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Some Ultrastructural Observations on the Midgut Epithelium of *Isohypsibius augusti* (Murray, 1907) (Eutardigrada)

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Summary. The midgut epithelial cells of the eutardigrade *Isohypsibius augusti* are organized into a convoluted monolayer. Only a single cell type could be distinguished although this cell type displayed considerable morphological variation. The midgut begins with crescent-shaped cells. More distally the cells are of variable height depending on the stored amount of nutritional material. No regenerative cells are present. Adjoining cells are held together by apical *zonulae continuae.* All the cells are characterized by a striated border, some basal infoldings, cytosis vesicles, numerous mitochondria, and abundant rough endoplasmic reticulum. Dictyosomes occur in small numbers. Ovoid or spherical inclusions (spherites), often concentrically laminated, are common. The cells, especially those along the middle part of the gut, are filled with large amounts of nutritional storage which includes polysaccharide material. The possible functions of the midgut in Tardigrada are discussed.

Key words: Midgut – Tardigrada – Spherites – Ultrastructure.

Zusammenfassung. Das einschichtige, stark gewundene Mitteldarmepithel des Eutardigraden *Isohypsibius augusti* besteht aus nur einem Zelltyp. Der Mitteldarm beginnt mit halbmondförmigen Zellen; die Höhe der sich anschließenden Zellen schwankt je nach der Menge der eingelagerten Nahrungsreserven. Regenerative Zellen fehlen. Benachbarte Zellen sind apikal durch *Zonulae continuae* verbunden. Alle Mitteldarmzellen zeichnen sich durch einen apikalen Mikrovillisaum, Cytosevesikel, zahlreiche Mitochondrien und viel rauhes endoplasmatisches Retikulum aus. Dictyosomen sind nicht allzu häufig. Verbreitet sind ovoide oder runde, oft konzentrisch geschichtete Einschlüsse (Spherite). Besonders die Zellen des mittleren Darmabschnittes können mit großen Mengen von Nahrungsreserven gefüllt sein, die zum Teil Polysaccharide enthalten. Mögliche Funktionen des Mitteldarms der Tardigraden werden diskutiert.

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Introduction

Three major divisions are recognized in the digestive tract of Tardigrada: the stomodaeum (foregut), the mesenteron (midgut), and the proctodaeum (hindgut). Both the foregut, consisting of the mouth tube, the pharyngeal bulb and the esophagus, and the hindgut are lined with a cuticle and generally are shorter and narrower than the midgut. In Eutardigrada eight muscle cells encircle parts of the alimentary tract at regular intervals; they originate at the esophagus and end a short distance before the hindgut. The digestive canal terminates in an anus in Heterotardigrada and a cloaca in Eutardigrada.

Eutardigrada are considered more advanced than Heterotardigrada (Marcus, 1929; Ramazzotti, 1972) and possess a less diverticulated intestine, crescent-shaped cells marking the transition between the esophagus and the midgut (Marcus, 1928, 1929; Dewel and Clark, 1973c) and three glands (vasa Malpighii) at the junction between the mid- and hindgut, which presumably have excretory function (Marcus, 1929).

Except for the description of the intestine by Marcus (1928, 1929) which was based on light-microscopical studies, only a few structural investigations have been carried out. The fine structure of the entire foregut of *Milnesium tardigradum* has been described by Dewel and Clark (1973a, b, c). The visceral muscles and the pharyngeal bulb of *M. tardigradum* and *Macrobiotus hufelandi* have been studied by Walz (1973, 1975a) and Shaw (1974). Recently Walz (1975b) reported some modified ciliary structures in the receptor cells in the mouth tube of the latter species.

At present no information is available on the ultrastructure of the midgut epithelium in Tardigrada. We therefore describe here some cytological details of midgut epithelial cells in the eutardigrade *Isohypsibus augusti*, a species which feeds primarily on algae and perhaps organic detritus and bacteria.

Material and Methods

Specimens of *I. augusti* were collected in spring 1973 and 1974 from a small pond near the Zoological Institute at Münster. Since great differences in the shape and size of the midgut may occur in different individuals of the same species due to different nutritional conditions (Marcus, 1929), mainly gravid females were selected for this investigation, for in general, growing oocytes inhibit females from feeding. Furthermore, *I. augusti* deposits eggs in the cast-off cuticle. Before moulting, however, the animals stop feeding and the midgut epithelium is therefore not filled excessively with stored food and the midgut lumen is empty in most cases (Marcus, 1929). Nevertheless, the height of the cells varies considerably, which is partly due to differences in the amount of stored food.

For electron microscopy the specimens were fixed in Karnovsky's fluid (Karnovsky, 1965) buffered with 0,25 m cacodylate-buffer (1 h) and postfixed in 1% osmium tetroxide (1 h). After dehydration in an ethanol series specimens were embedded in styrene-methacrylate (Kushida, 1962) or after dehydration in acetone, in Durcupan ACM (Fluka). Sections were cut with a Reichert Om U2, stained with lead citrate (Ruthmann, 1966) and examined in a Siemens 101 Elmiskop (grant of the Stiftung Volkswagenwerk).

