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Fine Structure and Function of the Digestive Tract of *Cyathura carinata* (Krøyer) (Crustacea, Isopoda)

Johann-Wolfgang Wägele[1], Ulrich Welsch[2], and Waltraud Müller[2]

[1] Fachbereich IV, Universität Oldenburg, Ammerländer Heerstr. 67–99, D-2900 Oldenburg, Federal Republic of Germany

[2] Anatomisches Institut, Universität Kiel, Olshausenstr. 40–60, D-2300 Kiel, Federal Republic of Germany

Summary. The entire gut of *Cyathura carinata* is lined by a cuticle indicating its completely ectodermal origin. By flattening of the epithelial folds and possibly also of reserve-folds of the plasma membrane the intestine is highly dilatable, an adaptation towards a rapid uptake of the food which is sucked in by means of specialized mouthparts, which pierce the body wall of its main prey, the polychaete *Nereis diversicolor*. Bundles of microtubules within the intestinal cells presumably represent cytoskeletal structures providing protection against mechanical stress. Spirally arranged muscle fibres, which form peculiar contact areas with the gut, can easily follow any dilatation. A few indications of the metabolic functions of the anterior gut epithelium have been found: Basally and apically located labyrinthine structures of the plasma membrane, apically located clear vesicles, positive reactions for lysosomal, mitochondrial and membraneous enzymes, a strikingly thin and loosely arranged cuticle through which food substances of low molecular weight may diffuse. The cells of the gut and also of the digestive caeca are interconnected by desmosomes, extensive pleated septate junctions, and gap junctions. In the pleon the gut is less dilatable and devoid of plasma membrane specializations. In this area tendon cells, particularly rich in microtubules, serve as attachment sites for the dilating muscles of the rectum. The digestive caeca synthetize and secrete digestive enzymes, mix food and enzymes in their lumen, resorb food molecules, store lipids and glycogen. In the glandular epithelium small cells, rich in rough ER, and a majority of large cells, rich in lipid droplets, occur which, however, are interconnected by a series of morphologically intermediate cells. All cells bear an apical brush border, form a basal labyrinth and contain high to medium activities of acid phosphatase, nonspecific esterases, ATPase, and succinic dehydrogenase. The ER-rich cells are far less frequent than in the omnivorous or herbivorous isopods (*Sphaeroma, Idothea,* Asellidae, Oniscoidea).

Offprint requests to: J.-W. Wägele

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A. Introduction

The anatomy of the Peracarida is generally less well-known than that of the decapod crustaceans, and a considerable number of questions concerning structure, function, and homologies of the individual organ systems find contradictory answers in the relevant literature. This is particularly true in respect of the different sections of the digestive tract. A common trait of all Peracarida is the fact that the distal stomach gives rise both to the midgut and the digestive caeca (= digestive glands = hepatic caeca = hepatopancreas) (Siewing 1954), a direct connection between entodermal digestive caeca and midgut thus being absent. The midgut of the Decapoda, Mysidacea, and Amphipoda is without doubt of entodermal origin, its lining cells resemble those of the digestive caeca by the presence of apical microvilli and the absence of a cuticle (Barker and Gibson 1977; Mykles 1979). The 'midgut' of the Cumacea, Tanaidacea, and Isopoda, however, is lined by a chitinous cuticle in the same way as the hindgut (Siewing 1954), which justifies the remark of Siewing (1954) that using the term 'midgut' in the crustacea does not necessarily imply that this part of the gut is an entodermal structure. Goodrich (1939) observed in early stages of *Porcellio* (Isopoda, Oniscoidea) embryos in which the proctodaeum and stomodaeum fuse, which means that the entire gut is of ectodermal origin. This observation was confirmed in other isopods by Jones (1968); Witkus et al. (1969); Clifford and Witkus (1971); Holdich (1973). Nevertheless, occasionally doubt is raised about the complete absence of an entodermal midgut (Schmitz and Schultz 1969). Holdich and Ratcliffe (1970) and Holdich (1973) assume, that the peritrophic membrane of *Dynamene* (Sphaeromatidae) as in other crustacean groups (Mykles 1979; Schlecht 1979) is formed by an entodermal midgut vestige.

Another peculiarity of the isopods is the alleged absence of lateral cell walls in the 'midgut' epithelium (Frenzel 1884; Schönichen 1899; Murlin 1902; Nicholls 1931; Siewing 1954; Schmitz and Schultz 1969). This statement, which was based on light microscopice studies has not been confirmed with the electromicroscope (Witkus et al. 1969; Holdich and Ratcliffe 1970; Schultz 1973).

The digestive caeca of the Isopoda have attracted much more attention than the 'midgut'. Various functions have been attributed to the caeca: Extra- and intracellular digestion, resorption, storage of energy-rich compounds, and excretion. In contrast to the digestive caeca of the Decapoda and Amphipoda, which are composed of four cell types (Amphipoda: Schultz 1976; Decapoda: Jacobs 1928; Stanier et al. 1968; Loizzi 1971; Storch and Welsch 1977; Barker and Gibson 1977; and others) those of the Isopoda ordinarily seem to contain only two cell types. The small, dark cells (S-cell of Frenzel 1884; storage cell of Steeves 1963; β-cell of Smith et al. 1975; A-cell of Hryniewiecka-Szyfter and Tyczewska 1979) contain a markedly granulated cytoplasm and few vacuoles (Smith et al. 1975), store glycogen (Steeves 1963) and lipid (Walz 1882; Steeves 1963; Jones et al. 1969; Moritz et al. 1973; and others) and are assumed mainly to be resorptive in function (Steeves 1963; Clifford and Witkus 1971) but also secretory (Donadey and Cesarini 1970). The second, larger cell (B-cells, 'secreto-

ry' cells, α-cells, B-cells) contain more vacuoles and less granulated cytoplasm (Schultz 1973), are said to be partly endowed with more ribosomes and rough endoplasmic reticulum than the smaller cells (Clifford and Witkus 1971) and thought to be mainly secretory but also have resorptive elements. On the whole rather contradictory interpretations are given in the literature. Jones et al. (1969) found a relatively uniform epithelium in starving *Eurydice* (Cirolanidae) and think that the described cell types are only functional stages, a view which these authors share with Stanier et al. (1968), who studied *Carcinus*. In the digestive caeca of marine isopods Frenzel (1884) describes one cell type which, however, has different age-dependent appearances. Storch and Lehnert-Moritz (1980) stress the rapidly changing morphology of the hepatopancreatic cells of *Ligia* under various conditions.

It is the aim of the present paper to analyse the relations between light and electron microscopical structure, enzyme-histochemistry and function of the gut and digestive caeca of *Cyathura carinata* (Krøyer) (Isopoda, Anthuridea), the feeding habits of which can be favourably observed in living animals because of their transparency. Findings on oesophagus and stomach will be reported in a different contribution (Wägele 1981).

B. Material and Methods

Adult specimens of *Cyathura carinata* were collected in the mesohaline Kiel – canal ('Lake of Flemhude') in July and October 1980. They were kept up to 14 days in water from the place of collection before fixation. Some of the animals were fed with *Nereis diversicolor* (Polychaeta) and fixed 2 h after food uptake. Living animals of all ages were observed in Petri dishes under a dissecting microscope during food uptake.

