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ULTRASTRUCTURAL OBSERVATIONS ON THE REDIA OF ECHINOSTOMA REVOLUTUM (FROELICH, 1802)

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Abstract. *E. revolutum* redia digestive and excretory system ultrastructure, as well as body wall tegument were studied in TEM. The body tegument protrudes in short microvilli and contains uni- and multiciliate sensory endings. The anterior part of the digestive system (pharynx, short oesophagus) is lined with body tegument, the caecum being covered with a flat epithelium with sporadic microvilli. Oesophageal gland cells are filled with minute electron-dense granules. The excretory capillaries joined to large flame cells are composed of spirally wrapped cells, in the cytoplasm of which there are clusters of microtubules. The special features of the digestive system of echinostome rediae, as well as their significance in the antagonistic relationship to the partenitae of other families of trematodes and their pathogenic effect on the intermediate host, are discussed.

The infection of molluscs by echinostome rediae acquired practical importance with the discovery of their antagonistic effect on the larval stages of other trematode species and their strong pathogenic effect on the intermediate host. Echinostome rediae are recommended by many authors (Lie 1966, 1967, Lim and Heyneman 1972, Ryšavý et al. 1974, Baruš et al. 1974, Combes 1982 and others) as competitive species for the biological control of human schistosomiasis. The basic principle of the antagonistic relationship between the larval stages of various trematode species in case of double infection is the predominance of rediae of more aggressive species, which mechanically damage and counsume less aggressive sporocysts or rediae. Echinostome rediae not only consume the sporocysts and rediae of other species, but also the rediae (Wesenberg–Lund 1934, Nasir 1962, Lie et al. 1968, Dobrovolskii et al. 1983) and the extraredial cercariae of their own species (Køie 1987). In a previous paper (Žďárská et al. 1987), we gave attention to the ultrastructure of multiciliate receptors of *Echinostoma revolutum* redia hitherto unknown in parthenogenetic trematode stages. These receptors faciliate good orientation for the rediae in the host in the case of attacking individuals of their own or another species. In antagonistic relationship towards other partenitae and in the damage of the host tissues, an important role is played, apart from the nervous system, by the digestive system of the redia. As has emerged from our ultrastructural study, *E. revolutum* rediae are not only morphologically but also functionally adapted to damage and consume less aggressive partenitae and the tissues of the host.

MATERIALS AND METHODS

We obtained *E. revolutum* rediae from the hepatopancreas of naturally infected *Planorbis corneus* (according to Kanev (1985), the larval stages from the family Planorbidae are apparently not identical with *E. revolutum* which according to him develops only in the molluscs of the family Lymnaeidae). The hepatopancreas with rediae was fixed in 3 % glutaraldehyde in 0.1 M cacodylate buffer of pH 7.2 at 4 °C for 2 hours and postfixed in 1 % OsO_4 for 2 hours. The material was then dehydrated in ethanol and aceton series and embedded in Durcupan. Ultrathin sections were obtained on Reichert's OM-U2 ultramicrotome, stained with uranyl acetate and Reynolds' solution of lead citrate, and examined in a Philips EM 420 and a Philips EM 300 electron microscopes.

RESULTS

A. Digestive system

1. Pharynx

E. revolutum redia has a robust pharynx (Pl. I, Figs. 1, 2) with strongly developed radial, equatorial and meridional muscle fibres. The muscle fibres are joined by means of hemidesmosomes to the lamina basalis. The muscle fibres are composed of both thin and thick myofilaments. Among the groups of myofibrils, mitochondria are concentrated in rows, giving an impression in transverse section as if they formed sheats dividing the content of the myocytes. The mitochondria have a small number of cristae. The α and β glycogen particles are concentrated among the mitochondria. The sarcoplasmic reticulum is formed of a system of vesicles and tubules in the muscle cells of the pharynx. The vesicles are concentrated closer to the sarcolemma. In transverse section the vesicles are flattened (Pl. I, Fig. 2, Pl. VI, Fig. 3). Among the muscle fibres there are situated sporadic cell processes with small spherical electron-dense granules (Pl. I, Fig. 2). The pharyngeal cavity is lined with tegument which is essentially identical with that of the redia body. The tegument (Pl. I, Fig. 1) inside the pharynx forms high folds and lacks microvilli. Under its apical plasma membrane the rod-shaped granules are arranged perpendicularly to its surface. No sensory endings were ascertained in the tegument of the pharynx.

2. Oesophageal gland cells

The bodies of these cells (Pl. IV, Fig. 1) are localized around the pharynx and their ducts open just behind the pharynx in the part termed oesophagus, which is covered with the same tegument as the pharynx. In the cytoplasm of the gland cells there is an abundance of small round electron-dense granules, cisternae of granular endoplasmic reticulum, Golgi apparatus and sporadic mitochondria. The nucleus has chromatine concentrated under the nuclear membrane and contains a nucleolus. The ducts of these cells are filled with electron-dense granules and are solidified by microtubules running through the cytoplasm close under the plasma membrane.

