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Light- and Electron Microscopical Studies on the Anatomy and Function of the Gills of Krill (Euphausiacea, Crustacea)

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Summary. The gills of the euphausiid crustaceans – *Euphausia superba* Dana, *Meganyctiphanes norvegica* (Sars) – contain two longitudinal channels separated by epithelial tissue. These channels, functioning as afferent and efferent vessels, are connected at regular intervals by transverse channels in the gill filaments. By contraction of the gill muscles the krill is able to draw back its gills against its body wall, thus reducing water-current resistance. By increasing the haemolymphic pressure, the gill filaments can perhaps be unfolded again. Besides the muscle cells and supplying nerves, fine-structural observations revealed several cell types in the euphausiid gills, considered from their morphological characteristics to be transport cells, respiratory cells, secretory cells serving a transepithelial ion transport, gas exchange and secretion. A further cell type (flat cells) presumably has a regulatory and/or filtering function on the haemolymphic current. The components are arranged in a complex order, reflecting the functional efficiency of the organs concerned. Similarities are pointed out with dendrobranchia of *Penaeus*.

Introduction

In the light of the economic interest that has been shown in krill in the past, studies of their biology (Marr 1962; Fischer 1976; Hempel and Hempel 1978) and ecophysiology (Lasker 1966; Kils 1978/79, 1979) have been advanced with a view to economical fishing and processing. Morphologically orientated studies are, on the other hand, less frequent (Herring and Locket 1978). The first-cited studies have shown that krill is capable of many remarkable achievements, the most outstanding being the amazing swimming ability of the antarctic krill, *Euphausia superba,* a phytoplancton filter feeder which avoids sinking into water depths void of light or food by means of its effective endurance swimming (Kils 1978/79, 1979). As has already been shown, the animals are dependent upon a high oxygen content in the water body. The present examination of the epipodite gills of the euphausiaceans aims to show how their structure can be interpreted as an adaptation to this high oxygen requirement.

Gills from Crustacea have long been the object of intensive research by electron microscopy. From the findings of Nagel (1935) it is known that in addition to respiratory and excretory functions, their gills also perform osmotic and ionic regulation. Consequently, the preferred experimental subjects have been species which are exposed or can be exposed to extreme conditions as regards their osmotic and ionic regulation: freshwater (Morse et al 1970; Bielawsky 1971; Fisher 1972), brackish water (Copeland and Fitzjarrel 1962), littoral (Storch and Welsch 1975; Foster and Howse 1978), terrestrial (Copeland 1968) and brine (Copeland 1967) shrimps or crabs. It has been concluded from fine-structure studies that in some cases the gills can no longer perform gas exchange, but are rather solely adapted to the other above-mentioned functions (Bielawsky 1971; Storch and Welsch 1975). Hypertonic regulators actively accept ions through the gill epithelium, sometimes over large concentration gradients: *Astacus* (Bielawsky 1964), *Carcinus* (Nagel 1935), *Callinectes* (Copeland and Fitzjarrell 1968). Hypotonic regulators actively excrete ions through the gill epithelium: *Artemia* (Copeland 1967). In *Gecarcinus* ions and water are absorbed by gill epithelia according to Copeland (1968) and Bliss and Mantel (1968). Recent studies on deep-sea animals are not known to us. However, it is to be expected that even these animals, in which osmoregulatory problems are less relevant, have mechanisms for ionic regulation (Robertson 1960; Spaargaren 1979). For this reason, the latter aspect is also a topic of this study.

Material and Methods

Euphausia superba (Dana) were collected during the Antarctic expedition of *RV Meteor* during austral summer 1980/81 in the Scotia sea. *Meganyctiphanes norvegica* (Sars) were caught in the Kattegat.

