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Histology of the siphons of *Macoma balthica* (Bivalvia: Tellinidae)

Marketta Pekkarinen

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The muscle fibres of the siphons of *Macoma balthica* (L.) have lateral projections, which contain mitochondria. The nuclei are also laterally located in the fibres. Connective tissue is not abundant in the siphonal walls and mucous gland cells are present only sparsely in the proximal inner wall of the exhalant siphon. A glandular area below ciliated cells is present at the inner base of the exhalant siphon. The epithelia of the siphons are richly vacuolated. Acid phosphatase activity, and sometimes also β-glucuronidase activity, was detected in the epithelial cells of the siphons. The microvillous layer of the epithelia often showed alkaline phosphatase activity. Certain cells, probably amoebocytes, within the siphonal walls showed strong β-glucuronidase activity and sometimes a weaker activity of acid phosphatase.

The zinc iodide – osmium tetroxide (ZIO) method revealed plenty of nerve fibres among the musculature. The six main longitudinal nerves send out branches laterally. Nervous connections with the outer parts of the siphonal walls run along the radial muscles. Bodian's silver impregnation method revealed the nerve fibres of sensory receptors, but in the main longitudinal nerves, and also among the musculature, it stained fewer nerve fibres than ZIO did.

Hill-like sensory receptors, the hill organs, are composed of a side cell which envelops two ciliated dendrites. One dendrite end is semicircular in cross section and it bears 7–9 cilia, and the other within the semicircle has a group of cilia. The perikarya of the neurones are far below the epithelium.

More complicated sense organs, the goblet organs, which are arranged as six longitudinal rows, have two-cell-thick epithelial side walls and a few central cells with long, stiff cilia projecting out of the organ. There could be up to five collar receptors of one kinocilium and nine stereocilia surrounded by up to dozens of supporting cilia in a goblet organ. A group of ganglion cells with thick nerve fibres was present further down beneath the goblet organ. There were also simpler receptors with different numbers of cilia in the epithelia of the siphons.

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1. Introduction

Tellinacean siphons are roughly similar in their general structure (cf. Rawitz 1892, Yonge 1949, Chapman & Newell 1956, Duval 1963, Mouëza & Frenkiel 1974, 1978, Armstrong & Millemann 1974, Eldon et al. 1980, Hodgson & Trueman 1981, Hodgson 1982a). They mainly consist of longitudinal, circular and radial muscles, collagen fibres and nerves. The proportions of these vary between species. The general structure of the siphons of *Macoma balthica* (L.) was given in Eldón et al. (1980). In that study one circular layer (outside the inner bundles of longitudinal muscle fibres, Fig. 3b) remained undescribed. For this reason and in order to obtain a better understanding of the diverse functions of the siphons further histochemical and electron microscopical studies on the siphons have been made in the present work.

In the paper of Eldon et al. (1980) the epithelial cells of the siphons were found to bear microvilli at the free surface. The idea of possible processes of active transport and digestion in these cells led to the demonstration of some enzyme activities in the siphons.

The siphons of *M. balthica* are capable of diverse flexing and rotating movements and great extension. They can be withdrawn suddenly after a disturbance. Their sense organs were generally described in Pekkarinen

(1984). The present study gives a more detailed description of the sensory receptors and innervation of the siphons of *M. balthica* to elucidate the coordination of siphonal functions.

2. Material and methods

Macoma balthica were collected from a muddy bottom, at a depth of 7–8 m (salinity 6–7‰), at Tvärminne Zoological Station on the southwestern coast of Finland. Paraffin sections (7 μm in thickness) of siphons fixed in Bouin's fluid were stained with HE = haematoxylin – eosin, HAOL = Crossmon's haematoxylin – acid fuchsin – orange – light green (Romeis 1968) or ABP = Mowry's alcian blue – PAS – Mayer's haematoxylin (Pearse 1968). Glycogen was demonstrated in celloidinized sections with PAS. Control sections were treated with diastase.

The innervation of the siphons was studied histochemically using two methods: Bodian's silver impregnation (Burck 1969) and ZIO = Champy & Maillet's zinc iodide – osmium tetroxide (Maillet 1963). Sections 7–20 μm thick were used.

Phosphatase activities were demonstrated in cryostate sections (8–10 μm in thickness) of siphons fixed in neutral 4% formaldehyde containing 1% $CaCl_2$: acid phosphatase with a modified Gomori method (Barka & Anderson 1963) and alkaline phosphatase with the Gomori Ca-Co method (Pearse 1968). Sequential sections, treated with arabic gum sucrose, were used in the demonstration of β-glucuronidase activity (Hayashi et al. 1964, after Pearse 1972). The incubation temperatures were 37–38°C, although room temperature (22°C) was also experimented with. Control sections (incubated similarly, but without substrate) were needed only in the demonstration of alkaline phosphatase.

In addition, siphons were fixed in 3% glutaraldehyde in 0.1 M phosphate buffer, pH 7.2, for 1.5–2 h. For TEM the siphons were post-fixed in 1.5% OsO_4 in the phosphate buffer, dehydrated and embedded in Epon. Semi-thin sections of them were stained with toluidine blue and subjected to light microscopical examination. Thin sections were stained with uranyl acetate and lead citrate (Reynolds 1963). Siphons for SEM preparations were cut open longitudinally and spread in brackish water between a slide and a cover glass. Glutaraldehyde solution (see above) was added between the glasses. Soon after the siphons had been fixed they were placed freely in the fixative. Thereafter they were dehydrated and dried through an ethanol series and the critical point and coated with gold.

Key to the symbols in the figures

A = amoebocyte
BB = basal body
C_1-C_4 = circular muscle
CN_1-CN_3 = circular nerve
CR = ciliary rootlet
D = dendrite
DC = detaching cell
G = glycogen
GA = glandular area at the base of the exhalant siphon
GB = Golgi body
GC = ganglion cell
GO = goblet organ
H = haemolymph space
IC = inner side cell of the goblet organ
IE = inner epithelium of the siphon
IS = intercellular space
K = knob in goblet organ
L_1-L_3 = longitudinal muscle
MC = mitochondrion
MN = nucleus of muscle cell
MV = microvilli
N = nerve
NF = nerve fibre
OC = outer side cell of the goblet organ
OE = outer epithelium of the siphon
ON = nucleus of an outer side cell
PK = perikaryon
R = radial muscle
SJ = septate junction
SV = synaptic vesicle
VM = vacuole containing Myofer aggregates
ZA = zonula adherens

3. Results

3.1. Muscles, haemolymph spaces and connective tissue

The arrangement of different sets of muscle fibres in the siphonal wall is shown in longitudinal section in Fig. 1a. Circular muscle fibres representing layer C_2 of some other tellinaceans (Yonge 1949) are present in *M. balthica* (Fig. 1b). But in some individuals these are sparse, at least in the distal parts of the siphons. In contracted siphons these circular fibres are embedded in the main longitudinal nerves. A few oblique muscle fibres were also detected here and there in the walls. In cross and longitudinal sections of the siphons these usually appeared as spindle-shaped refractile structures.

The muscle fibres of the siphons bear lateral cytoplasmic and membranous projections (Fig. 1c), which contain mitochondria and which probably attach to other muscle fibres. The nuclei are also located in the lateral parts of the fibres. The longitudinal fibres in the bundles (L_1 and L_2) are quite large. It was not clear whether they had one nucleus or more per fibre. In ZIO and Bodian material some large longitudinal fibres had a dark-staining centre (Fig. 2f). In contracted siphons the outermost longitudinal muscle fibres (L_3) and the epithelium are puckered. Occasionally some of these fibres or their branches attach to the neighbourhood of the outer epithelium.

The radial muscles sometimes cross each other obliquely, and they are also split into branches at their ends. Longitudinal sets of

