

## THE ULTRASTRUCTURE OF THE INTEGUMENT OF *ULOPHYSEMA OERESUNDENSE* BRATTSTRÖM, 1936 (CRUSTACEA, ASCOTHORACICA)

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### ABSTRACT

*Ulophysema oeresundense* Brattström, 1936, is a highly specialized crustacean that spends its adult life enclosed in different organs of its sea urchin host. The morphological adaptations of the integument of *U. oeresundense* for making close contact with the host cells were studied. The body is enclosed in a double-walled mantle covered on the outside by a single layer of choanocyte-like cells of host origin. The outer mantle epithelial cells underlie a thin electron-dense epicuticle, which has a dense network of highly differentiated villi-like structures.

The wall of the mantle contains branches of the intestine, but the gut epithelium in adult specimens shows pronounced degeneration and its role in nutrient uptake is doubtful. The mouth parts are atrophied.

The mantle cavity functions as a brood chamber, and its integument is provided with "anchoring" hooks that, together with the long and hairy projections of the body surface, probably prevent the eggs and larvae from being expelled.

A great number of sensory organs with a putative rheoreceptive function are observed among the outer epithelial cells of the mantle cavity.

The specialized epicuticle and the microvilli of the epithelial cells of the mantle are considered a route for molecular interchange.

The Ascothoracica, an order of the subclass Cirripedia, are parasitic crustaceans living as endo- or ectoparasites in different species of coelenterates and echinoderms. A peculiar feature of their morphology is the presence of a soft bivalve carapace or mantle enclosing the entire body. In females of some species the mantle is highly modified, developing a branching system of roots extending into all parts of the body cavity of the host, and containing the gut.

*Ulophysema oeresundense* Brattström, 1936, is an endoparasite of irregular sea urchins. It spends its adult life most often attached to the genital glands of the sea urchin, but is also found unattached in the perivisceral cavity.

The larval development, part of the life cycle, and gross morphology of *U. oeresundense* have been described by Brattström (1947, 1948a, b). The present paper deals with the ultrastructure of the integument of the parasite, with the purpose of understanding the process of nutrition. As far as we know, no work of the ultrastructural level has been published, except for a paper by Grygier (1982) concerning sperm ultrastructure, and a short note by Bresciani and Jespersen (1983).

### MATERIAL AND METHODS

Specimens of *U. oeresundense* were collected from the host *Echinocardium cordatum* (Pennant) dredged at Disken, Øresund, south of Helsingør, at a depth of 7-9 m. The sea urchins were taken in May and June 1982, brought to the laboratory alive, and dissected. The infestation was rather high (20-25%). Small specimens (2-3 mm) were found free in the coelomic cavity of the host, while older specimens (up to 20 mm in length and with folded mantles) were attached to the degenerated gonads.

Small pieces of the mantle and body of the parasite were fixed for electron microscopy in trialddehyde (Lake, 1973) or in 3% glutaraldehyde in filtered sea water, blockstained for 2 h at room temperature in 0.5% aqueous uranyl acetate, and postfixed in 1% osmium for 1 h at 4°C.

Araldite or an Epon-Araldite mixture was used as embedding medium for all the material.

The sections were cut with a diamond knife on a Reichert Om3U ultramicrotome, stained with uranyl acetate and lead citrate, and examined with a Siemens Elmiskop I. For scanning electron

microscopy, individuals of different sizes were fixed in 3% glutaraldehyde in 0.1 M cacodylate buffer for 2 h at room temperature and postfixed in 2% osmium for another 2 h. Following dehydration, the specimens were critical-point dried and coated with 200 nm of gold for observation in a Jeol JSM-T 20 and in a Cambridge Stereoscan.

## RESULTS

In all stages of *U. oeresundense*, the mantle is covered by a single layer of cells belonging to the host (Figs. 2, 10, 11). This layer consists of choanocytes which make it easily recognizable (Figs. 4, 11) in the electron microscope.

*The Cuticle of the Outer Mantle Wall.*—The cuticle is 0.2–0.6  $\mu\text{m}$  thick and consists of an outer epicuticle and an inner procuticle. The epicuticle is very thin, about 20 nm, and appears at many section angles to be provided with small knoblike processes. These actually represent the basal part of villi-like protuberances (Fig. 12). They are membrane-bounded and have a diameter of about 25 nm. The term microvilli will be used in the following description according to the term used by other authors (Bouligand, 1966a, b; Gharagozlou-van Ginneken, 1976; Gharagozlou-van Ginneken and Bouligand, 1975; Hubert, 1978; Hubert *et al.*, 1979; Bocquet-Vedrine *et al.*, 1977) for similar studies in copepods and Rhizocephala.

The epicuticular microvilli, long and slender, fill the narrow space between the mantle and the covering host endothelium. In this space, among the microvilli, a network of collagen is seen (Figs. 10, 11).

The procuticle is 0.2–0.6  $\mu\text{m}$  thick in different parts of the mantle. It is a network of chitin and protein filaments which gives rise to the parabolic patterns seen in the electron microscope (Fig. 12).

*The Cuticle of the Inner Mantle Wall.*—The basic constitution and dimensions of the cuticle are similar to those of the outer mantle wall. The surface, though, has quite a different appearance thanks to numerous long “hair-projections” (Figs. 9, 13). The “hairs” are about 400  $\mu\text{m}$  long and 0.3  $\mu\text{m}$  in diameter and contain procuticle surrounded by epicuticle. They seem to be clustered in small tufts and some of them are provided with “anchoring hooks” (Fig. 6).

Microorganisms, with the morphology of bacteria, are occasionally found on the surface of the inner mantle wall.