One µm sections, unstained or stained with toluidine blue—borax or Nile blue A (Mc Gee Russel and Smale, 1963) or subjected to the PAS-reaction (Ruthmann, 1966) were studied in the light microscope. Carbohydrates were localized by staining ultra-thin sections by the periodic acid thiosemicarbazide (TSC)-silver proteinate method of Thiéry (1967). Staining in TSC was restricted to 40 min for the identification of glycogen, or was extended to 24 h and 56 h for other carbohydrates.

Observations

In *I. augusti* the structure of the midgut is more or less uniform throughout. Generally all of the cells are of a single basic type which shows some morphological variation, such as different amounts of nutritional storage and different dimensions (Fig. 1 a, b). Nevertheless, there is no division into distinct regions, although the anterior portion of the midgut is represented by crescent-shaped cells (= cardia; Marcus, 1928, 1929) which lack nutritional storage (Fig. 2b); the posterior cells seem to possess more basal infoldings (Fig. 4) and may become progressively smaller.

The midgut epithelium is composed of a single layer of cells which often become so flat that the cells range in height from 0,5 to 10 µm, including the striated border. This monolayer is highly convoluted and forms small diverticula which serve to increase the secretory and absorptive area (Figs. 1 b, 3 d).

The cells rest on a basal lamina which closely follows the convolutions of the epithelium separating the intestine from the hemocoel. The basal lamina, in which fine filaments either run parallel to the basal surface of the midgut or are arranged irregularly, is separated from the basal midgut cells by a small clear region (Figs. 2a, 3d).

The apical cell surfaces of the midgut cells are covered with slender microvilli. Each finger-like projection, the outermost tip of which is often very electron-dense (Fig. 2a), is approximately 0,25 µm long. In some cases, however, areas of the apical surface are devoid of microvilli which probably do not maintain a constant length and diameter, and which sometimes seem to disintegrate (Fig. 3b) especially at the surface of the crescent-shaped cells (Fig. 2a). Transverse sections through the microvillus border show that the projections are arranged irregularly (Fig. 3 a, inset). The coating of mucopolysaccharide glycocalyx which characterizes many other absorptive epithelial cells can be recognized as fuzzy filamentous material covering the exterior surface of the microvilli (Figs. 2a, 3a). Each microvillus contains a few filaments, which run parallel to the long axis of the projection, but lacks tubules (Fig. 3a). Filaments or tubules are also absent from the apical cytoplasm. A terminal web is not apparent.

Moderately electron-dense vesicles and globules, and membrane-like structures often fill the midgut lumen and the spaces between the microvilli (Figs. 2a, 3a, b). The origin and function of these structures are at present unclear. However, the occurrence of similar vesicles in the apical cytoplasm and of vesicular invaginations in the plasma membrane between the microvilli perhaps reflects a mechanism whereby fluid or small particles are absorbed or secreted by the cell. In *I. augusti* these pit-like invaginations are very common, but a number of them are apparently devoid of content (Figs. 3a, 6a). Vesicles with finely granular material of moderate electron density are also concentrated in the apical cytoplasm of the crescent-shaped cells (Fig. 2a, see also Figs. 3a, 5a).