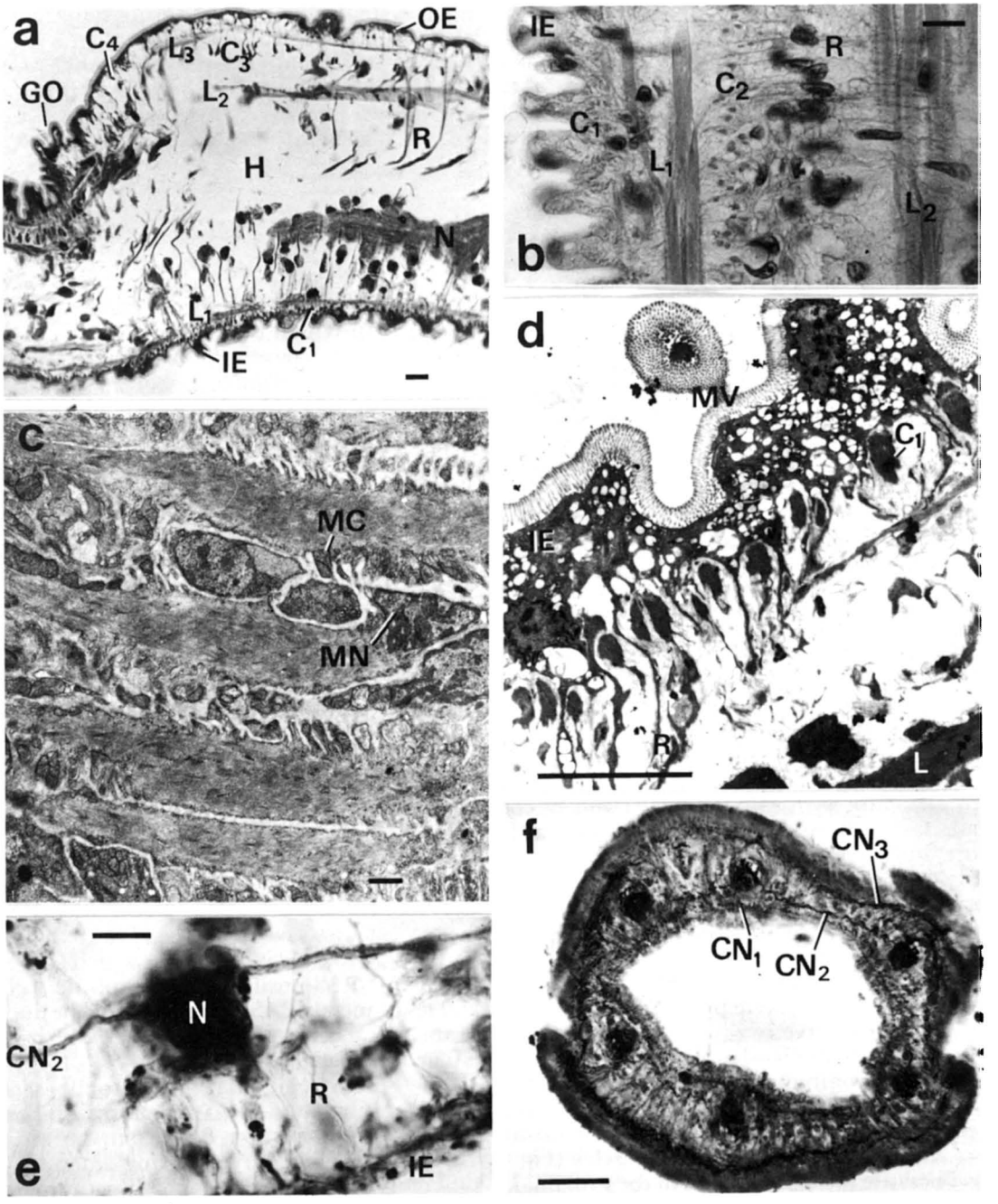


Fig. 1. General structure of the siphons of *Macoma balthica*. — a. Longitudinal Epon section of a siphon wall stained with toluidine blue, showing the surface epithelia (IE, OE), a longitudinal nerve (N), haemolymph space (H) and sets of circular (C), longitudinal (L) and radial (R) muscles. A sense organ (GO) is also visible in the outer epithelium. — b. Longitudinal paraffin section from the inner side of a wall showing the circular muscles C_2. HE staining. — c. Electron micrograph of longitudinal muscle fibres with their lateral projections. Mitochondria (MC) and nuclei (MN) are located laterally in the muscle cells. — d. Electron micrograph of the inner side of a wall sectioned longitudinally. The epithelium bears microvilli (MV). The circular muscles C_1 are partially enveloped by processes of the epithelium. — e. Cross section at the site of a longitudinal nerve (N), which has stained black with ZIO. Larger lateral branches (CN_2) leave the nerve. — f. Cross section of a siphon stained with ZIO. The six main longitudinal nerves and circular nerve fibres (CN) among circular muscles appear black. Bars 1 μm in c, 10 μm in a, b, d, e and 100 μm in f.

radial muscles partially separate longitudinal haemolymph channels. One or two (dorsal and ventral) of these channels are usually wider than the others, at least in the proximal parts of the siphons. The crossing over of the radial muscles is best seen beside these wider channels. The radial muscles are probably attached to the inward processes of the epithelial cells. If the longitudinal and radial muscles are somewhat contracted, the innermost and outermost circular muscles (C_1 and C_4) are partially enveloped by the epithelial cells (Fig. 1d). In the extended state the epithelium is stretched and the circular muscles separate from the epithelium (Fig. 1a).

The lateral projections of the siphonal muscles contain glycogen. PAS-positivity of some muscle fibres proper did not disappear totally in diastase treatment. Amoebocytes were present in the haemolymph spaces. Sometimes the spaces in proximal parts contained detached vacuoles and due to these and the projections of the muscles the spaces appeared "foamy". Crossmon's staining showed that connectice tissue was not abundant. Electron micrographs revealed some fibrils around muscle fibres.

3.2. Nerves of the siphons

The six main longitudinal nerves stained almost totally with ZIO (Figs. 1e,f and 2a,c). Some large fibres of the main nerves stained more intensively than the others (Fig. 2a). Only a few large fibres in the outer side of the nerves stained with Bodian's method (Fig. 2b). Nuclei could be seen occasionally within the nerves. Large cells were present outside the lateral and inner sides of the main nerves, but smaller cells (glial?) were present on the outer, free side of the nerve.

Larger and smaller lateral branches from the main longitudinal nerves run in the "layer" of circular muscle fibres C_2 (Fig. 1e,f). Plenty of nerve fibres stainable with ZIO run also among the other circular muscles (Fig. 1f). These are most prominent in the proximal outer parts of the siphons. Only a few nerve fibres among the musculature stained with Bodian's method.

Thin nerve fibres run along the radial muscles (Fig. 2c,e). Nerve fibres also sometimes run along longitudinal muscle fibres (Fig. 2d). Sometimes in Bodian's silver impregnation light reddish staining, thicker, fibres were seen on neighbouring radial muscles beside the main longitudinal nerves. In Figs. 2e and 2f there is a nerve cell nucleus on radial muscles and its thicker fibre with a lateral branch is visible.

3.3. Surface epithelia, glands and amoebocytes of the siphons

The epithelial cells are cuboidal or columnar. The proximal outer epithelium is highest. The epithelial cells of the inner surface are lower and more irregular in shape. The microvilli of the inner epithelium are slightly shorter than those of the outer epithelium. The epithelial cells contain numerous vacuoles (Fig. 1d). Occasionally septate junctions were detected between the cells (Fig. 3a). Sometimes the epithelial cells contained alcianophilic granules. The microvillous layer stained with PAS and alcian blue. Some glycogen was present in the epithelia. PAS-positivity of the cytoplasm did not disappear totally with diastase. The inner surfaces of the siphons were often covered by alcianophilic mucus. Detached vacuoles, probably pinched off from the inner epithelium, and occasionally detached cells, were detected in the lumen of the siphon tube. PAS-positive gland cells were present only in proximal parts of the exhalant siphon. They were not numerous. Their cell bodies were located deep in the muscular layer and often their ducts led between large vacuoles to ciliated elevations at the inner surface. At the inner ventral base of the exhalant siphon there is a glandular area which is composed of PAS-positive–alcianophilic cells and fewer merely PAS-positive cells. The ducts of the gland cells protrude between overlying ciliated epithelial cells.

The surface epithelial cells usually show acid phosphatase activity (Fig. 3b). Alkaline phosphatase activity was detected in the microvillous layer (Fig. 3c) in varying amounts in different individuals. Weak β-glucuronidase activity was sometimes apparent in the epithelium (Fig. 3e), but more activity was apparent within the siphon walls in cells which could be amoebocytes and in the glandular area at the base of the exhalant siphon (Fig. 3d). This area also sometimes showed acid phosphatase activity. Weak acid phosphatase activity was also detected in some amoebocytes.