*The Cuticle of the Body Wall.*—The thickness of the cuticle of the body proper of the adult *U. oeresundense* varies in different parts of the body. An 8–10  $\mu\text{m}$  thick cuticle is seen on the four dorsal horns. The epicuticle was only 20 nm thick. Cuticular projections of variable length and shape are seen. The cuticle of the four dorsal horns is extended into “hairs” of about 100  $\mu\text{m}$  in length (Fig. 5), while other parts of the body surface are smooth (Fig. 14) or provided with short, broader extensions arranged in small rows.

*The Epithelial Cells of the Mantle.*—The epithelial cells of the outer mantle wall underlying the cuticle appear to be columnar at the light-microscopic level (Figs. 7, 8), but when observed in the electron microscope, the lateral and basal borders are highly infolded. The apical surface of the cells is provided with many microvilli (Figs. 10, 11, 12, 16), projecting from an irregular relief of cytoplasmic depressions and elevations. They are tightly packed toward the cuticle, but in some areas they may line a subcuticular space of variable width. The tips of the microvilli appear to be filled with numerous particles.

One characteristic of the epithelial cells (Figs. 10, 16) is their large nucleus and the presence of numerous membrane-bounded vacuoles filled with either ho-

mogenous contents, cell debris, or profiles of concentrically arranged layers of membranous material. The Golgi bodies are small and numerous, and surrounded by a profusion of vacuoles and vesicles. The elongate mitochondria are aggregated at the apical portion of the cell close to the cuticle.

Tonofilaments attached to the cuticle, microtubules, lipid inclusions, and numerous septate junctions are frequently seen. The cytoplasmic matrix contains ribosomes, microtubules, discrete profiles of rough and smooth endoplasmic reticulum, and patches of elongate parallel filaments in the long axis of the cells.

The mantle contains striated muscles running from the outer to the inner wall and diverticula of the ovary and the gut (Figs. 1, 3, 7). The gut diverticula (Fig. 17) are lined by a single-layered cubical epithelium. In young stages of *U. oeresundense* (2–3 mm), the epithelium showed a regular brush border about 10  $\mu\text{m}$  tall, while the brush border disappeared in older stages (18–20 mm), and only few microvilli remained on the laminal surface. The cells were filled with dense osmiophilic material and showed advanced degeneration.

Glandular cells and sensory cells are incorporated in the epithelium (Fig. 8). The sensory cells (Fig. 15) are observed in different parts of the mantle. They are seen as sensilla with peripheral guard cells.

From light-microscopical sections through the mantle wall it can be seen that an apical protrusion from the sensory organ penetrates the coelomic epithelium of the sea urchin and bulges out into the coelom (Fig. 8).

#### DISCUSSION

The integument of the outer mantle wall of *U. oeresundense*, in close contact with the host body cavity, is obviously adapted to function as a route for molecular exchange, something which has been observed in other parasitic crustaceans. The

