron-dense granules. Among them is the Golgi complex and solitary mitochondria. The ducts of these cells are filled with irregular granules laying close to one another and possess a large number of longitudinally running microtubules at the periphery under plasmalemma (Plate IV, Figs. 1, 2, 3; Plate III, Fig. 1). The ducts of frontal gland cells penetrate the layer of longitudinal and circular muscles, the layer of connective tissue, lamina basalis and tegument. Their openings are fixed by a circular septate desmosome to the plasmalemma of tegument (Plate IV, Fig. 3). The anterior part of body of *L. perturbatum* metacercaria contains also praepharyngeal gland cells opening between pharynx and oral sucker. Their structure is identical with that of frontal gland cells.

The tegument of the posterior part of oral sucker and pharynx differs structurally from the body tegument. In its basal part, there are large lacunae (Plate II, Fig. 2) filled with fluid, which arise by separation of plasmalemma from lamina basalis. The plasmalemma of tegument is fixed by hemidesmosomes to lamina basalis only in some points. Similar hemidesmosomes connect the muscle fibres with lamina basalis on the opposite side. Behind the pharynx, this type of syncytial tegument is replaced by cellular covering of caeca. The caecal cells are fixed to lamina basalis surrounded with a layer of connective tissue and muscles. The cell cytoplasm of intestinal branches contains mitochondria with a small number of cristae, large lipid vacuoles and electron-dense bodies. The nucleus of these cells is large, chromatin is accumulated in clusters under the nuclear membrane and the nucleolus is compact. The apical part of intestinal cells protrudes in numerous microvilli connected with one another by a thick layer of electron-dense substance (Fig. 1). Even in the microvillous zone of intestine, there are large lipid vacuoles and electron-dense bodies. The basal plasmalemma of intestinal cells forms numerous invaginations.

B. Sporocyst

The body surface of the sporocyst is covered with tegument protruding in long, thin microvilli covered with glycocalyx. This outer covering cements the microvillous zone in a compact layer. The cytoplasm of tegument contains single mitochondria and dense granules and the basal plasmalemma forms numerous invaginations extending up to three fourth of tegument thickness. The basal plasmalemma adheres to lamina basalis under which is a thick layer of connective tissue surrounding the layer of muscles. The fibres of longitudinal and circular muscles are permeated with processes of pigment cells filled with large pigment granules of variable size, mitochondria and β-particles of glycogen (Plate VI, Fig. 1). The processes of subtegumental cells communicate with tegument, whereas the processes of pigment cells terminate in the layer of circular muscles. The perinuclear parts of tegument and pigment cells are localized under the layer of longitudinal and circular muscles. Coloured bands of sporocyst sac protrude above the surface. They arise by the accumulation of circular muscles and processes of pigment cells. The lumen of the sporocyst sac is bordered with cells the surface of which forms lamellae. The lamellae are more numerous in the distal part of sac. The nuclei of these cells contain chromatin situated in clusters under nuclear membrane and a conspicuous nucleolus. The cytoplasm is filled with many large lipid vacuoles, solitary membrane structures and particles of glycogen (Plate VI, Fig. 2).

DISCUSSION

The ultrastructure of the body tegument of *L. perturbatum* metacercaria is almost identical with that of other hitherto studied species of this genus. The structure of the filaments of the high glycocalyx is identical, but the calcium inclusions in *L. perturbatum* metacercaria differ in shape from that in the metacercaria of *L. paradoxum* (Žďárská 1981, Storch and Welsch 1970), *L. variae* and *L. holostomum* (Bakke 1982). In all of these four species the individual particles are spherical, but in *L. paradoxum*, *L. variae* and *L. holostomum* they do not accumulate in larger structures. In *L. perturbatum*, individual particles form conglomerates of various shapes, consisting of 2—6 particles connected by electron-dense substance. Consequently, in *L. perturbatum*, the calcium salts occur not only in form of individual particles, as in the other three species, but also in form of conglomerates, distinguishing thus the body covering of this metacercaria from that of the others. In contrast to *L. variae* and *L. holostomum* (Bakke 1982), the glycocalyx of *L. perturbatum* and *L. paradoxum* (Žďárská 1981) contains large, electron-dense bodies and that of *L. perturbatum* also crystalline inclusions.

It still remains unclear what is the origin of calcium particles in glycocalyx — are they products of metacercaria or of sporocyst? Some authors assume that excretions from the excretory bladder are involved (Bakke 1982). However, according to some authors (Kagan 1952, Bakke 1982), the opening of the excretory bladder does not continue through a pore to the surface of glycocalyx and, consequently, the excretions would accumulate in the inner layer around the excretory pore. The calcium particles, however, occur mostly in the superficial layer of glycocalyx and we therefore assume that they are produced by the sporocyst wall and incorporated into the glycocalyx produced by metacercaria (Žďárská 1981). Nevertheless, cytochemical studies would be necessary to confirm this hypothesis.