Electron microscopy: The animals were cut into 1–2 mm thick slices which were processed in the following way: 2 h in 3.5% phosphate buffered glutaraldehyde (pH 7.5), repeated rinses in phosphate buffer (pH 7.5), 1.5 h post-fixation in 2% OsO_4, dehydration in ethanol, immersion in propylenoxyde, embedding in araldite. Thin sections were stained with uranyl acetate and lead citrate. Semithin sections were stained with azure II-methyleneblue. Electron microscope: Philips EM 301.

Scanning electron microscopy: Air-dried, formalin-fixed material was coated with gold and investigated in a Cambridge S 4-10 scanning electron microscope.

Enzyme histochemistry: 10 µm thick fixed and unfixed cryostat sections were used for the demonstration of the following enzymes: Acid and alkaline phosphatase, ATPase, β-glucosaminidase, α-naphthyl-acetate esterase, indoxylacetate esterase, succinic dehydrogenase, acetylcholine esterase. Methods according to Pearse (1961) and Lojda et al. (1976).

C. Results

1. Mouthparts and General Structure of the Alimentary Tract

The mouthparts of *Cyathura carinata* (Fig. 2A) are adapted to its predatory habits: the second maxillae are reduced, the first maxillae are slender, stiletto-like structures which are endowed distally with pointed teeth, the mandibles bear a sharp lamina dentata (Wägele 1979) instead of the setal row of other Peracarida. The mouth opening is between upper lip and hypopharynx. The elongated oesophagus widens only in the second pereonite to become the stomach. In

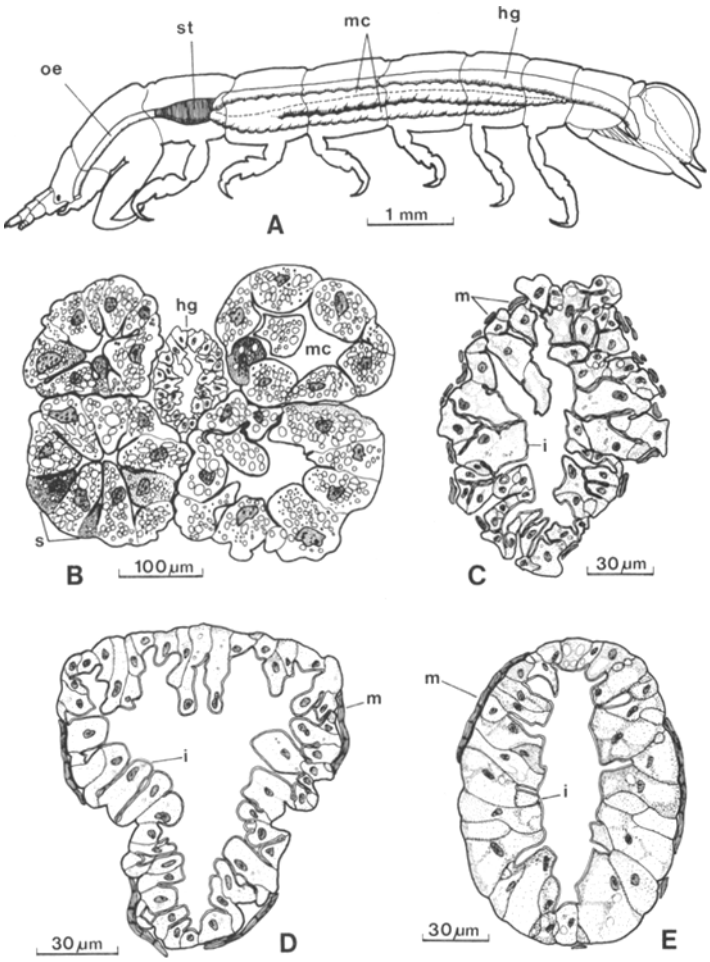


Fig. 1. **A** Alimentary tract of *Cyathura carinata*, semischematic; *oe* oesophagus; *st* stomach; *mc* midgut caeca; *hg* hindgut. **B** Cross-section of midgut caeca (*md*) and hindgut (*hg*); *s*: dark secretory cells. **C** Cross-section of pereonal hindgut with folded epithelium; *m* muscle; *i* intima. **D** Cross-section of hindgut in pereonite 7. **E** Hindgut in pleon; *m* muscle; *i* intima

most Isopoda the stomach is located in the cephalothorax, the oesophagus thus being rather short. Two caudally situated exits leave the stomach, the dorsal one leading via lamina dorsalis posterior (Scheloske 1976) into the intestine (the part of the alimentary tract following the stomach = hindgut, since a typical midgut is absent – see above), the ventral one via an atrium into the digestive caeca. The intestine is a straight tube terminating with its anus in the pleotelson. *Cyathura* has two pairs of digestive caeca (Fig. 1A), the ventral ones being shorter and branching off from the dorsal ones in the third pereonite. The relatively large cells of the digestive glands are arranged in rings surrounding the lumen (Fig. 2B) and become progressively smaller near the distal end of the glands.

2. *Feeding Habits*

All developmental stages of *Cyathura carinate* are predators. They puncture and suck out polychaetes, in the biotope studied predominantly *Nereis diversicolor*. The necessary negative pressure is generated by the pumping action of the muscles of oesophagus and stomach. The act of sucking normally lasts only a few minutes; the polychgetes frequently survive the injury. Initially the liquid food is stored for some minutes in the intestine, which therefore enlarges to a remarkable extent. Then, the food is passed back into the stomach in small portions and is pressed through the gastric filter system into the digestive caeca. Here a lively peristalsis forces the food from the right caeca into the left ones and vice versa, which presumably enhances the process of mixing of food and enzymes. The contents of the digestive caeca rapidly takes a dark coloration and can be stored here for weeks. Freshly obtained animals usually contain dark food within their caeca. The formation of faeces can be observed in the hindgut after several hours.

The observations indicate that the food of *Cyathura carinata* contains almost no firm constituents and that its proportion of proteins and also lipids is higher than in the majority of isopods, which are of herbivorous or omnivorous habits.

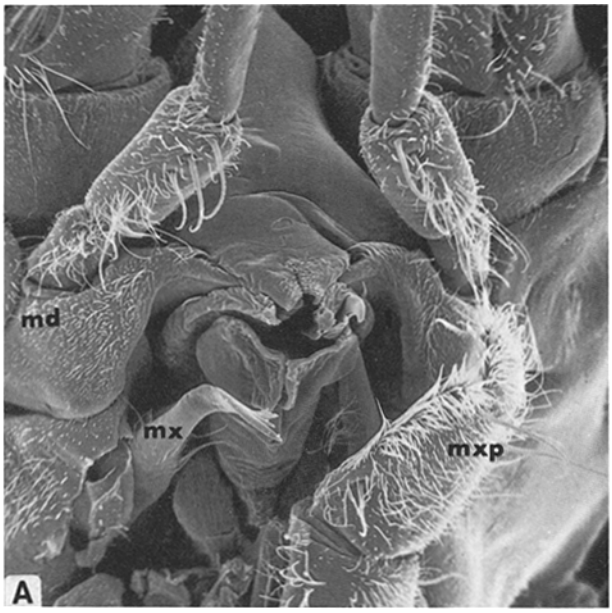
3. *Light Microscopy*

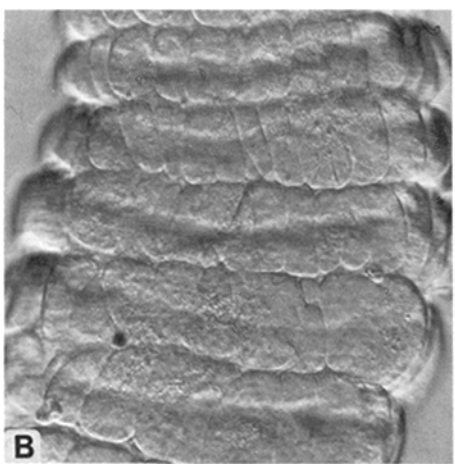
Series of longitudinal sections demonstrated the presence of an uninterrupted cuticular lining of the entire alimentary tract. There is no vestige of a typical entodermal midgut. The digestive caeca including their atrium, however, are devoid of a cuticular intima.

