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ULTRASTRUCTURE OF THE DIGESTIVE TRACT OF BRACHYLAIMUS AEQUANS (TREMATODA: BRACHYLAIMOIDEA)

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Abstract. The foregut of *Brachylaimus aequans*, i.e. the oral sucker cavity, prepharynx, and pharynx are lined with a tegument, which is essentially identical with the body tegument. The tegument of the oral sucker and pharynx differs by the presence of a lacunal system in its basal part. This lacunal system arises by the attachment of the tegument by hemidesmosomes to lamina basalis at several points. Large lipid vacuoles are present in the tegument of the pharynx. The openings of gland cells into the prepharynx have been demonstrated for the first time in an adult digenetic trematode. Their ducts are reinforced by microtubules and attached to the prepharynx tegument by septate desmosomes. The secretion granules are large, irregular, and electron-dense. The caeca are lined with a syncytial epithelium, the apical part of which projects into long, thin microvilli covered with glycocalyx. The cytoplasm contains numerous mitochondria, large lipid vacuoles, Golgi complexes, rough endoplasmic reticulum, single electron-lucid vesicles, lysosomes, autophagosomes, and residual bodies. The basal plasma membrane of the caecal syncytium forms numerous invaginations. The functional importance of the structures of individual parts of the digestive tract is discussed.

This paper is a continuation of the histochemical studies of this trematode (Žďárská and Soboleva 1987) and it is a part of complex investigations of adult trematodes of the superfamily Brachylaimoidea, the life cycle of which is bound to the terrestrial environment. This is our first ultrastructural study of an adult trematode. The aim of this study, as well as of the following ones, is to elucidate at the ultrastructural level the changes in the morphology of adult trematodes whose previous developmental stages are dependent on terrestrial snails. Some of the peculiarities of the life cycle of this trematode is the cercaria freely moving in the terrestrial environment and non-encysted metacercaria in the second intermediate host. At the beginning of its development, the metacercaria actively feeds on the snail tissues. Therefore the digestive system is well developed not only in the adult trematode, but already in the metacercaria. The studies of the ultrastructure of the oral sucker, prepharynx, and pharynx amplify our knowledge of the digestive system in adult trematodes.

MATERIALS AND METHODS

Adults of *Brachylaimus aequans* (Looss, 1899) at the age of 6—8 days were obtained by experimental feeding of white laboratory mice with metacercariae of the snail *Macrochlamys schmidti*. The trematodes isolated from the intestine were washed in saline and fixed in 3% glutaraldehyde in 0.1 M cacodylate buffer (pH 7.2) at 4 °C for 2 h, and postfixed in 1% OsO_4 at 4 °C for 2 h. After dehydration through an alcohol series the material was embedded through acetone in Durcupan. Ultrathin sections were cut using LKB 8800 Ultrotome III ultramicrotome, contrasted with 20% uranyl-acetate and Reynolds solution of lead citrate, and examined in Philips EM 420 and Philips EM 300 electron microscopes.

RESULTS

1. Oral sucker

The oral sucker (Pl. I, Fig. 1) is lined with a tegument identical with the body tegument, except for its basal part. The folded tegument surface is bordered by a plasma membrane connected with a thin glycocalyx. The basal plasma membrane of the tegument does not adhere evenly to lamina basalis, but it is attached to it by hemidesmosomes only at some points. In this way there arise cavities between the basal plasma membrane and lamina basalis forming a lacunal system in the whole posterior part of the oral sucker. The same type of tegument occurs also inside the pharynx, but not inside the prepharynx. The tegument cytoplasm of the oral sucker contains single electron-lucid vacuoles, mitochondria, and a large number of rod-shaped electron-dense granules arranged perpendicularly to the plasma membrane, particularly near the surface. The lipid vacuoles are lacking in the tegument cytoplasm. A thick connective tissue layer is situated under lamina basalis and under this layer, there are strongly developed meridional, equatorial, and radial muscles. The tegument of the posterior part of the oral sucker passes to the tegument of the prepharynx (Pl. I, Fig. 1).

2. Prepharynx

The tegument of the prepharynx (Pl. II, Fig. 1) contains the same cellular organelles as the tegument of the oral sucker. The rod-shaped granules are concentrated mostly in its surface layer, whereas the mitochondria occur mostly in its middle layer. Like in the tegument of the oral sucker, there are no lipid vacuoles. The basal plasma membrane forms single invaginations and adheres to lamina basalis. Under the lamina basalis, there is a thick connective tissue layer and under it single muscle fibres. Prepharyngeal gland cells (Pl. II, Fig. 2) open into the prepharynx and they are localized around it, i.e. between the oral sucker and pharynx. The prepharyngeal gland cells contain large, irregular, electron-dense granules. Their ducts are reinforced by microtubules below the plasma membrane (Pl. II, Figs. 1, 2; Pl. VI, Fig. 1). The plasma membrane of the duct of gland cells is fixed through a septate desmosome to the plasma membrane of the tegument at the site of the opening near the tegument surface. The tegument of the prepharynx passes to the tegument of pharynx (Pl. I, Fig. 1).

