Cell Tiss. Res. 180, 367–381 (1977)

Cell and Tissue
Research

Material Transport within Specialised Ciliary Shafts on *Rhabdopleura* Zooids

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Summary. The surface of the *Rhabdopleura* zooid is ciliated. The cilia of the cephalic shield and tentacles have paddle-like swellings of the shaft. These swellings are usually about 0.6–1 μm in diameter and most frequently found in the distal 1–2 μm of the ciliary shaft. Others are found in other positions along the length of the cilium and it is suggested that at least some of these swellings represent material transport within the cilium.

Paddle shaped cilia are probably more efficient than normal cilia in moving water and food particles. If these cilia are involved in the building of the tubular coenecium then their distribution suggests that the tentacles as well as the cephalic shield are actively involved in tube building.

Key words: Paddle-cilia – *Rhabdopleura* – Transport – Coenecium – Building – S.E.M.

Introduction

The shafts of cilia usually have a simple cylindrical shape, but there are descriptions of cilia with much more complicated morphology, thought to be an adaption related to some specialised function (Afzelius, 1969; Bonsdorff and Telka, 1965; Cobb, 1969; Dirksen et al., 1971; Doolin and Birge, 1966; Fawcett, 1961; Hayes, 1971; Hookes et al., 1967; Horridge, 1965, a, b; Kanda and Hilding, 1968; Rhodin and Dalham, 1956; Rivera, 1962; Sleight, 1962; Tamm, 1972). Nearly all of these reports discussed either the fusing together of several ciliary shafts to make a complex multicilium, or modification of the usual 9+2 tubules, causing modifications of the smooth cylindrical shaft of the cilium. Recently,

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* I should like to thank the director and staff of the Marine Biological Laboratory, Plymouth, for collecting the material and the generous loan of facilities during the preparation of the material. Mr. R. Moss provided skillful technical and photographic assistance

a new type of cilium associated with the formation of byssal attachment discs in *Mytilus californianus* has been described (Tamarin et al., 1975).

These cilia had a paddle-like biconcave flattened disc at their distal ends. The disc was formed by a 360° curvature of the axoneme tip within the ciliary membrane. They suggested that these specialised cilia function as microscopic spatulae for the application of the adhesive plaque material to substrate surfaces.

Rhabdopleura secretes its surrounding tube-like coenecium using the ciliated cephalic disc, and it was of interest to examine the cilia that take part in the production of the complex coenecium to see if they have any similar morphological modifications.