In the pereon the intestinal epithelial cells are of highly irregular shape, frequently resulting in a bizarre outline of the gut lumen (Fig. 1C). In some places the lumen almost reaches the basement membrane, in other places the basement membrane extends into epithelial projections and seems to branch out here. A typhlosolis, as known from Oniscoidea (Murlin 1902), is lacking. All cells are covered by a thin cuticle. The small nuclei are in midcellular or apical position. After a short transitory zone in the last pereonite (Fig. 1D) the intestinal epithelium in the pleon is of a regular shape, there are almost no epithelial folds and the basement membrane is ring-shaped in the cross-section of the gut (Fig. 1E). Here the cells frequently contain large intracellular vacuoles, which at least in part seem to be identical with fields of glycogen as can be seen in the electron microscope (see below). In the light microscopical section cell boundaries are hardly detectable in the hindgut.

On cross-section through the gut the accompanying muscle fibres are cut longitudinally, obliquely, and transversally. This is due to the spirally arranged muscle fibre system which can be analysed in whole mount preparations of the gut. Frequently the muscle fibres form ramifications (Fig. 2C).

The cells of the digestive caeca are remarkably larger than those of the gut. Their apices usually bulge into the lumen which in the fixed material is reduced to a star-shaped cleft (Fig. 1B). There are numerous large and a few small cells interconnected by intermediate cells. These different cell forms are of irregular distribution over the cross-section. The clear cytoplasm of the





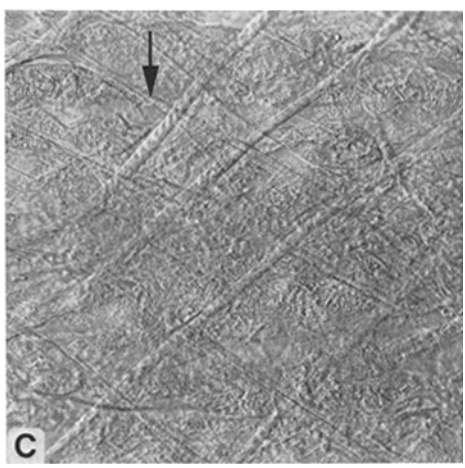


Fig. 2. **A** Cephalothorax with mouthparts in ventral view, right mxp removed, right mx in unnatural position; *md* mandible; *mx* first maxilla; *mxp* maxilliped (×240). **B** Digestive gland with circular arrangement of cells (×220). **C** Muscle network of gut epithelium, arrow showing ramification of muscle (×350)

dominating large cells is filled with lipid droplets and additionally contains variable amounts of small granules; their voluminous nuclei exhibit frequent basally directed extensions and a distinct chromatin pattern: A few irregular distributed coarse particles are to be found within a multitude of tiny heterochromatin particles (Fig. 7A). The rare small cells are characterized by a darker cytoplasm, numerous small granules and only a few lipid droplets.

4. Electron Microscopy

As seen in the light microscope, the intestinal cells of the pereon are of variable height and shape. They possess lateral cell membranes. Neighbouring cells extend numerous and irregularly arranged finger-shaped projections thus forming complex interdigitations between the cells. Three types of cell junctions can be distinguished: (a) a narrow apical zonula adhaerens; (b) a pleated septate junction (Noirot-Thimothée and Noirot 1980) of large dimensions (Figs. 3D and 8); (c) gap junctions in basal or midcellular position below the septate junction (Fig. 3E).

Apically the cells are lined with a thin cuticle (Figs. 3B and 8). It is built up by a thin epicuticle which is covered by a layer of fine-flocular material, and a broad electron transparent endocuticle. On the whole, this cuticle is thin and its endocuticle does not exhibit layers of regularly arranged filaments.

The apical plasma membrane forms narrow invaginations, apparently of variable depth. Also the basal plasma membrane is characterized by labyrinth-like infoldings, thus the entire cellular surface is considerably enlarged. In the apical cytoplasm clear vesicles, coated vesicles, and individual dense granules occur. Mitochondria are concentrated in an apical and basal zone near the corresponding invaginations. A striking feature of the cytoplasm are frequent bundles of microtubules which mainly run in parallel to the lateral and apical cell borders (Figs. 3B and 8). Other organelles are of sparse occurrence, like a few short rough ER-profiles, a small Golgi apparatus, infrequent lysosome-like bodies. Free ribosomes and small fields of glycogen particles (α-particles) are distributed throughout the cytoplasm. The basement lamina is of variable width and texture.

Muscle cells and intestinal epithelial cells are interconnected in a particular way. Between the basement laminae of the gut and the muscle cells a dense, fine particular material can be observed. Extensions of this material may bulge into the muscle cells at the level of the Z-lines. Here the Z-line reaches the plasma membrane and takes the shape of a desmosomal structure (Figs. 3A and 4A). In the contracted muscle cells these peculiar junctional complexes become clearly recognizable, since the indentations at the level of the Z-lines become deeper and the plasma membrane in between bulges to the outside. The muscle cells are of the tonic slow type (Fahrenbach 1967) with a large number (about 12) of actin filaments which surround one myosin filament. The connection of the above mentioned fine particular material between the basement laminae with the gut epithelium does not show structural specializations.

In the pleon the intestinal epithelium is lower. The cuticle is relatively thick and its endocuticle is of a layered appearance (Fig. 3C). Apical and basal invaginations of the plasma membrane are rare, the cytoplasm contains large clear membrane-bound vacuoles and rather extensive fields of glycogen. Specialized epithelial cells (tendon cells) mediate the contact between cuticle and muscle cells dilating the posterior hindgut. Dense peg-shaped projections of the cuticle extend into the tendon cells, the surrounding plasma membrane is of halfdesmosome-like structure (Fig. 4B and C). Profuse bundles of microtubules (diameter