3. Pharynx

The tegument of the pharynx (Pl. III, Fig. 1), in contrast to previous parts of the foregut, contains in addition to a small number of rod-shaped granules (Pl. I, Fig. 2), mitochondria and electron-lucid vesicles, also large lipid vacuoles (Pl. III, Fig. 2), which are most numerous in its upper part. The outer lamina of the trilaminal plasma membrane of the tegument is connected with single filaments of the glycocalyx. The basal plasma membrane forms some invaginations, passes to the septa of lamina basalis and demarcates the lacunal system at the base of tegument (Pl. III, Figs. 1, 2) identical with the lacunal system in the oral sucker. Lamina basalis forms septa projecting into the tegument and between muscle fibres. The connective tissue layer is lacking. The tegument is connected with lamina basalis through hemidesmosomes at some points. Muscle fibres are attached by hemidesmosomes to the lamina basalis on the opposite side. Cytoplasmic processes occur between radial muscle fibres of pharynx. They contain spherical, electron-dense structures with single cristae, inside which a small spherical structure is present (Pl. VI. Fig. 2).

4. Caeca

The oesophagus is not developed in *B. aequans*. The pharynx tegument passes imediately to the lining of the caeca. Their lining adheres to lamina basalis beneath which is a thick connective tissue layer and beneath this longitudinal and circular muscles (Pl. V, Fig. 1). Cytoplasmic processes of myocytes and parenchymal cells penetrating through lamina basalis up to the base of caecal syncytium are visible in some sections. They form gap junctions with the syncytium (Pl. V, Figs. 1, 2). The basal plasma membrane of the caecal syncytium forms numerous invaginations. The cytoplasm of the syncytium contains nuclei with a nucleolus (Pl. IV, Figs. 1, 3), numerous small mitochondria with an electron-dense matrix and single cristae, electron-lucid vesicles, Golgi complexes, rough endoplasmic reticulum, lysosomes, autophagosomes, residual bodies, and large lipid droplets (Pl. IV, Figs. 1, 3), which often cause that the apical part of the caecal syncytium is evaginated into the microvillous zone. The microvillous zone is formed by numerous long, thin microvilli (Pl. IV, Figs. 1, 3) covered by glycocalyx (Pl. IV, Fig. 2).

DISCUSSION

The digestive tract of *B. aequans*, like that of other trematodes (Robinson and Halton 1983, Leitch et al. 1984), is bordered by two different components. The syncytial tegument, which covers the body surface of the trematode, lines also the cavity of the oral sucker, prepharynx, and pharynx, whereas the caeca are lined with syncytial epithelium with long, thin microvilli.

Considering that the superfamily Brachylaimoidea belongs to the order Strigeatoidea La Rue, it may be supposed that the ultrastructure of the digestive tract will be most similar to that of the members of the genus *Schistosoma*, which have been studied most intensively. The ultrastructure of the tegument of individual parts of the foregut somewhat differs from the ultrastructure of the body tegument in the presence of individual organelles and in the thickness of glycocalyx. The rod-shaped granules are less numerous and the glycocalyx is thinner. The morphology of mitochondria does not change in the whole digestive tract — they possess an electron-dense matrix and single cristae.

Several authors (Lumsden 1975, Robinson and Halton 1983 and others) have demonstrated that the contents of rod-shaped granules are discharged by exocytosis to the tegument surface and are used for the formation of glycocalyx. The rod-shaped granules are produced in the Golgi apparatus of subtegumental cells and they are transported into the syncytium. The majority of these granules accumulate in the tegument beneath its apical plasma membrane. When the contents of the rod-shaped granules are discharging, both membranes fuse and the granule contents get to the surface (exocytosis). The discharged granule contents have a protective function during the change of the surface membrane and the glycocalyx connected with it. There is unequivocal autoradiographic evidence that the glycocalyx of parasitic plathelminths is elaborated through the secretory activity of the tegumental cell bodies (Lumsden 1975), and is becoming increasingly apparent from the ultrastructural immunochemistry studies that the glycocalyx turnover in a number of these worms prevents host immune complexes or inflammatory cells from damaging the parasite surface (Hanna 1980a, b).

Considering that particularly the body tegument and of the digestive tract only oral sucker tegument get into immediate contact with the host, the smaller number of rod-shaped granules and thinner glycocalyx in the prepharynx and pharynx may be explained.

The gland cells localized between the oral sucker and pharynx and opening into the prepharynx are the first finding of these glands in adult digenetic trematodes. They are termed prepharyngeal gland cells. These glands are identical with the circumpharyngeal glands described by Halton (1972) in the aspidogastrid trematode, *Aspidogaster conchicola*. These gland cells conform to Halton's description not only in the localization and opening into the prepharynx, but also in their ultrastructure. Similar gland cells opening into the prepharynx are the prepharyngeal gland cells in Monogenea (Halton et al. 1974, Smyth and Halton 1983). The secretion of the prepharyngeal gland cells of *B. aequans* is of protein nature; it contains a large amount of tryptophan and exhibits the activity of acid phosphatase (Žďárská and Soboleva 1987).

Similar gland cells, which surround the pharynx, but do not open into the digestive tract, have been described by Halton (1967) and Halton and Dermott (1967) in *Haplometra cylindracea* and *Opisthioglyphe ranae*. These cells are evidently identical with the frontal gland cells, which open onto the body surface around the oral sucker of digenetic trematodes. Their ultrastructure is identical also with that of frontal gland cells in *Leucochloridium paradoxum* and *L. perturbatum* metacercariae (Žďárská and Soboleva 1984, Žďárská 1986) and with penetration gland cells preserved in young *Gorgoderina vitelliloba* (Hoole et al. 1983).