3. The caecum

The caecum is lined with flat cells, the apical part of which protrudes in sporadic short microvilli (Pl. II, Figs. 1,2). The lumen of the caecum is filled with a highly electron-dense substance (Pl. II, Figs. 1,2; Pl. III, Figs. 1,2), which is probably the haemolymph of the host which contains haemoglobin in the case of the *Planorbis* genus. The gastrodermal cells are interconnected by means of long septate desmosomes (Pl. II, Fig. 1; Pl. III, Fig. 1). The cytoplasm of these cells contains Golgi apparatus, granular endoplasmic reticulum, lysosomes, mitochondria, autophagosomes, membraneous corpuscles, vesicles and vacuoles. The nucleus contains a dense nucleolus. Under the gastrodermis there is a thin lamina basalis, under which there are fine muscle fibres, and processes of the parenchymal cells (Pl. II, Figs. 1,2; Pl. III, Figs. 1,2). No special gland cells were observed in the gastrodermis.

B. Excretory system

The flame cells (Pl. V, Figs. 1, 2) are attached to excretory capillaries (Pl. VI, Fig. 1), which open into two collecting excretory ducts. The excretory ducts run along the redia body wall and open separately on its surface. There is no excretory bladder. The flame cells and the excretory capillaries are larger than in the cercaria. The nucleus of the flame cell, with chromatine situated in clusters under the nuclear membrane, is surrounded by a narrow border of cytoplasm, in which at the pole facing the excretory capillary, the rootlets and basal bodies of the cilia are embedded. The plasma membrane of the flame cell is connected by gap junctions to the processes of the parenchymal cells. Microvillus-like processes (internal leptotriches) project to the lumen around the flame (Pl. V, Fig. 1). They are apart of the flame cell. Similar processes (external leptotriches) extend from the outer side of the first cell of the excretory capillary into the intercellular substance. At the point where the flame cells are connected to the first cell of the excretory capillary, the finger-like processes of the cytoplasm of both cells fit into one another. The plasma membranes of these interdigitations are joined by means of a very thin fibrous layer (Pl. V, Fig. 1). The excretory capillaries are formed of spirally wrapped cells, the plasmalemma of which is joined together by means of septate desmosomes at the point of contact (Pl. V, Figs. 1,2). The wall of excretory capillaries is reinforced with clusters of microtubules (Pl. V, Fig. 2). The cytoplasm of the excretory capillary cells contains, in addition to microtubules, granular endoplasmic reticulum, glycogen and sporadic mitochondria. The nucleus is flattened. The collecting excretory ducts are provided with lamellae.

C. Tegument

The tegument of the redia body (Pl. IV, Figs. 1,2; Pl. V, Fig. 1) protrudes in short, less numerous microvilli. It is bordered by a surface and basal plasma membrane and contains irregularly arranged, rod-shaped electron-dense granules, sporadic spherical electron-dense granules, mitochondria, lipid droplets and granular endoplasmic reticulum. The syncytial part of the tegument is connected by means of cytoplasmic processes to the subtegumental cells situated underneath the muscle layer. In the tegument of the anterior end of the redia there are numerous uniciliate (Pl. IV, Fig. 2) and sporadic multiciliate (see Žďárská et al. 1987) receptors. The uniciliate receptors have a long cilium with a basal body and a well-developed striated rootlet, which is anchored at the bulbous part of the nerve fibre. The bulb is reinforced with a dense ring and contains sporadic mitochondria, neurotubules and electron-lucid vesicles. The plasma membrane of the bulb is attached at the level of the dense ring by means of a septate desmosome to the plasma membrane of the tegument. Under the basal plasma membrane of the tegument there is a thick lamina basalis, to which the tegument is attached by means of hemidesmosomes. Under the lamina basalis there are well-developed both circular and longitudinal muscle fibres, which facilitate the migration of the redia in the tissues of the host. The cytoplasmic parts of the myocytes contain numerous mitochondria, glycogen particles, nucleus with dense chromatine under the nuclear membrane, and the nucleolus.

D. The embryonal epithelium

The inner part of the parenchymal layer of the redia body wall forms an embryonal epithelium at the place of the germ balls. This epithelium consists of processes of the parenchymal cells which envelop the embryos and later also the developing cercariae. After the formation of definitive cercarial tegument the embryonal epithelium degenerates and its remains, together with the released cercariae, are situated in the body cavity of the redia.