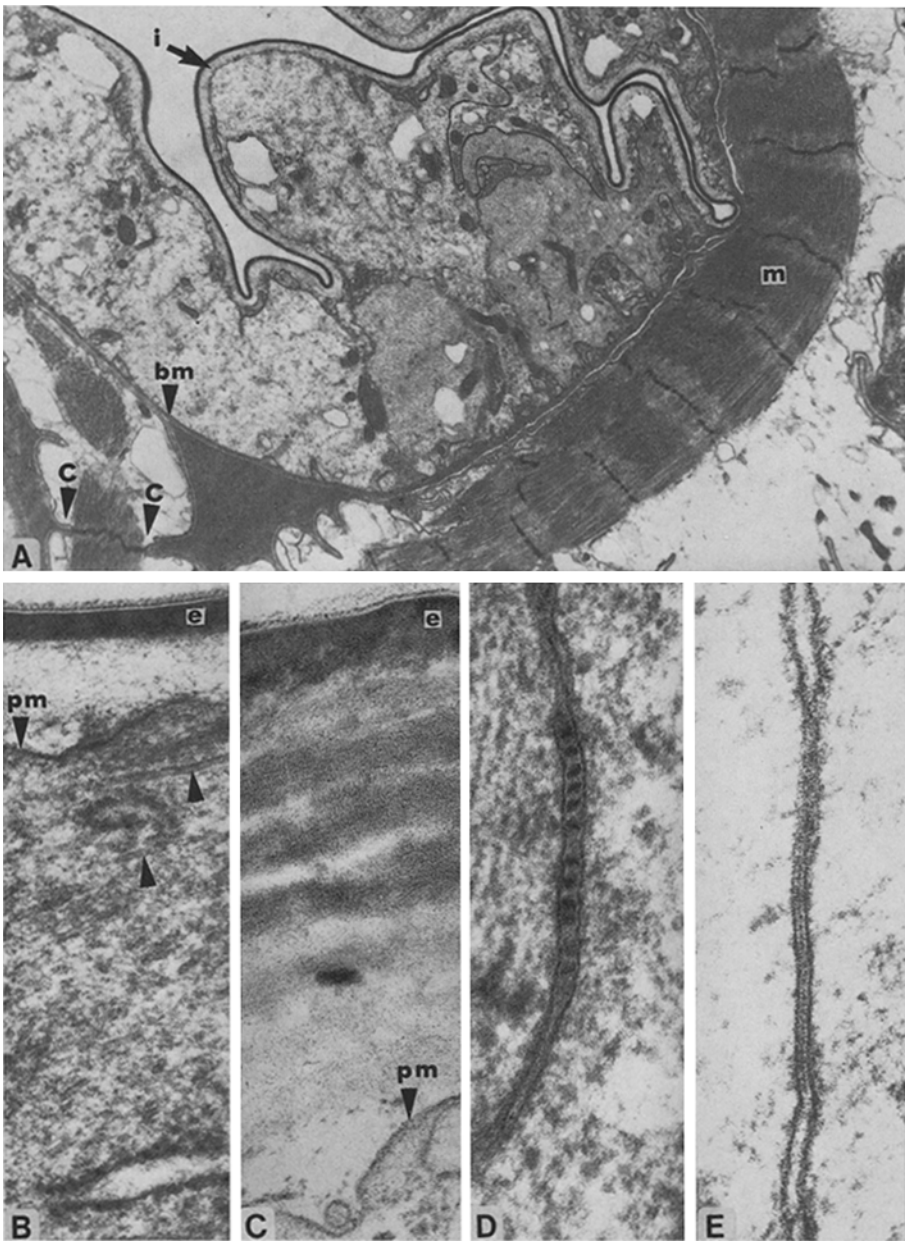
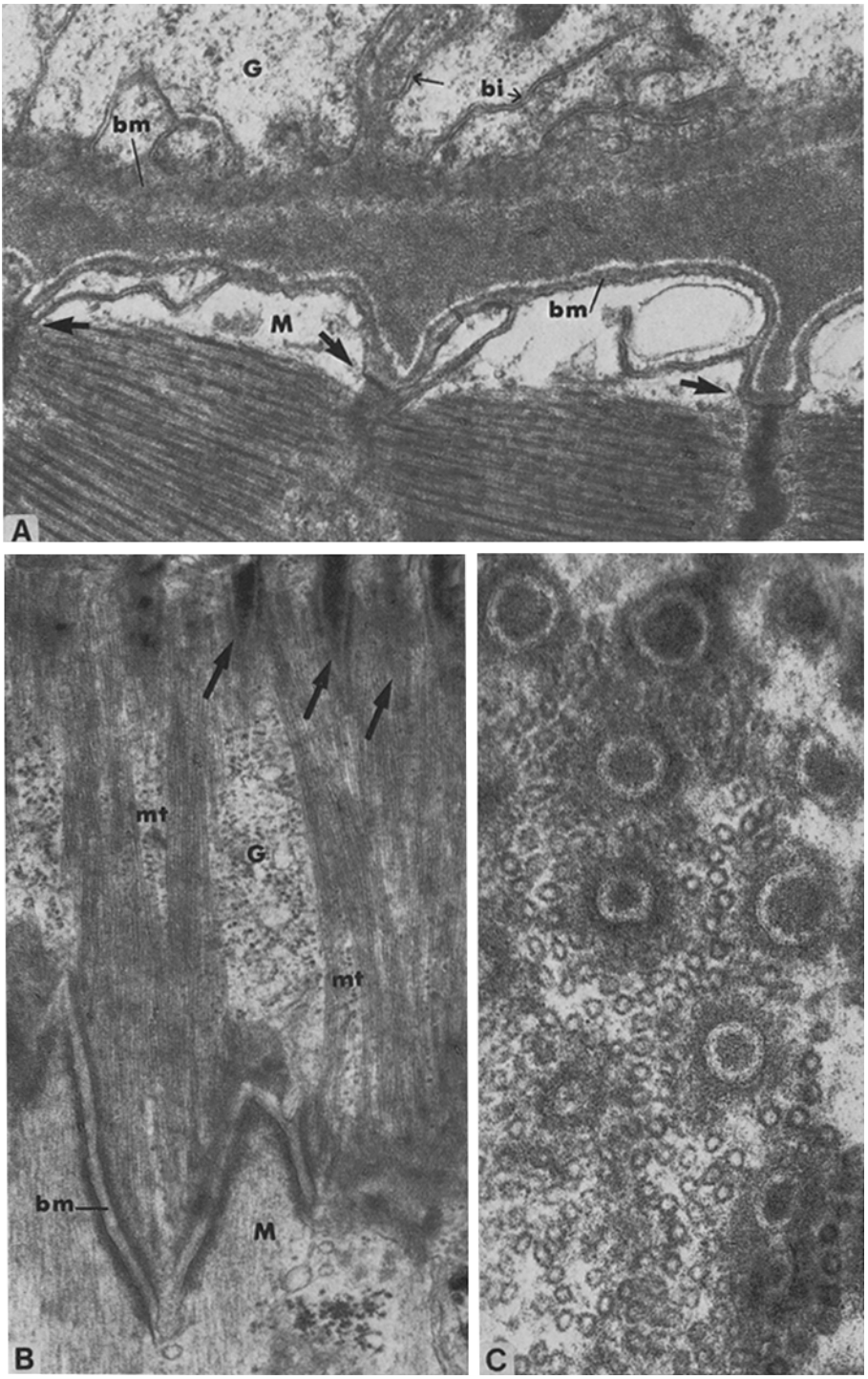


Fig. 3A–E. Hindgut of *Cyathura carinata*. **A** Cross-section of gut in pereonite 4; *bm* basement membrane; *c* contact between Z-line and basement membrane; *i* intima; *m* muscle (×4,500). **B** Apical region of gut in pereonite 4, intima with dark epicuticle (*e*) and electron transparent endocuticle; *pm* apical plasma membrane; *arrows*: microtubules (×37,000). **C** Intima of gut in pleon with dark epicuticle (*e*) and layered endocuticle; *pm* apical plasma membrane (×60,000). **D** Pleated septate junction between gut cells (×120,000). **E** Gap junction (×60,000)