The prepharyngeal gland cells have already been demonstrated by histochemical (Žďárská et al. 1984) and electron-microscopical (unpublished) methods in *Leucochloridium perturbatum* metacercariae. Adult specimens of this trematode species have not yet been studied by us. Also another morphological structure of the foregut is identical in adults of *B. aequans* and metacercariae of *L. perturbatum* (Žďárská and Soboleva 1984, Žďárská 1986) and *L. paradoxum* (Žďárská 1983). It is the lacunal system at the base of tegument in the posterior part of the oral sucker and in pharynx. The special arrangement of the basal part of the tegument in the oral sucker and pharynx is explained by the presence of well developed muscles, for which the simple folding of tegument at the moment of contraction would be insufficient. This type of tegument, which is attached to lamina basalis only at some points, ensures its better flexibility. This function of the lacunal system is indicated also by the fact that this system is lacking in the prepharynx, where the muscles are not so developed. Remarkable is the presence of large lipid vacuoles in the pharynx tegument of *B. aequans*. They have not been observed in this region in any of the studied digenetic trematodes.

The caeca of *B. aequans* are lined with syncytial epithelium projecting in the apical part in long, thin microvilli. In this way, the resorption surface of caeca is increased several times. The microvilli are covered by a thin layer of glycocalyx. Similarly as in other trematodes, the cytoplasm of caecal syncytium contains mitochondria, Golgi complexes, rough endoplasmic reticulum, lysosomes, autophagosomes, residual bodies, large lipid vacuoles, and nucleus with nucleolus at regular distances. The basal plasma membrane forms numerous invaginations and cytoplasmic processes of muscle and parenchymal cells penetrate through lamina basalis to the base of caecal syncytium forming gap junctions with it.

A similar caecal syncytial epithelium has been described also in *Schistosoma mansoni* (Senft et al. 1961, Morris 1968, Spence and Silk 1970), *S. haematobium* (Sodeman et al. 1972), *S. japonicum* (Fujino and Ishii (1979), *Schistosomatium douthitti* (Shannon and Bogitsh 1969), *Gorgodera amplicava* (Dike 1967), *Gorgoderina attenuata* (Davies and Bogitsh 1971), *Megalodiscus temperatus* (Bogitsh 1972b, Morris 1973), *Echinostoma hortense* (Fujino and Ishii 1979), *Eurytrema pancreaticum* (Fujino and Ishii 1979), *Corrigia corrigia* (Panin et al. 1981), and *Corrigia vitta* (Robinson and Halton 1983). An intermediate form of the caecal epithelium of digenetic trematodes, i.e. a combination of syncytial and cellular gastrodermis, has been described by Halton (1982) in *Fellodistomum fellis*. Other previously studied trematodes have a typical cellular gastrodermis.

The cytoplasmic processes of muscle and parenchymal cells in the adult *B. aequans* terminating in the syncytial epithelium by the gap junctions enable, like in other trematodes, a transport of nutrients from the caecal epithelium into body parenchyma. According to Morris (1973), the caecal syncytium is connected by junctional complexes with the muscle cells enabling the distribution of nutrients into the whole body by means of the same connections with other tissues. Similar junctional complexes have been described by Gallagher and Threadgold (1967), Bennett (1975) and Robinson and Threadgold (1975) in *Fasciola hepatica*, by Morris (1968) and Spence and Silk (1970) in *Schistosoma mansoni*, by Bogitsh (1972a) in *Haematoloechus medioplexus*, by Matricon-Gondran (1980) in *Echinostoma caproni*, and by Panin et al. (1981) in *Corrigia corrigia*. According to Smyth and Halton (1983), the parenchymal cells are structurally connected not only with one another, but also with the tegument, digestive, excretory and reproductive systems, and muscles by means of gap junctions. These junctional complexes should be considered sites of intercellular communications, which, due to the absence of a circulatory system, enable the transport of nutrients in the whole body of the trematode.

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УЛЬТРАСТРУКТУРА ПИЩЕВАРИТЕЛЬНОЙ СИСТЕМЫ ТРЕМАТОДЫ *BRACHYLAIMUS AEQUANS* (TREMATODA: BRACHYLAIMOIDEA)

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Резюме. Передняя часть пищеварительной системы трематоды *Brachylaimus aeguans*, т. е. полость ротовой присоски, предглотка и глотка, выстланы тегументом, который в сущности совпадает с тегументом тела. Он отличается только тем, что в базальной части тегумента ротовой присоски и глотки находится лакунарная система. Тегумент глотки содержит, кроме того, также большие липидные вакуоли. Впервые было обнаружено впадение железистых клеток в преглотку. Выводные протоки этих преглотковых железистых клеток содержат микротрубочки и прикреплены к тегументу предглотки септированной десмосомой. Секрет образует большие, нерегулярные, электронноплотные гранулы. Ветви кишечника выстланы синцитиальным эпителием, апикальная часть которого переходит в длинные, тонкие микроворсинки, покрытые гликокаликсом. Ядра содержат ядрышко и цитоплазма многочисленные митохондрии, большие липидные вакуоли, комплексы Гольджи, эндоплазматический ретикулум и отдельные электронно-прозрачные везикулы, лизосомы, аутофагосомы и резидуальные тела. Базальная плазматическая мембрана синцитиального эпителия ветвей кишечника образует многочисленные инвагинации. Обсуждается функциональное значение структур отдельных частей пищеварительной системы.