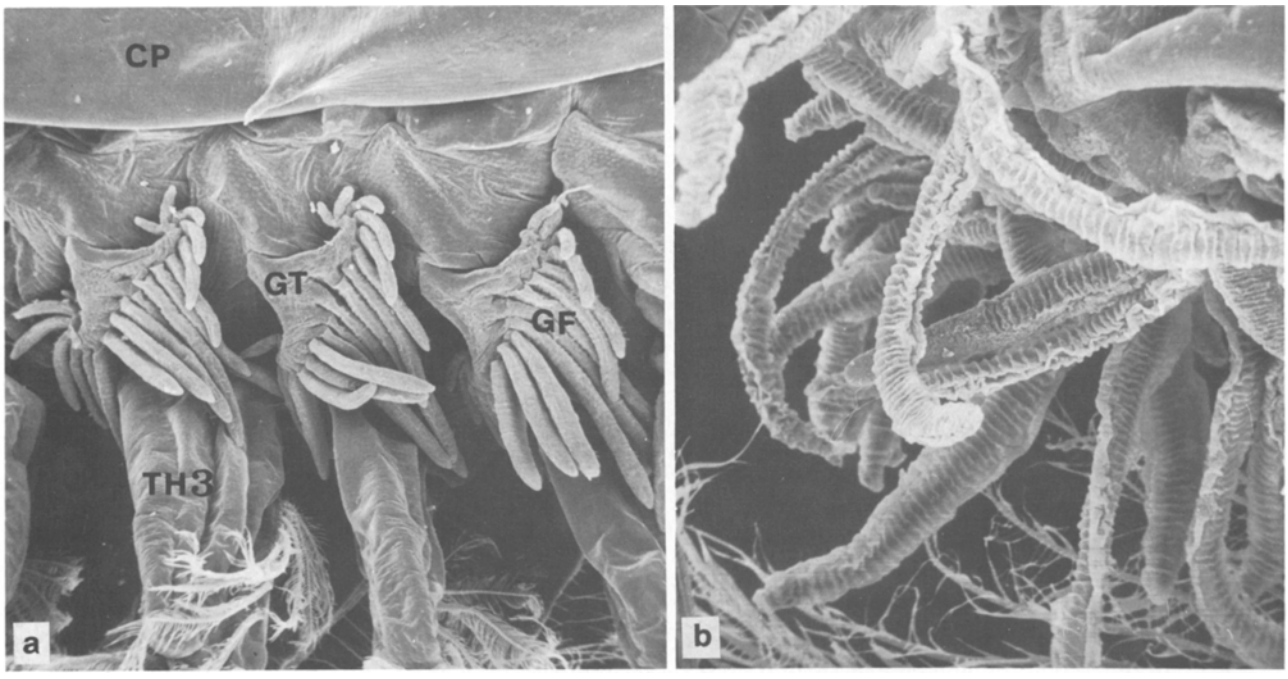

Fig. 1. **a** *Meganyctiphanes:* lateral view of gills of thoracopods 3 – 5 × 40. **b** *Euphausia:* gill filaments of thoracopod 6. Note the characteristic surface relief (obvious through artificial shrinking) ×100. *CP* = carapace; *GF* = gill filaments; *GT* = gill trunk; *TH* 3 = thoracopod 3

Directly after their capture the specimens were cut with a razorblade into several pieces, which were then immersed in 3.5% glutaraldehyde (phosphate-buffered, pH 7.4; 4 °C). After 2 h the tissues were repeatedly rinsed in phosphate buffer (pH 7.4), postfixed for 2 h in 2% OsO_4 and cleansed in the buffer solution for 10 min. The tissues were preserved in 70% ethanol until further processing in Germany, where the samples were dehydrated over various ethanol stages and embedded in araldite using propylenoxide as an intermediate medium. Ultramicrotome: Reichert OMU 2.

Sections stained according to the method of Richardson (1960) served as a general guideline.

The ultrathin sections were contrasted for 5 min with uranyl acetate (saturated solution in 70% methanol) and lead citrate. Electron Microscope: Zeiss EM 9 S2.

Specimens fixed in formalin were utilized for scanning-electron microscopy. These were dehydrated over ethanol stages and dessicated with Frigen 11 and CO_2 in a "critical-point" apparatus from Balzers. The gold-sputtered objects were then studied with a Cambridge S4/10 scanning-electron microscope.

Results

The eight pairs of thoracopods of the examined euphausiaceans have tubular gills (epipodites) on their coxopodites (Kaestner 1967) (Fig. 1). Their structures are increasingly complicated from the anterior to the posterior. Whereas the epipodite of the first thoracopod is a simple pointed appendage, the following epipodites are divided near their base into a dorsally (in *Euphausia* less prominent) and ventrally bent trunk ("Doppelschnecke", Zimmer 1956). Gill filaments branch off these gill trunks on their convex side. Especially in the area of the last two thoracopods there is a more intensive branching of the gill trunks, whereas the endopodites and exopodites here are more *(Euphausia)* or less *(Meganyctiphanes)* reduced (Zimmer 1956). The epipodite of the first thoracopod was not included in our studies. The distal parts of the gill trunks as well as the gill filaments of the thoracopods 2 – 8 showed no mentionable histological or cytological differences. Apart from a variation in size, no essential differences were noticed between the two studied species. Figure 1a shows gills from the central thorax region (Th 3 – 5). In this area, the gills are developed as a "Doppelschnecke". The gill filaments, appearing more or less rectangularly in the cross-section, lie relatively parallel to the thorax body surface when the epipodites are adjacent to the body. Two sides can be differentiated: one directed towards the body (inner side = morphologically, the posterior side) and the other away from the body (outer side = morphologically, the anterior side). Whereas the narrow edges of the gill filaments often show a groove-like longitudinal furrow, the adjacent surfaces of neighbouring gill filaments show a regular, fine, transverse ribbing (Figs. 1, 2a).

A gill trunk is traversed by two haemolymphic channels, which are separated by a thickening of the epithelium of the concave side of the bent gill trunks (Fig. 2a). The haemolymphic channels are situated on the outer (anterior) and inner (posterior) sides of the gill trunks. A strong longitudinal muscle runs parallel to the epithelial separative tissue on the inner side. The separative tissue itself shows a conspicuous metachromatic, reddish-purple colour upon dying with toluidine blue.

As the electron microscopic photo shows, this colour reaction might be due to vacuoles of large secretory cells situated between long, extended, supportive cells rich in microtubuli (Figs. 2a, 3a, b).