Fig. 4. **A** Contact between hindgut (*G*) and muscle (*M*), *arrows* showing adhesion of Z-line to basement membrane (*bm*); *bi* basal infoldings of plasma membrane (×28,000). **B** Tendon cells of gut (*G*) in pleon; *bm* basement membrane and hemidesmosomes; *mt* microtubules; *M* muscle; *arrows* showing invagination of intima (×38,000). **C** Cross-section of apical zone of tendon cell, with microtubules and cuticular pegs (×120,000)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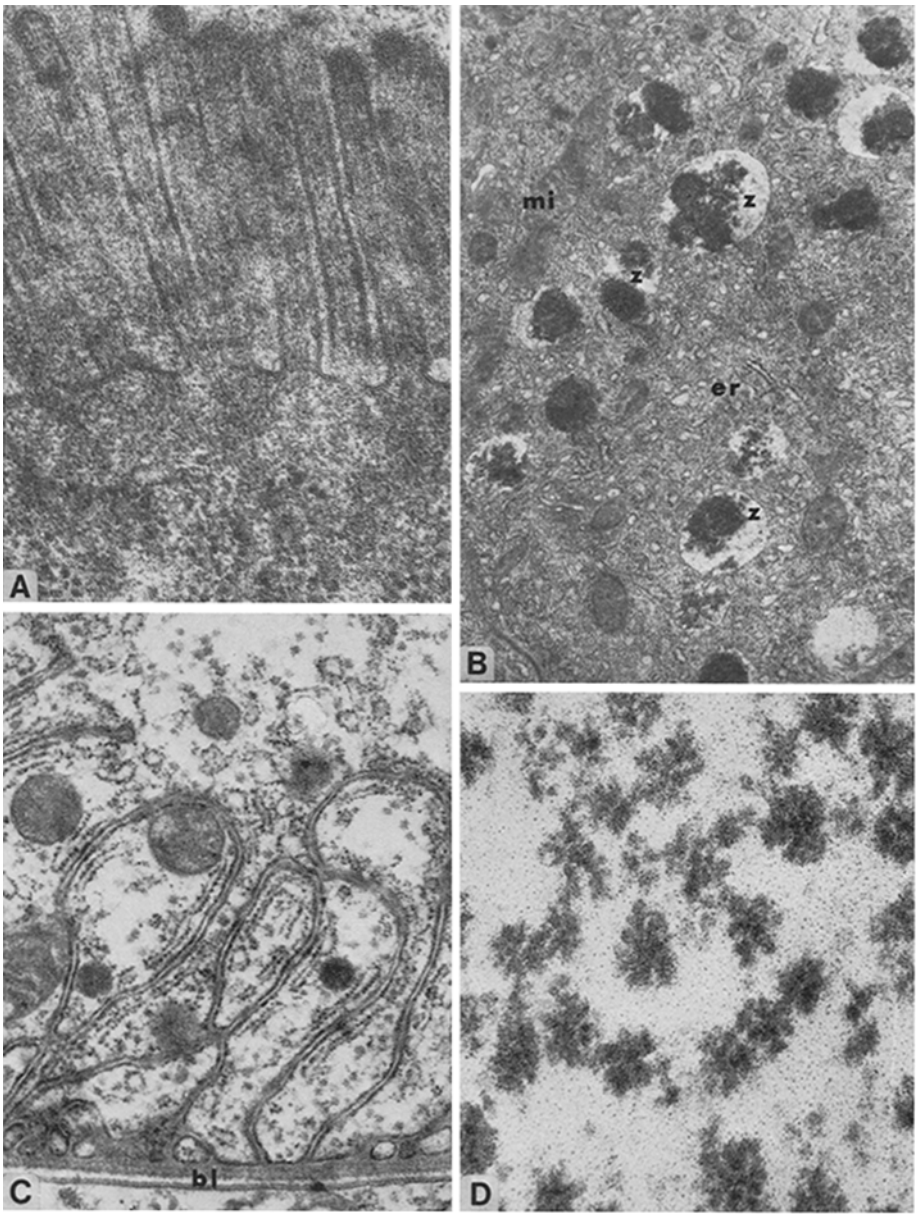


Fig. 5A–D. Digestive glands of *Cyathura carinata*. **A** Apical microvilli (×60,000). **B** Secretory cell with rough endoplasmic reticulum (*er*) and zymogen granules (*z*); *mi* mitochondria (×12,000). **C** Basal lamina (*bl*) and infoldings of basal cell membrane (×20,000). **D** Particles of α-glycogen in digestive gland (×120,000)

about 250 Å) run from the apical indentations, containing the cuticular peg, down to large halfdesmosomes of the basal plasma membrane which is invaginated by processes of the muscle cells. A narrow space containing the basal laminae of epithelial and muscle cells is interposed between the adjoining cell surfaces (Fig. 4B).

The cells of the digestive caeca are not covered by a cuticle and bear an apical seam of microvilli, which contain a core of microfilaments. The base of the microvilli occasionally seems to be slightly thinner than the tip, which may be due to a contraction of the contractile proteins within the microvilli (Fig. 5A). The lipid droplets of the large cells are electron transparent. Structural details of the large cells beside their numerous lipid droplets are: A deep basal labyrinth with associated mitochondria (Fig. 5C), numerous free ribosomes, fields of glycogen (α-particles), lysosomal inclusion bodies, which in some cells are frequent and mainly in basal and midcellular position; granules with regularly arranged fine particular contents, which presumably present secretory (zymogen) granules, possibly individual small peroxisomes (without cristalline core, usually near rough ER-cisterns), individual granules with concentrically arranged dense and light material. The small darker cells are characterized by fairly abundant cisterns of the rough ER which often forms stacks and abundant secretory granules (Figs. 5B and 9). These cells, too, however contain glycogen, lipid and lysosomal structures. The slender muscle cells surrounding the digestive caeca are of the tonic type, too.

5. Histochemistry (Plates 6 and 7)

Lipids (Figs. 7A and B). Sudan black stains lipid droplets in all cells of the digestive caeca. These droplets are bigger and more abundant in the large cells than in the smaller dark cells. The lipid is stored in the central and basal parts of the cytoplasm. The intestinal cells do not contain lipid droplets.

Glycogen (Fig. 5D). With the electron microscope glycogen (α-particles) has been demonstrated in the gut and digestive caeca (see above).

Acid Phosphatase (Fig. 7E). A relatively diffuse reaction of weak to medium intensity is present in the gut epithelium. In the cells of the digestive caeca the reaction is granular and of medium to strong intensity. The frequency and distribution of these lysosomal granules varies considerably from animal to animal and from cell to cell. They are, however, usually concentrated in the basal and central cytoplasm. In fed animals the reaction is stronger than in starving ones.

β-Glucosaminidase. A weak reaction, in part granular, in the intestinal epithelium was found. In the caeca a number of cells give an almost identical reaction as the acid phosphatase, i.e. the reaction is granular of medium to strong intensity and stains numerous lysosomes. In the majority of cells, however, the reaction is confined to small groups of granules which give a medium to weak reaction.