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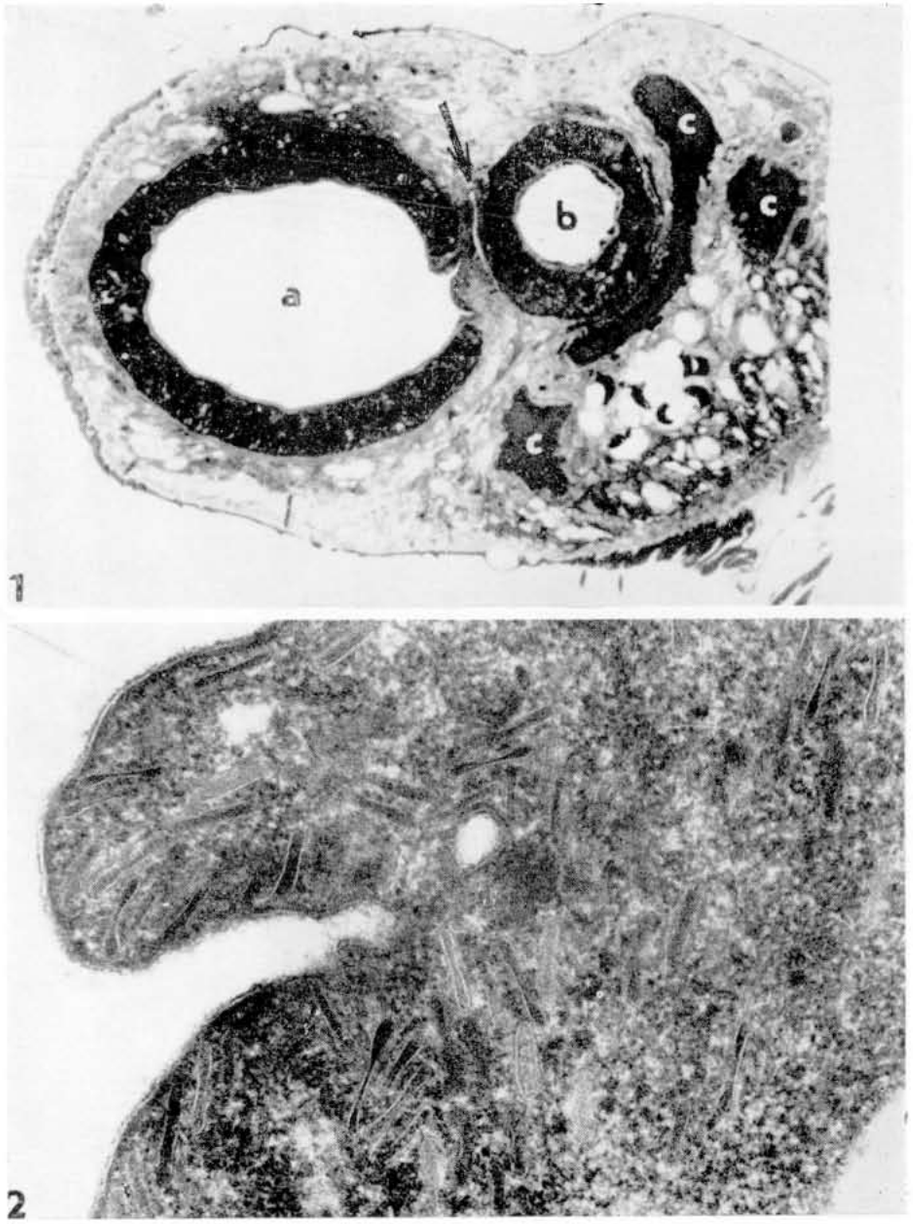

Fig. 1. Semithin section through the anterior part of *B. aequans*. a — oral sucker, b — pharynx, arrow — prepharynx, c — intestine (toluidine blue) (×265). **Fig. 2.** Tegument of pharynx contains electron-dense rod-shaped granules arranged beneath apical plasma membrane (left) perpendicularly to its surface (G, Os, UAc, Pb) (×75,000).