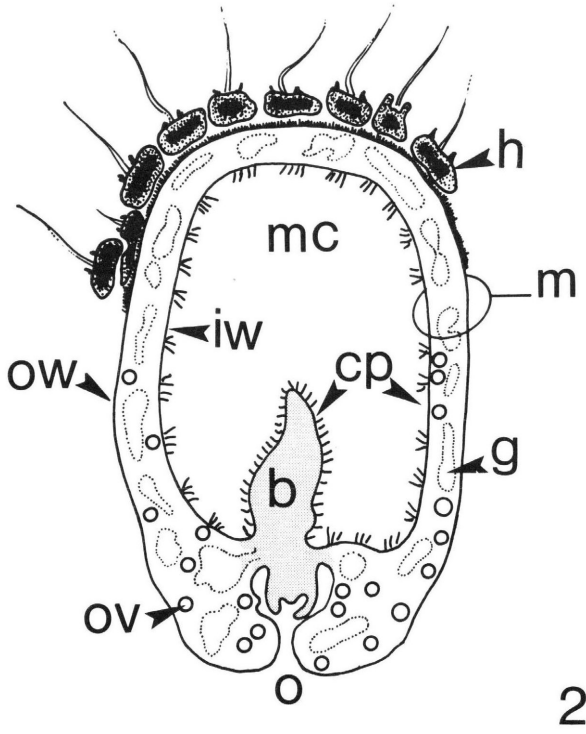
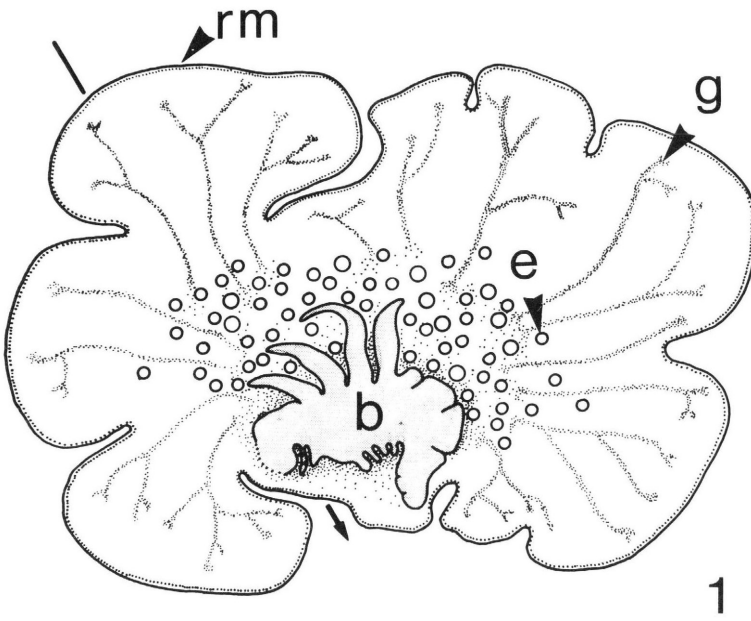
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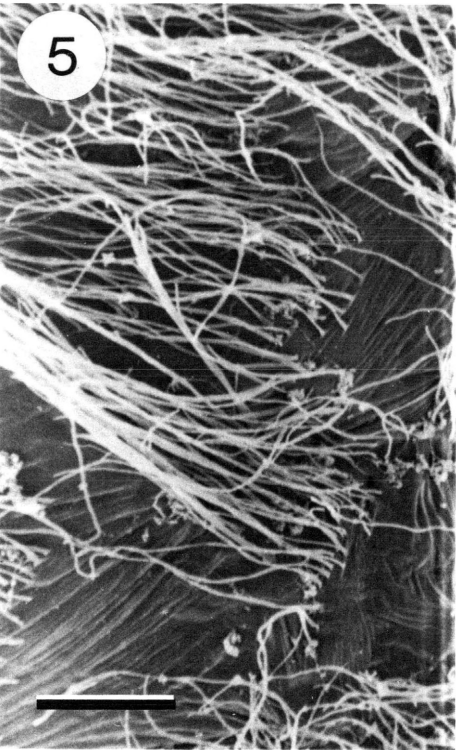
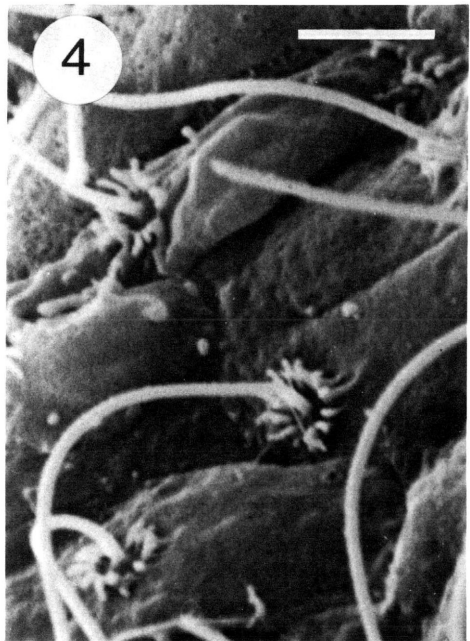
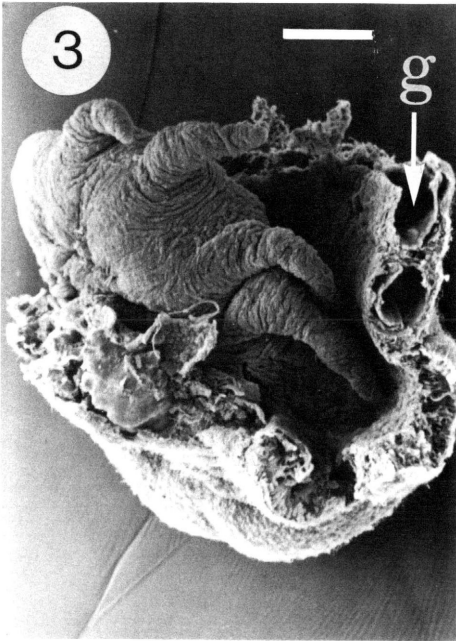
Figs. 1, 2. (1) Diagram of *Ulophysema oeresundense*, adult specimen, 20 mm in length. The body (b) is surrounded by the mantle. The left mantle wall is removed, the right mantle wall (rm) is exposed and contains ovary diverticula with eggs (e) and branches of the gut (g). (2) Diagram showing a cross section of *Ulophysema oeresundense*. (The arrow in Fig. 1 shows the plane of the section). The mantle (m) is enclosing the body (b) in a mantle cavity (mc). The mantle is covered by a membrane, belonging to the host, composed of a layer of choanocytes (h). The outer mantle wall (ow) has a cuticle with microvilli. In the mantle tissue ovary diverticula (ov) and branches of the gut (g) are seen. The inner mantle wall (iw) as well as the body surface have a cuticle with projections (cp) into the mantle cavity. Mantle opening (o).