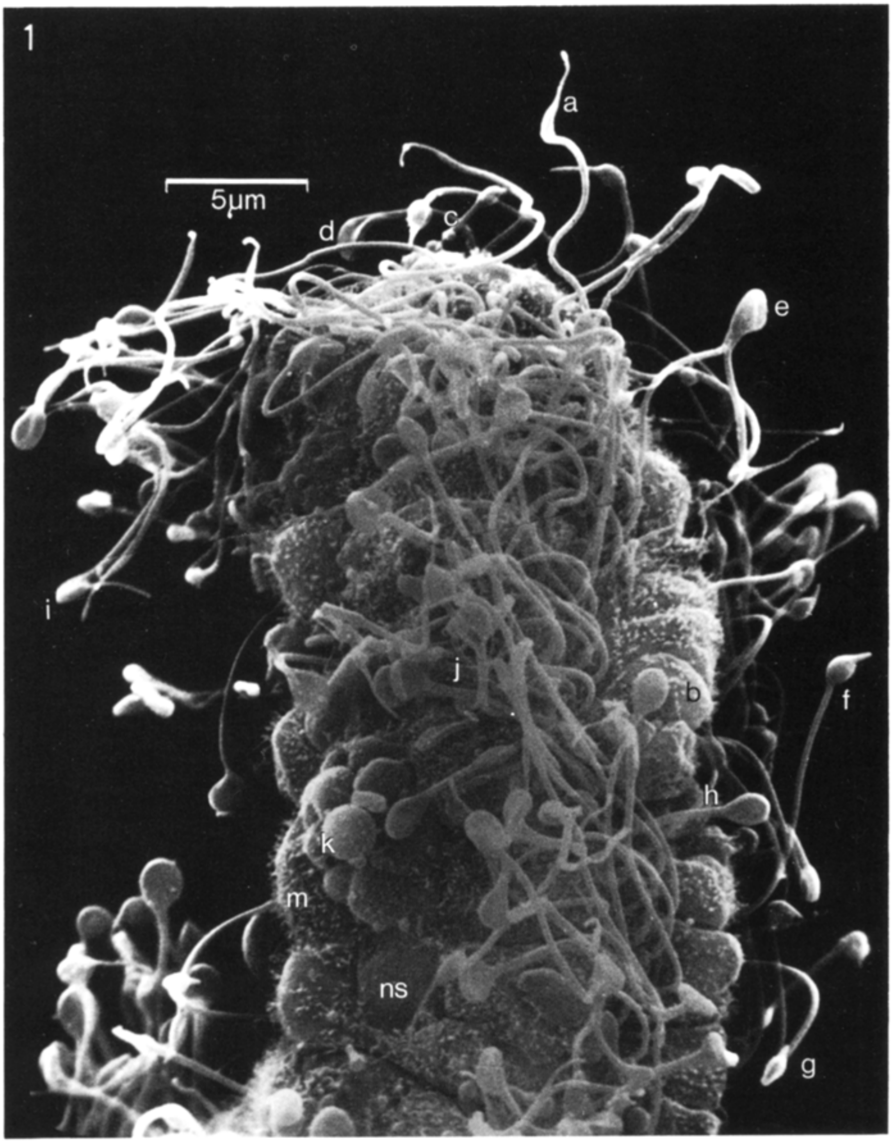
Materials and Methods

Colonies of *Rhabdopleura compacta* were obtained by dredging near Stoke Point, Plymouth, England. The zooids were removed by breaking the erect tubes of the coenecium from the repent part and removing the tube leaving the zooid attached to the repent tubes by the stalk. The colonies were then narcotised using MS222 (Sandoz). When the lophophores had become extended the colony was flooded with 5% glutaraldehyde buffered to pH 7.4 using cacodylate buffer. After 5 h the zooids were cut free using iris scissors, and the zooids transferred using a bacteriological pipette to 2% Osmic acid buffered to the same pH using the same buffer. After 2 h, the zooids were washed in buffer, dehydrated through graded ethanol solutions and then some were transferred via freon 113/alcohol graded mixtures to pure freon 113. The specimens were critical point dried, mounted on aluminium studs using double-sided cellotape. The specimens were then coated with gold in a sputter coater, and examined in a Cambridge IIa scanning microscope at 30 KV. Other specimens were taken and immersed in 8% Uranyl acetate in absolute ethanol, washed for fifteen minutes in epoxy propane and embedded in Araldite, sectioned using glass knives in a Porter Blum microtome, mounted on carbon coated grids, stained with lead hydroxide and examined in a Siemens 1a Elmiskop.

Figs. 1–18. It is difficult to attach meaningful dimension marks to scanning electron micrographs because of the obliquity of the specimen to the scanning beam. However, in this paper as a result of T.E.M. sections, it is known that the ciliary shafts are 0.2 μm in diameter, and the scale has been calculated using that observation

Abbreviations: aa acute angle bend of the ciliary shafts; *ap* assymetric particle; *cs* part of the main body of the cephalic shield; *er* empty ring; *fl* flat disc; *hl* hook-like loop; *jz* junctional zone of the cephalic shield that extends as an annulus separating the lip from the central region; *l* lip region of the cephalic shield; *m* microvilli; *ns* a cell surface devoid or only sparsely covered with microvilli; *p* possible pore aperture leading onto the surface; *ra* right angle bend; *sb* spherical bodies; *sc* short narrow shafted cilia; *st* single thickness ciliary shaft; *t* tapering terminal μm or so of a ciliary shaft; *tm* thin membrane; *ts* twin thickness ciliary shaft