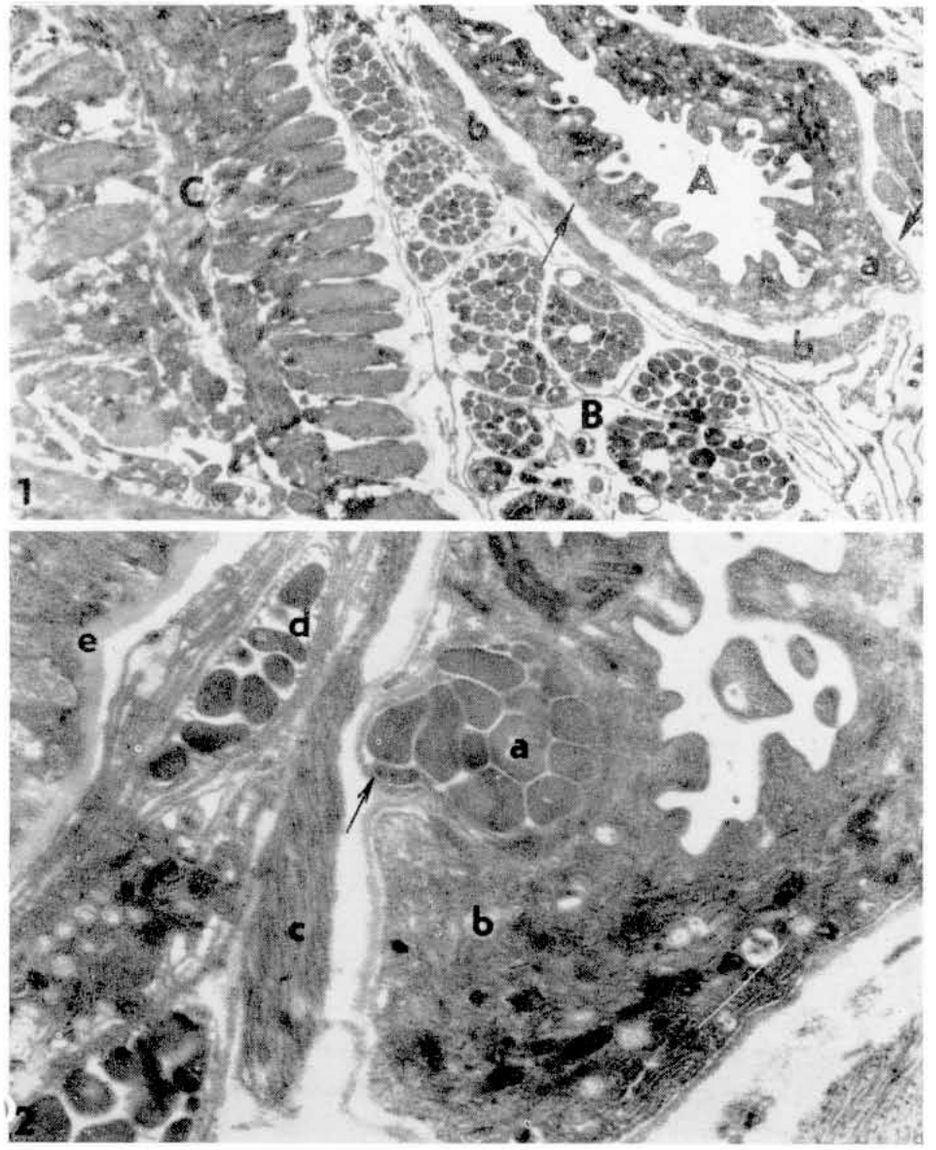

Fig. 1. Prepharynx (A), prepharyngeal gland cells (B) and pharynx muscles (C) of *B. aequans*. Lamina basalis (arrows) and thin muscle layer are beneath the prepharynx tegument (a). (G, Os, UAc, Pb) (×6,500). **Fig. 2.** Oblique section through the opening of prepharyngeal gland cell (a) in the tegument of prepharynx (b). The duct contains irregular large, dense granules and is reinforced by microtubules (arrow) beneath the plasma membrane. Note a large number of mitochondria with electron-dense matrix and rod-shaped granules in the tegument of prepharynx. c — prepharynx muscles, d — transverse section through the duct of prepharyngeal gland cells in the parenchyma with conspicuous microtubules, e — pharynx (G, Os, UAc, Pb) (×21,800).