Another question is the purpose for which this thick body covering of metacercaria is formed. We assume that the thick incrusted glycocalyx protects the metacercaria against friction during the rhythmical pulsation of the sporocyst sac and against dehydration. In the opinion of Lewis (1974 a, b, 1977), the formation of this type of "cyst" is a form of adaptation which should prevent the dehydration when the tentacles of the snail rupt and the metacercariae are released into terrestrial environment. This hypothesis, however, cannot be accepted considering that such a thick glycocalyx occurs also in other metacercariae of the superfamily Brachylaimoidea, as *Leucochloridiomorpha constantiae* (Harris et al. 1974), *Hasstilesia ovis* (Žďárská and Soboleva 1982) and *Brachylaimus aequans* (Žďárská 1983), which cannot be accidentally released from the snail. In our opinion, the hygroscopic, thick glycocalyx of the cercariae and metacercariae of the superfamily Brachylaimoidea represents an ecological adaptation to the existence under terrestrial conditions. It does not concern only the genus *Leucochloridium*, but also other genera with different type of life-cycle. Also Bakke's (1982) hypothesis that the "cyst" protects metacercaria against the effect of digestive enzymes in the definitive host is worth consideration.

The character of secretion and presence of microtubules in the ducts of frontal and praepharyngeal gland cells in *L. perturbatum* metacercaria are identical with that of frontal gland cells in the metacercaria of *L. paradoxum* (unpublished), gland cells opening around the oral sucker and into oesophagus of *Microphallus similis* metacercaria (Davies 1979, 1980) and frontal gland cells in young specimens of *Gorgoderina vitelliloba* (Mitchell 1973). They are also identical with lappet glands producing A secretion in *Diplostomum phoxini* (Bibbi and Rees 1971) and very similar to penetration gland cells in various species of cercariae. However, these are not the cystogenic gland cells reported by Bakke (1982). The praepharyngeal gland cells in *L. perturbatum* metacercariae are identical in their localization with the gland cells of *Urogonimus macrostomus* described by Schmidt (1964) and seem to have a digestive function. The same may be supposed also about the frontal gland cells opening in the rim around the oral sucker. If we admit that the metacercaria takes nutrients from the lumen of sporocyst, then the two types of gland cells would function already in the metacercaria.

Sensory receptors in metacercariae of the genus *Leucochloridium* are described for the first time at ultrastructural level. They were previously characterized histochemically in *L. paradoxum* (Žďárská and Soboleva 1981) and *L. perturbatum* (Žďárská et al. 1984). The metacercaria of *L. perturbatum* possesses two types of receptors without cilia, which do not communicate with the tegument surface. The type with well developed rootlet resembles very much one of the three types of receptors in *Gyrocotyle rugosa* described by Allison (1980) and the aciliated sensory ending in young *Fasciola hepatica* (Bennett 1975), the rootlet of which, however, is not so well developed.

The ultrastructure of caecal branches and pharynx in *L. perturbatum* metacercaria is identical with that in *L. paradoxum* (Žďárská 1983).

The ultrastructure of sporocyst wall in *L. perturbatum* resembles in the main features that in *L. paradoxum* (Žďárská et al. 1982). The pigment granules in the two species are different and this difference is expressed both in the colour and ultrastructure. In *L. paradoxum* sporocyst (of green colour), the pigment granules are compact and strongly electron-dense, whereas in *L. perturbatum* (of red-brown colour), they are granular and less electron-dense. They resemble the pigment granules of red-brown sporocysts of *L. variae* and *L. holostomum* (Bakke 1982). The chemical composition and source of pigment in trematode larvae was studied in detail by Nadakal (1960 a, b). The pigment in the sporocyst wall of trematodes of the genus *Leucochloridium* seems to play an important role in transmission ecology (Holmes and Bethel 1972).

The cells in the inner layer of sporocyst sacs of *L. perturbatum* contain a large number of lipid vacuoles which are considered by Bakke (1982) to be secretory globules. In our opinion, however, these are metabolic products deposited in form of neutral fats. Since the rhythmical contractions of the sporocysts wall depend on the intensity of light (Mönnig 1922, Halik 1931, Hecker and Thomas 1963, Kagan 1952, Lewis 1972), Bakke (1982) tried to find photoreceptors in the sporocyst wall of *L. variae* and *L. holostomum*. He did not find typical photoreceptors (pigmented or non-pigmented), but he regards as photoreceptors the undulated membranous structures. It is remarkable that neither pigmented nor non-pigmented photoreceptors have ever been found in the photosensitive sporocyst sacs in the genus *Leucochloridium*, though they are known to occur in the trematodes both in sporocysts and cercariae. Pigment eye-spots in sporocysts were described by Faust (1918), Basch and Sturrock (1969), Pond and Cable (1966) and Arvy (1975). Photosensitive non-pigmented eye-spots were reported by Isseroff and Cable (1968).