DISCUSSION

Whereas the trematode sporocysts feed only osmotically, the nutritional means of rediae are diverse, as a result of the presence of a digestive system. In addition to osmotic nutrition via the tegument, the rediae also absorb nutrients in the digestive system consuming the tissues of the mollusc. In this case then we can speak of histiophagia (Dobrovolskii et al. 1983). If in case of double infections the rediae consume the rediae, sporocysts and cercariae of other species, we can speak of predation (Lim and Heyneman 1972), and if they consume individuals of their own species then it is cannibalism (Wesenberg–Lund 1934; Nasir 1962; Lie et al. 1968; Dobrovolskii 1983; Køie 1987). It has been histochemically proved that acid phosphatase activity is present in the pharynx, caecum and oesophageal gland cells of *E. revolutum* rediae (Žďárská and Našincová 1985), as is the case with other rediae (Cheng 1964, Probert 1966, Krupa et al. 1968, Dobrovolskii et al. 1983). We have demonstrated ultrastructurally in these parts of the digestive system the presence of lysosomes and dense secretory granules which probably also contain this enzyme. From the morphological, histochemical and ultrastructural viewpoints it is evident that *E. revolutum* rediae, like other rediae (Dobrovolskii et al. 1983), are able to feed not only by resorption of nutrients via the tegument, but also by means of active consumption of the host tissue (histiophagia) or of the partenitae and larvae of trematodes (predation, cannibalism). This phenomenon has been observed, particularly in the case of double infections, by many authors (Lie 1966, 1967, Lim and Heyneman 1972, Ryšavý et al. 1974, Baruš et al. 1974, Combes 1982), whose conclusions are recommended for application in the biological control of human schistosomiasis.

The study of the ultrastructure revealed that *E. revolutum* rediae are equipped for the consumption of tissues with well-developed nervous system with special sensory endings (Žďárská et al. 1987) and digestive system with frontal gland cells, pharynx, oesophageal gland cells and caecum with microvilli. They have highly developed musculature, not only in the pharynx, but also in the body wall. Smyth and Halton (1983), Rees (1966), Wilson (1972), Dobrovolskii et al. (1983) attribute a digestive function to the oesophageal gland cells. The frontal gland cells, which open into the tegument around the oral opening of the redia, can also be considered a part of the digestive system. It is probable that the secretion of the frontal gland cells also assists in extracorporal digestion in *E. revolutum* rediae as in the hermaphrodite trematode generation (Žďárská 1986). According to Køie (1971) the extracorporal digestion of rediae is also facilitated by enzymes released from the tegument.

The excretory system of *E. revolutum* rediae differs from that of miracidia, cercariae and adults in the conspicuously large size of the flame cells, excretory capillaries and ducts. Dobrovolskii et al. (1983) have already drawn attention to the striking large size of the flame cells of some partenitae. Apart from some details, the excretory system of rediae is ultrastructurally identical with those of other trematode developmental stages. The excretory capillaries of rediae differ in the presence of clusters of microtubules both from the excretory capillaries of miracidia (Chia-Tung 1980), in which microtubules were demonstrated only in the cytoplasm of the flame cells, and from the excretory capillaries of cercariae (Ebrahimzadeh and Kraft 1971) as well as from mature digenetic trematodes (Senft et al. 1961, Pantelouris and Threadgold 1963, Soboleva et al. 1988), where they have not been demonstrated at all. Owing to the presence of clusters of microtubules in the walls of the excretory capillaries, the excretory system of *E. revolutum* rediae most closely resembles that of the Aspidogastrea, in which groups of microtubules are present both in the flame cells and in the excretory capillaries as well as in the collecting excretory ducts (Rohde 1971). As in other trematode stages, the flame cells of *E. revolutum* rediae are likewise provided with both internal and external leptotriches, and there are no pores among the interdigitations.

As far as, the tegument structure of *E. revolutum* redia is concerned, it is evident that it is less dependent upon feeding through the tegument than the sporocysts and rediae with short caecum (Krupa et al. 1967, Ginetsinskaya 1968, Reader 1972). The microvilli are short and their density is low. Otherwise the basic structure of the tegument corresponds to the structure generally known in rediae and sporocysts. The thin synticial layer of tegument is joined by means of cytoplasmic processes with the subtegumental cells situated under the layer of strongly developed circular and longitudinal musculature. Ultrastructurally, however, *E. revolutum* rediae differ from hitherto described rediae in the equipment of the anterior body and tegument with special multiciliate sensory endings (Žďárská et al. 1987) similar to the sensory endings of free-living miracidia and cercariae (Žďárská et al. 1988). The presence of these receptors in the tegument of *E. revolutum* rediae indicates that the partenitae are capable of good orientation in their environment, particularly when obtaining food, whether by histiophagia, predation or cannibalism.