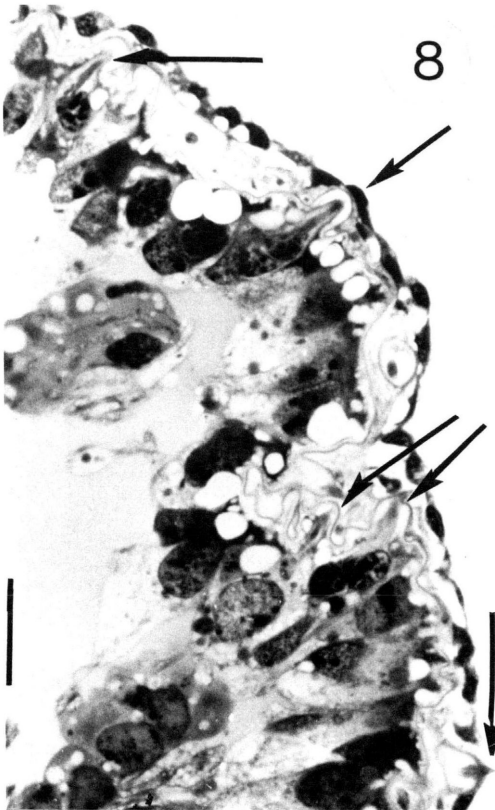
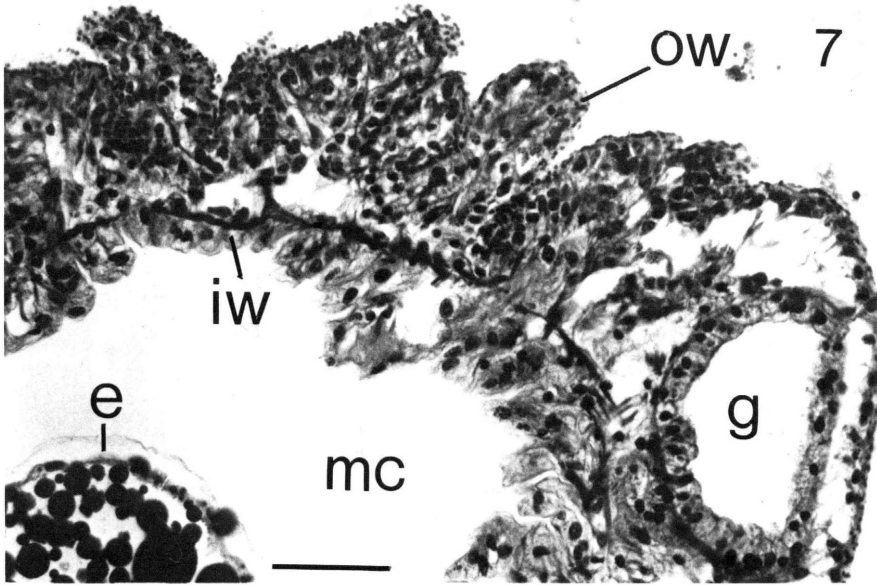
Figs. 3–6. (3) SEM-micrograph showing the dorsal part of the body of a small *Ulophysema oeresundense* (3 mm); most of the mantle is cut off. The four unpaired “horns” of the body are seen as fingerlike extensions. Branches of the gut are seen in the mantle (g). Scale bar = 100  $\mu\text{m}$ . (4) SEM-micrograph of the host epithelium with choanocytes covering the outer side of the mantle of *Ulophysema oeresundense*. Scale bar = 2  $\mu\text{m}$ . (5) SEM-micrograph showing detail of the body surface (dorsal part). Scale bar = 20  $\mu\text{m}$ . (6) SEM-micrograph of the inner mantle wall of an adult (20 mm) *U. oeresundense*. The hairlike cuticular projections, some of them provided with anchoring hooks, are seen. Scale bar = 3  $\mu\text{m}$ .

Figs. 7–9. (7) LM-micrograph of the mantle of *Ulophysema oeresundense*. The mantle cavity (mc) contains embryos (e). The inner wall (iw), the outer wall (ow), and a branch of the gut (g), are seen. Scale bar = 100  $\mu\text{m}$ . (8) LM-micrograph of the mantle, showing several sensory organs (arrows). Scale bar = 15  $\mu\text{m}$ . (9) LM-micrograph of the inner wall (iw) of the mantle of *U. oeresundense*, with cuticular projections (cp). Scale bar = 2  $\mu\text{m}$ .









morphological evidence supporting this assertion is to be found not only in the present work but also in the study of the integument of the Rhizocephala and the Copepoda.

The Rhizocephala are parasitic on decapod crustaceans. They have no alimentary canal, so the absorption of nutrients has been taken over by a well-developed root system that penetrates into the host haemocoel. Bocquet-Vedrine *et al.* (1977) and Hubert (1978) described the roots of *Sacculina carcini* Thompson. Hubert *et al.* (1979) investigated *Loxothylacus panopei* (Gissler). Bresciani and Lützen (1980) extended these studies to *Lernaediscus porcellanae* F. Müller, *Peltogaster paguri* Rathke, and *Clistosaccus paguri* Lilljeborg. Finally Payen *et al.* (1981) investigated *S. carcini* with the help of the scanning electron microscope. In all these specimens, the roots are lined by a thin electron-dense epicuticle composed of an inner homogenous layer and an outer system of microvilli. The procuticle with its characteristic structures is no longer detectable.

Comparing the shape and structure of the microvilli of the epicuticle in the two orders, the microvilli of *S. carcini* occupy a particular position in that they, according to Bocquet-Vedrine *et al.* (1977), are "true microvilli, belonging to the epithelial cells underlying the cuticle." This is not the case in other Rhizocephala or in *U. oeresundense*.

Among the Copepoda, the other crustacean group that can be drawn into this discussion, some of their parasitic representatives show morphological adaptations comparable with those of *U. oeresundense*, for example, reduction or absence of a digestive system, rudimentary or obsolete mouth parts, and modified cuticular surface. The first example is to be found within the family Lamippidae, associated with Anthozoa. In this group, studied by Bouligand (1966a, b), only a thin epicuticle is present, associated with microvilli similar to those described in *U. oeresundense*. In some of these copepods a poorly developed intestine is present.

The integument of other endoparasitic copepods, such as *Gonophysema gullmarensis* Bresciani and Lützen in ascidians, *Aphanodomus terebellae* (Levinsen) in the polychaete *Thelepus cincinnatus* (Fabricius), and *Antheacheres duebeni* M. Sars in actinians, have been investigated by Bresciani and Lützen (1972, 1974).