УЛЬТРАСТРУКТУРА МЕТАЦЕРКАРИИ И МЕШКА СПОРОЦИСТЫ *LEUCOCHLORIDIUM PERTURBATUM* POJMANSKA, 1969

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Резюме. Метацеркарии и мешок спороцисты *L. perturbatum* изучали с помощью трансмиссионной электронной микроскопии. Тело метацеркарии покрыто толстым гликокаликсом, который в периферической части инкрустирован большим количеством известковых частиц, накопленных в конгломераты разного размера. Среди филаментов гликокаликса встречаются кристаллоидные включения и продольные, компактные, сильно электронноплотные строения. Гликокаликс крепко соединен с тегументом, содержащим большое количество палочковидных и овальных гранул, шипики и два типа безреснитчных сенсорных рецепторов. На поверхность тегумента открываются в передней части тела метацеркарии выводы фронтальных железистых клеток с продольными микротрубочками. Выводы фиксированы к плазмалемме тегумента через круглые, разделенные перегородками десмосомы. Как тела, так и протоки этих клеток выполнены секреторными гранулами нерегулярной формы. Предглотковые железистые клетки имеют одинаковую структуру. В пищеварительной системе находятся два различных покрова. В задней части ротовой присоски и в глотке — тегумент с характеристическими лакунами и во ветвях кишечника — клетки с сильно развитой зоной микроворсинок. Зона микроворсинок тегумента образует поверхность спороцисты. В пигментированных полосах мешка накоплены циркулярные мышцы и пигментные клетки. Полость мешков спороцисты отграничена клетками с большим количеством липидных вакуолей и пластинчатовидными отростками.

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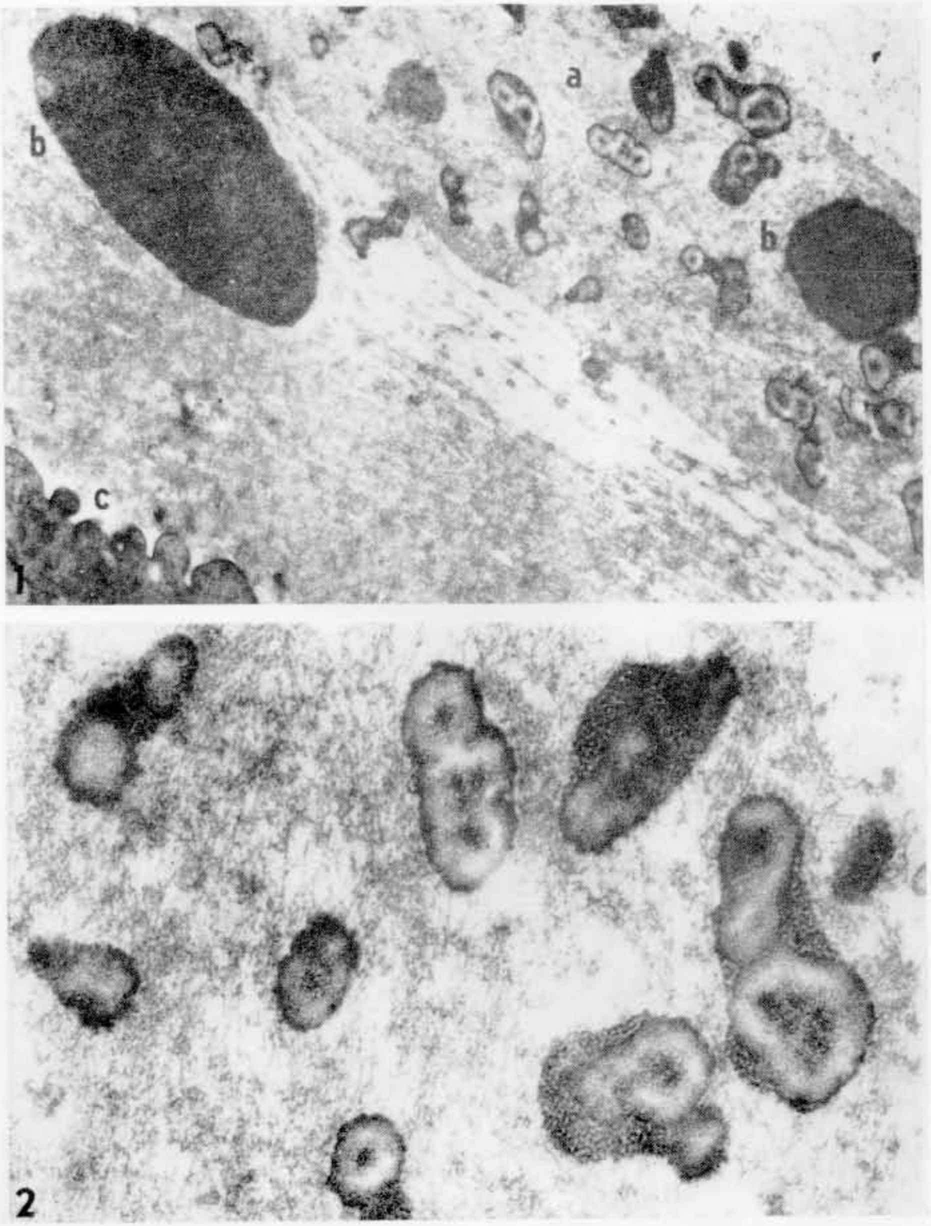