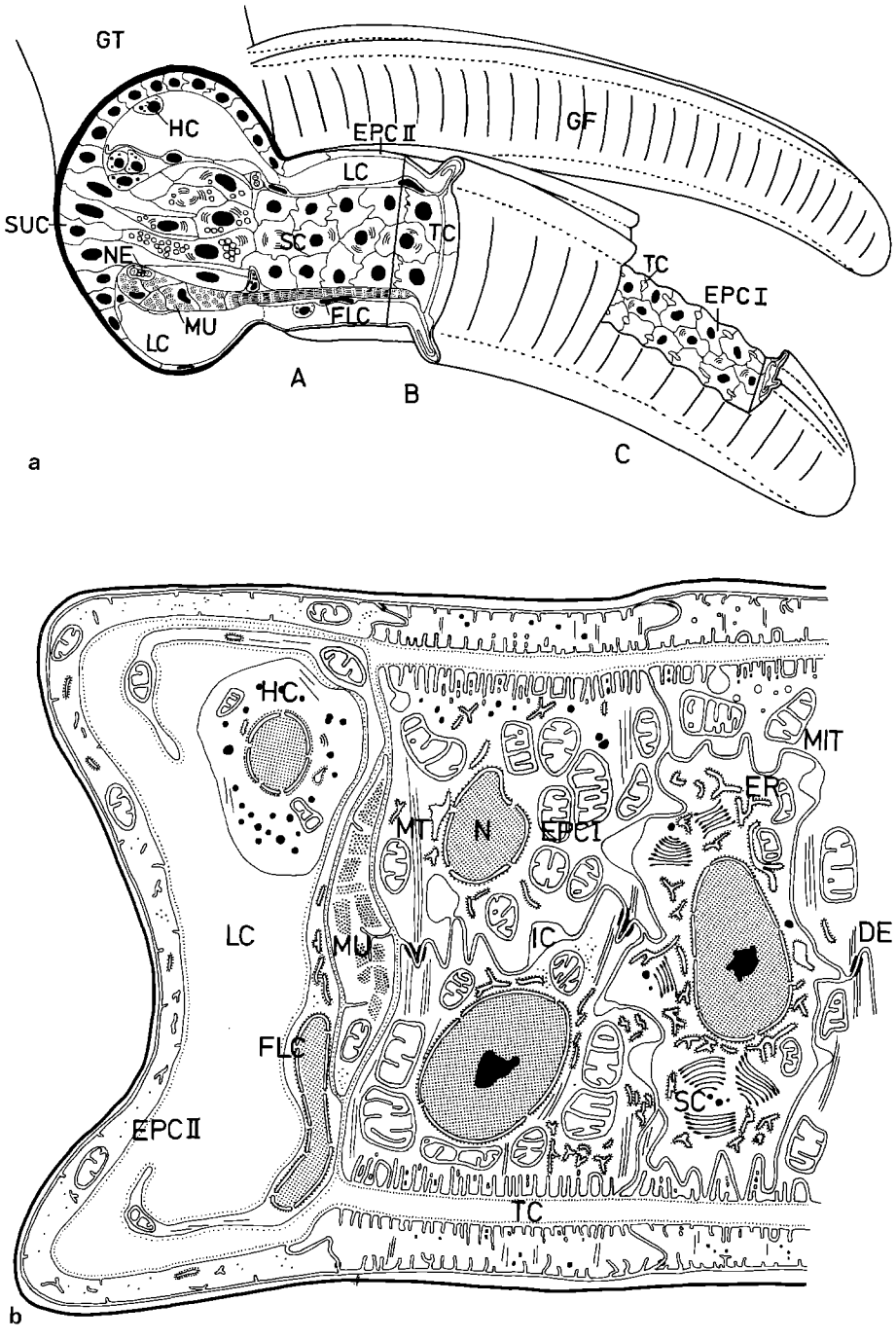

Fig. 2. a Diagram of gill trunk and two gill filaments. *A, B, C* different section planes (compare Figs. 4–6). **b** Diagram of a transverse section of a gill filament (section plane B, turned by 90° compared with **a.** *DE* = desmosome; *EPC I* = epithelial cell I; *EPC II* = ep. cell II; *ER* = endoplasmic reticulum; *FLC* = flat cell; *GF* = gill filament; *GT* = gill trunk; *HC* = haemocyte; *IC* = intercellular space; *LC* = longitudinal channel; *MIT* = mitochondria; *MT* = microtubules; *MU* = muscle cell; *N* = nucleus; *NE* = nerve; *SC* = secretory cell; *SUC* = supportive cell; *TC* = transverse channel

In addition to these cell types, haemocytes are regularly present, characterized by numerous granules, small rough ER vesicles of irregular form, single microtubules and relatively small cristamitochondria. Their cell nuclei are large and rounded-off. Particularly characteristic for these cells are numerous small, often dumb-bell-shaped structures. The blood cells often push deep into the narrow crevices between the basal laminae of the separative tissue and the epithelium of the opposite side. A transverse connection between both haemolymphic, longitudinal channels does not seem to be present in this region. Other cells are found here that lie on the separative tissue or also push themselves between muscle and separative tissue. They have an irregular and flattened form in contrast to the spherical blood cells in the free blood space. They also differ from the blood cells in that an extracellular electron-dense layer is present which corresponds to the density and strength of the basal lamina of the epithelial cells.

A nerve runs between the longitudinal muscle and the separative tissue, the axons of which are enveloped by glia cells. A further nerve was observed lying adjacent to the separative tissue in the outer channel.

Whereas the separative tissue has a complicated structure, the peripheral walls of the longitudinal channels are more simply formed. However, the epidermis