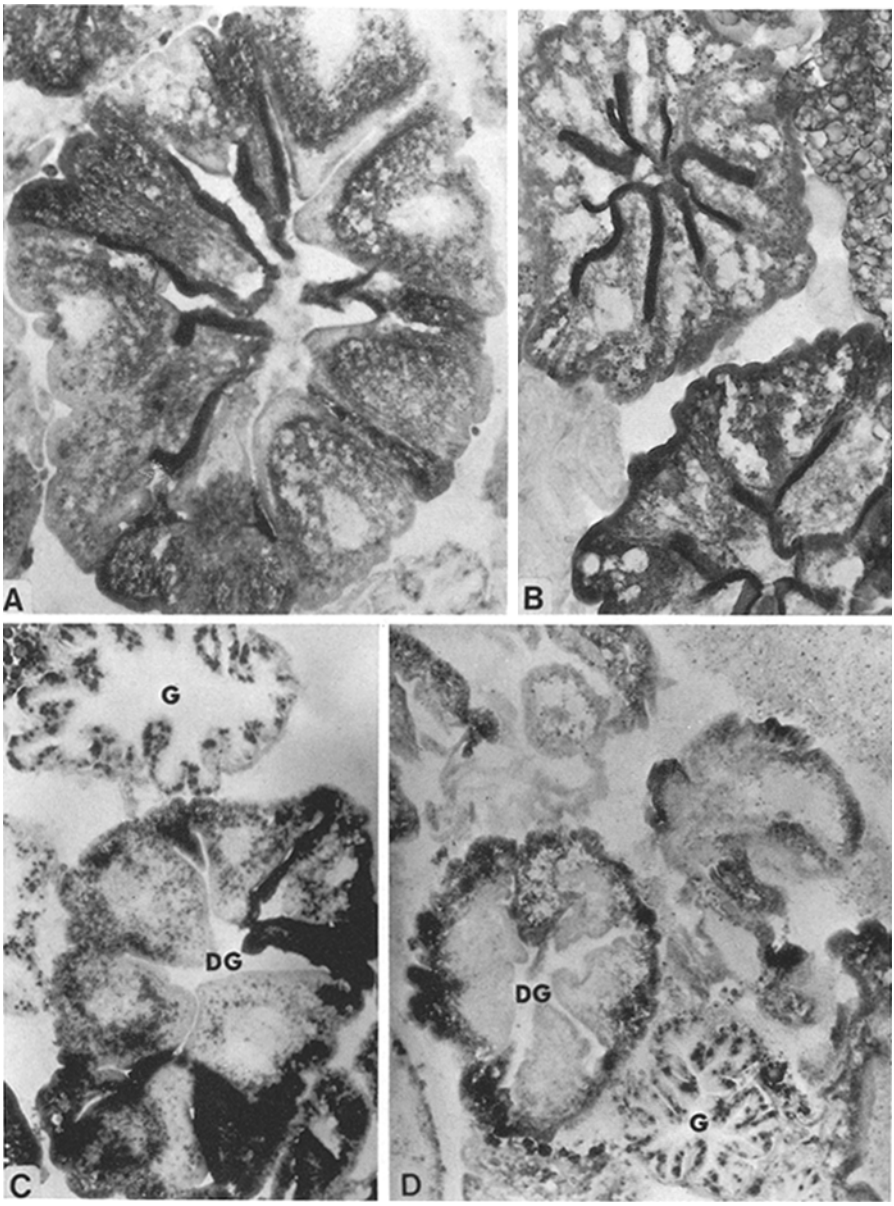
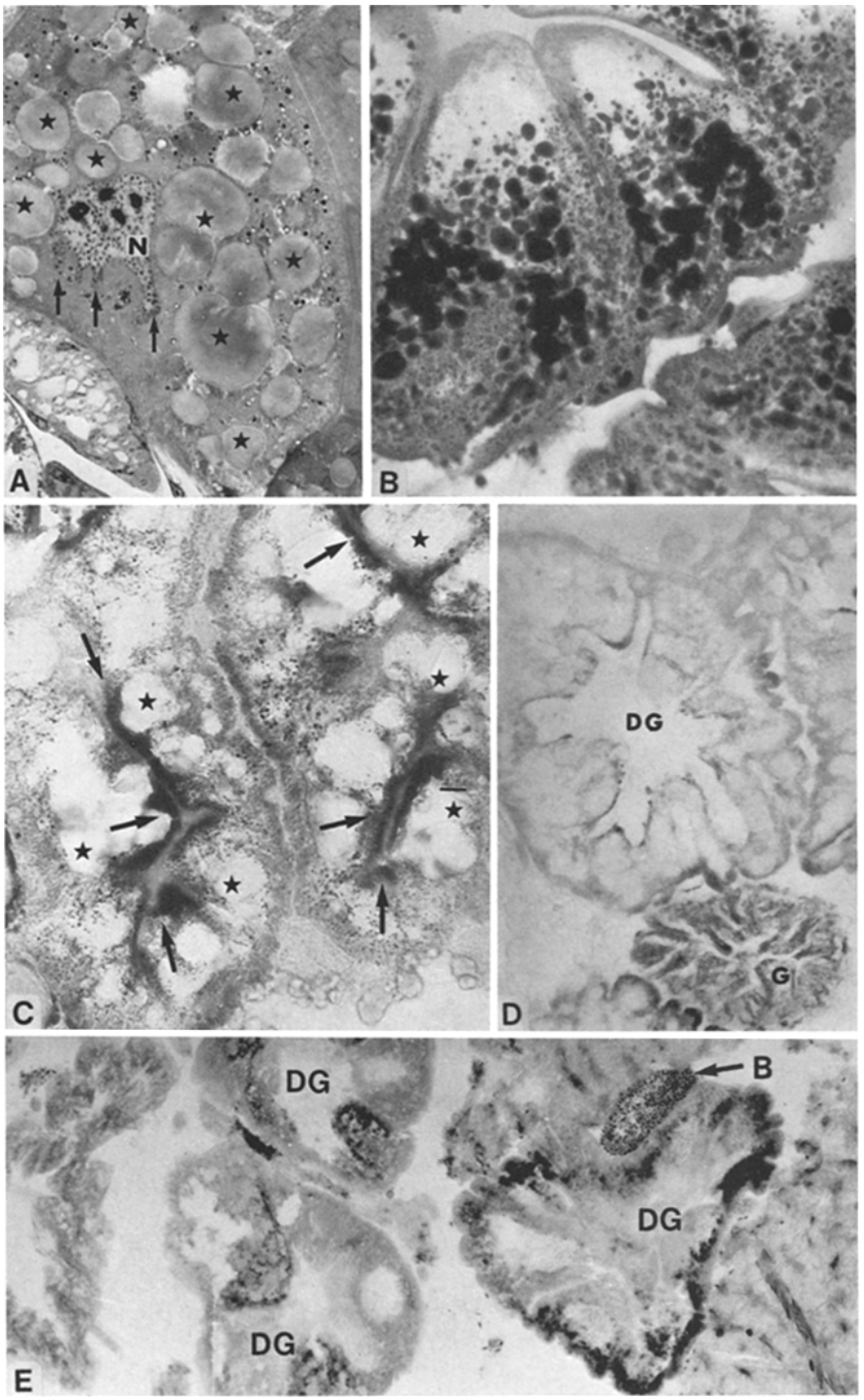


Fig. 6A–D. Non-specific esterases. **A, B** α-naphthylacetate esterase in the digestive glands, note differences in enzyme activity in different cells (**A**) and caeca (**B**). **C, D** Indoxylacetate esterase in the gut (*G*) and digestive glands (*DG*), note variable enzyme activity in different cells and caeca. A × 220, B × 140, C × 140, D × 140

Fig. 7A–C. Histochemistry of digestive glands. **A, B** Lipid droplets in the epithelial cells of the digestive glands. **A** Methyleneblue, araldite embedded material; *asteriscs*: lipid; *N* nucleus with coarse and fine chromatin; note basally directed nuclear processes (*arrows*) (× 560). **B** Sudan black coloration of lipids (× 350). **C** ATPase reaction (*arrows*) in the brush-border of the digestive caeca; asteriscs: lipid (× 220). **D** SDH in digestive gland (*DG*) and gut (*G*) (× 120). **E** Acid phosphatase in the digestive caeca, note different distribution and activity in different cells and caeca; *DG* digestive gland; *B* parasitic bacteria. (× 220).)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α-naphthylacetate Esterase, Indoxylacetate Esterase (Plate 6). Both enzymes give an identical reaction, which stains a moderate number of coarse granular inclusions of the intestinal epithelium. In the digestive caeca the reaction is very variable. The large cells often contain strongly reacting granules which occupy the apical and basal cytoplasm. In the smaller cells often the entire cytoplasm can be stained in a diffuse fashion. Occasionally only the peripheral zones of the cells give a positive reaction. E-600-inhibited esterases are of very similar distribution and intensity if compared with the non-inhibited enzymes.