Fig. 1. Tangential section through the glycocalyx of *L. perturbatum* metacercaria. The outer layer (a) contains a large amount of concrements and single dense structures (b). c — tegument. (G, Os, UAc, Pb) (×15 200). **Fig. 2.** Glycocalyx with conglomerates of calcium particles (detail from Fig. 1). (G, Os, UAc, Pb) (×36 000).

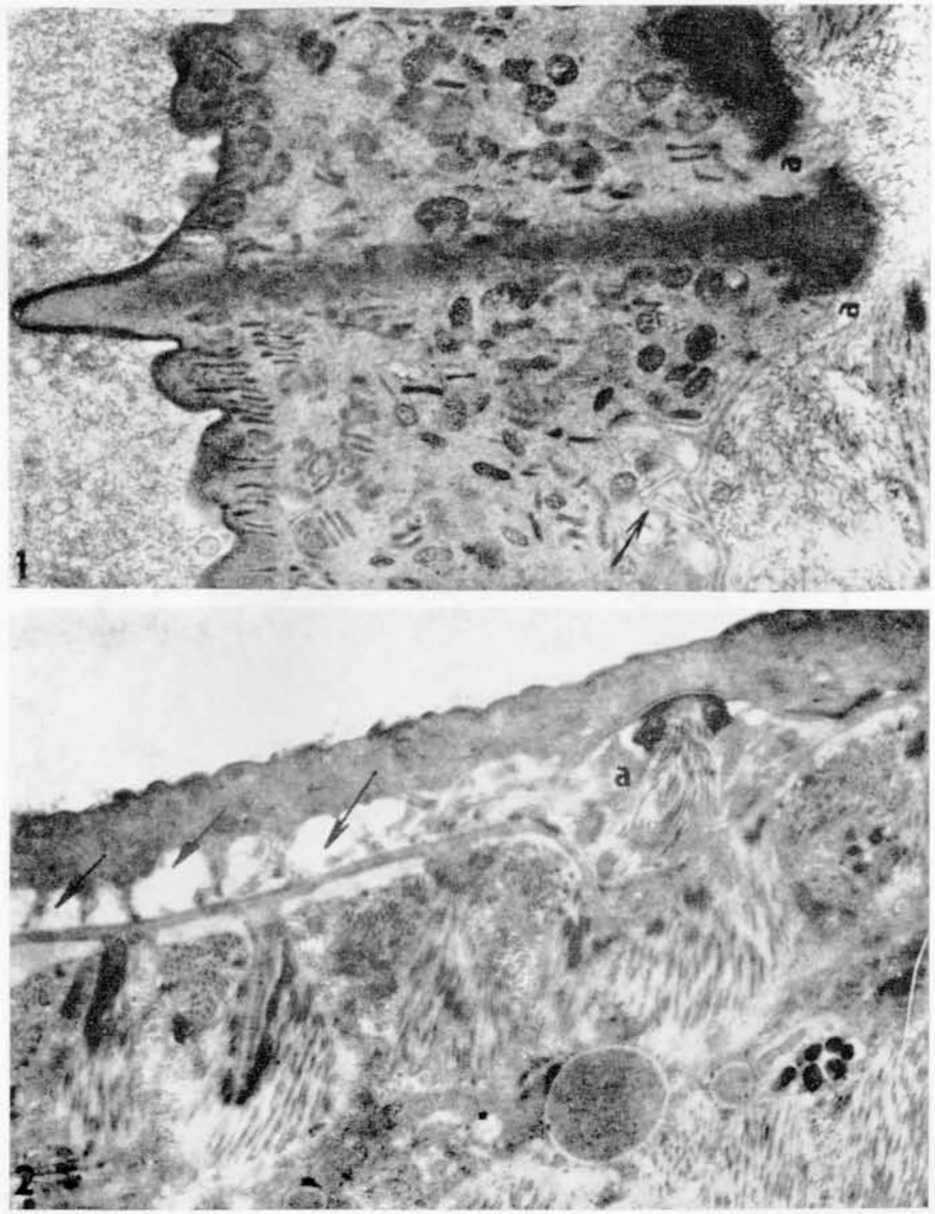

Fig. 1. Longitudinal section through a spine of *L. perturbatum* metacercaria. Its widened base (a) adheres to lamina basalis and its tip raises the plasmalemma of the tegument above the tegument surface. The basal plasmalemma of tegument forms numerous invaginations (arrow). Note the arrangement of rod-shaped dense granules near the surface of tegument and connection of glycocalyx with plasmalemma. (G, Os, UAc, Pb) (×22 350). **Fig. 2.** Longitudinal section through posterior part of oral sucker metacercaria at the site where the typical body tegument turns to tegument with lacunae in the basal part (arrows). A sensory receptor (a) is situated at this site. (G, Os, UAc, Pb) (×15 000).