Fig. 1. Montage of the distal tip of a tentacle of *Rhabdopleura compacta* showing the general covering of spatulate cilia, their wide variety and the irregular microvilli covered surface of the cells that bear them: *a* tapering terminal part of the shaft with a bulge suggesting that the contents of the bleb have been discharged; *b* a flat terminal paddle; *c* a spherical juxtaterminal enlargement



of the shaft; *d* a biconcave spatulate enlargement showing the ciliary shaft as a peripheral ridge; *e* either two ciliary shafts contributing to a single paddle or an enlargement in the middle part of the length of a shaft; *f* a peaked terminal, suggesting the shaft is associated with one side of the enlargement, and tapers beyond it; *g* one of the spherical blebs surrounded by a recurved hook of the ciliary shaft that remains distinct; *h* a flattened enlargement surrounded by the ciliary shaft which is fused together to make a double thickness stalk; *i* a flattened disc, with a longer distal narrow portion of the ciliary shaft; *j* a cilium with double shafts made by the single shaft encircling the disc and remaining fused to the proximal part of its course; the T.E.M. suggests that these shafts are often contained within a single ciliary membrane; *k* a spherical particle resting on the surface of the tentacle. It is attractive to speculate that some of these particles are picked up and transported by the cilia, and correspond to the swellings enclosed in bends in the ciliary shafts

Results

The cilia vary considerably in size in differing places on the surface of the zooid. There are four major ciliated areas, the tentacles, the cephalic shield, the body and the stalk, and the cilia are different in each of these regions.

The Tentacles

The tentacles have all variety of cilia (Figs. 1–9). The majority of them have distended shafts. The swellings themselves can occur in many places along the length of the shaft. There is usually only one swelling per shaft, and these cilia occur together with cilia that appear to have lost their blebs, and others whose shafts have the typical uniform cylindrical shape.

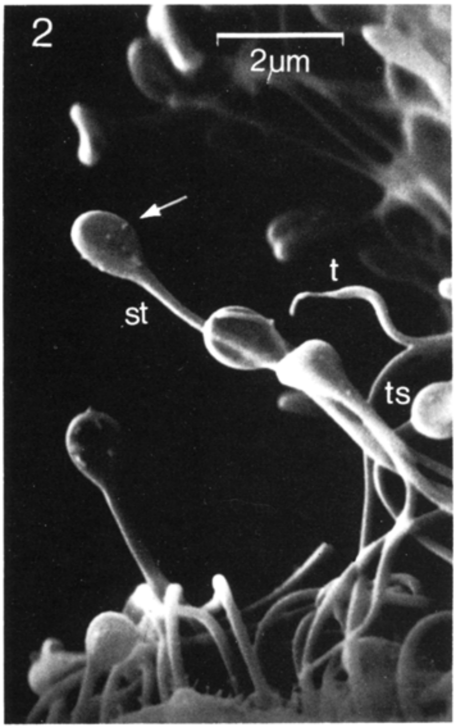
Initially, most of the cilia appear to have a flat terminal paddle, but closer inspection reveals that there is a wide variation amongst the cilia (Fig. 1). Some of the swellings do not occur at the distal tip of the shafts but about 1 μm before the tip (Figs. 7, 8). These swellings vary considerably in shape from flat biconcave discs to apparent turgid spheres (Figs. 2–9). The shaft can pass around a meridian (Fig. 7) or apparently traverse the polar axes of the sphere (Fig. 8). Frequently, the distal part of the shaft is narrower than the proximal shaft and tapers to an even narrower diameter (Figs. 2, 3, 7, 8), although quite often the taper ends in a terminal bleb about 0.25 μm in diameter. The distal part of the cilium often bends through an acute angle compared with the general direction of the main shaft (Figs. 1, 7). Sometimes, the change of direction can be so dramatic as to extend more than 270–360° from the preswelling direction (Figs. 3, 5). It is unlikely that all of these swellings are contained within the ciliary membrane, and occasionally it appears as if the swelling is independent from, but encircled by the ciliary shaft (Fig. 5), or simply attached to the shaft surface (Fig. 9). The enclosed material can have an irregular shape

Fig. 2. Two spatulate cilia on a tentacle, one with a standard shaft, and one with a double thickness shaft. There is also a tapering cilium nearby. The surfaces of the enlargements have small particles attached to them (arrow). The swellings appear flat whereas adjacent ones appear to have a concave face about their transverse axes

Fig. 3. A flat and a spherical enlargement of the ciliary shaft of cilia from the tentacles. The ciliary shaft encircles the disc-like ending and the ciliary membrane appears continuous across it. The tapering distal part of the shaft can be seen against the proximal shaft. The adjacent spherical enlargement has surface ridges. Sometimes it is possible to observe several ridges and they suggest that they are related to the 9 + 2 microfilaments of ciliary axoneme. A tapering cilium with small particles attached is also present