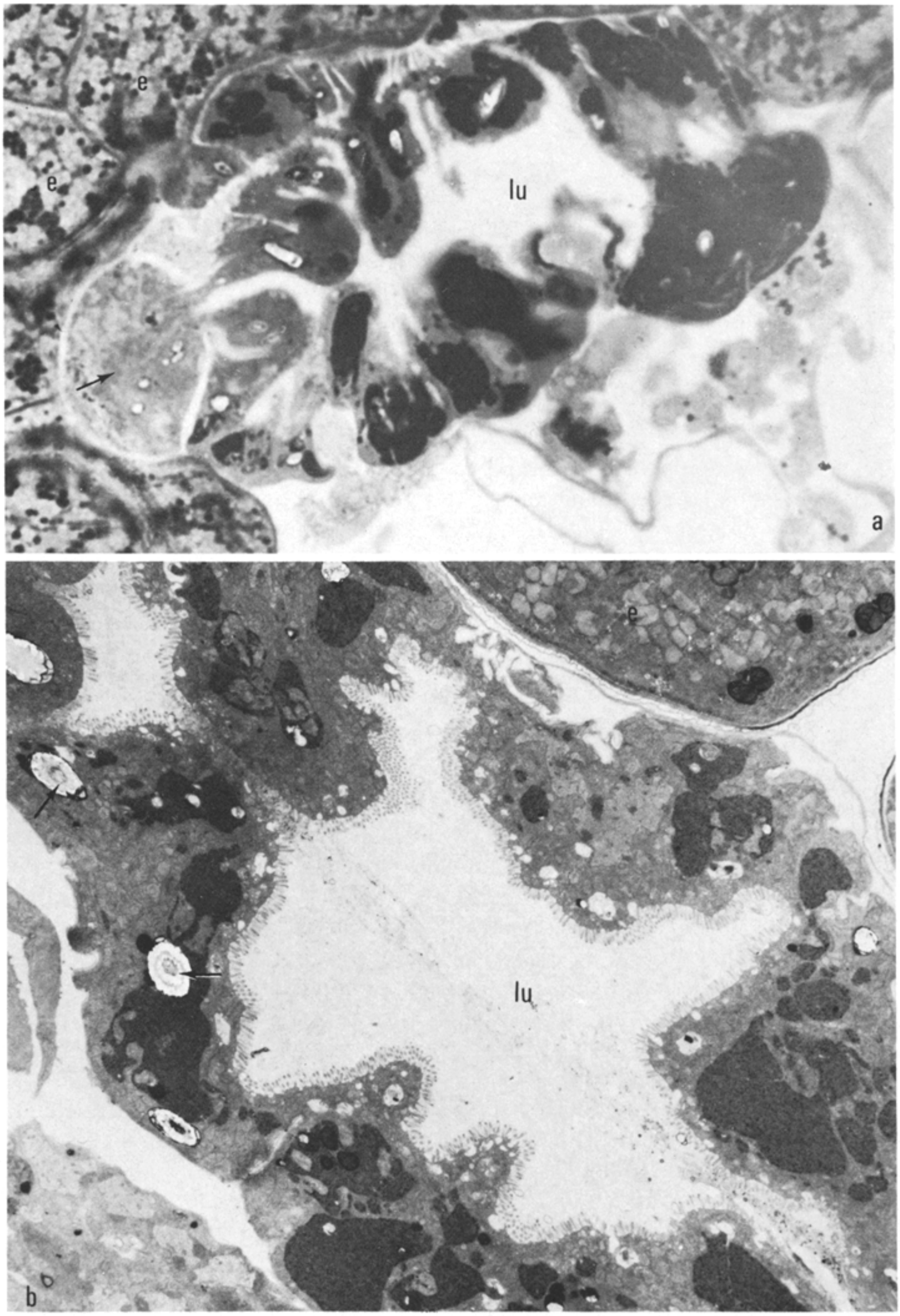


Fig. 1 a and b. Midgut of *I. augusti*. (a) Light microscopical view of the middle part of the intestine (longitudinal section). Note the dark-stained nutritional storage material. The anterior portion is formed by crescent-shaped cells (→). × 640. (b) Diverticulated midgut with nutritional storage and numerous spherites (→). Eggs (*e*), lumen (*lu*). × 4,200