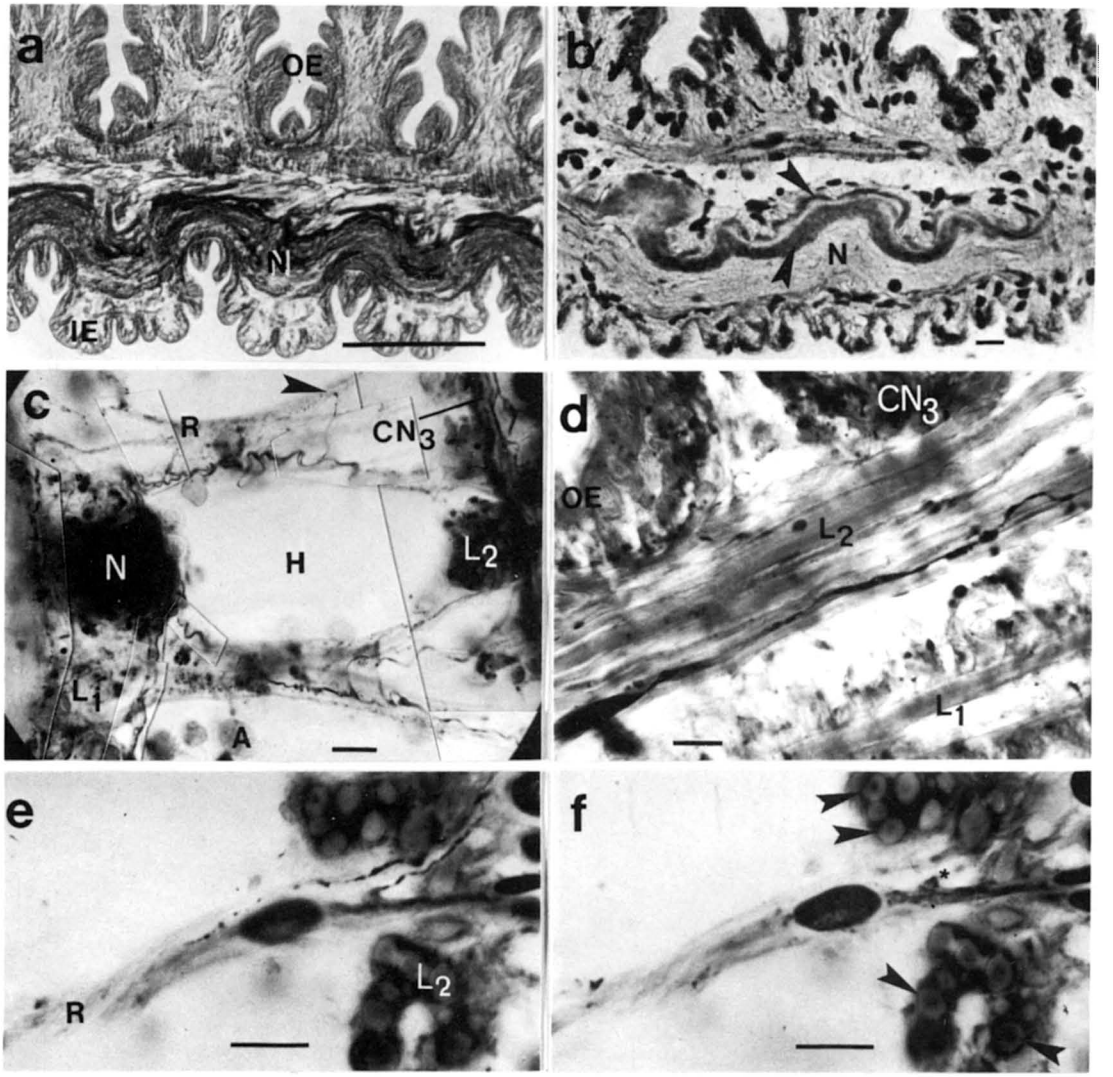


Fig. 2. Innervation of siphonal tissues. — a. Main longitudinal nerve (N) stained with ZIO. — b. Another main longitudinal nerve impregnated using Bodian's method. The arrows show fibres which have stained in the otherwise pale nerve. A round nucleus is also visible within the nerve. — c. A picture representing a combination of several photographs focused at different planes in a cross section stained with ZIO. Thin nerve fibres on radial muscles are visible. The arrow indicates a possible neuromuscular junction. A lateral branch from the main nerve (N) runs downwards in the picture. A few amoebocytes (A) are present in the lower haemolymph space. — d. A nerve fibre on a longitudinal muscle fibre of L_2. ZIO. — e and f. Bodian's silver impregnation. A nerve cell soma (indicated by a large nucleus) lies on radial muscles. Its nerve fibre on the right has a lateral branch, which is indicated with an asterisk in picture f. Another nerve fibre by-passes the soma in picture e. The arrows in picture f point to muscle fibres which have darkly staining centres. Scale bars 100 μm in a and 10 μm in the other pictures.

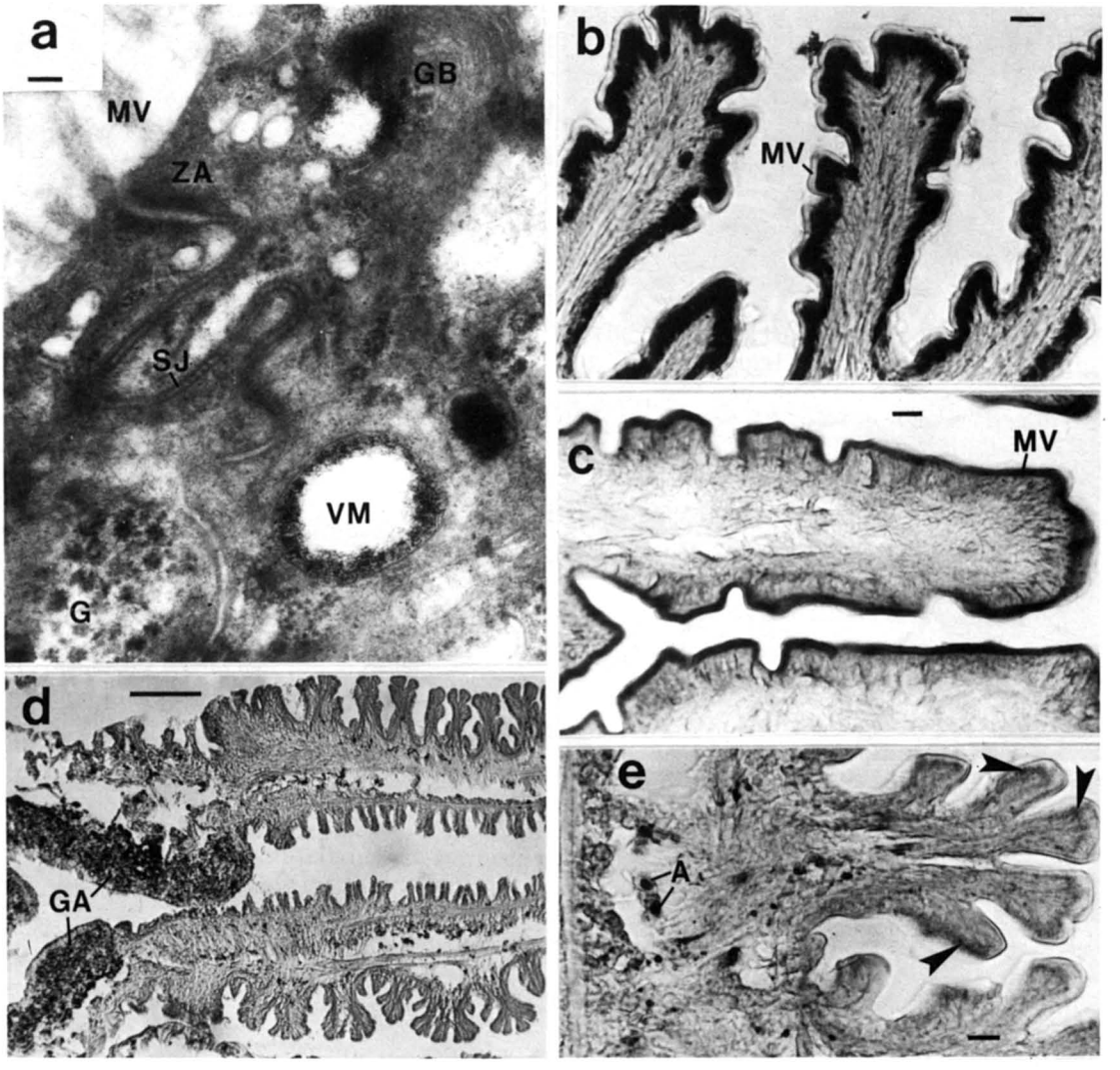
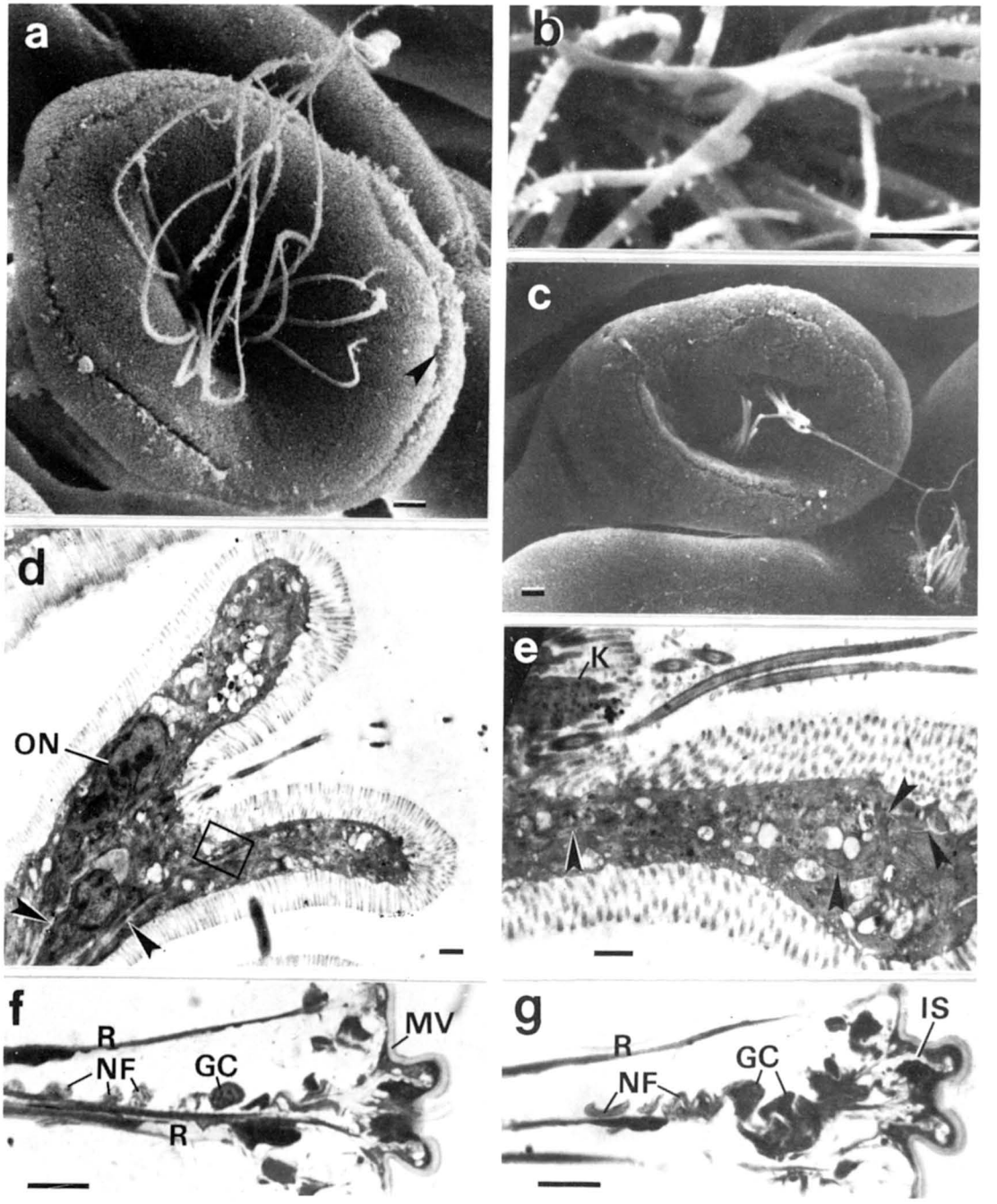