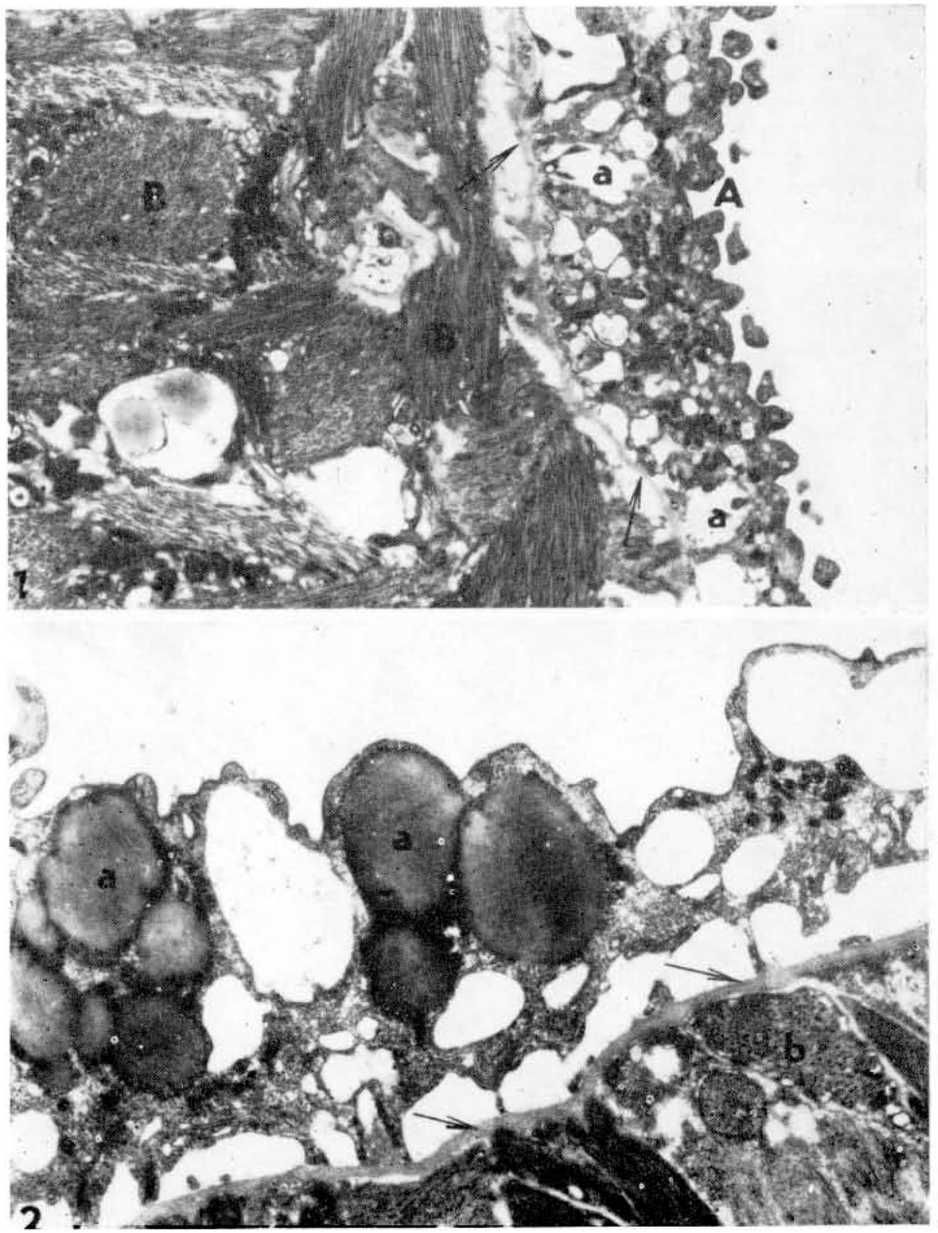

Fig. 1. Tegument (A) and muscles (B) of pharynx of *B. aequans*. Note the lacunal system (a) at the base of tegument. Arrows-lamina basalis (G, Os, UAc, Pb) (×8,250). **Fig. 2.** Section through the tegument of pharynx at the site with a large number of lipid vacuoles (a); arrows — lamina basalis, b — pharynx muscles (G, Os, UAc, Pb) (×13,650).