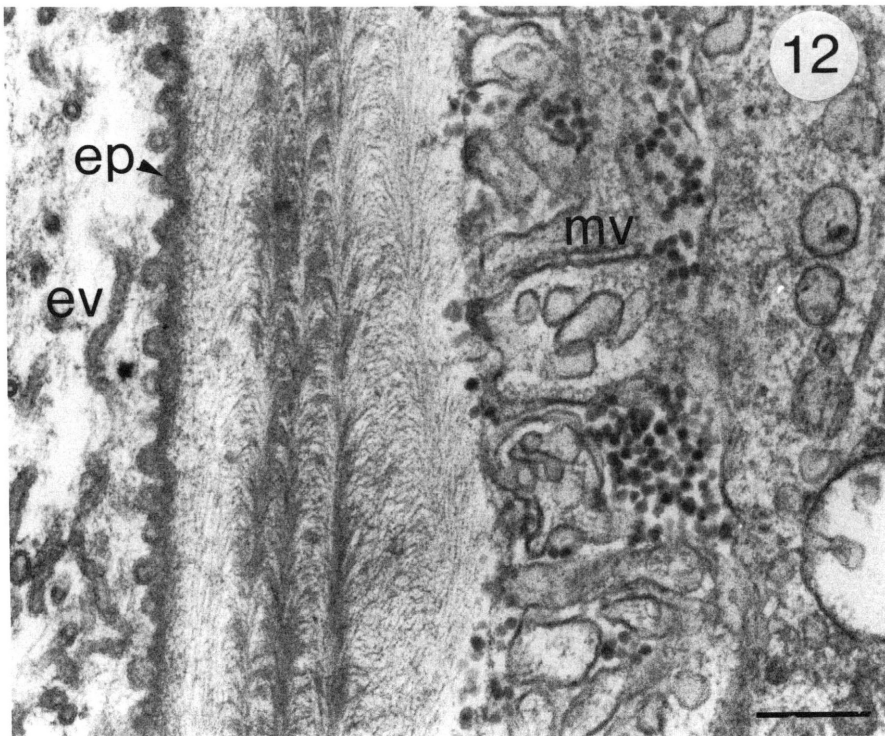
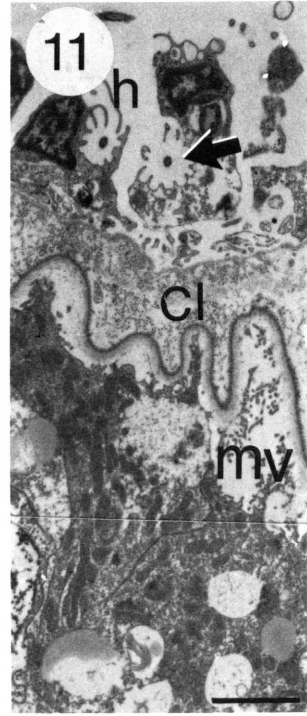
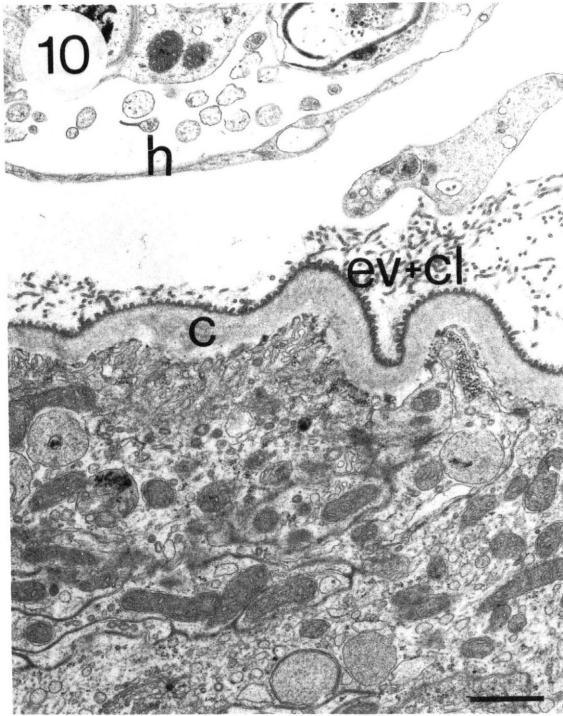
*Gonophysema gullmarensis* has no intestine and its fibrillar cuticle is provided