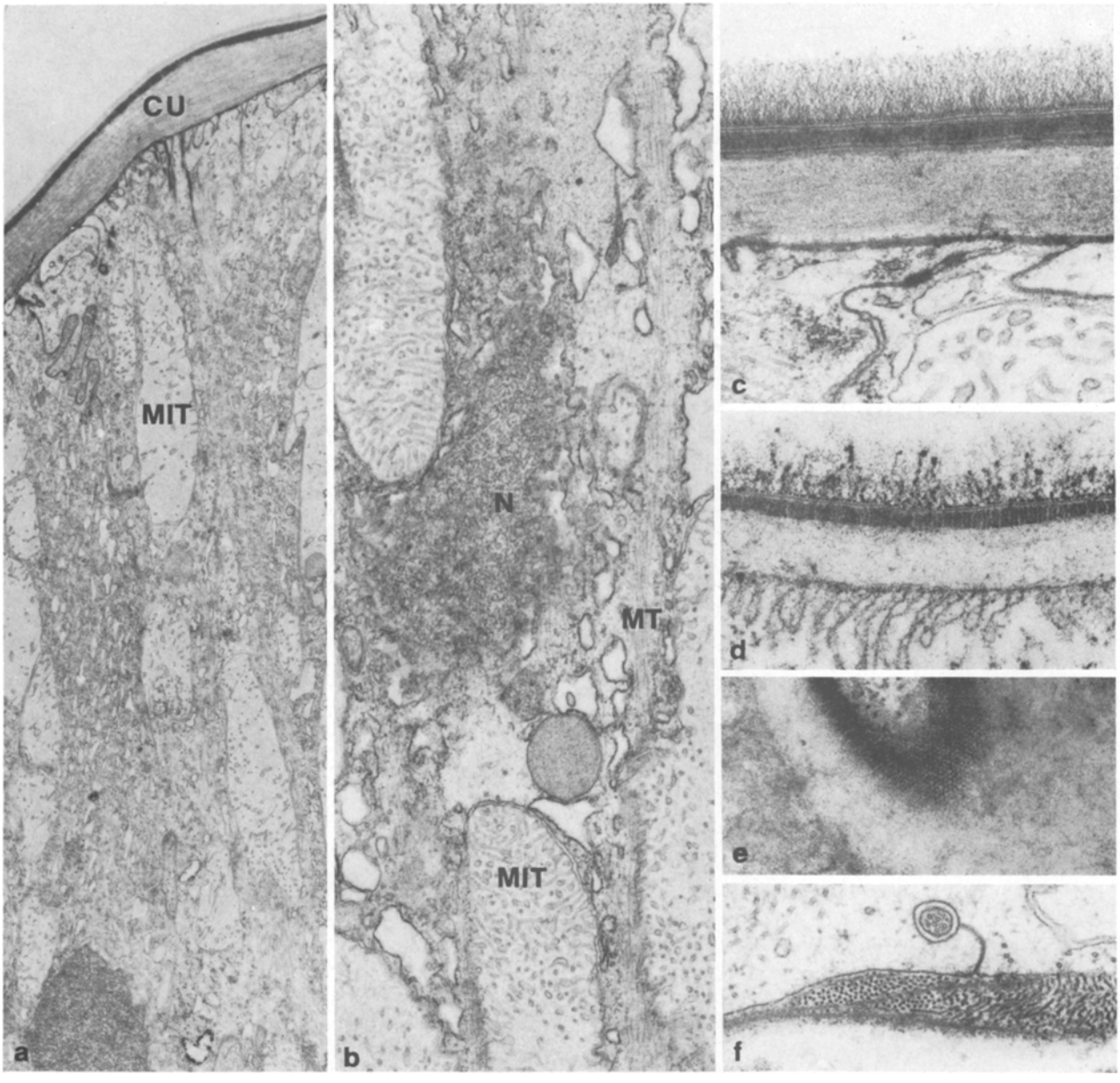

Fig. 3. **a** *Meganyctiphanes:* gill trunk; supportive cells of separative tissue. ×5,700. **b** *Euphausia:* mitochondria and microtubules in supportive cells of gill trunk. ×14,250. **c–e** Cuticle of gill filaments; **c** *Meganyctiphanes.* ×28,500. **d, e** (tangential) *Euphausia.* ×28,500. Note different layers of the epicuticle. **f** *Meganyctiphanes:* gill trunk; note microtubuli in extension of epithelial cells and fibrils below the cell base. ×28,500. *CU* = cuticle; *MIT* = mitochondria; *MT* = microtubules; *N* = nucleus

and cuticle differ in thickness. The outer channel has a cuboidal epithelium, the inner channel a flattened one. The cuticle on the outer side is clearly thicker than on the inside. The cuboidal cells have basal membrane infoldings, numerous microtubuli perpendicular to the surface and large crista mitochondria. The flattened cells of the inner channel show some particularities: basal invaginations, which frequently disintegrate into the cell centre in pearl-chained vésicle rows, some large mitochondria, and often enlarged, rough ER cisternae. The cell apex is folded in some places.

In rare cases (especially large, basal channels or basal parts of the gill trunks) conspicuous fibril systems were found between the basal laminae and the cell membrane (Fig. 3f).

The cuticle is basically uniform in all the examined areas of the gills and contains four layers visible on electron microscopy. Only the inner layer differs in thickness depending on its location. It is relatively electron permeable and will be designated here as procuticle. Few fibrils are found in its light ground substance and these contribute to the formation of lamellae in the gill trunks and the basal parts of the gill filaments. On the concave side of the gill, from where the separative tissue originates, extensions of the procuticle link together with the epidermis cells. In this area, one also finds denser areas in the