Acetylcholine Esterase. No reaction was seen in the epithelia studied.

Alkaline Phosphatase. This enzyme shows a weak reaction in the apical cytoplasm of the intestinal cells and no reaction in the digestive caeca, except for its muscle cells which stain brightly.

ATPase (Fig. 7C). A weak reaction in the apical zone of the intestinal cells was found. A dense reaction product is found in the apical zone of most cells of the digestive caeca; the basal cytoplasm of these cells exhibits a weak reaction. Individual cells contain almost no ATPase.

Succinic Dehydrogenase (Fig. 7D). Reaction of medium intensity in the intestinal epithelium, relatively strong reaction in the apex of numerous and in the basis of several cells of the digestive caeca.

D. Discussion

Although the intestine of *Cyathura* is not endowed with specialized structures, which might indicate resorption of food or secretion of digestive enzymes it seems to perform certain metabolic tasks: The demonstration of alkaline phosphatase, ATPase, succinic dehydrogenase, apical and basal labyrinth-like structures with associated mitochondira and apical vesicles, which at least in part represent pinocytic vesicles, indicates transport processes, which may concern ions and water, as has been postulated in other species by Smith et al. (1969); Holdich and Ratcliffe (1970); Mykles (1979). Possibly low-molecular substances diffuse through the thin and loosely arranged cuticle into the cells where they may in part be degraded by esterases, phosphatases, and glucosaminidase. Murlin (1902) has described the uptake of sugars into the gut epithelium of terrestrial isopods, thus demonstrating that resorptive processes in principle are possible in the isopod gut. Steeves (1963) observed the appearance of glycogen five minutes after feeding in the gut of *Lirceus*. Glycogen also occurs in the intestine of *Cyathura*. Nicholls (1931) found indications for resorptive abilities in the intestine of *Ligia* after feeding iron saccharate. In the hindgut of terrestrial isopods apical labyrinthine structures are very prominent – more so than in *Cyathura* – (Holdich and Mayes 1975) and it is known that these animals absorb water through the hindgut (Gruner 1966). As in *Cyathura*, clear vesicles, interpreted to be pinocytotic vesicles, have been described in the apical cytoplasm under the cuticle of the intestinal cells of *Armadillidium* (Vernon et al. 1974) and *Mesidothea* (Hryniewiecka-Szyfter and Tyczewska 1979).

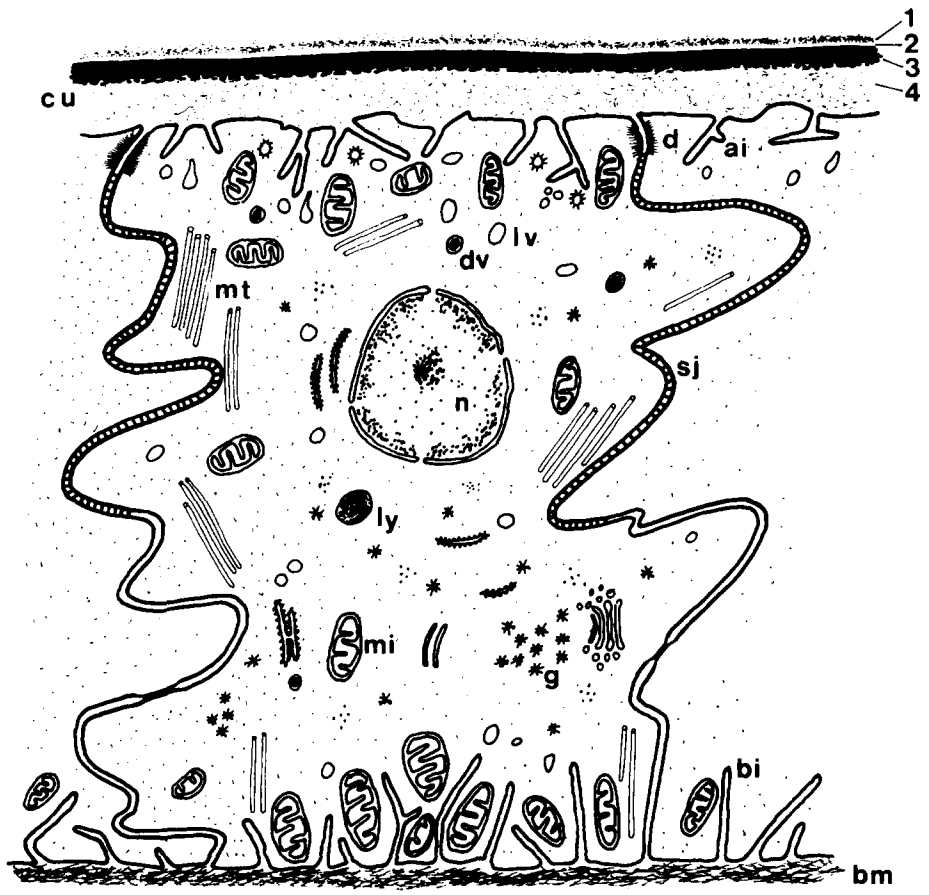

Fig. 8. Schematic drawing of hindgut cell. *ai* apical infoldings; *bi* basal infoldings; *bm* basement membrane; *cu* cuticle with floccular layer (1), electron transparent zone (2), epicuticle (3), endocuticle (4); *d* desmosome; *dv* dense vesicle; *g* glycogen; *lv* light vesicle; *ly* lysosome; *mi* mitochondria; *mt* microtubules; *n* nucleus; *sj* septate junction

The principle task of the gut, however, presumably is a more mechanical one, which is also indicated by the small inconspicuous cellular nucleus. Observations of the living animals have shown that the gut of *Cyathura* is dilatable to a marked degree. The morphological correlate of this ability are numerous folds of the intestinal epithelium which are followed by the apical cuticle and basement membrance. At the ultrastructural level infoldings and interdigitations of the plasma membrane may represent a sort of membrane reserve. It is uncertain whether the intestinal muscle cells play an active part in dilating the intestine (except for the dilating muscles of the rectum). Flattening of the epithelial, cuticular and basal-laminar folds greatly increases the intestinal volume without exerting an undue stretch onto these structures. Probably the observed bundles of microtubules in the intestinal epithelium have a cytoskeletal function. They have also been found in the intestine of other crustacea, e.g. *Homarus* and *Procambarus* and various isopods (Komuro and Yamamoto 1968; Holdich and Ratcliffe 1970; Mykles 1979). The considerable dilatability is of importance,

since *Cyathura* is a predator which in a short period of time has to suck up as much food as possible. The intestine of Gnathiidae and Cirolanidae is of identical function (Monod 1925; Jones 1968). In *Eurydice* only the anterior intestine is a storage organ which is delimitated from the posterior gut by a sphincter muscle (Jones 1968). The spirally arranged muscle fibres can easily follow each increase or decrease in volume of the *Cyathura* intestine. The specialized contacts between muscle cell and intestinal epithelium as observed in *Cyathura* deserve further analysis. So far there is no information on the peculiar dense extracellular material interspersed between the basement membranes of muscle and intestinal cells. It seems to be part of the attachment system in which the Z-lines of the muscle cells also play a role. Z-lines occasionally also reach the plasma membrane in other Isopoda (Donadey 1971; Fig. 6 in Talbot et al. 1972). Evidently they can thus take the function of a hemidesmosome.