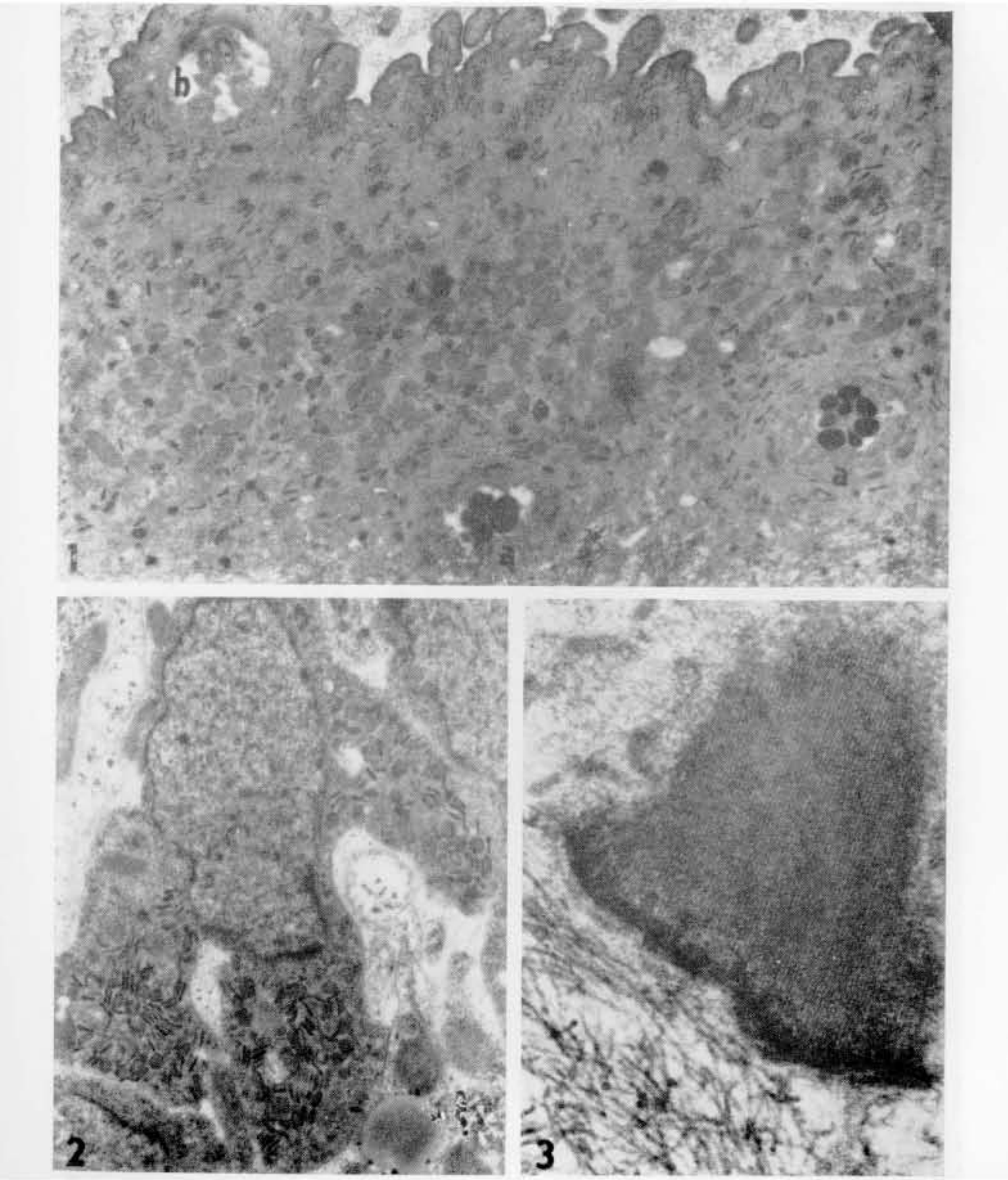

Fig. 1. Metacercaria of *L. perturbatum* — oblique section through the tegument of rim in front of the oral sucker at the site of ducts of two frontal gland cells (a) and aciliated sensory receptor (b) with two basal bodies. (G, Os, UAc, Pb) (× 12 870). **Fig. 2.** Lobular body of subtegumental cell with a large nucleus and finely dispersed chromatin and cytoplasm filled with rod-shaped dense granules and mitochondria. (G, Os, UAc, Pb) (× 15 000). **Fig. 3.** Oblique section through a spine with a conspicuous crystalline lattice and dense substance at its base. (G, Os, UAc, Pb) (× 53 640).