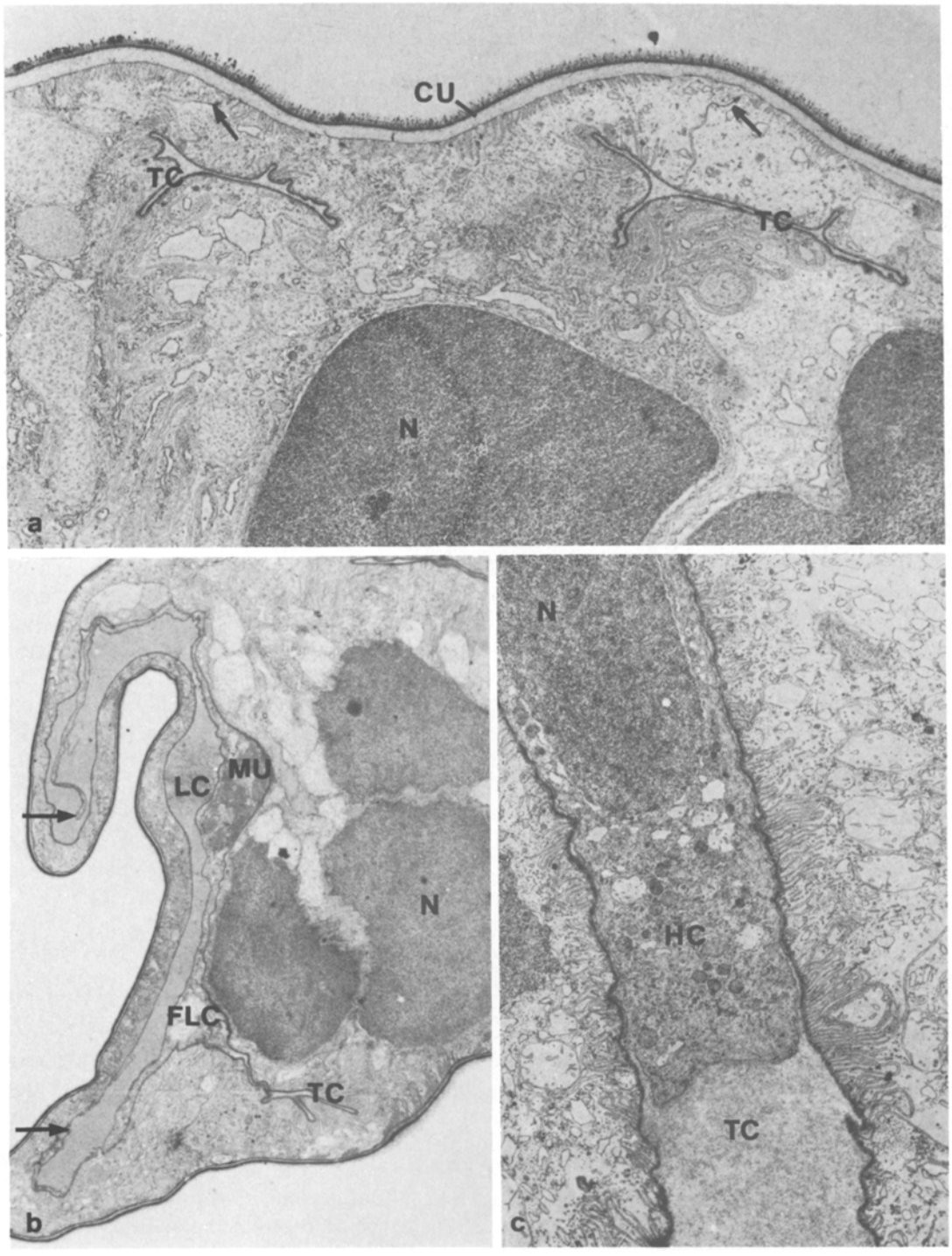

Fig. 4a–c. Gill filament. **a** *Euphausia* (section plane C): epithelial cell I bordering transverse channels. *Arrows:* cell junctions. ×5,700. **b** *Meganyctiphanes* (section plane B). Opening of transverse channel into longitudinal channel covered by flat cell. *Arrows* indicate extension of flat cell. ×3,220. **c** *Meganyctiphanes* (section plane A, near periphery): transverse channel containing haemocyte. Note plication of cell bases. ×5,700. *CU* = cuticle; *FLC* = flat cell; *HC* = haemocyte; *LC* = longitudinal channel; *MU* = muscle cell; *N* = nucleus; *TC* = transverse channel

procuticle, perpendicularly aligned to the surface. According to our interpretation, the peripheral layers are parts of the epicuticle. The procuticle is followed by an electron-dense layer showing a vertical striping. The tangential cross-section shows a comb-formed arrangement of light channels (?). Above this structure and separated by a bright slit lies a very thin electron-dense layer, which is also separated by a light cleft and followed by the outer layer. This layer is characterized by a diffuse system of very fine fibrils, which seems to be quite uniform in *Meganyctiphanes;* in the case of *Euphausia,* dark granules are embedded here (Fig. 3c–e).

The gill filaments show a structure that is similar to that of the gill trunks (Fig. 2), and are similarly traversed by longitudinal channels between which lies a separative tissue of epithelial nature. These channels run along the narrow inner and outer edges of the gill filaments and are responsible for the previously described longitudinal furrows. They originate from the corresponding longitudinal channels of the gill trunks and communicate with each other at the distal end of the gill filaments. The separative tissue of the gill filament is connected to that of the gill trunk. It shows a complicated structure and contains two types of cells: epithelial cells I and secretory cells (Fig. 2b). The former are clearly more abundant.

The shape of the epithelial cells I is determined by the formation of regular transverse channels connecting the longitudinal channels, which run along both the opposite sides and contribute to the surface transverse ribbing (Figs. 1b, 2). The transverse channels are situated between two cells coupled length-wise and run near to their apical region (Fig. 4a). From the cross-section it can be seen that several epithelial cells I take part in the bordering of a transverse channel. Their number is reduced at the distal ends of the gill filaments. The epithelial cells I of the opposite sides border each other without basal laminae developing. This is different to the conditions previously mentioned in the gill trunk. In this area, small desmosomes are present, especially in the interdigitating peripheral cell areas (Figs. 2b, 6b, e). Basal laminae are developed towards the haemolymphic area of both longitudinal and transverse channels. The cell apices show extensive plications, especially in regions between the transverse channels (Fig. 5b). Neighbouring epithelial cells I are attached to each other apically by zonulae adhaerentes and occasional septate junctions. The epithelial cells I are characterized by very large and numerous mitochondria of the crista-tubular type, as well as by many transverse microtubuli. Less characteristic is the extensive system of rough, often enlarged ER vesicles, various large vacuoles and the rounded nucleus (Figs. 2b, 4a, 5c, d). A particular feature is the cell base in the region of the transverse channels. It is strongly folded in this region, adjacent cells being interdigitated. One often observes the transition of membrane folds into vesicle rows. Intercellular spaces are quite often enlarged (Fig. 6b, d). Electron-optically, their content resembles that of the haemolymphic spaces. Blood cells were rarely observed in these intercellular areas (Fig. 6d).