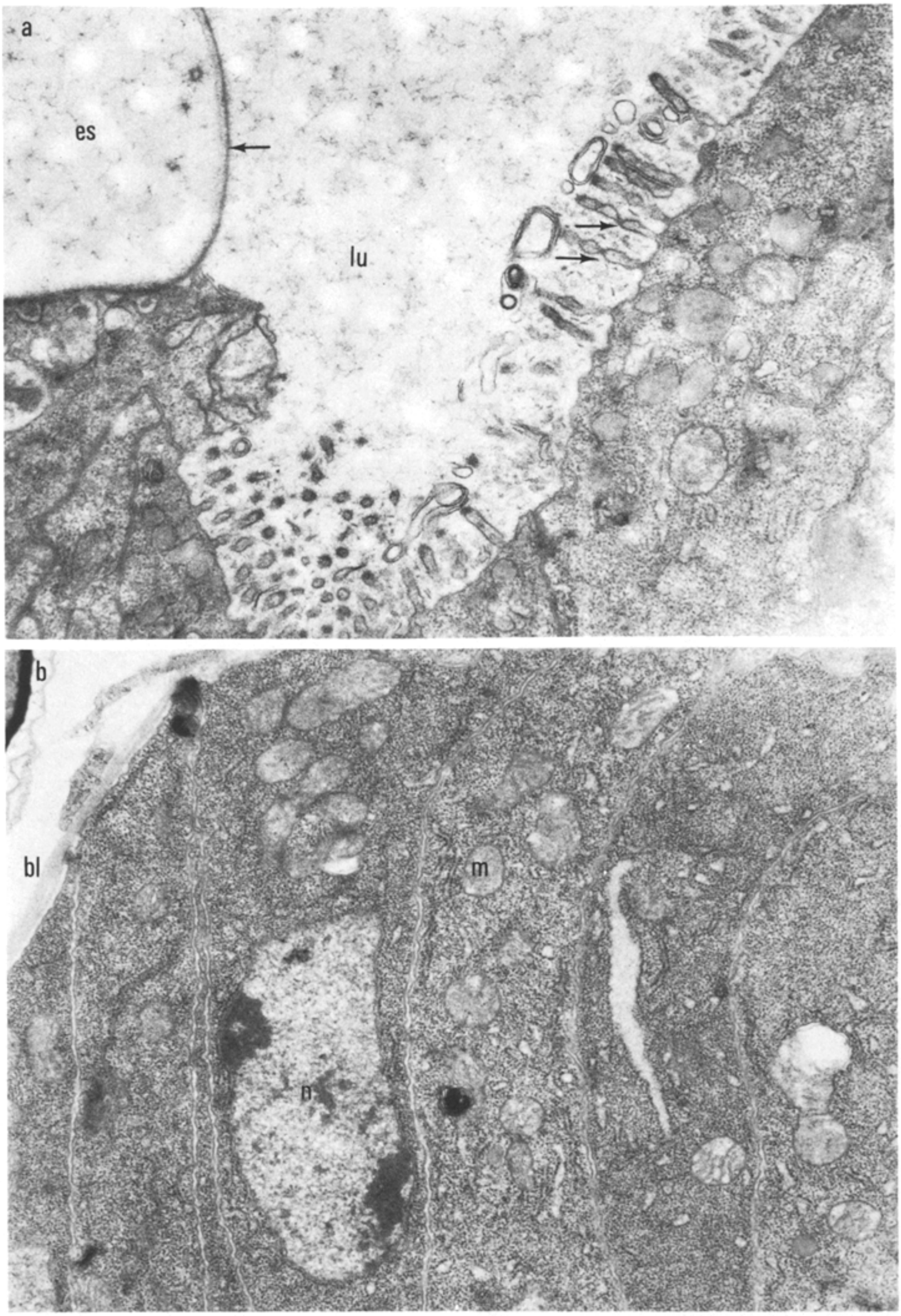


Fig. 2a and b. The anterior portion of the midgut. (a) Transition from the esophagus to the crescent-shaped cells. The esophageal lining (→) extends into the midgut lumen. The microvilli covered with a surface coat appear to disintegrate (→). Moderate electron dense vesicles are concentrated in the cell apex. × 24,000. (b) Cytoplasm of the crescent-shaped cells. Basal lamina (*bl*), esophagus (*es*), lumen (*lu*), mitochondrion (*m*), nucleus (*n*). × 18,000