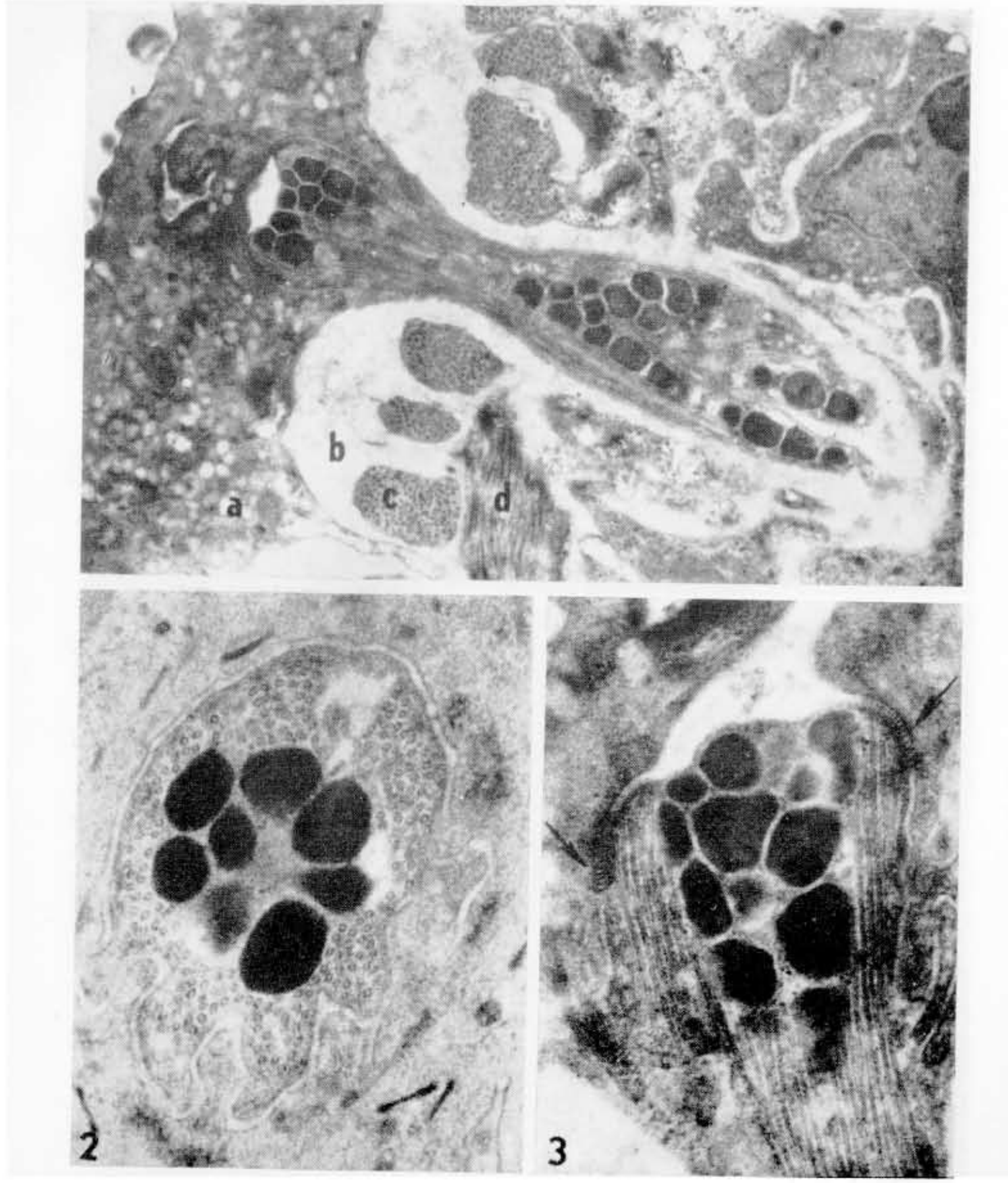

Fig. 1. Longitudinal section through frontal gland cell duct of *L. perturbatum* metacercaria with distinct longitudinal microtubules and lumen filled with irregular, dense granules. a — tegument, b — layer of connective tissue, c — circular muscles, d — longitudinal muscles. (G, Os, UAc, Pb) (× 15 200). **Fig. 2.** Transverse section through frontal gland cell duct. Note microtubules localized at the periphery. (G, Os, UAc, Pb) (× 35 760). **Fig. 3.** Detail of longitudinal section through frontal gland cell duct with distinct microtubules and septate desmosome (arrows). (G, Os, UAc, Pb) (× 31 300).