The second type of cell, the secretory cell, is rarer (Figs. 2, 6c) and mainly characterized by the conspicuous golgi complexes consisting of numerous narrow cisterns, which form small droplets. These accumulate to make up only a few larger vacuoles; thus, these cells clearly differ from those of the separative tissue of the gill trunks. In contrast to the adjacent epithelial cells I, microtubuli are less abundant and the mitochondria are smaller. On the other hand, the rough ER is very conspicuous. The content of the cisterns appears somewhat more electron-dense than that of the epithelial cells I. The basal laminae lining the transverse channels are reached by extensions of the secretory cells (observed once). They apparently have no contact with the cuticle. They are, therefore, limited to the central region of the gill filaments and represent a cell row here within the separative tissue which is otherwise made up of epithelial cells I. Cell junctions between secretory cells and epithelial cells I were not observed.

The flatter epithelial cells II border the epithelial cells I (Figs. 2b, 6a). They comprise the peripheral walls of the longitudinal channels. Only one cell is presumably involved in the cross-section. These cells are more simply built than the epithelial cells I and correspond for the most part to those of the inner channels of the gill trunks.

The cuticle of the gill filaments differs in thickness, as in the case of the gill trunks. The greatest thickness is reached above the separative tissue, especially in the basal area of the gill filaments. A muscle cell which branches off the longitudinal muscle of the gill trunk (Figs. 2, 4b, 6b) runs along the inner side of the separative tissue. A large, flat cell lies on this muscle cell or the separative tissue of the outer side and has constant contact with the neighbouring cells only in this area. An electron-dense layer overlies the plasmalemma of the flat cell, which corresponds electron-optically to the basal laminae of the epithelial cells. The peripheral parts of the flat cells often loosen themselves from the walls of the haemolymphic channels and protrude more or less into the haemolymphic space (Fig. 4b). The length-wise extension of the flat cells stretches approximately over six transverse channels. They have a large, flat nucleus, which is seen only seldom due to the cell size. Otherwise, there are only few particularities to be seen: single cristamitochondria, rough ER cisterns and some microtubuli.

Discussion

The present study shows that the gills of Euphausiacea are very complex and comparable to those of the related Decapoda. The following sum up the main characteristics: regularly occurring transverse channels, the differentiation of various cell types, and muscle cells in the gill filaments. The gills of euphausiaceans are best comparable at this time to the dendrobranchia of *Penaeus* (Decapoda) (Foster and Howse 1978). Like the gill filaments of *Penaeus,* those of Euphausiacea are traversed by longitudinal channels which communicate distally and in which an afferent and an efferent vessel can be seen according to the observations of Zimmer (1912) and Mauchline (1958) on live animals. According to Mauchline's representation, it seems that the outer channel is the afferent vessel. The occurrence of transverse channels in Euphausiacea has its corresponding structures in the so-called subcuticular lacunae of *Penaeus,* which are found in the gill filaments (Foster and Howse 1978). Similarities are also to be recognized on the cellular level with the occurrence of different cell types (see below) in the gills of