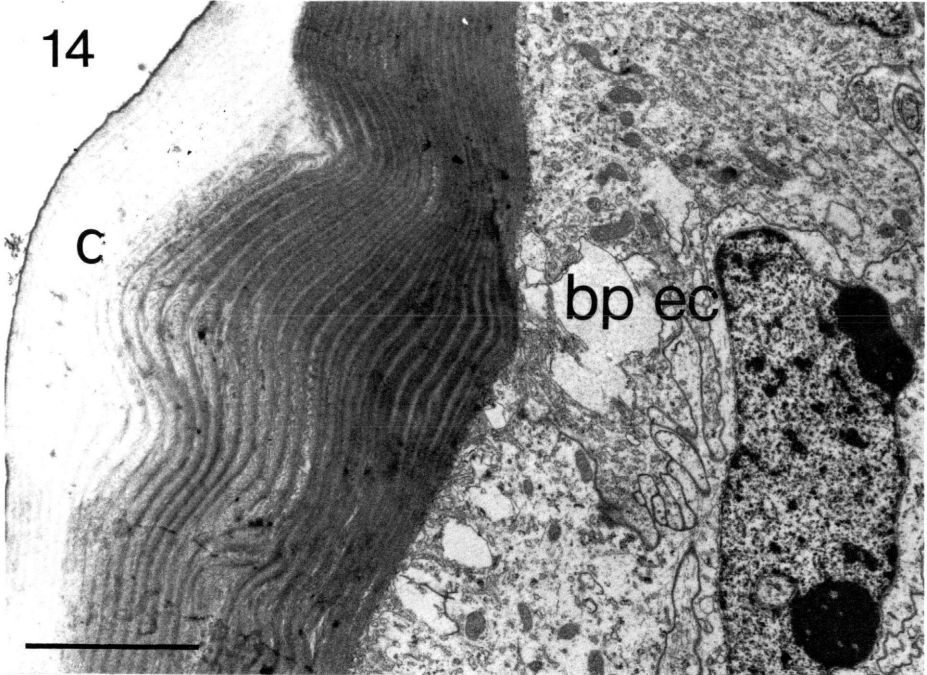
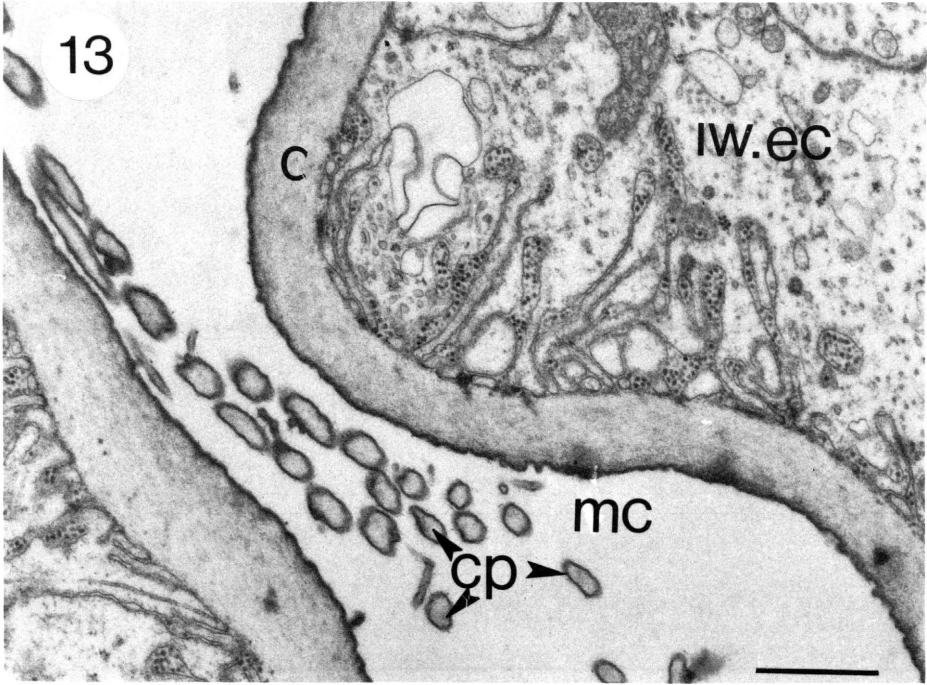
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Figs. 10–12. (10) TEM-micrograph of the outer wall of the mantle of *Ulophysema oeresundense*. The cuticle (c) and the layer of collagen and microvilli (ev + cl) are seen below the choanocytes (h), which belong to the sea urchin. The mantle epithelial cells of *U. oeresundense* are provided with microvilli and numerous mitochondria and vesicles in their apical part. Scale bar = 1  $\mu\text{m}$ . (11) TEM-micrograph of the cuticle surrounded by collagen (cl). The apical part of an epithelial cell with its microvilli (mv), and some choanocytes (h) are seen. Note the flagellum (→). Scale bar = 0.5  $\mu\text{m}$ . (12) TEM-micrograph of the outer mantle wall cuticle with microvilli (ev). Note the thin epicuticle (ep) and the microvilli (mv) of the epithelial cells. Scale bar = 200 nm.

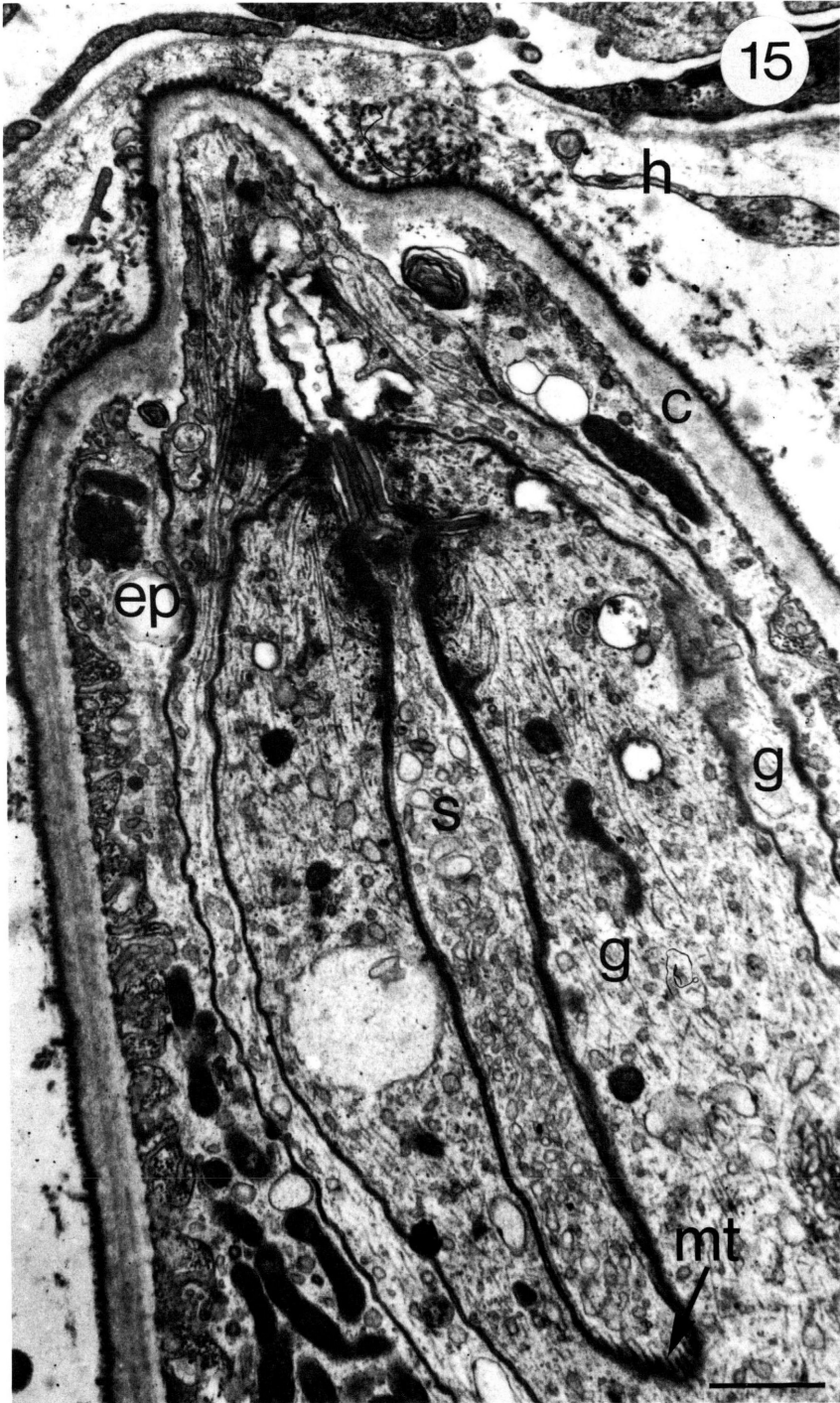
Figs. 13, 14. (13) TEM-micrograph of the inner wall of the mantle of *Ulophysema oeresundense*. The cuticle (c), the cuticular projections (cp) in the mantle cavity (mc) and the apical part of the epithelial cells of the inner wall (iw.ec) are seen. Scale bar = 0.5  $\mu\text{m}$ . (14) TEM-micrograph of the body of *Ulophysema oeresundense*. The thick cuticle (c) and part of an epithelial cell (bp ec) are seen. Scale bar = 5  $\mu\text{m}$ .