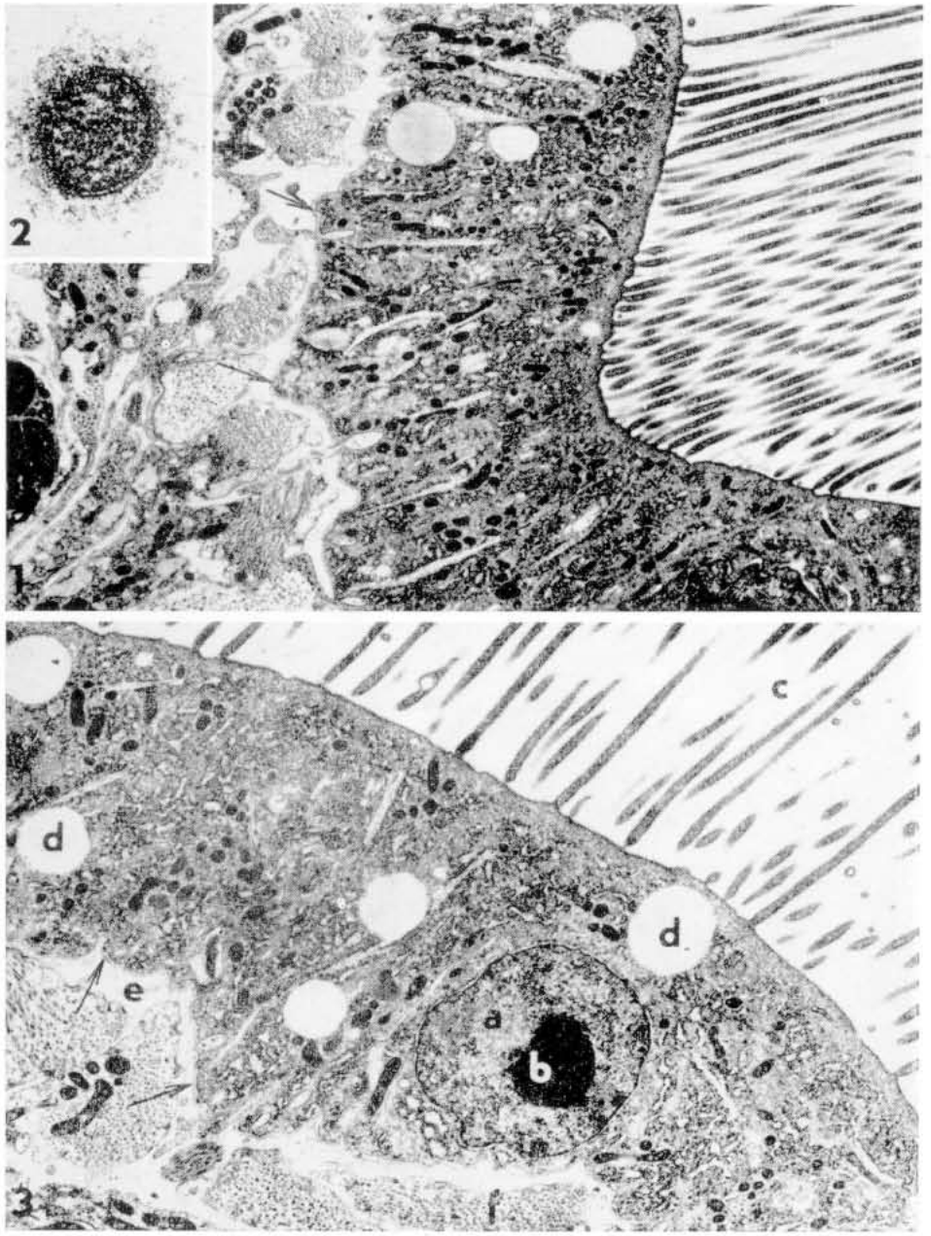

Fig. 1. Transverse section through syncytial gastrodermis of *B. aequans* with microvillous zone (right). Thin lamina basalis (arrows) beneath the gastrodermis and connective tissue and muscle layer beneath lamina basalis (left) (G, Os, UAc, Pb) (×7,650). **Fig. 2.** Detail of microvillus surrounded by glycocalyx (G, Os, UAc, Pb) (×147,000). **Fig. 3.** Detail of gastrodermis of caecum in the region of nucleus (a); b — electron-dense nucleolus, c — microvillous zone, d — lipid droplets, arrows — lamina basalis, e — connective tissue layer, f — muscle layer (G, Os, UAc, Pb) (×10,000).