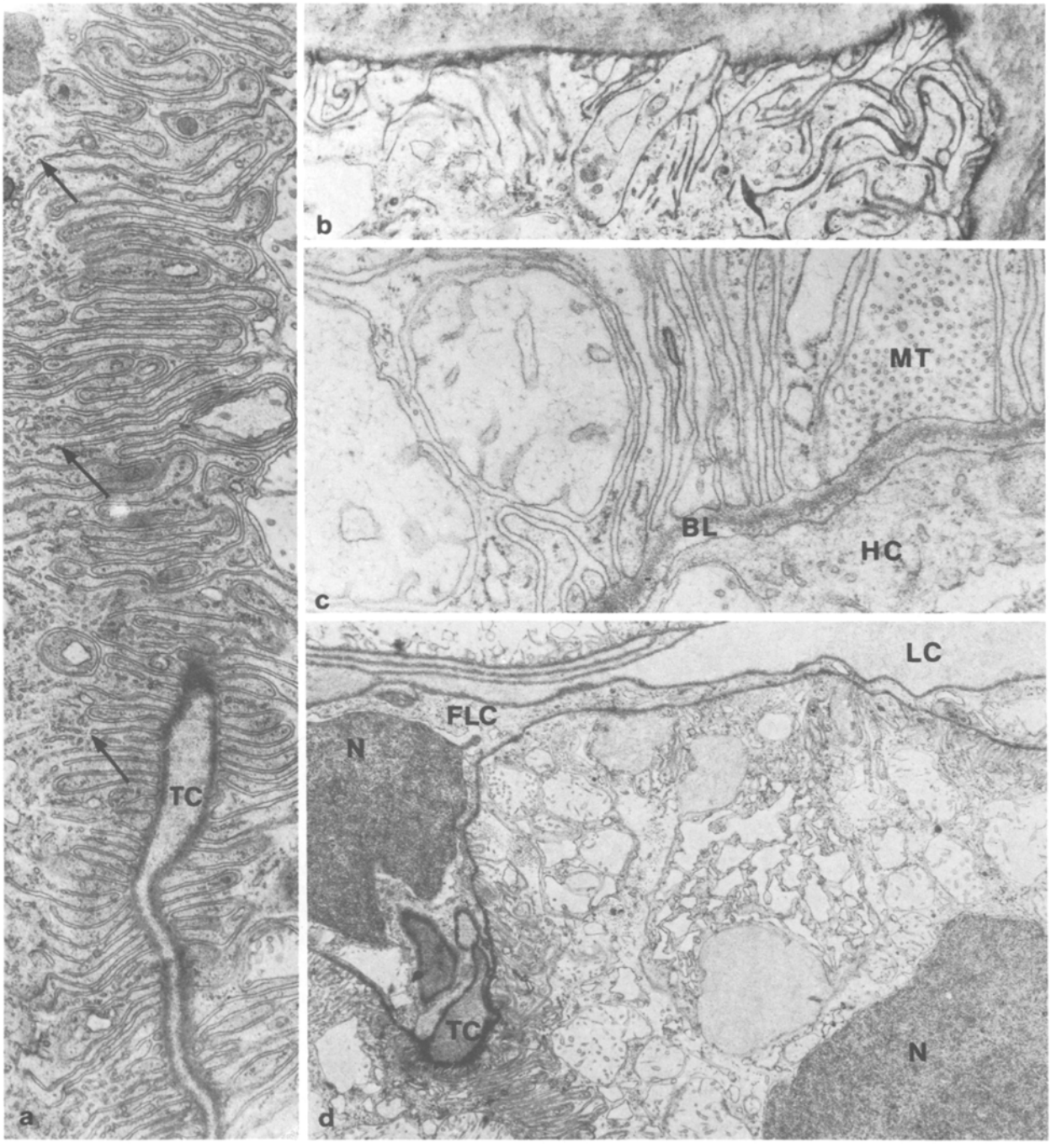

Fig. 5a – d. Gill filament of *Meganyctiphanes*. **a** Section plane A, near periphery. Note interdigitations of epithelial cells I below transverse channel, which can also partly be seen. Invaginations of plasmalemma often disintegrate into small vesicles (*arrows*). ×14,250**b** Epithelial cells I (oblique section): plication of cellapex below procuticle. ×14,250. **c** Epithelial cell I (section plane A) bordering transverse channel. Note numerous microtubuli and large mitochondria. ×28,500. **d** Longitudinal channel with opening of transverse channel covered by flat cell (section plane A). ×5,700. *BL* = basal lamina; *FLC* = flat cell; *HC* = haemocyte; *LC* = longitudinal channel; *MT* = microtubules; *N* = nucleus; *TC* = transverse channel

both eucarid groups. Thus, these structures may be homologous and reflect systematic relationships.

In *Astacus astacus* or other related species *(Astacus leptodactylus, Pacifastacus leniusculus)*, the epithelium of the trichobranchia comprises only one cell type (Bock 1925; Morse et al. 1970; Bielawsky 1971). This is characterized by a differentiation in a flattened part, directed towards the cuticle, with numerous mitochondria and membrane folds, as well as a bag-shaped part protruding into the haemolymphic space containing the cell nucleus. These nuclei-containing cell areas of neighbouring epithelial cells can lie adjacent to or be separated from one another, so that an irregular lacunary system originates between them and the flattened cell parts. The fine struc-