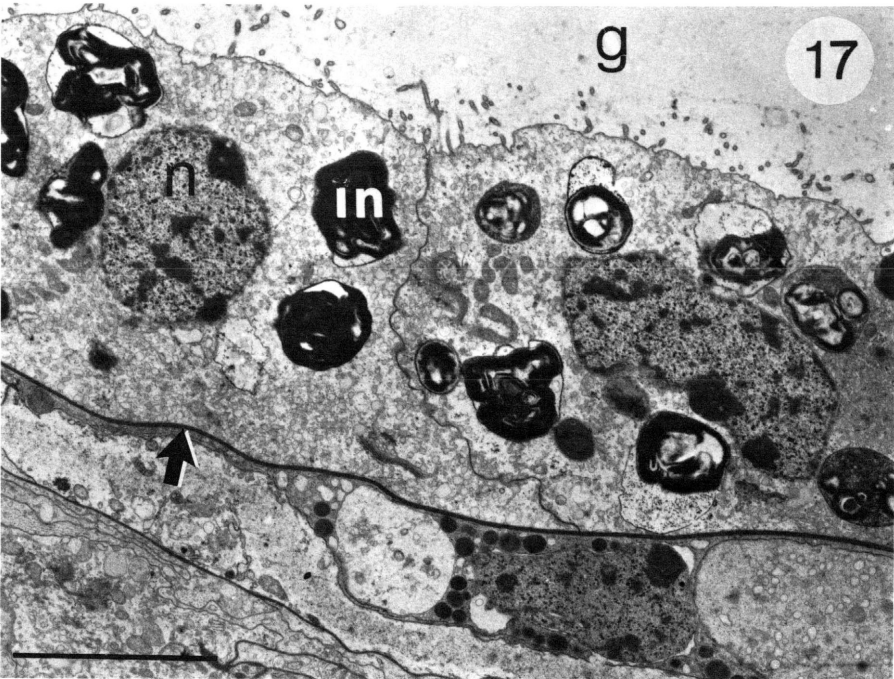
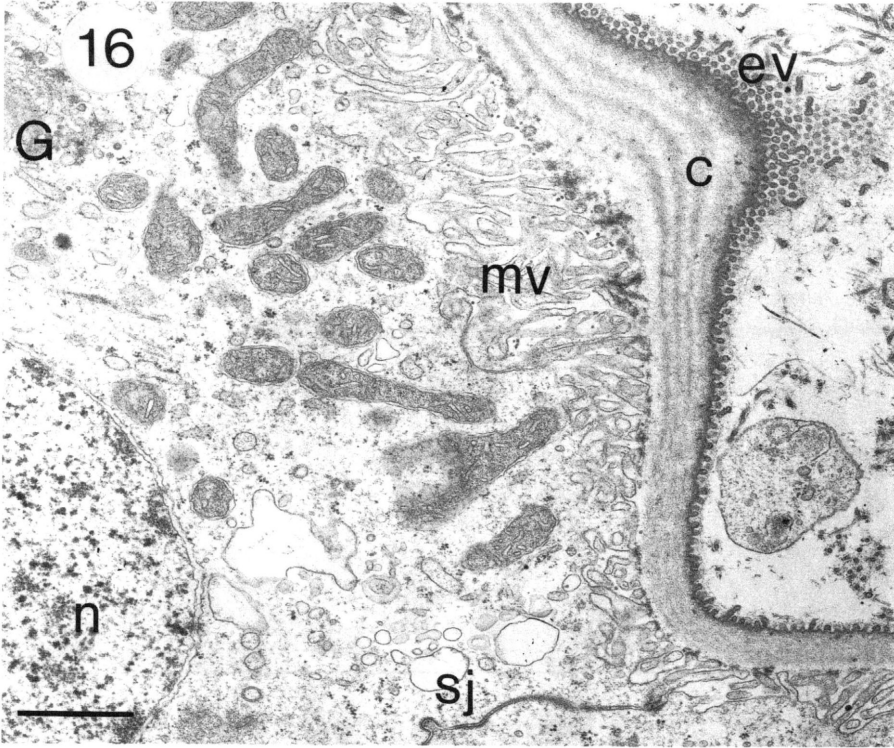
Fig. 15. TEM-micrograph of the apical part of a sensory organ from the outer mantle wall of *Ulophysema oeresundense*. The sensory cell (s) with microtubules (mt), guard cells (g), and epithelial cells with cuticle (ep, c), and cells belonging to the covering sea urchin (h) are seen. Scale bar = 1  $\mu\text{m}$ .











with very long (5–6  $\mu\text{m}$ ) and slender microvilli. In *A. terebellae* the female located in the body cavity of the host is provided with a kind of intestine called the axocoel, but the integument, in close contact with the host coelom, is provided with numerous and densely packed microvilli. *Anthecheres duebeni* shows a cuticle very loose in structure and also provided with long microvilli (3–4  $\mu\text{m}$ ). The mouth parts are rudimentary, probably nonfunctional, and the intestine lacks an anus and exhibits a degenerate epithelium.