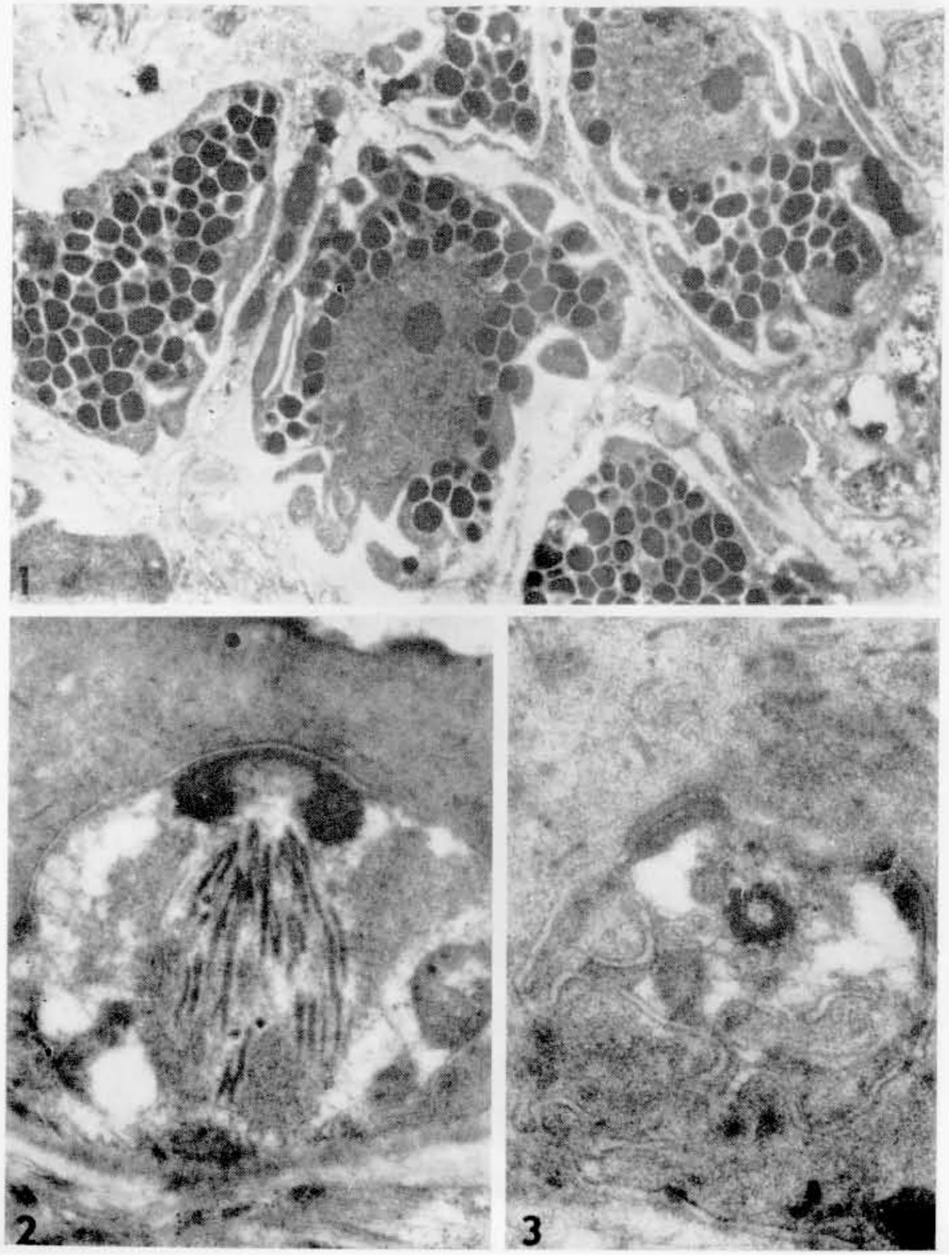

Fig. 1. Section through lobular bodies of frontal gland cells of *L. perturbatum* metacercaria filled with dense granules. The nucleus contains a dense nucleolus. (G, Os, UAc, Pb) (×10 700). **Fig. 2.** Aciliated sensory receptor with dense collar and well developed rootlet. A mitochondrion is situated on the right in the bulb. (G, Os, UAc, Pb) (×22 200). **Fig. 3.** Section through aciliated sensory receptor with one basal bcdy. Compare with sensory receptor with two basal bodies shown in Plate III, Fig. 1. (G, Os, UAc, Pb) (×31 290).