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НАБЛЮДЕНИЕ ЗА УЛЬТРАСТРУКТУРОЙ РЕДИИ *ECHINOSTOMA REVOLUTUM* (FROELICH, 1802)

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Резюме. С помощью метода трансмисионной электронной микроскопии изучали ультраструктуру пищеварительной и экскреторной систем и тегумента редии *E. revolutum*. Тегумент тела образует короткие микроворсинки и содержит одно и многоресничные чувствительные окончания. Передний отдел пищеварительной системы (глотка, короткий пищевод) покрыт тегументом, кишечник покрыт плоским эпителием с одиночными микроворсинками. В пищевод впадают пищеводные железистые клетки заполненные мелкими электронпоглощающими гранулами. Экскреторные тубулы, являющиеся продолжением больших мерцательных клеток, образованы спирально закрученными клетками, в цитоплазме находятся скопления микротрубочек. В работе дискутируются особенности пищеварительного тракта редий эхиностом и их значение для антогонистического отношения к партенитам других семейств trематод и для патогенного эффекта по отношению к промежуточонму хозяину.

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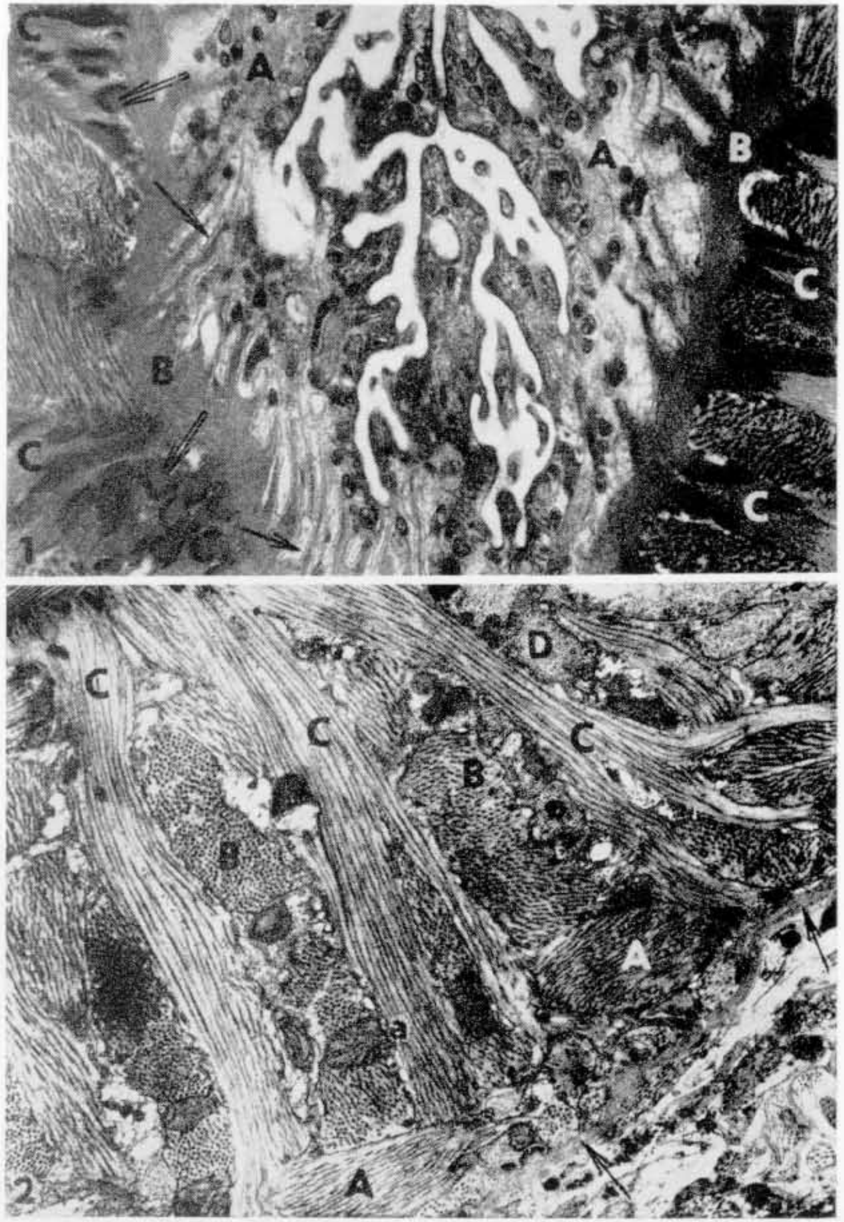


Fig. 1. Transverse section through the pharynx of *E. revolutum* redia. The pharynx cavity is bordered with folded tegument (A), containing rod-shaped and sphrerical dense granules. The basal plasma membrane (arrows) follows the septa of the substantially developed lamina basalis (B) on the opposite side of which the radial muscle fibres (C) are attached by means of hemidesmosomes (double arrows). (G, Os, UAc, Pb) (×16 800). **Fig. 2.** Transverse section through the pharynx muscles. A — equatorial muscle fibres, B — meridional, C — radial, D — cytoplasmic part of muscle cell, arrows — lamina basalis, a — mitochondria (G, OS, UAc, Pb) (×13 500)