Fig. 3. Epithelia and amoebocytes of the siphons. – a. Junctions between two cells of the outer epithelium: ZA = zonula adherens, SJ = septate junction. G = glycogen, GB = Golgi body, MV = microvilli, VM = vacuole containing Myofer (iron-dextran complex) aggregates (the clam was kept in brackish water containing 1 % Myofer for 24 h). – b. Acid phosphatase activity in the outer epithelium in a siphon in July. – c. Alkaline phosphatase activity in the microvillous layer of the outer epithelium of an inhalant siphon in July. – d. β-glucuronidase (β-GU) activity in the glandular area (GA) at the inner base of an exhalant siphon. The dark dots within the siphon wall are probably amoebocytes which show strong β-GU activity. – e. Weak activity of β-GU (arrowed) in the outer epithelium below the microvillous layer in April. A = amoebocytes. Bars 0.1 μm in a, 100 μm in d and 10 μm in others.

Fig. 4. The goblet organs of the siphons. – a. Surface view of a goblet organ. The normally straight cilia have collapsed during the preparative processes. Note the projections on the ciliary shafts. The arrow indicates the boundary between inner and outer side cells of the organ. – b. Figure showing minute projections on the ciliary surfaces. – c. A goblet organ with two separate foci of cilia. The cilia may have been broken during preparation of the sample. – d. General view of a goblet organ sectioned longitudinally. Intercellular space between inner and outer side cells is marked with arrows. Nucleus of an outer side cell is marked with ON. The other nucleus in the lower left hand corner may belong to



an inner side cell (the section is not exactly median). The square indicates the region which is more highly magnified in Fig. 5a. – e. Part of a goblet organ showing a protruding knob (K) at the centre, and minute sacs on the ciliary membranes. The boundary between the inner and outer side cells is indicated by the arrows. – f and g. Association of some of the radial muscles (R), and ganglion cells (GC) and their nerve fibres (NF) with a goblet organ in Epon sections stained with toluidine blue. The intercellular space (?) (IS) between the side cells is distended. Scale bars 1 μm in a–e and 10 μm in f and g.

3.4. The goblet organs of the siphons

The goblet organs (Pekkarinen 1984) (Figs. 1a, 4) are located on the outer surface in six longitudinal rows following the courses of the main nerves beneath. The organs are about 10–20 μm in diameter and the smallest organs are usually in the lagunae of the puckered surface. The long (about 15–20 μm) stiff cilia in the organs could number up to several dozen. There were minute sac- or club-like projections on the ciliary membranes (Fig. 4a,b,e). The walls of the organs are formed by a two-cell-thick layer. The boundary between these side cells is usually readily visible in SEM preparations (Fig. 4a,c). The distal part of the boundary between the side cells is tortuous. Sometimes the intercellular space (?) is quite wide (Fig. 4f,g). The space contained minute electron-opaque granules (Fig. 5a). Sometimes it appeared longitudinally fibrous as if there were microfilaments or microtubules present. These may belong to nervous or other cellular processes which cruise in the space. A few or several small processes were sometimes noticed in the space in cross-sectioned goblet organs. A process in contact with the outer side cell is visible in Fig. 5a. The inclusions in the process may be small clear synaptic vesicles or microtubules in cross section.

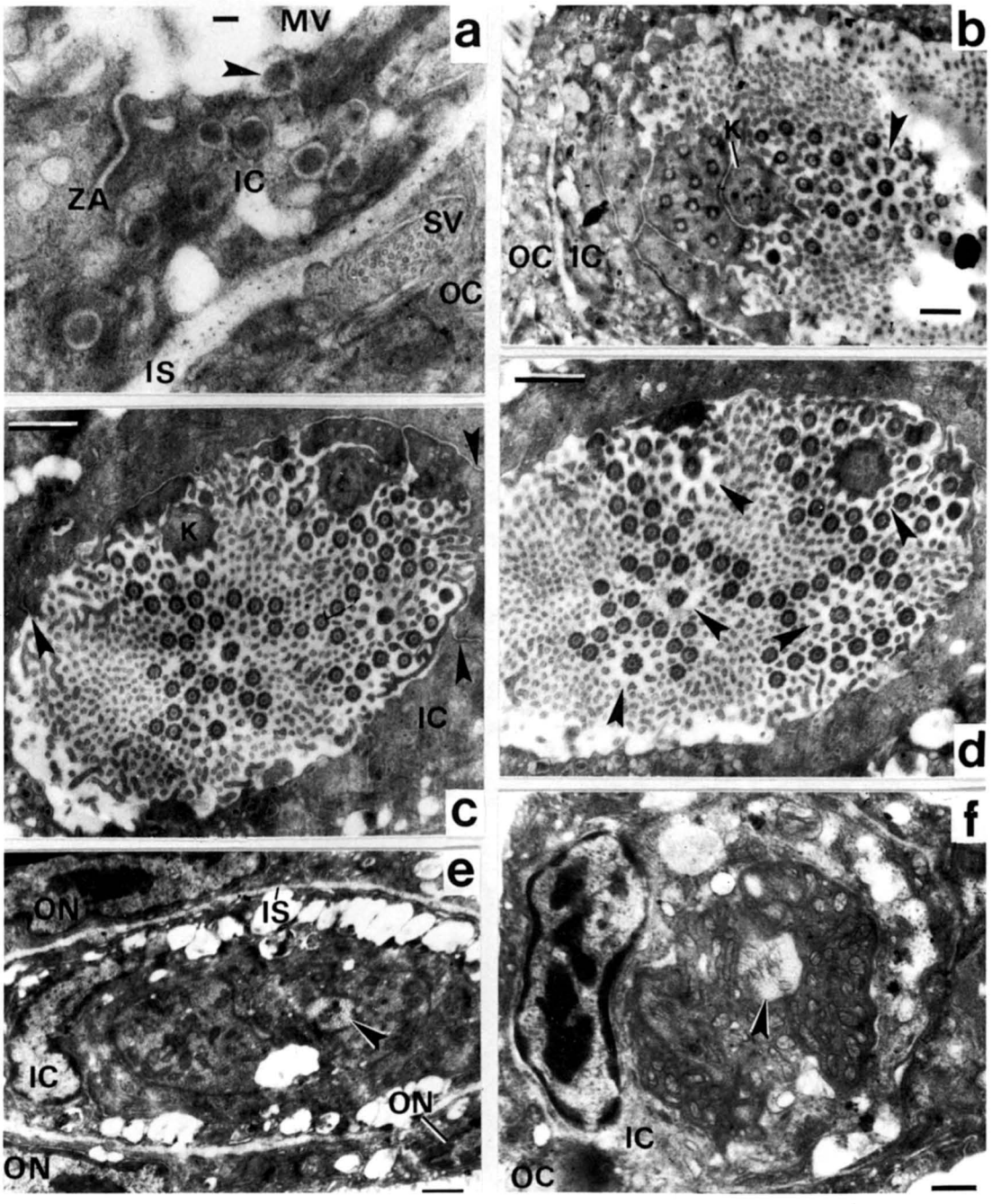
The nuclei of the side cells are never located in the distal parts (Fig. 4d,e). The cytoplasm of these cells bears numerous smaller or larger vacuoles, and moreover the inner side cells contain electron-opaque globules (Fig. 5a). Many nuclei could be seen in the shaft of the goblet: up to three nuclei belonging to the outer side cells (Fig. 5e) and two belonging to the inner side cells. A few central nuclei were detected when living organs were viewed from the top. It is not known whether these nuclei really were located in the shaft or whether the nuclei of the cluster of ganglion cells present beneath the organ (Figs. 4f,g; 8b) were discernible. Some radial muscles attach to the organ; protrusion and retraction of living organs were detected.

A protruding knob could sometimes be seen at the centre point of the goblet organ (Fig. 4e,f). The distal parts of the central cells usually made lateral indentations in the neighbouring cells. The cells contained elongated mitochondria, microtubules or microfilaments. Long striated ciliary rootlets were detected a few times in the central cells. The cilia in the goblet organs were arranged as one or more foci. A two-centered goblet organ is visible in Fig. 4c. In this organ, however, the foci are located exceptionally far from each other. The organ in Fig. 5b may also be two-centered: one centre is indicated by a protruding knob (cross-sectioned) and the other is marked by a "collar arrangement" of nine stereocilia which encircle a kinocilium. These foci are surrounded by supporting cilia. The stereocilia are triangular in cross section. In Figs. 5c and 5d there are cross sections of a goblet organ with five foci. The arrangements of the kinocilium and stereocilia probably arise from knobs (knob K in Fig. 5c has turned out to bear this arrangement in a more superficial section in Fig. 5d). Cross sections from deeper parts of goblet organs (Fig. 5e,f) show numerous mitochondria in the central cells. A light centre is also visible.