The reversible peristalsis of the muscle layer supports food uptake, transport of stored food into the stomach and digestive caeca, and finally of the faeces to the anus. Ide (1892) had already pointed out that differences in the arrangement of the muscle cells exist in isopods. In *Oniscus asellus* there is a circular and a longitudinal layer, in *Asellus aquaticus* a circular and a spirally arranged layer. In *Cyathura* there is only a network of spirally arranged fibres, which however, are of a specialized structure. They can form ramifications, which have also been described in *Procambarus* (Loizzi 1971), and within one cell there are fibrils of different orientation, in part at right angles towards each other.

In the rectum of *Cyathura* specialized tendon cells occur in the intestinal epithelium which serve the attachment of the rectal dilators. These cells are of the same structure as comparable cells which are found intercalated between muscle and cuticle of the body in other arthropods (Bouligand 1962; Lai-Fook 1967; Smith 1972).

A liquid food-juice, free of setae and other chitinous material, is delivered from the gastric filters into the digestive caeca of *Cyathura*, the cells of which are not protected by a cuticle and thus cannot be injured during the process of mixing the food with digestive enzymes by the peristalsis of the muscle fibres surrounding the caeca. Peristaltic movements of the caeca have also been observed in other isopods. Nicholls (1931) and Jones (1968) speculate that such movements might force enzymes from the caeca into the stomach and intestine where they could enhance liquifaction of the food. Within the epithelium of the caeca of *Cyathura* two cell types occur, which, however, represent only extreme forms of a whole morphological series with many intermediate forms. The smaller cells with stacks of the rough ER and numerous granules which are mostly apparantly zymogen granules, have a predominantly synthetizing function, whereas the large cells mainly store lipids and glycogen and contain larger numbers of lysosomes, indicating digestive function. Acid phosphatase, a marker enzyme for lysosomes, increases activity after food uptake. However, there is no exclusive character for one of these two cells: Lipid droplets, glycogen and phosphatase, brush border with ATPase activity and basal labyrinth are to be found in both types. It seems probable to us that the larger storage

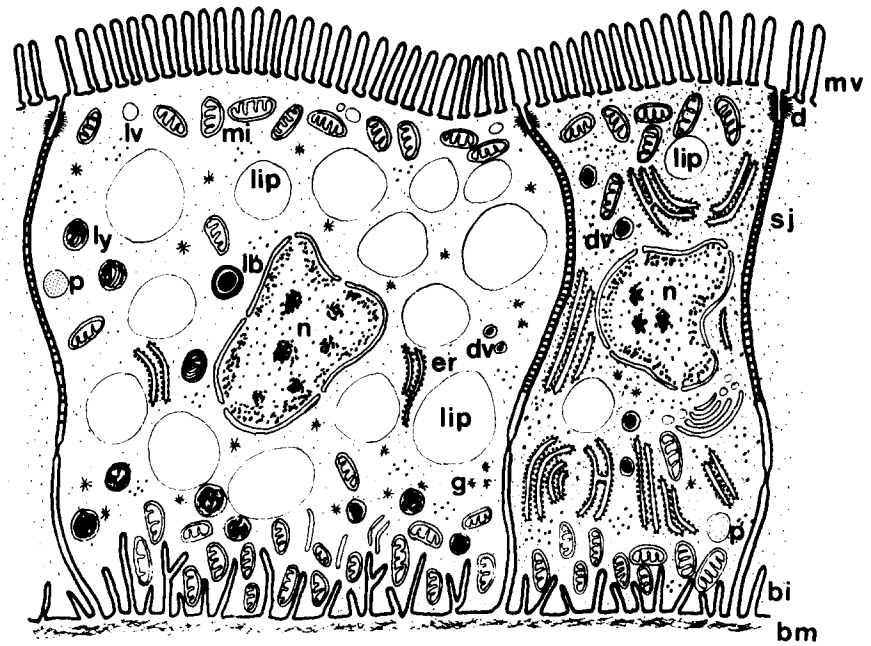

Fig. 9. Schematic drawing of storage cell (left) and secretory cell (right) of digestive glands. *bi* basal infoldings; *bm* basement membrane; *d* desmosome; *dv* dense vesicles; *er* rough endoplasmic reticulum; *g* glycogen; *lb* lamellated body (calcium?); *lip* lipid; *ly* lysosome; *mi* mitochondria; *mv* microvilli; *n* nucleus; *p* peroxisome; *sj* septate junction

and digestive cells arise from the secretory cells. A similar view had been put forward by Frenzel (1884). Also Jones et al (1969) assumed that the different cells observed in the caeca of *Eurydice* represent stages of one cell type, in starving animals all cells are of the same appearance. This is in contrast to observations in *Ligia* (Storch and Lehnert-Moritz 1980) in which under conditions of starvation the two cell types are particularly evident. These and other omnivorous and herbivorous isopods have a stronger functional specialization of the caecal cells. That different functional stages may occur in the *Cyathura* caeca is not only suggested by the studies of ultrastructure, but also by the enzyme histochemical results, e.g. the distribution of β-glucosaminidase, α-naphthylacetate, and indoxylacetate esterases is very variable, and the activity of ATPase varies to some degree, too. In *Eurydice* the ER-rich cells are of a similar irregular distribution within the epithelium as in *Cyathura*; in *Asellus, Idothea, Sphaeroma* and the Oniscoidea, however, they are arranged completely regularly, one small cell always being intercalated between two large cells. But also in these animals there is no absolute morphological and functional separation of the two cells (Clifford and Witkus 1971; Smith et al. 1975). Steeves (1963) analysed the secretory cycle in the digestive caeca of *Lirceus* (Asellidae) and came to the conclusion that in this animal also there is no definite separation of function between the cell types, and, finally, Donadey and Cesarini (1970) found evidence for secretory activity in all cells of the digestive gland of the Sphaeromatidae.

This interpretation – one cell type with various functional stages – is also supported by the morphology of the cellular nucleus, which is strikingly voluminous and possibly even polyploid (Clifford and Witkus 1971). In a few Malacostraca even two nuclei per cell occur.

The comparatively low number of ER-rich cells in the predators *Cyathura* and *Eurydice* if compared with the omnivorous isopods may be related to the easily digestible food of these predators.

In *Cyathura* and other isopods all cells of the digestive caeca have a well developed basal labyrinth, indicating active ion and water transport. So far there is no firm evidence as to whether such a labyrinth in addition indicates an excretory function, which has been ascribed to the caeca in the Oniscoidea by Semenova (1970). Donadey (1966) observed granules with concentric lamellae in the caeca of *Sphaeroma*, which according to this author might represent deposits of uric acid. Other investigators (e.g. Becker et al. 1974) have presented evidence that such granules, which occur in *Cyathura*, too, represent storage organelles for calcium. Their number varies according to the moulting stage.

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