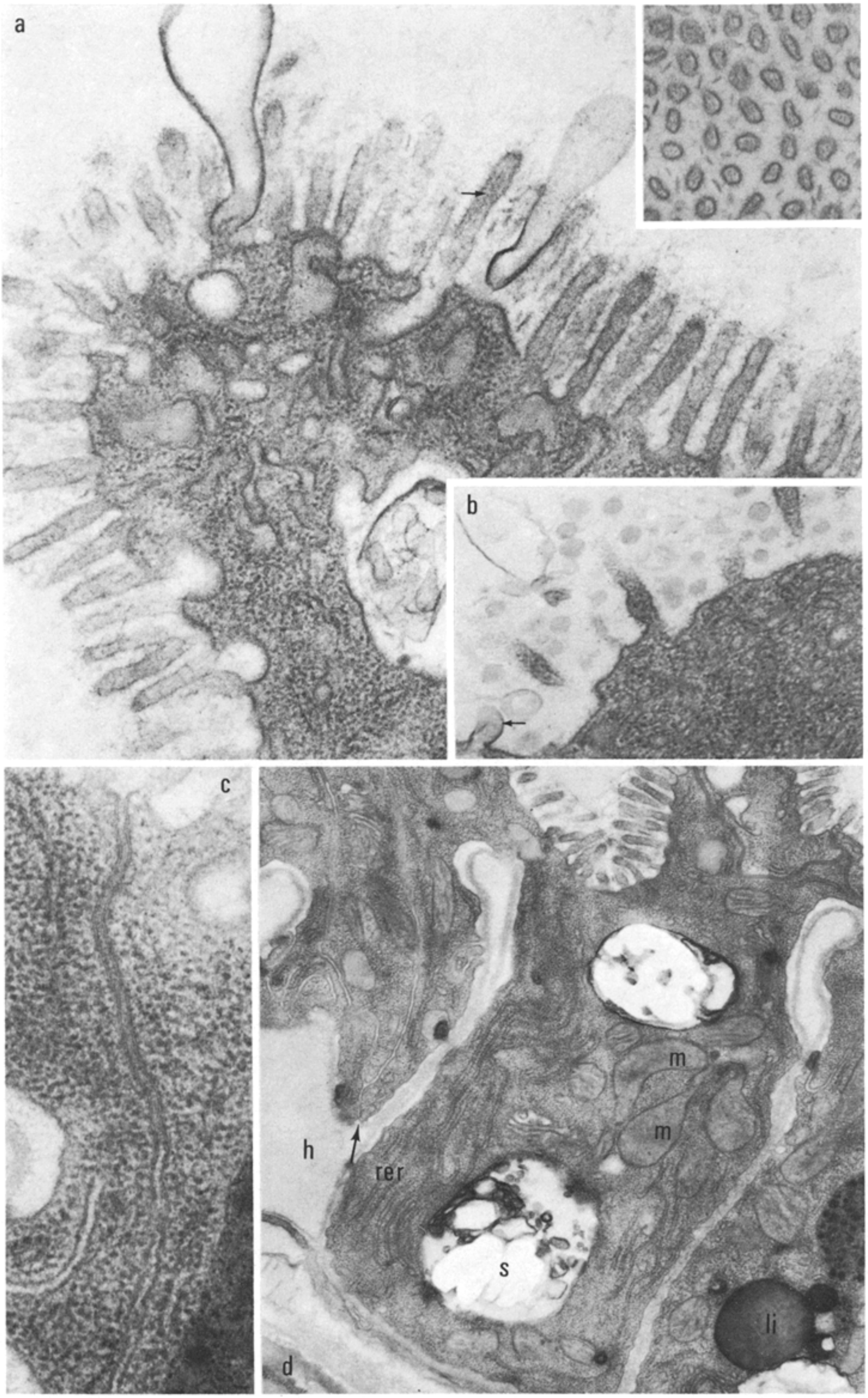


Fig. 3a–d

There is not such a significant morphological difference between the microvilli and glycocalyx of the crescent-shaped cells and the striated border of the other midgut cells, as reported to be the case in the eutardigrade *Milnesium tardigradum* by Dewel and Clark (1973c). As in this species, the cuticle of the esophagus in *I. augusti* extends freely a short distance into the lumen of the midgut. The cuticle covers, but does not attach to the microvilli (Fig. 2a). Ultrastructurally the crescent-shaped cells resemble "normal" midgut cells. Their special shape and the absence of large amounts of nutritional storage material, suggest additional unknown functions (see Dewel and Clark, 1973c).

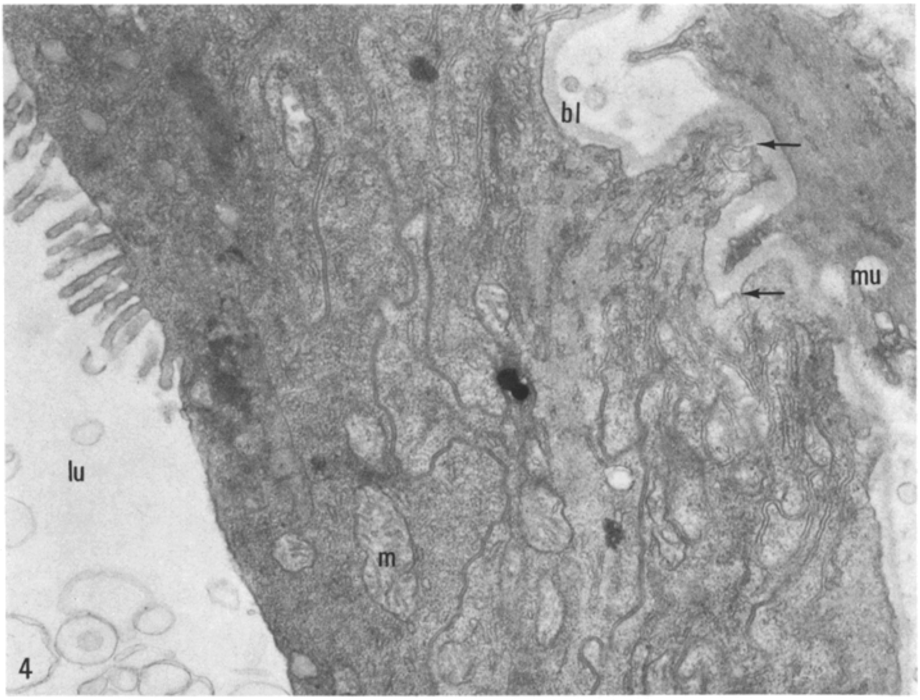
The cells near the hindgut sometimes lack nutritional storage material. These cells are highly interdigitated and possess more basal infoldings than other cells, but the striated border is reduced or is absent from the luminal surface (Fig. 4). There are also highly vacuolized cells which mark the openings of the vasa Malpighii. A detailed description of this zone including the vasa Malpighii will be published elsewhere.

In general, the lateral cell boundaries are straight but sometimes interdigitations occur between adjacent cells. Intercellular adhesion may be facilitated by the presence of *zonulae continuae* between the apical plasma membranes of adjacent cells (Fig. 3c). In the *zonula continua* or continuous junction the intercellular space between the parallel membranes is filled with a continuous, granular material. It is unknown whether the function of continuous junctions differs from the function of septate junctions. *Zonulae continuae* have been observed in the midgut of some insects (Noirot and Noirot-Timothée, 1972; for review see Staehelin, 1974). The length of the junctions is variable. The plasmalemma is invaginated, resulting in sinous folds extending into the body of the cell (Figs. 3d, 4). The basal lamina does not penetrate the infoldings. The invaginations are not as frequent as those in many other resorbing epithelia. There are no specialized intercellular junctions at the basal aspect of the midgut cells.