3.5. The hill organs of the siphons

The hill organs (Pekkarinen 1984) are well-bordered ciliated hills (Fig. 6a–d), which can probably be withdrawn. The tips of their cilia are often tapered and curved. Cross sections at the level of the cilia disclose 7–9 cilia in a semicircle and a bundle of cilia within the semicircle (Fig. 6d, insert). Probably only one side cell envelops the ciliated central cells (Fig. 6f, h). The side cell(s) of the hill organs contained electron-opaque globules (Fig. 6e), as also did the inner side cells of the goblet organs. The basal feet of the ciliary basal bodies were sometimes detected (Fig. 6g). The sensory cells usually had indentations protruding into their neighbouring cells on the distal parts of their lateral walls (Fig. 6e). Often the ciliated cells were more electron-opaque than the side

Fig. 5. Structure of the goblet organs. – a. Greater magnification in the region indicated in Fig. 4d (but not in the same section). Minute granules are present in the intercellular space (IS), which separates the inner (IC) and outer (OC) side cells, and larger electron-opaque globules are present in the inner side cell. One globule (arrowed) is present just beneath the outer surface and might have been extruded. The zonula adherens (ZA) probably connects two inner side cells. A process which contains small clear synaptic vesicles (SV) or microtubules cross-sectioned is in contact with the outer side cell. – b. Cross section showing a collar arrangement of nine stereocilia (arrowed) around a kinocilium, a knob (K) and



multiciliate cell(s) at the centre of an organ. — c. Cross section of a goblet organ with five foci (knobs or kinocilium — sterocilia arrangements) surrounded by supporting cilia, microvilli and parts of three inner side cells (IC, boundaries arrowed). Note the electron-opaque globules in the inner side cell in the lower left hand corner. — d. A more superficial section from the same organ as in c. The knob (K) in c has turned out to bear a collar arrangement. Different foci are arrowed. — e and f. Cross sections from deeper parts of goblet organs. In e three nuclei (ON) belonging to outer side cells are partially visible. A lighter centre (arrowed) is visible in both pictures. Bars 100 nm in a and 1 μm in the others.

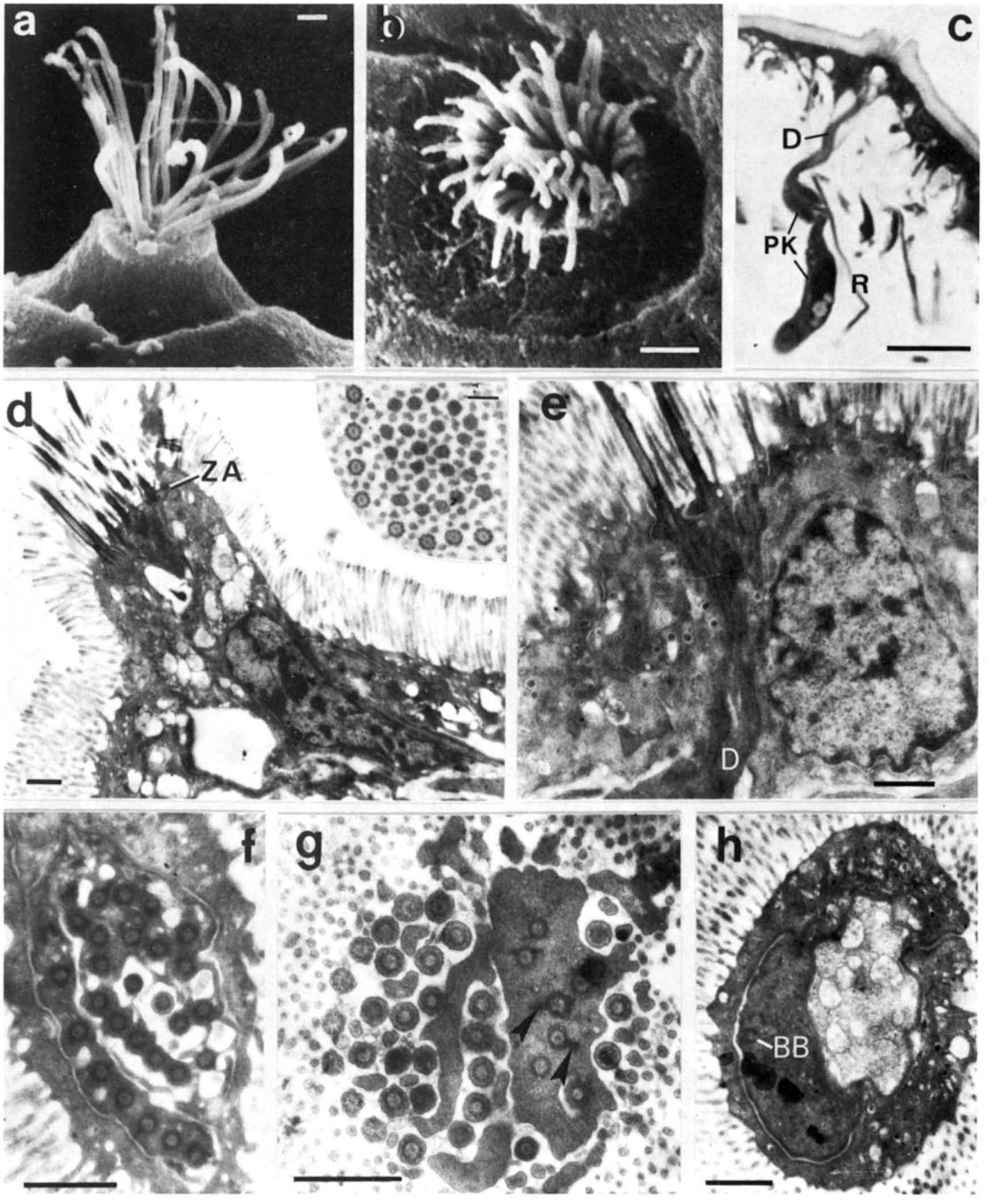


Fig. 6. The hill organs of the siphons. — a and b. Side and top views. — c. Epon section showing a hill organ in the epithelium, and its dendrites (D) and perikarya (PK) far beneath the epithelium. Toluidine blue. — d. A protruded hill organ sectioned longitudinally. There are at least two ciliated central cells (dendrite ends) (three zonulae adherentes visible, one marked with ZA). Insert: Cross section at the ciliary shafts. A semicircle of eight cilia and a group of apically sectioned cilia among microvilli are visible. — e. The dendrites of a hill organ. The distal parts of the dendrites make lateral indentations into the neighbouring cells. Pigment or secretory globules are present in the side cells. — f. Cross