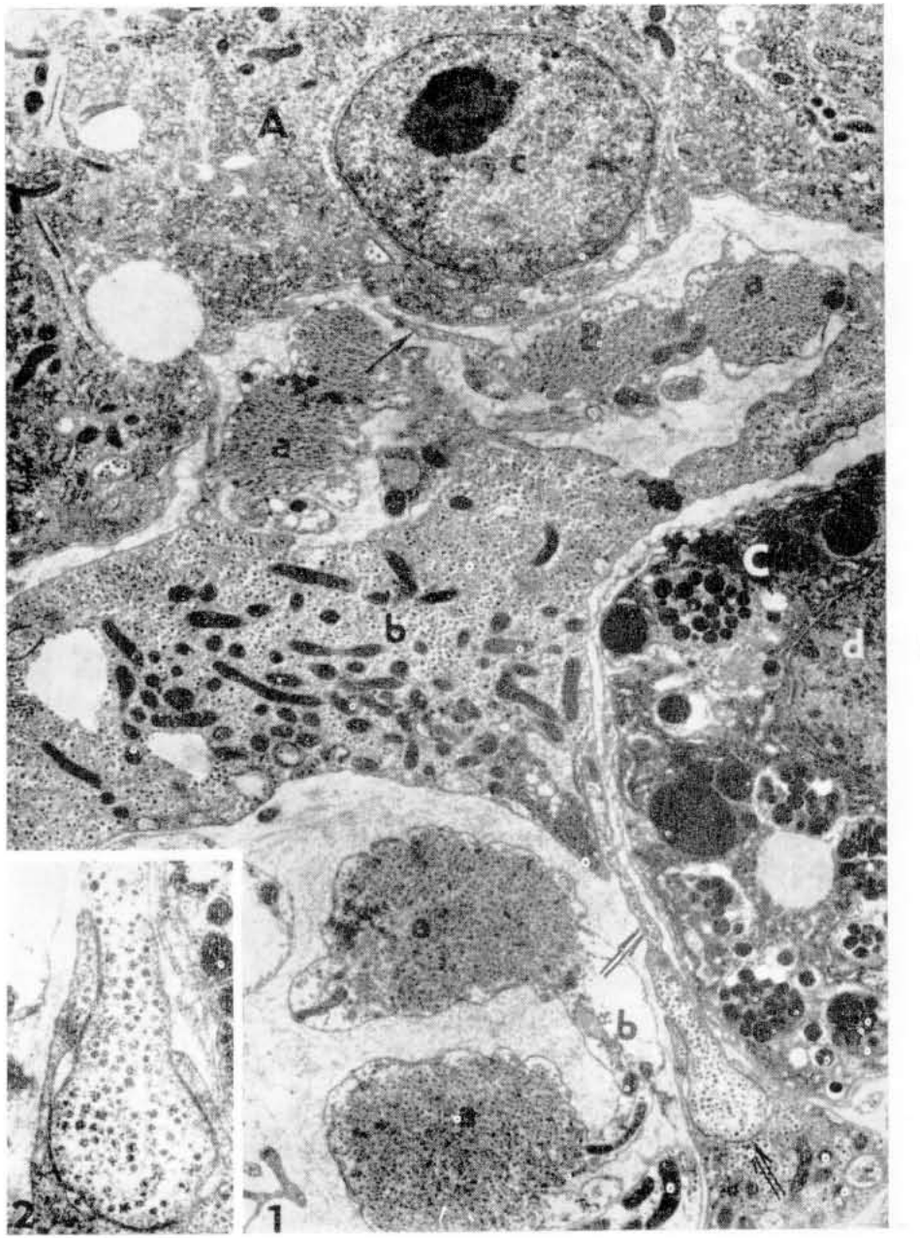

Fig. 1. Transverse section through the basal part of gastrodermis (A), muscle layer (B) and vitelline cell (C). Muscle layer (B) consists of contractile (a) and cytoplasmic (b) parts of myocytes. Cytoplasmic processes of myocytes penetrate not only into the basal part of gastrodermis (arrow), but also into the parenchyma (double arrow), where they form gap junctions with other cells; c — nucleus of gastrodermis, d — nucleus of vitelline cell (G, Os, UAc, Pb) (×8,900). **Fig. 2.** Detail of cytoplasmic process with gap junctions from Fig. 1 (G, Os, UAc, Pb) (×18,100).

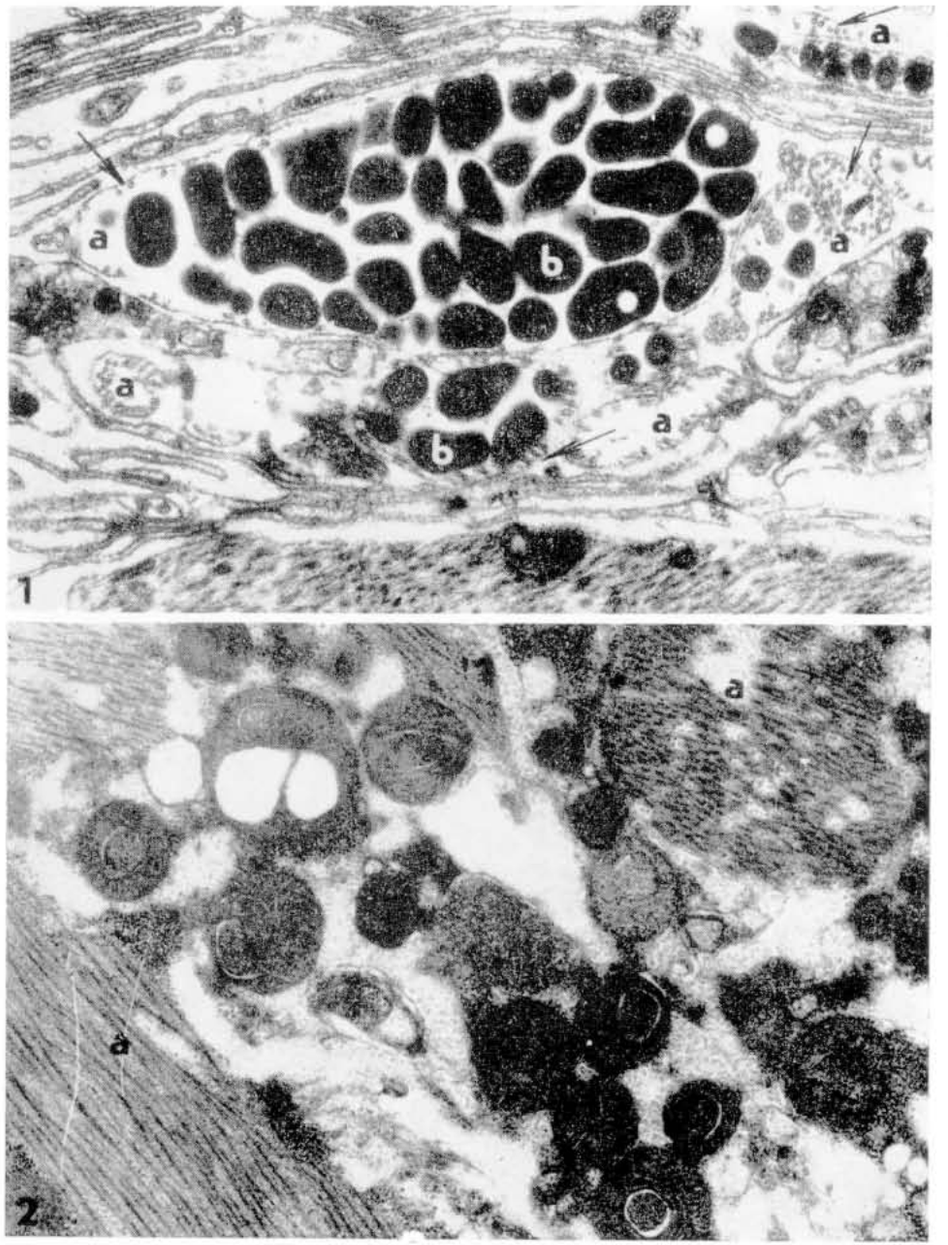

Fig. 1. Section through *B. aequans* in the region around prepharynx with numerous ducts of prepharyngeal glands (a) with microtubules (arrows). Some of them are filled with electron-dense secretory granules (b) (G, Os, UAc, Pb) (×31,000). **Fig. 2.** Section through pharynx muscles with numerous spherical structures with cristae and a spherical structure situated inside between the muscle fibres (a) (G, Os, UAc, Pb) (×22,800).