The centrally located lobed nuclei contain a conspicuous nucleolus. Clumps of heterochromatin are scattered throughout the nucleoplasm and along the inner nuclear membrane. The outer membrane of the nuclear envelope is studded with ribosomes (Fig. 5a).

Numerous mitochondria are distributed throughout the cytoplasm, some of which have very few cristae (Figs. 2b, 3d). Dictyosomes, which occur in small numbers, are usually located close to the spherical inclusions or nutritive material or the rough endoplasmic reticulum (Fig. 5a, b). Smooth endoplasmic reticulum appears to be absent. The smooth vesicles in the cytoplasm may have arisen from the dictyosomes. The abundant rough endoplasmic reticulum is not restricted to one part of the cell. Ribosomes cover the entire surface

Fig. 3a–d. Midgut cells. (a) Apical portion of a cell containing vesicles of different electron density, and invaginations between the microvilli. The fuzzy coating of the striated border is distinct. Microvilli contain only a few filaments (→). ×40,000. Inset: Transverse section through irregularly arranged microvilli. ×32,000. (b) Globules between disintegrating (→) microvilli. ×40,000. (c) *Zonula continua* between two apposed cells. ×70,000. (d) Three adjacent midgut cells. Note the basal infoldings (→). Hemocoel (*h*), lipid droplet (*li*), mitochondrion (*m*), rough endoplasmic reticulum (*rer*). ×18,000



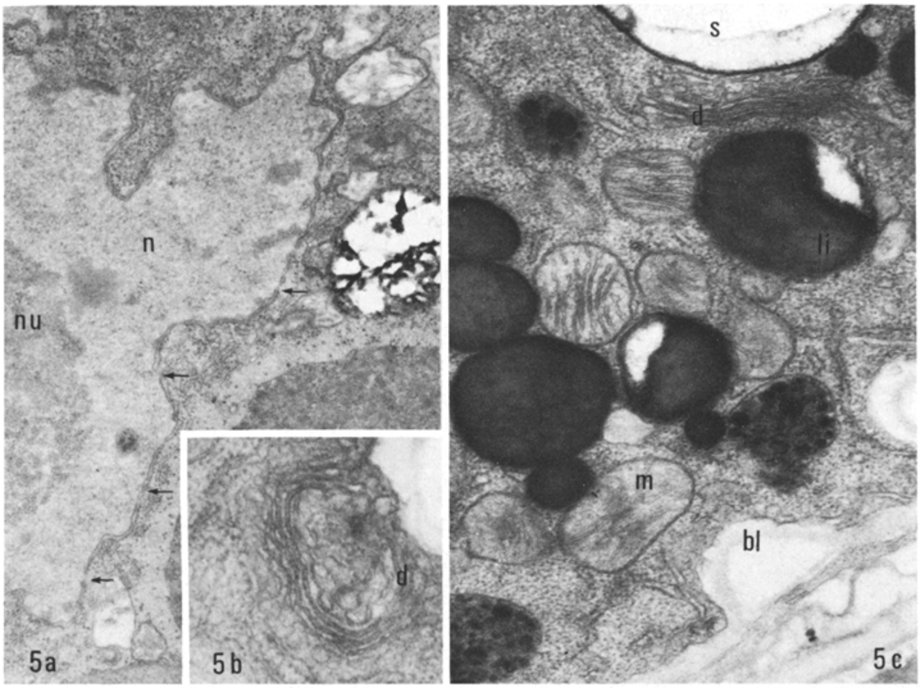


Fig. 4. Posterior portion of the midgut. Some cells are devoid of microvilli. Note the interdigitations between adjacent cells and the basal infoldings (→). Basal lamina (*bl*), midgut lumen (*lu*), visceral muscle (*mu*). ×20,000

Fig. 5a–c. Organelles of the midgut cells. (a) The nucleus (*n*) contains a conspicuous nucleolus (*nu*) and a perforated envelope (→). ×18,000. Dictyosomes (*d*) near the rough endoplasmic reticulum (b) and between a spherite (*s*) and lipid droplets (*li*) (c). (b) ×40,000. (c) ×28,000