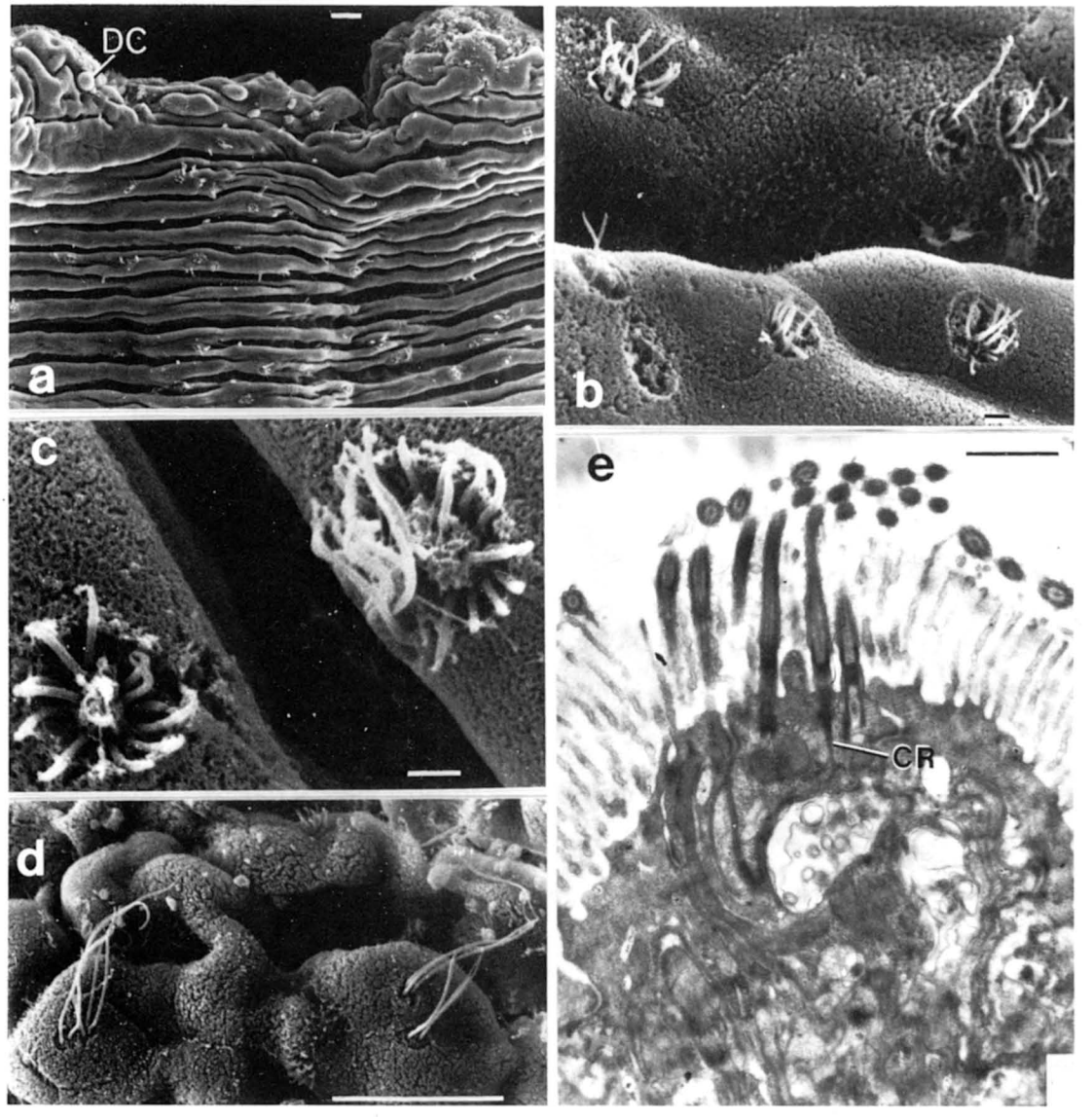


Fig. 7. Ciliated cells on the inner surfaces of the siphons. — a. Distal inner surface of an inhalant siphon. Two of the six projections ("fingers") of the tip are visible. Ciliated cells are numerous. DC = detaching cell. — b. Ciliated and non-ciliated pits in the inner surface of an inhalant siphon. — c. Ciliated circles in the inner epithelium of an exhalant siphon. — d. Longer cilia projecting out of the inner surface of an exhalant siphon. — e. A ciliated receptor sectioned longitudinally. There are striated ciliary rootlets (CR), and a protruding small knob at the apex of the cell. Bars 10 μm in a and d and 1 μm in the others.

section of a hill organ showing one surrounding side cell, the basal bodies of eight cilia in a semicircular cell left of another central cell with ciliary bases. — g. The semicircular cell may be to the left in this hill organ (7—9 cilia). Basal feet (arrowed) of two cilia in another cell are visible. — h. This hill organ is composed of three cells: one side cell, and one darker and one lighter central cell. BB = basal body. The dark flecks are artefacts. Bars 10 μm in c, 0.5 μm in the insert in d, and 1 μm in the others.

cells. Large vacuoles were often present in or under the organs (Fig. 6c,d). The perikarya of the sensory cells are situated deep down under the epithelium (Fig. 6c). In addition to the hill organs simpler ciliated structures were also probably present in the outer epithelium.

3.6. Ciliated cells of the inner surfaces of the siphons

Hill organs are present probably only in the distal parts of the inner siphonal surfaces. Ciliated organs, or cells, are, however, numerous on the inner surface (Fig. 7). The number and length of the cilia vary greatly. There are round pits with a few or many short (2–5 μm) cilia (Fig. 7b). Sometimes a circle of cilia surrounded a centre carrying no, or just a few, cilia (Fig. 7c). Such a receptor may be present in Fig. 7e sectioned longitudinally. There is a small knob at the centre. Striated ciliary rootlets were found a few times. There were also long (about 10 μm) solitary or grouped cilia (Fig. 7d). Bundles of motile cilia were also sometimes detected on the inner surfaces of living siphons.

3.7. Appearance of the receptors after nerve staining

The staining of the goblet organs varied in different batches of ZIO and also within the same batches. Sometimes black fibres could be observed to cruise between the side cells of the goblet organs (Fig. 8a). At other times the inner side cells stained as shown in Fig. 8c. Then the tortuous contour of the distal part of the inner cell against the outer cell became evident. Often the organs stained totally, but sometimes they remained unstained. In Bodian's silver impregnation the ganglion cells and the nerve fibres below the organ stained as well as the basal bodies of the cilia (Fig. 8b). The nerve fibres of the goblet organs were thicker than those of the hill organs (Fig. 8b,d,e). The perikarya of the central cells of the hill organs and those of other ciliated receptors sometimes had a centripetal knob (Fig. 8d,e). The hill organs did not stain with ZIO. ZIO stained some epithelial cells (Fig. 8f). Most epithelial cells stained at the distal parts of the siphons. Dark-staining slender endings were occasionally seen between the outer epithelial cells of the proximal half of the siphon (Fig. 8g).

4. Discussion

4.1. Siphonal muscles, haemolymph spaces and collagen

According to Yonge (1949) the middle circular muscle layer, C_2, outside the inner longitudinal bundles is lacking in the siphons of Tellinidae and Semelidae. He takes *Scrobicularia plana* (da Costa) as an example from the Semelidae. In *Donax* species (Donacidae) it is present (*D. vittatus* L.: Yonge 1949; *D. rugosus* L.: Duval 1963; *D. trunculus* L.: Mouëza & Frenkiel 1978) and in members of Psammobiidae (e.g. in *Gari tellinella* (Lam.) and *G. faeroensis* (Chemn.): Duval 1963; and in *Tagelus dombeyi* (Lam.): Hoffmann 1914). However, according to Duval's (1963) descriptions and the present study the subject in question is not so acutely restricted: some members of Tellinidae do have the middle circular muscle layer C_2 in their siphons. Some confusion may result from erroneous interpretation of structures. The layer which is visible in the siphon of *M. balthica* in place of C_2 in Fig. 3 in Eldon et al. (1980) has now turned out to consist of nerves and also of some muscle fibres. The siphons of *S. plana* contain much collagen according to Chapman & Newell (1956). According to Hodgson & Trueman (1981) this statement is partly incorrect, some collagen only being present among the circular muscles. Wade (1969) interprets the circular layers of the siphons of *D. denticulatus* L. as collagenous, except for the circular muscles at the tentacular region of the tip. The circular layers in *D. trunculus* are composed of connective tissue and some muscle fibres (Mouëza & Frenkiel 1978). The siphons of *M. balthica* contain hardly any collagen.

The lateral projections of the siphonal muscle fibres of *M. balthica* keep the muscle fibres together and strengthen the siphons. The crossing and branching of the radial muscles contribute to the strength of the muscular skeleton of the siphon. Beside the larger haemolymph channels the arrangements of the radial muscles appeared very strong. The larger longitudinal haemolymph channels are usually two in number, if they are present, in siphons which are separate (Duval 1963). *M. balthica* has numerous smaller longitudinal channels in its siphons. In certain functional states of the siphons these channels are quite wide and they permit the free flow of haemolymph. The wider channels are usually indis-