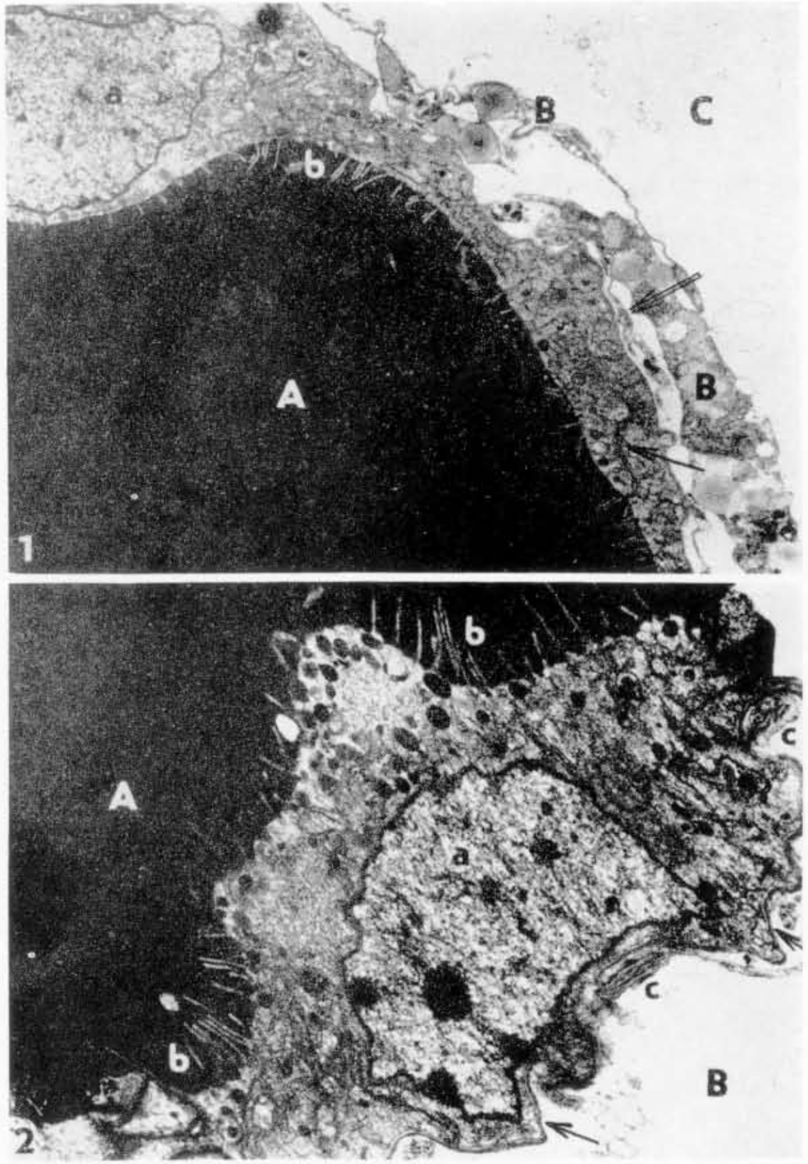


Fig. 1. Transverse section through the dilated wall of *E. revolutum* redia caecum. The lumen of the caecum (A) is filled with dense liquid containing haemoglobin of the host. The apical part of the epithelial cells of the gastrodermis protrudes in short microvilli (b). The cells are interconnected by a septate desmosome (arrows). Under the lamina basalis there are sporadic fine muscle fibres (double arrow) and under these processes of parenchymal cells (B). a — nucleus of epithelial cell, C — body cavity of redia (G, Os, UAc, Pb) (×6 460). **Fig. 2.** Detail of epithelial cell of gastrodermis with numerous dense vesicles in the apical part, A — lumen of the caecum, B — redia body cavity, a — nucleus, b — microvilli, c — fine muscle fibres, arrows, — lamina basalis (G, Os, UAc, Pb) (×12 450)