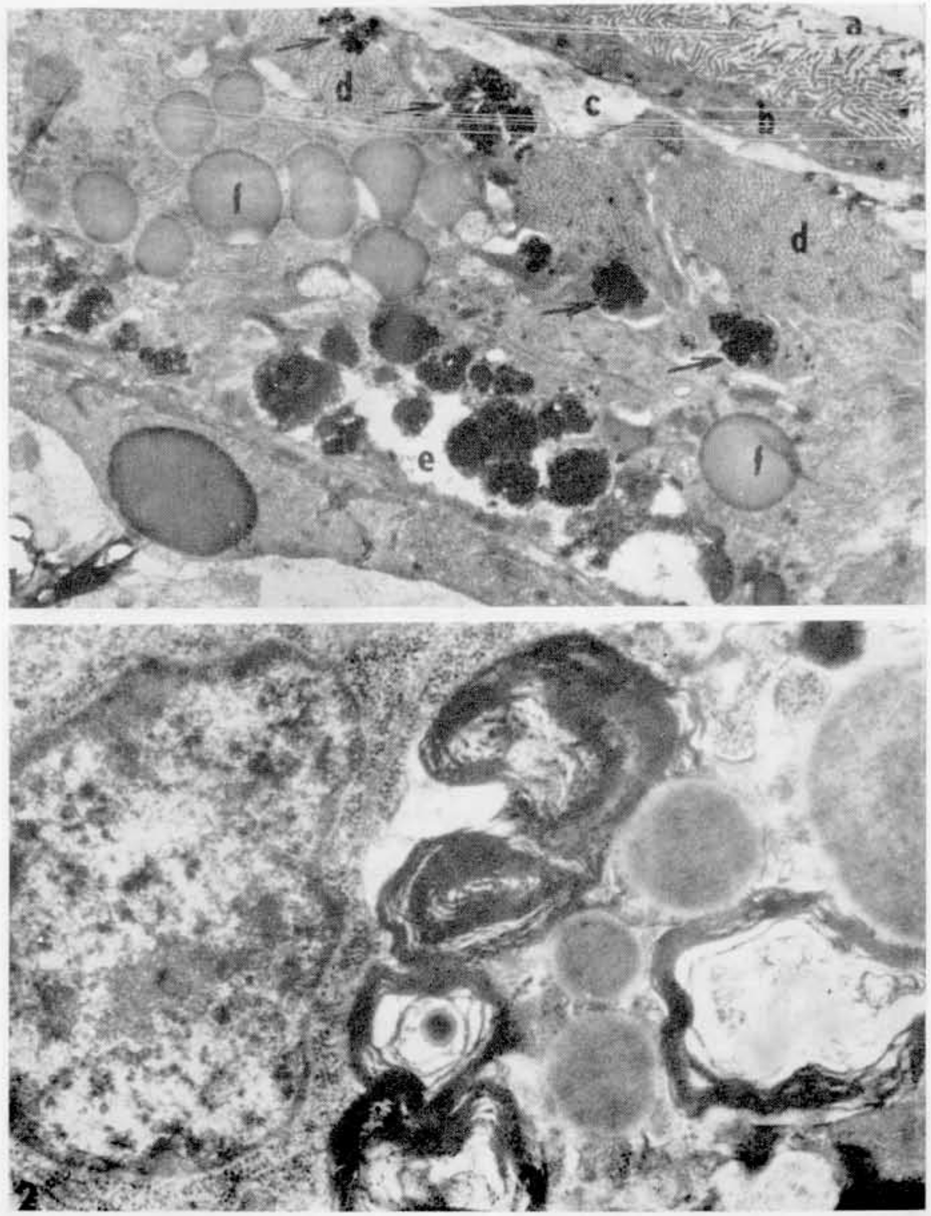

Fig. 1. Longitudinal section through the wall of sporocyst sac of *L. perturbatum* with irregularly finely granulated, dense pigment granules. Processes of pigment cells filled with pigment reach up to circular muscles (arrows). a — microvillous zone of tegument, b — tegument, c — connective tissue layer, d — circular muscles, e — pigment, f — lipid vacuoles. (G, Os, UAc, Pb) (×13 400). **Fig. 2.** Cell of inner limiting layer of sporocyst wall with membranous structures and lipid vacuoles. (G, Os, UAc, Pb) (×31 900).