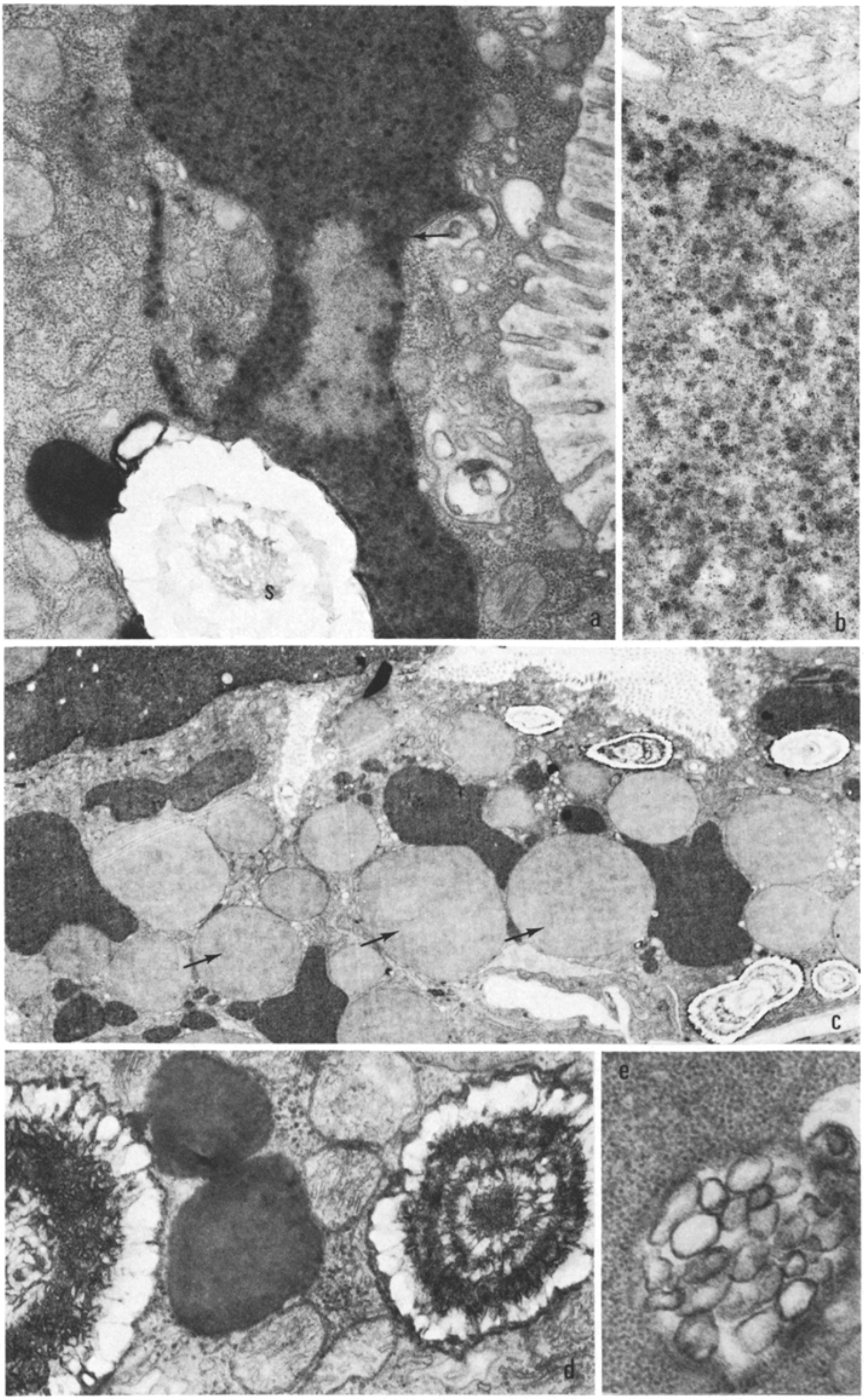


Fig. 6a–d. Inclusions of the midgut cells. (a) A large area of granular material. ×20,000. (b) Positive reaction after Thiéry's method. ×26,000 (unstained). (c) Large membrane-bounded spherules of moderate electron density (→). ×4,800. (d and e) Different ultrastructural appearances of spherites. (d) ×30,000, (e) ×40,000

of the cisternae and free ribosomes are also abundant. Some cells contain lysosome-like bodies containing residual material. Lipid droplets of varying size and number are stored within all cells (Fig. 5c), whereas glycogen deposits could not be observed in gravid females.

In all specimens investigated the cells of the middle part of the intestine are filled with large amounts of granular material which is irregularly distributed in distinctive areas of the cytoplasm (Figs. 1a, b, 6a). Sometimes these accumulations seem to be membrane-enclosed. Using the PAS-method only a very weak positive reaction was observed. This material is faintly stained by Thiéry's method (Fig. 6b), whereas the glycogen of the cavitary cells and the developing eggs is strongly stained.

We have also found large membrane-bounded spherules of moderate electron density between the granular material in some cells (Fig. 6c). Both substances are believed to represent nutritional storage.

The midgut cells, including the crescent-shaped cells of the anterior portion and the small cells of the posterior part, contain numerous spherical or ovoid inclusions ranging in diameter from 0.5 to 4 μm. The number encountered in a section was from three to more than 30 (see Fig. 1b). Most of these bodies were characterized by a distinct concentric-ring (lamellar) arrangement of opaque and clear zones and a boundary membrane (Figs. 1b, 6a, d, e). Often the contents of these inclusions appear to fall out during sectioning, leaving holes in the cytoplasm (Fig. 3d). They almost certainly contain material that only partly survives processing for electron microscopy. Possibly the appearance of the inclusions also depends upon the plane of section and their stage of development, as they show some morphological variation (Figs. 1b, 6a, d, e). The origin of these bodies has not been investigated. Sometimes they could be observed beneath the apical cytoplasm and between the microvilli, indicating a discharge into the midgut lumen.