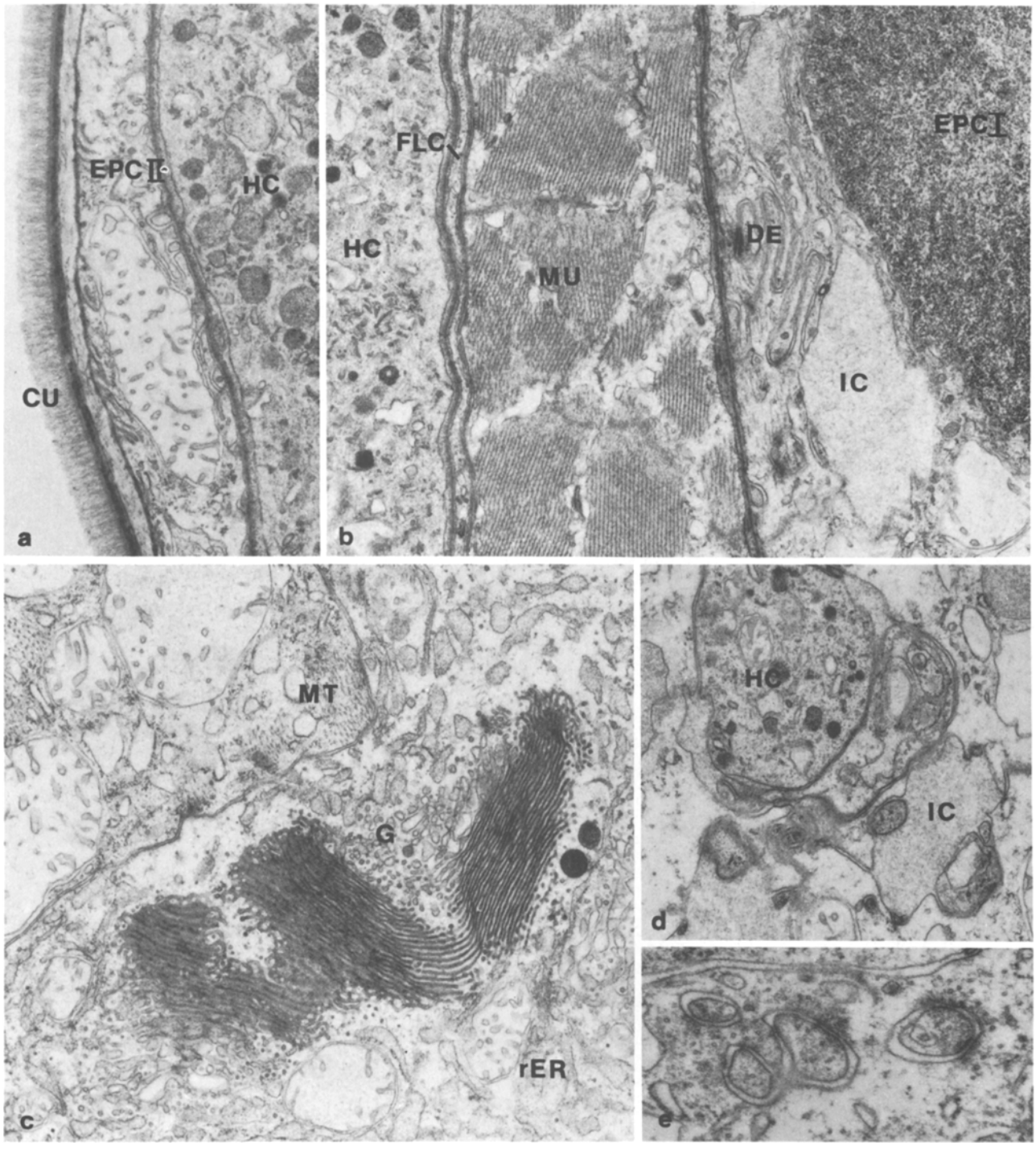

Fig. 6a–e. Gill filament of *Meganyctiphanes*. **a, b** Section plane B (compare Fig. 2b): components bordering longitudinal channel (with haemocyte). Note intercellular spaces between epithelial cells I. ×14,250. **c** Epithelial cell I and secretory cell with extended golgi apparatus. ×14,250. **d** Intercellular space between epithelial cells I containing haemocyte. ×14,250. **e** Desmosomes between epithelial cells I connecting interdigitations (section plane C, compare Figs. 2b, 6b). ×28,500. *CU* = cuticle; *DE* = desmosome; *EPC I* = epithelial cell I; *EPC II* = epithelial cell II; *FLC* = flat cell; *G* = golgi complex; *HC* = haemocyte; *IC* = intercellular space; *MT* = microtubules; *MU* = muscle cell; *rER* = rough endoplasmic reticulum

tural features of the trichobranchia of these freshwater crabs indicate an osmoregulatory function, according to Morse et al. (1970) and Bielawsky (1971).

The division of the longitudinal bloodstreams takes place in the flattened gill filaments of the Euphausiacea (rectangular cross-section) by the large epithelial cells I situated opposite. These correspond to the pillar cells, which are known from the gills of many Malacostraca (Bernecker 1909; Drach 1930; Balss 1944; Siewing 1957; Storch and Welsch 1975), and seem most probably to

take over the function of stabilizing the gill cross-section, as shown by the large number of microtubuli running perpendicular to the longitudinal axis of the gill. A particular feature is the lack of basal laminae between opposite epithelial cells I and the development of interdigitations bearing desmosomes (maculae adhaerentes).

With the development of a complicated haemolymphic channel system, a differentiation into two different epithelial cell types has been developed. The more or less cuboidal epithelial cells I bordering the transverse channels are characterized not only by abundant microtubuli, but also by numerous large mitochondria and extensive membrane folds; the epithelial cells II in the area of the longitudinal channels are characterized by their flattened form, relative lack of organelles and thin cuticle.

In agreement with numerous studies on gills and gill-like organs of representatives of various animal groups (Philpott and Copeland 1963; Newstead 1967; Bierther 1970; Storch and Welsch 1975; Haase 1975; Babula and Bielawsky 1976; Babula 1977; Komnick 1977; Foster and Howse 1978; Schipp et al. 1979; Kümmel 1981; Wägele 1982), the following can be assumed for the epipodite gills of Euphausiacea: the region of the epithelial cells I is responsible for ionic regulation occurring through active trans-cellular transport, whereas the area around the gill filaments, comprising epithelial cells II, is responsible for the gas exchange through diffusion.

The gill filaments thus exhibit a clear morphological arrangement, possibly reflecting the functional efficiency of this organ.

However, the function of the transverse channels is not yet completely clear. According to the observations of Mauchline (1958), they are included in the haemolymphic stream between the afferent and efferent vessels. For this reason, they could be important for the gas exchange as part of an extensive capillary system. Our observations, however, possibly contradict this, as we have found the transverse channels to be in the area of the epithelial cells I and recognized as transport cells. Their position near the cuticle makes it possible that they are involved in the respiration process too. The situation is, however, more difficult due to the unusual position of the large, flattened cells in front of the opening of the transverse channels into the longitudinal channels. From their arrangement, it may be concluded that the flattened cells function as valves, separating the transverse channels from the main stream of the longitudinal channels. This would explain the frequent collapsing of the transverse channels in our sections. As the main stream of the haemolymph is connected over the transverse channels with the epithelial cell I (presumably involved in the ionic regulation), the flat cells possibly have an indirect regulatory function when operating as valves. On the other hand, Foster and Howse (1978) have observed nephrocytes lining the efferent channel of *Penaeus aztecus* in a similar position, occupied by flat cells in Euphausiacea in both longitudinal channels. From ultrastructural evidence (podocyte-like cell structure) it has been concluded that the nephrocytes of *Penaeus* are involved in filtering the haemolymph. The flat cells could serve the same function, as the haemolymph stream has to pass them before entering the transverse channels. However, no structures characteristic of ultrafiltration have been observed.

By means of the transverse channels, products of the secretory cells are able to reach the haemolymphic main stream and drainage of the liquid of the intercellular spaces can take place. Further studies, especially on live krill, are necessary in order to elucidate these questions.

Secretory cells from the gills of decapod crabs have already been reported (Bock 1925; Balss 1944; Foster and Howse 1979; Doughtie and Rao 1982). In this case they are, at least partially, exocrine mucous glands possibly involved in cuticle formation. Until now, we have not been able to find any evidence of an exocrine extrusion of secretions. According to Green and Neff (1972) the comparable "intraepidermal connective tissue cells" of the fiddler crab might provide the cuticle-forming cells with their secretory products. A similar transfer could take place from the secretory cells towards the epidermal cells (epithelial cells I and II in the gill filaments) of euphausiaceans. Haemocytes were only occasionally seen in the transverse channels and in intercellular spaces of the separative tissue. The above-mentioned haemocytes must be considered as belonging to the granulocytes. According to Maynard (1960), Mix and Sparks (1980) granulocytes are capable of amoeboid-like migrations.

A further feature of the krill gills is the presence of muscle cells. This can perhaps be seen in connection with the unprotected position of the gills, easily enabling a supply of fresh water. The consequences are, however, a larger risk of injury and technical flow problems. Due to the arrangement of the longitudinal muscles, the gills can be drawn against the body, the gill filaments being bent. A folding-out of the gills presumably occurs as a result of a rise in haemolymphic pressure.

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