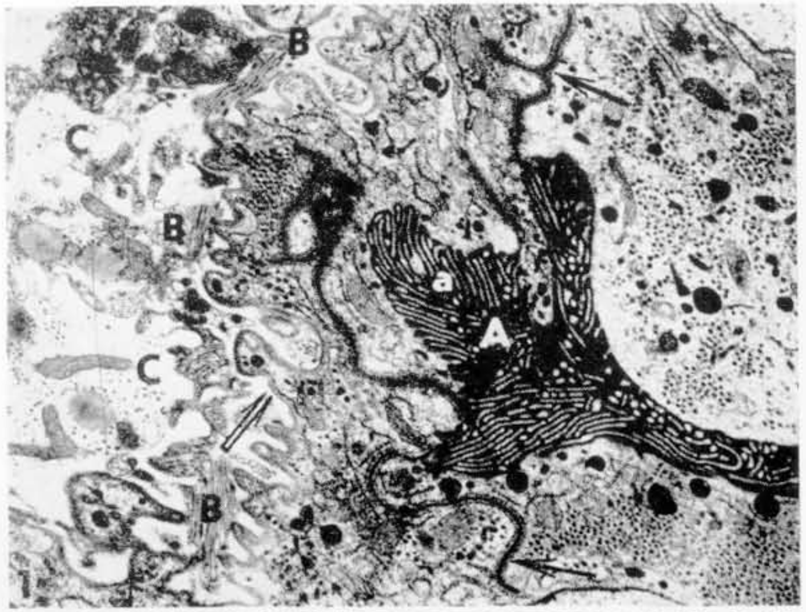
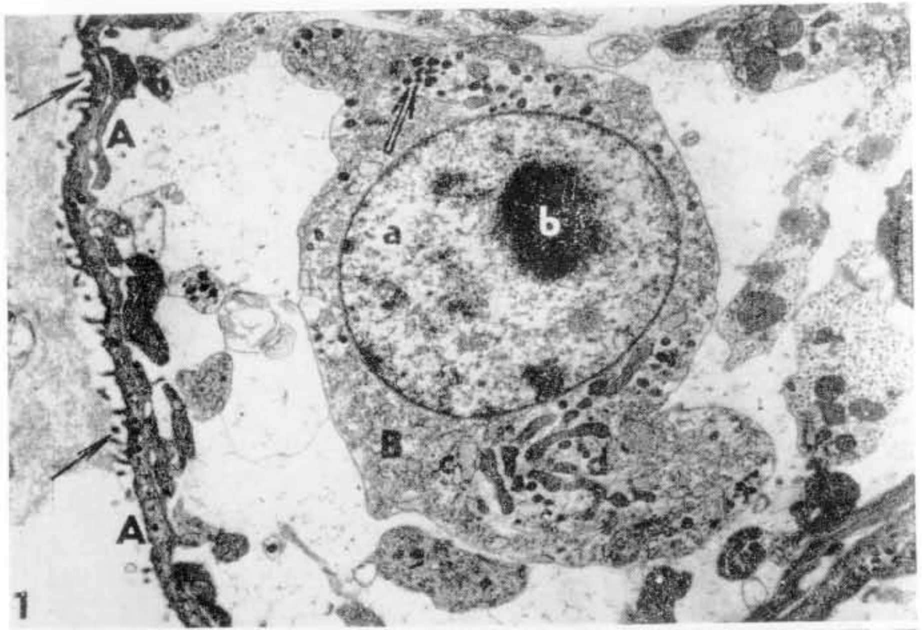


Fig. 1. Section through the contracted caecum of *E. revolutum* redia, A — lumen of caecum, a — microvillous zone of epithelial cells, arrows — desmosomes joining individual cells, double arrow — lamina basalis, B — muscle layer, C — parenchymal cell processes (G, Os, UAc, Pb) (×10 600). **Fig. 2.** Horizontal section through cell of gastrodermis at the level of the nucleus (a) with nucleolus (b). Note the large abundance of α — glycogen particles (top right), c — microvillous zone, d — redia body cavity, e — fine muscle fibres, arrow — lamina basalis (G, Os, UAc, Pb) (×10 600).