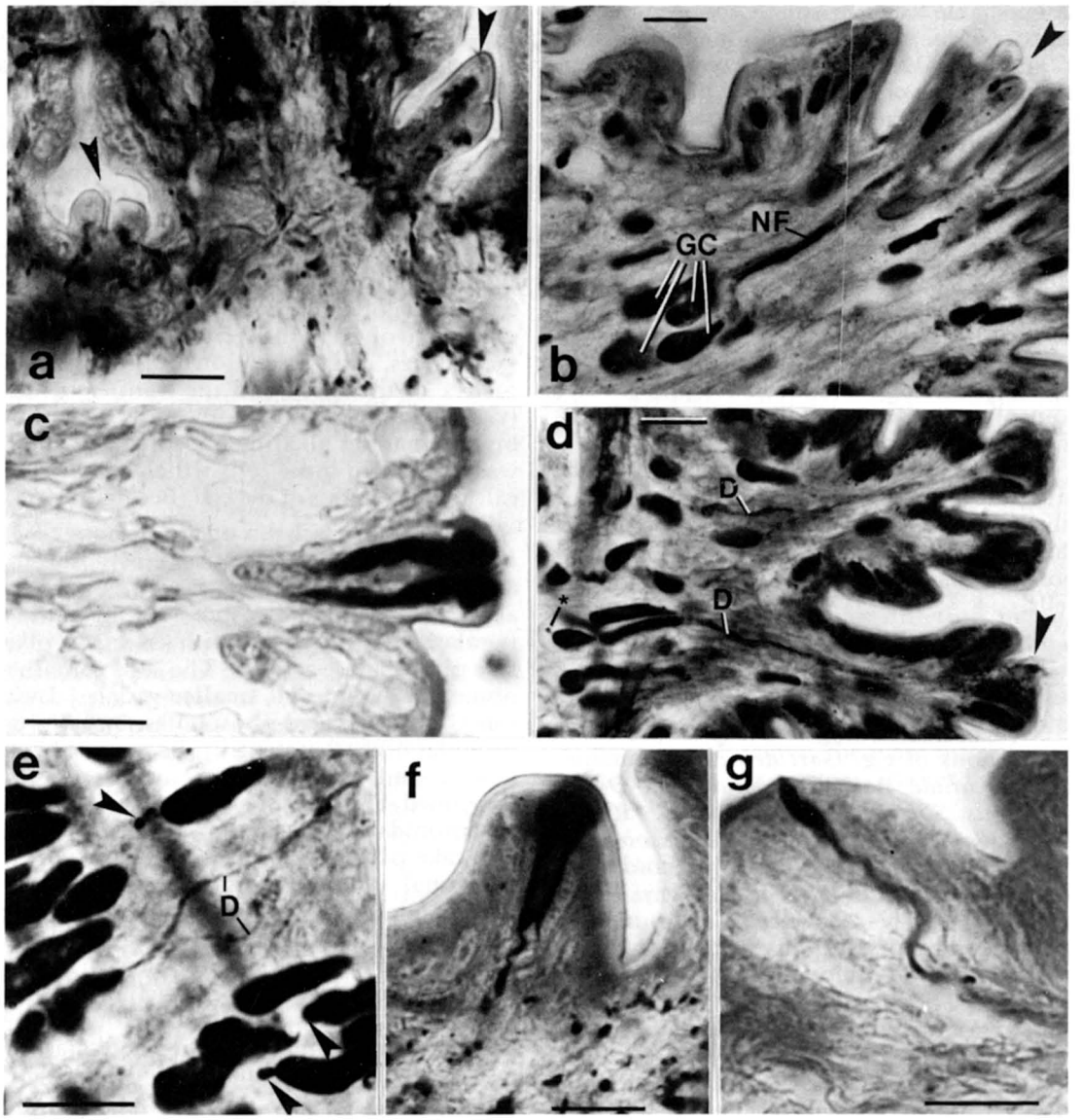


Fig. 8. Nerve stainings in the sense organs and other epidermal structures of the siphons. — a. Nerve fibres stained with ZIO invade the side walls of two goblet organs (arrowed). — b. Bodian's silver impregnation showing a group of ganglion cells (GC), and nerve fibre(s) (NF) between these and a goblet organ (arrowed). The basal bodies of the cilia stained dark. — c. The inner side cells of this goblet organ stained with ZIO. Note the tortuous contour of the inner side cells against the outer cells. — d. Dendrites (D) and perikarya of hill organs (one organ indicated by the arrow, the other being out of the plane in the upper right hand corner). The asterisk indicates a small knob at the base of a perikaryon. — e. Perikarya of sensory cells, some of which have centripetal projections (arrowed). — f. A Zn-osmiophilic epithelial cell in the proximal part of a siphon. — g. A slender Zn-osmiophilic process in the outer epithelium. Scale bars 10 μm in all pictures.

tinguishable from the smaller ones in the distal part of the siphon. According to Hodgson & Trueman (1981) extension and movements of the siphons of *Scrobicularia plana* are performed by contraction of the intrinsic muscles and redistribution of the haemolymph, and by the pressure of water from the mantle cavity into closed siphons. Radial muscles in the animal's siphons may act as a valve mechanism and control the flow of haemolymph. Hodgson & Trueman thought that siphonal extension may take place in a similar way in *M. balthica*. The outermost longitudinal fibres, which sometimes attach to or near the outer epithelium of *Macoma* siphons, may control the puckering of the outer surface during siphon retraction.

The nuclei and the mitochondria of the muscle cells are located laterally outside the fibrillar cores. The lateral projections enlarge the surfaces of the cells, promoting the transport of ions and metabolites to and from the cells.

4.2. Glands, surface epithelia and amoebocytes

Numerous mucous gland cells are present in the siphons of e.g. *Gari depressa* (Pennant), *Tellina nitida* Poli, *T. planata* L., *Donax trunculus, Solecurtus strigillatus* L. (according to Rawitz 1892) and *S. chamasolen* (da Costa) and *S. scopula* (Turton) (according to Yonge 1949) and of *Tagelus dombeyi* (Hoffmann 1914). In *Macoma balthica* mucous gland cells are present only in proximal parts of the exhalant siphon, and they are few in number. There is, however, a specialized glandular area present at the inner base of the exhalant siphon.

According to Péquignat (1973) in the sluggish, primitive pelecypods, transepidermal tissue nutrition and respiration are widespread phenomena. Direct epidermal nutrition may take place, especially in the palleo-gill system of bivalves. According to Ryder & Bowen (1977) the foot epithelium of the slug *Agriolimax reticulatus* (Müller) can function as a digestive epithelium and it possesses a vacuolar system in which heterophagic and autophagic material is hydrolysed. Endocytosis of ferritin and peroxidase could be demonstrated in the epithelium. Large vacuoles or multivesicular bodies acquired hydrolytic enzymes to become secondary lysosomes. In snails, *Lymnaea stagnalis* L., epidermal cells may absorb particulate matter from the external medium by pinocytosis and digest this material within the lysosomal system (Zylstra 1972a). Acid phosphatase is localized primarily in the lysosomal and Golgi bodies of the dorsal head epidermis and the inner mantle epithelium of the snails. Alkaline phosphatase has been considered to be involved e.g. in the active transport of materials across membranes. Alkaline phosphatase activity is associated with the microvilli of the outer mantle epithelium of *Helix pomatia* (L.), and there it may be involved in the secretion of mucopolysaccharides, the formation of the organic matrix of the shell, and the transfer of Ca^{2+} (Ganagarajah & Saleuddin 1972). In some bivalve mantles alkaline phosphatase activity was greatest in those cells which secrete non-calcareous regions of the cell (Beedham 1958).

The surface epithelia of the siphons of *M. balthica* possess characteristics of absorbing and/or secreting epithelia, as well as cells capable of intracellular digestion. The free surface is enlarged by microvilli with associated alkaline phosphatase activity. The cells contained numerous larger and smaller vesicles. Lysosomal enzymes (acid phosphatase and β-glucuronidase) were present in the cells. The digestion and trasnsport of materials may be continued by the amoebocytes, in which β-glucuronidase and acid phosphatase activities also take place. In the gills of *Mytilus edulis* epidermal uptake of dissolved amino acids from natural sea water was not, however, transepidermal (Jørgensen 1982). Because special mucous gland cells were infrequent in *M. balthica* siphons, the surface epithelial cells may themselves secrete some mucus (they sometimes contained alcianophilic and diastase-resistant PAS-positive material).

Invertebrates generally have septate junctions in the epithelial tissue in place of tight junctions. In addition to serving as attachments between epidermal cells, the septate junctions probably also provide an epithelial permeability barrier, as well as a means of communication between neighbouring cells (Zylstra 1972b, Newell & Skelding 1973). Phosphatase enzymes were present along the septate junctions and not along the other regions of the lateral plasma membrane of the epithelial cells of slugs, and it is thus probable that the junctions are also involved in the active transport processes (Newell 1977). Septate junctions were also detected in *M. balthica*.

4.3. Innervation of siphonal tissues

The siphons of *Scrobicularia plana* are rather insensitive to mechanical stimuli (Hodgson 1982b). Hodgson was unable to demonstrate any peripheral nerve network within these siphons. The siphons do in fact possess sensory receptors, but these are probably chemosensory in nature (Hodgson, personal information). The siphons of *Egeria radiata* Lam., too, are comparatively insensitive to mechanical stimuli (Purchon 1963). There is little innervation in the siphonal walls of *Donax denticulatus* and there are no obvious sense organs in either the inner or outer epithelium (Wade 1969). Small stimuli on the siphons of a non-tellinacean, *Spisula solidissima* (Dillwyn), cause local reflexes in the siphon musculature (Prior 1972a,b). A medium-intensity stimulation causes siphon retractor muscle activation along with local reflex activity. Siphon retraction is centrally mediated (Prior 1972a,b, Hodgson 1982b). Clusters of efferent neurone somata occur at the peripheral branching points of the siphonal nerves at the bases of the siphons of *S. solidissima*. These cells receive synaptic input from a set of touch-sensitive afferents from the siphon wall. According to Prior none of the peripheral cells from which records had been obtained provided any indication of being sensory in function.

In *M. balthica* the nervous connection of the siphons with the visceral ganglion is via paired visceropallial connectives, pallial ganglia and siphonal nerves (n. siphonalis analis dorsalis and ventralis, n. siphonalis branchialis dorsalis and ventralis) (Lammens 1969). Lammens found a small ganglion, so-called siphonal ganglion, in the n. siphonalis branchialis ventralis near the siphon retractor muscle. According to the present study the siphonal tissues are richly innervated. The two methods stained neurones differently. Usually only a few outermost longitudinal fibres of the main nerves stained with Bodian's silver impregnation. (Probably the same fibres showed most intense staining with ZIO.) Fibres connecting the sensory receptors stained with the silver impregnation, but fibres among the musculature stained more rarely. With ZIO many fibres of the main nerves stained and this method revealed a dense nervous supply among the musculature. The results suggest a different chemical composition in the neurones, and hence their functions may also be different. However, according to Gilloteaux (1972) other osmiophilic elements among muscle fibres may confuse the identification of neurones.

4.4. Sensory receptors

Sensory receptors with brush cells (Pinselzell, Flemming 1869) on the siphons of some tellinacean bivalves were described by Rawitz as early as 1892. Recently Hodgson et al. (1982) and Hodgson & Fielden (1984) have described the ciliated siphonal receptors of some bivalves. In *Macoma balthica* siphons, simple ciliated receptors were found by Eldon et al. (1980), and the ciliated sense organs of its siphons were generally described by Pekkarinen (1984).

Hodgson & Fielden (1984) classified the simpler siphonal receptors of *Donax sordidus* Hanley into two categories differing in the numbers and lengths of their cilia. According to the present study the cilia of the simpler receptors of the *Macoma* siphon surfaces varied greatly, and a strict classification could not be made. Moreover, there are tufts of motile, possibly non-receptor, cilia on the inner surface as well.

The ciliated receptor cells of *M. balthica* usually had indentations on their lateral distal parts similar to those visible in the siphonal receptor cells of *Solen capensis* and *Donax sordidus*, described by Hodgson et al. (1982) and Hodgson & Fielden (1984). The receptor cells of *Donax sordidus* often appeared more electron-opaque than the surrounding cells, as did also some receptor cells in *M. balthica*.