Other copepods with a cuticle comparable to that of *U. oeresundense* are *Porcellidium viride* (Philippi) and *P. fimbriatum* Claus investigated by Gharagozlouvan Ginneken and Bouligand (1975) and *Alteutha depressa* Baird studied by Gharagozlouvan Ginneken (1976). *Porcellidium viride*, *P. fimbriatum*, and *A. depressa* live on green algae of the genus *Ulva* and have a well-developed and functional intestine, but, although they have a typical cuticle, this is covered with a system of highly specialized microvilli. The presence of microvilli in the cuticle of free-living copepods is surprising, and the authors are of the opinion that the system of microvilli is apparently related to the presence of a bacterial microflora covering the dorsal cuticle and some ventral part of the animals.

The bacterial layer shows signs of cytolysis and Gharagozlouvan Ginneken and Bouligand (1975) advanced the idea that this "could result from the action of the microvilli; perhaps the microfilaments which coat the microflora are involved in this cytolysis."

Filshie and Smith (1980) reported that the cuticle covering the gills of the crayfish *Panulirus argus* (Latreille) has a system of elaborated microvilli. Similar structures have also been reported from non-crustaceans, namely, in a parasitic nematode related to the genus *Bradynema* Strassen, in which Riding (1970) described a cuticle covered by long microvilli. In *Bradynema* sp., the mouth and anus often atrophy and the intestine is in this case not in connection with the oesophagus. It is supposed that the food must be absorbed through the body wall.

It may therefore be concluded that the presence of microvilli in the integument of the species mentioned above shows that such structures, together with degeneration of or absence of a digestive system, can be correlated. Even in the case of species with a functional intestine, the presence of microvilli is associated with a presumptive absorptive function.

The following morphological evidence supports the concept that the outer mantle wall of *U. oeresundense* is the site of nutritional and respiratory exchanges: (a) The extremely thin cuticle, 0.2–0.6  $\mu\text{m}$ , is comparable to similar absorptive structures; (b) The presence of microvilli of the epicuticle affords a considerable increase of the mantle surface; (c) The numerous microvilli of the epithelial cells enlarging the area of the plasma membrane; (d) Mitochondria are abundant in the apical part of the epithelial cells; and (e) The atrophied mouth parts, the lack of an anus (Brattström, 1948b), and the degenerate epithelia of the intestine in adult specimens, together with histochemical and cytochemical studies of the roots of the Rhizocephala, showed that they are the site of active nutrient transport. Bresciani

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Figs. 16, 17. (16) TEM-micrograph of the outer wall of the mantle of *Ulophysema oeresundense*. Cuticle (c), microvilli of the cuticle (ev), microvilli of the epithelial cells (mv), septate junctions (sj), nucleus (n), and a Golgi apparatus (G). Note the numerous mitochondria. Scale bar = 1  $\mu\text{m}$ . (17) TEM-micrograph showing two intestine epithelial cells from an adult 20-mm specimen of *Ulophysema oeresundense*. Towards the lumen (g) the cells have low irregular microvilli, and they are filled with inclusions (in). Nucleus (n) and basal lamina (→). Scale bar = 10  $\mu\text{m}$ .



and Dantzer (1980) localized nonspecific acid phosphatase in the epithelial cells and in the outer part of the epicuticle covering the roots of *C. paguri*.

Payen *et al.* (1983) clearly demonstrate synthesis, absorption, and transport of substances in the roots of *L. panopei*, and show the presence of micropinocytotic transport in the epithelial cells. It is therefore suggested that the same type of transport mechanism may be involved in *U. oeresundense*, although tracer studies and enzyme histochemistry have not yet been performed.

The presence of choanocyte cells covering the mantle of *U. oeresundense* is not surprising, since this type of cell has been found in different groups of invertebrates other than sponges where it has been considered a unique feature. Choanocytes are normal elements of the perivisceral epithelium of echinoderms. Nørrevang and Wingstrand (1970) summarized and added new observations concerning the occurrence of such cells in invertebrates. Brattström (1948b) noted this layer as a "thin covering membrane of foreign origin, which can be removed with difficulty from the mantle wall."

The structure of the cuticle covering the body wall of *U. oeresundense* is of the common arthropod type and comparable to that of the Calanoida (Bouligand, 1966b, and Raymont *et al.*, 1974) and Harpacticoidea (Gharagozlou-van Ginneken, 1976).

The mantle cavity functions as a brood chamber. The cuticular hairs of the inner wall of the mantle of the body surface will contribute to the protection of the eggs and the larvae, since the mantle and the body with the dorsal fingerlike horns are provided with contractile elements, and constantly perform movements. Thus the anchoring hooks of the hairs could prevent larvae and eggs from being expelled.

The sense organs found in *U. oeresundense* show similarity with the sense organs reported from *Notopterophorus papilio* Hesse, an endoparasitic copepod from ascidians (Gotto and Threadgold, 1980), who suggested that they could be important in rheoreception and detection of hydrostatic pressure in connection with optimal larval release by the copepod.

The concept that the sense organs found in *U. oeresundense* may have a similar function is at this point of the investigation only speculative. Further work on the nature of these organs would be extremely interesting.

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