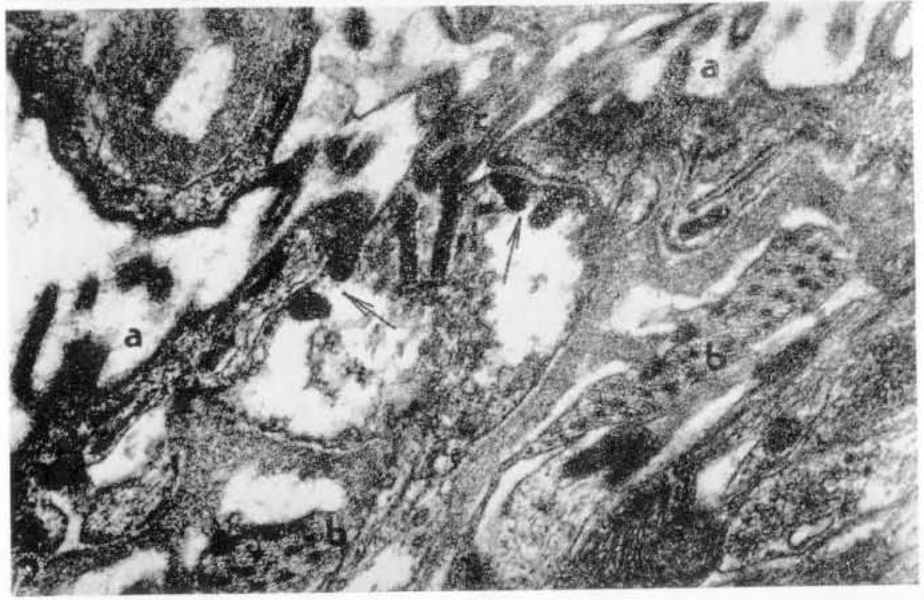


Fig. 1. Body wall (A) and oesophageal gland cell (B) of *E. revolutum* redia. The body tegument of the redia protrudes in short microvilli (arrows). The oesophageal gland cell (B) contains a nucleus (a) with nucleolus (b), cisternae of granular endoplasmic reticulum (c), Golgi apparatus (d) and spherical electron-dense granules (double arrow) (G, Os, UAc, Pb) (×7 840). **Fig. 2.** Detail of redia body tegument with uniciliate receptor, a — microvillous zone of tegument, b — circular muscle fibres, c — cilium, d — basal body, arrows — electron-dense rings in the receptor (G, Os, UAc, Pb) (×38 400).

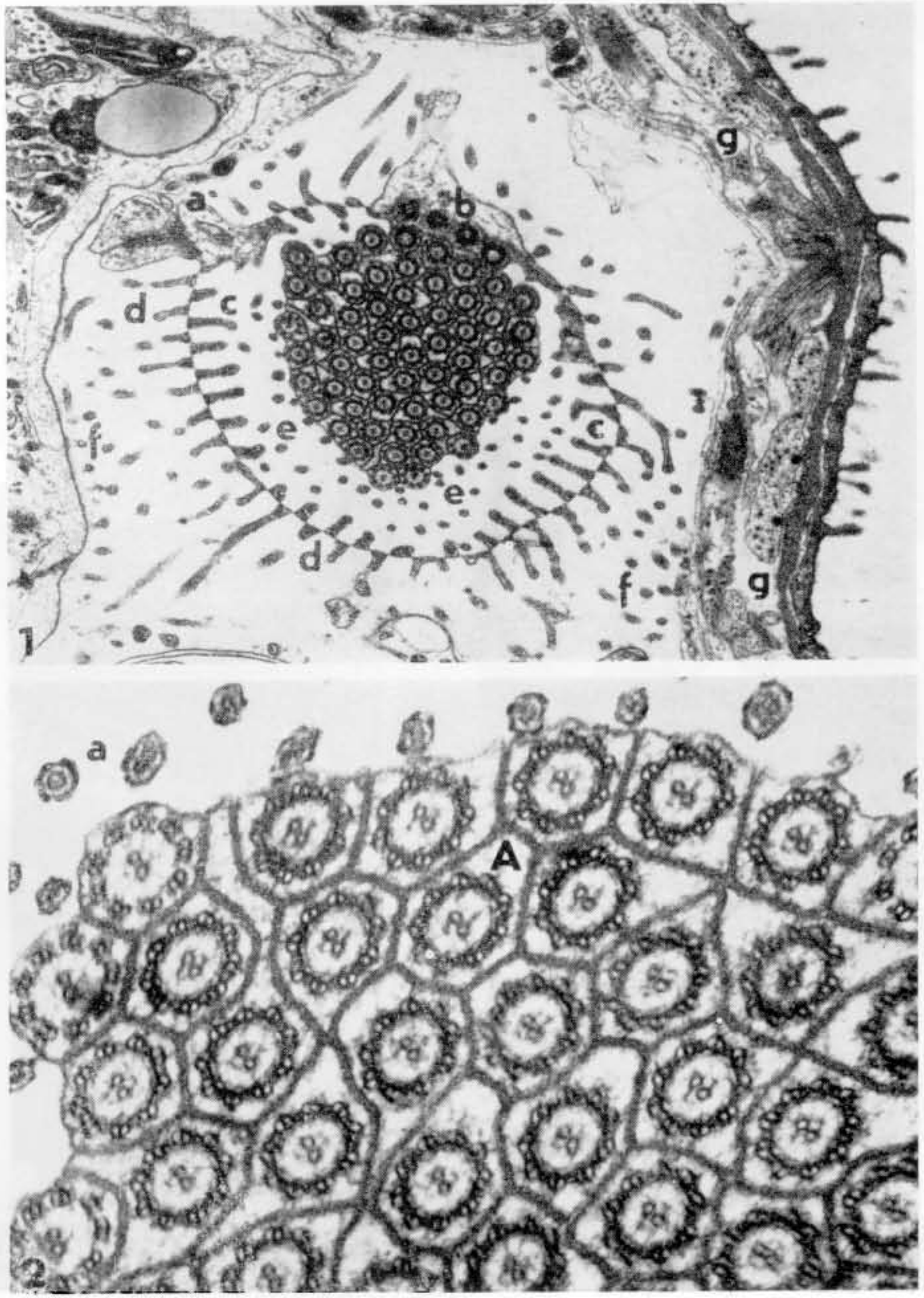


Fig. 1. Transverse section through flame cell of *E. revolutum* redia, a — part of first cell of excretory capillary in the region with septate desmosome, b — basal bodies of cilia, c — internal ribs, d — external ribs, e — internal leptotriches, f — external leptoriches, g — redia body wall (G, Os, UAc, Pb) (×16 800). **Fig. 2.** Detail of cilia (A) and internal leptotriches (a) from Fig. 1. (G, Os, UAc, Pb) (×79 200).