It must be emphasized, however, that in fed animals – which were not investigated in this study – the size and number of cell organelles and inclusions increase enormously.

Apparently regenerative cells are absent from the entire midgut of *I. augusti*. This may be in conformity with the trend towards cell constancy of some tissues in Tardigrada (Marcus, 1929; Bertolani, 1970; Ramazzotti, 1972).

Discussion

The main functions of the midgut in Tardigrada, as in other invertebrates and vertebrates are the digestion and absorption of nutritional substances. The midgut cells exhibit a number of ultrastructural specializations which may be correlated with these roles. The most prominent of these is the amplification of the apical and the basal plasma membranes, although basal infoldings in *I. augusti* are less prominent than in many other species. A microvillus border and basal infoldings are features of most absorptive epithelia (see Berridge and Oschman, 1972).

We do not know how nutritient molecules are taken up from the lumen of the gut into the lining cells or how the digestive enzymes are secreted. The occurrence of a well developed rough endoplasmic reticulum might be taken as morphological evidence of enzyme synthesis but there is little evidence of dictyosome activity or of products of the endoplasmic reticulum. The presence of vesicles between the microvilli may represent the secretion of enzymes or the absorption of nutrient substances by cytosis. The disintegration of microvilli may be a mode of secretion (Heinrich and Zebe, 1973). In the gravid females investigated we never found an extracellular sheath resembling a peritrophic membrane separating the luminal contents from the apical surface. This does not mean that a peritrophic membrane which is widely spread in the animal kingdom (for review see Peters, 1969) is really absent in Tardigrada. Light microscopical observations revealed the existence of a "membranous" structure surrounding the faeces of Tardigrada (Marcus, 1929); some EM-pictures of the midgut of *Isohypsibius granulifer* show a structure very similar to a peritrophic membrane (Greven, unpublished). In some insects the peritrophic membrane is believed to be formed along the length of the midgut, presumably as a secretory product of the epithelial cells (Smith, 1968; Wigglesworth, 1972). It is possible that the luminal vesicles and membrane-like structures contribute in some manner to the formation of such a sheath. The cuticle of the esophagus which extends a short distance into the midgut lumen, obviously does not function as a peritrophic membrane (Dewel and Clark, 1973c).

Spherical granules with a more or less distinct concentric lamination have been demonstrated by electron microscopy in a number of different tissues (for references see Turbeck, 1974). In many invertebrates they occur in the epithelial cells of the malpighian tubules (if they are present) (Smith, 1968; Wigglesworth, 1972) or in the gut cells (i.g. Nematoda, Jenkins, 1973; Onychophora, Lavallard, 1967; Crustacea, Donadey, 1967; Insecta, Smith, 1968; Ballan-Dufrancais, 1972; Wigglesworth, 1972; Humbert, 1974). Generally they are believed to have an excretory function. Possibly they serve also as stores of material used later in the growth of cells (Turbeck, 1974). These midgut inclusions, for which the common name "spherites" has been proposed (Turbeck, 1974), contain among other substances P, Cl, Ca, and Mg in a glycoprotein matrix (Ballan-Dufrancais, 1972).

The present results show that the midgut cells of Tardigrada also contain spherites, often with a concentric lamination. It was Marcus (1928, 1929) who observed polygonal crystal-like inclusions not only in the midgut cells but also in the midgut lumen and in the faeces of several tardigrades. He suggested that they represent excretory products and that the midgut of Tardigrada may perform an excretory function contrasting with its primarily digestive role and independent of the presumed function of the malpighian tubules (Marcus, 1929).

Furthermore, there is evidence that the midgut cells of *I. augusti* are engaged in storage of nutritive material (see also Marcus, 1929), a function in which the cavitary cells are also involved (Marcus, 1929; Rosati, 1969; Weglarska, 1975). Lipid storage is distinctly localized within the midgut cells (Marcus, 1929). In most of the specimens of *I. augusti* studied with the light microscope the midgut cells were filled with green or yellow nutritive material ("körnchenartige Klumpen", Marcus, 1929) mainly of vegetal origin, which is diminished during growth, moulting or starvation. These substances correspond with the large amounts of granular material and the membrane-bounded spherules seen in ultra-thin sections. It may be concluded from our results that the granular substance at least contains some polysaccharide material. Further histochemical studies concerning this material are in progress.

Plant-eating insects (Smith, 1968; Wigglesworth, 1972) and crustaceans such as *Artemia salina,* which resists desiccation at high salinities, are known to use the midgut in ion transport (Hootman and Conte, 1974). Some of the structures described for the midgut epithelium in *I. augusti* are believed to be indicative of such a function. It is documented that the eutardigrade *Macrobiotus hufelandi* tolerates high salinities (Collin and May, 1950). The midgut or at least parts of the midgut of Tardigrada may therefore play a role in osmoregulation. However, as these mechanisms have not been studied in Tardigrada and as the organs involved in osmoregulation are, as yet, unknown, this last suggestion must be regarded as highly speculative.

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