The hill organs described by Rawitz (1892) in *Gari depressa* consisted of two supporting side cells with a ciliated cell at the centre. The side cells contained granules which stained brownish with osmic acid. The sensory knobs of the cephalic tentacles of prosobranch snails had pigment granules in the lateral supporting cells (Storch & Welsch 1969). Some ciliated cells at the bases of ciliated papillae on the tentacles of giant scallops, *Placopecten magellanicus* (Gmelin) also contained pigment granules (Moir 1977a). The side cells of the siphonal hill organs of *M. balthica* contained electron-opaque globules. These may be pigment or some secretory product. The globules, both in the side cells of the hill organs and in

the inner side cells of the goblet organs of *M. balthica*, also resembled the ultrarhabdite secretory grains in the epithelium of catenulid turbellarians (Moraczewski 1981). Some globules in the inner side cells of the goblet organs were close to the plasma membrane (Fig. 5a), and they may be extruded outside it.

In the pallial tentacles of *Lima hians* (Gmelin) specialized gland cells were combined with sensory cells (Owen & McCrae 1979). No evident gland cells were present in the hill organs of *M. balthica*. The occasional PAS-positive gland cells of the inner surface of the exhalant siphon, however, sometimes opened at ciliated tufts. The gland cells were not found or identified in TEM material. The ciliated tufts and pits in the inner siphonal surfaces viewed in SEM closely resembled the sensory cilia tufts and gland openings described by Owen & McCrae (1979) on the pallial tentacles of *L. hians*.

The so-called collar receptors may be fairly common in the animal kingdom (cf. Ehlers & Ehlers 1977, Haszprunar 1985). In such receptors a kinocilium is surrounded by a collar of nine microvilli or stereocilia, or the number may in some species be around nine (Knapp & Mill 1971, Lyons 1973, Ehlers & Ehlers 1977, Moir 1977a). Among bivalves collar receptors have been reported as occurring in the pallial tentacles of giant scallops by Moir (1977a) and of *Lima hians* by Owen & McCrae (1979), and in the so-called Stempell's organ of *Nucula* species by Haszprunar (1985). In the present study we have another example of a bivalve which possesses such collar receptors, in this case in the goblet organs on the siphons.

In some species the collar microvilli are triangular in cross section, e.g. in the earthworm, *Lumbricus terrestris* (Knapp & Mill 1971), in *Lima hians* (Owen & McCrae 1979) and in *Nucula* (Haszprunar 1985). Those of the *M. balthica* collar receptors are also triangular. The number of microvilli (9) equals the number of peripheral microtubule doublets in the kinocilium. A starlike plate formed by fibrous material which is associated with the stereocilia and the basal body of the kinocilium was noticed at the proximal part of the basal body by Owen & McCrae (1979) and by Haszprunar (1985). The collar arrangements of the *Nucula* Stempell's organ arise on protruding knobs (Haszprunar 1985), as they do in the goblet organs of *M. balthica*.

In scallop tentacles the central cells of the sensory papillae had up to five collar arrangements at their apices (Moir 1977a). In the goblet organs of *M. balthica* collar arrangements could be up to five in number, but they were possibly in different cells. Multiciliated cells probably surrounded the collar cells, as they do in the sense organ of the earthworm (Kapp & Mill 1971).

Eisig (1879) suggested a common existence of goblet organs in aquatic and terrestrial animals. Rawitz in his detailed description (1892) of some tellinacean siphons suggested that the "lateral organs" (Seitenorgane) of the siphons of *Gari depressa* are analogous to the lateral line organs of other animal classes. According to him the hill organs (dreiteiligen Organe) of *G. depressa* detect direct tactile stimuli and the lateral organs also detect the smallest vibrations in the water. Owen & McCrae (1979) also suggested that the collar cells of *Lima hians* were vibration receptors. Tactile reception has also been suggested as a function of the collar receptors in some species (Table 1 in Haszprunar 1985). According to Lyons (1973) the hair cells of the vertebrate acoustico-lateralis system could be regarded as a collar cell type but with the "stereocilia" of the collar rearranged to one side of the "kinoflagellum". Lyons also suggested phagocytosis of food particles and transport as possible roles of the collar cells in the "ciliary" tracts of filter-feeders (e.g. in hemichordates, protochordates and brachiopods).

In scallop tentacular papillae the basal feet of different cilia are oriented in different directions even within the same cell. Thus, the receptor cells would be able to respond to stimuli from a number of different directions (Moir 1977a). In the multiciliary cluster cells of the gland cell/sensory cell complex of *Lima hians* the basal feet of the cilia tend to project outwards along a line radiating from the centre of the cluster of the ciliated cells (Owen & McCrae 1979). The semicircular cells of different hill organs on the *Macoma* siphons were randomly arranged on different sides of the hills.

Knapp & Mill (1971) somewhat tentatively suggested that the widely distributed multiciliate sensory cells of the earthworm may be tactile receptors, while the less abundant uniciliate (collar) cells may function as chemoreceptors. Membrane modifications of cilia have been detected a few times in receptors suggested as chemosensory; such are swellings and

vesicles in the ciliary shafts (Reese 1965, Moir 1977b). Certain artefacts of cilia, the so-called paddle cilia, can result from hypertonic fixatives or an abnormal ionic composition of the medium (Ehlers & Ehlers 1978). The outward projections on the cilia of the goblet organs of *M. balthica* may be genuine ciliary structures (or some small ectosymbionts). The sacs, if they are structures of the ciliary membrane, may enhance reception of chemical stimuli. They may also provide additional resistance to water currents and thus increase sensitivity to vibrations.

The intercellular space between the two side cells of the goblet organs contained minute dark grains. Sometimes it had a fibrous appearance. It may be composed of a narrow glial cell (cf. the glial processes and sheaths in other molluscs: Zylstra 1972c, McLaughlin & Howes 1973, Owen & McCrae 1979, Elekes et al. 1985) or a pigment cell. The occasional fibrous appearance of the intercellular space in longitudinal sections and the light vesicles or microtubules in certain processes suggest nerve fibres (axons or dendrites) running in the space. ZIO staining sometimes supported this. The ZIO stain appears at unmasked lipids associated with proteins (Maillet 1963, Gilloteaux 1968). According to Gilloteaux (1972) the two antagonistic nerve endings of molluscs, cholinergic and tryptaminergic, cannot be differentiated with ZIO. Clear synaptic vesicles in pulmonate synapses were thought to be involved in the cholinergic transmission of nerve impulses (Gerschenfeld 1963). Aronova et al. (1979) noted that when ZIO impregnation was used, the electron opaque precipitate was seen in the light synaptic vesicles and in the neurotubules. Axon terminals may control the function of the side cells of the goblet organs. Alternatively, there may be dendrites which transmit information from chemical stimuli. Some radial muscle fibres, which retract the organ, may also invade the intercellular space and attach to the side cell membranes. The intercellular fluid and vacuoles in the side cells may function as a hydroskeleton of the organ.

There were no signs of typical light sensitive receptors in the siphons of *M. balthica*. The siphonal lateral organs of some tellinaceans (*Egeria radiata* Lam. and *Iphigenia brasiliensis* Lam.; Purchon 1963 and Narchi 1972, respectively) are surrounded by pigment. Pigment in and around the goblet organs of *M. balthica* was so scarce that it was not visible either with the naked eye or under the light microscope. *M. balthica* responds to vibratory stimulation of at least five seconds by digging movements after a delay of 25 seconds (Mosher 1972). It reacts to the switching on of a bright light with burrowing movements after a similar lag (unpublished results of the present author). The site of the light receptor(s) is not known. They may be located in the CNS or peripheral nerves, or in the epidermis (cf. Kennedy 1958, Braun & Job 1965). The "light off" receptors of gastropod skin may have sensory endings with microvilli or a few cilia (Zaitseva & Bochrarova 1981). The function of the microvillated Zn-osmiophilic epithelial cells of the siphons of *M. balthica* is not known. The narrow endings shown in Fig. 8g may be tactile (pressure) receptors which provide information about the degree of gaping of the valves, preventing injury of the extended siphons between the shells.

The nuclei of invertebrate receptors are often located below the epidermis. In freshwater snails the cell bodies of sensory receptor cells are frequently found in discrete groups (10–40 nerve cells) forming small ganglia (Zylstra 1972c). Rawitz (1892) found ganglion cells beneath the sensory cells of the lateral organs in the siphons of *Gari depressa*. Nerve fibres associated with the radial muscles connected the ganglion cells with the main nerves. In the siphons of *Tagelus dombeyi* a band of tissue rich in nuclei runs from the sensory papillae inwards within the tissue of the siphon (Hoffmann 1914). The sensory cells in the siphons of *Donax trunculus* are connected with the main nerves via nerve fibres running along the radial muscles (Mouëza & Frenkiel 1974). It is not known whether the central cells of the goblet organs of *M. balthica* are primary, or secondary, sensory cells. Ganglion cells connect the organs with the main nerves. It is not known whether the neuron in Fig. 2e,f is a ganglion cell of a goblet organ or an additional interneuron. The connection of the sensory cells of the hill organs or free sensory cells with the main nerves is not quite evident. The centripetal projections of the cell bodies might be sites of synapses. These receptors might function with tactile stimuli primarily in local reflex pathways, but the goblet organs may mediate to the CNS signals from threatening vibrations, to be reacted to by siphon retraction and digging movements.

Probably some of the siphonal receptors described above detect chemical stimuli. As to the number and diversity of sensory receptors in both the inner and outer surfaces and the rich innervation of the siphons, *Macoma balthica* possesses effective equipment for the reception and coordination of information from its medium.

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