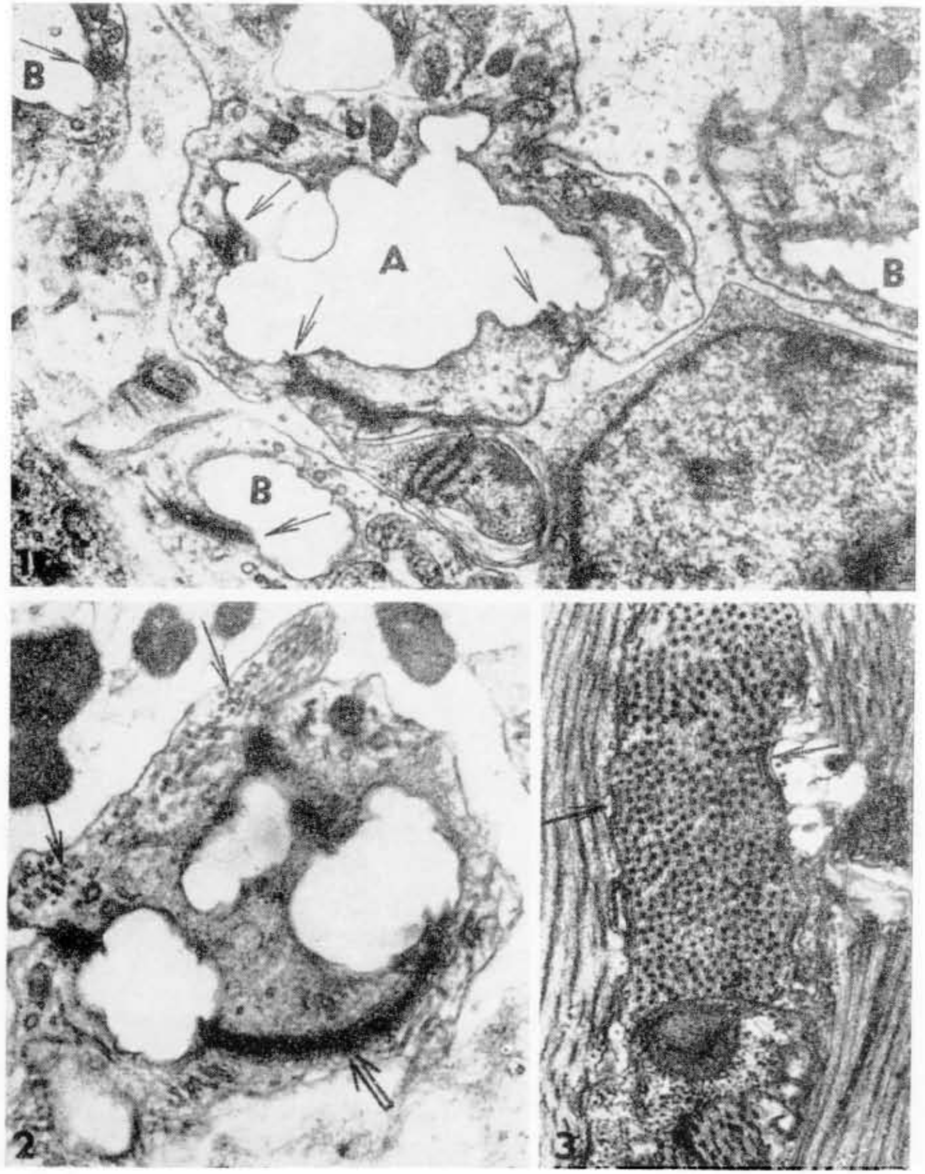


Fig. 1. Detail of excretory duct (A) and excretory capillaries (B) of *E. revolutum* redia. The spirally wrapped cells of the capillaries and the duct cells are joined by means of septate desmosomes (arrows), b — mitochondria (G, Os, UAc, Pb) (×20 000). **Fig. 2.** Detail of excretory capillary, the wall of which is reinforced with clusters of microtubules (arrows). Note the desmosome joining the edges of the spirally wrapped cell of the excretory capillary (double arrow) (G, Os, UAc, Pb) (×72 000) **Fig. 3.** Detail of flattened vesicles of sarcoplasmic reticulum (arrows) of pharynx muscle fibres from Plate I, Fig. 2. (G, Os, UAc, Pb) (×29 600).