Fig. 4. A cilium from the tentacle with a terminal swelling and the proximal and distal shafts separating after several μm. The adjacent cilium swelling has a concavity about it' longitudinal axis

Fig. 5. A swelling about mid-way along a ciliary shaft with a near 360° encirclement by the shaft, but the proximal and distal parts of the axoneme remain separate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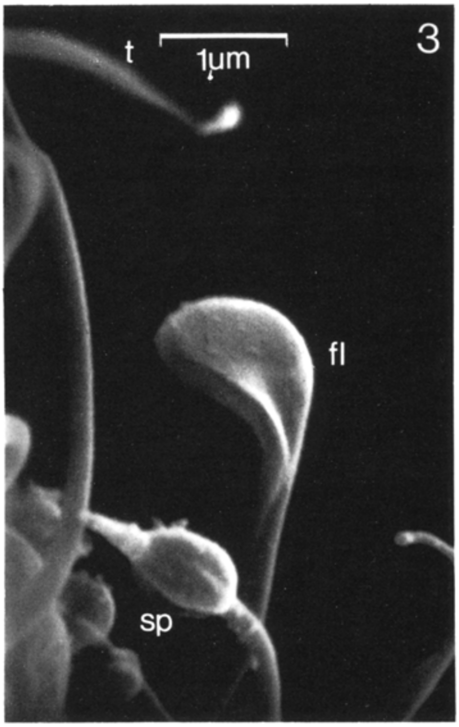
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within the curve of the ciliary shaft, and in extreme cases can appear either as a thin curtain of membrane, or a droplet (Figs. 11, 13). Some of the swellings are asymmetrical, the larger portion extending to one side of the ciliary hook.

Extreme cases of ciliary shaft encirclement occur when the distal and proximal shafts meet (Figs. 2–5). There can either be only a short distance of contact before the distal fragment peters out (Fig. 3), or the two shafts can part and the distal fragment can extend for several μm. Sometimes, the distal and proximal ciliary shafts can remain fused together for much of their length, giving the appearance of being surrounded by a single ciliary membrane and producing a ciliary shaft of double thickness (Fig. 4). Sometimes, it also appears as if two separate ciliary shafts can support a single paddle without being fused along their shafts (Fig. 1e). Finally, there are some spherical bodies to be found associated with the ciliary shafts a good distance from their distal regions (Fig. 9).

There are spherical swellings on the surfaces of some of the cells of the tentacles. Some of these surface swellings have the same dimensions as the blebs associated with the cilia, and beside these swellings the tentacle cells have a rich covering of short microvilli. The cells themselves do not form an even contour, but rather each cell is associated with a dome-like bulge from the tentacle surface. There are other cells on the tentacle whose surface is smooth and without microvilli. These cells do not usually have cilia either. Each zooid has numerous tentacles and the total area of paddle cilia from this part of the animal is much greater than that of all the other regions combined. Suggesting that whatever the specialised functions of these cilia are, then the tentacles must be important in that activity.

Cephalic Shield

The cephalic shield has two main areas of differing sorts of cilia. First, there are those associated with the lip. The lip is an annular ring around the edge of the shield. The cilia on the lip are usually the regular cylindrical sort, whereas secondly those over the main body of the shield have spatulate endings (Fig. 16). The two regions are abruptly separated from one another and there appears to be a line of cobblestone-like cellular projections between them.

The long cilia of the lip are about 15 μm in length and 0.2 μm in diameter, longer than those of the rest of the shield, but in the region of the junction between the two shield areas, these long cilia are associated with shorter and narrower cilia near their bases. These cilia are about 1.0 μm long and 0.1 μm

Fig. 6. A flat terminal paddle just enclosed by the distal part of the shaft. No evidence of the distal tip emerging from the enlargement can be seen

Fig. 7. Juxta terminal swellings where it appears that the ciliary shaft passes meridionally to the spherical enlargement, and ends in a short steep taper

Fig. 8. Another juxta terminal swelling where it appears this time as if the ciliary shaft passes axially through the polar axis of the enlargement in the ciliary membrane

Fig. 9. A spherical body that appears to rest on a ciliary shaft. This body may have a separate enclosing membrane distinct from that of the cilium


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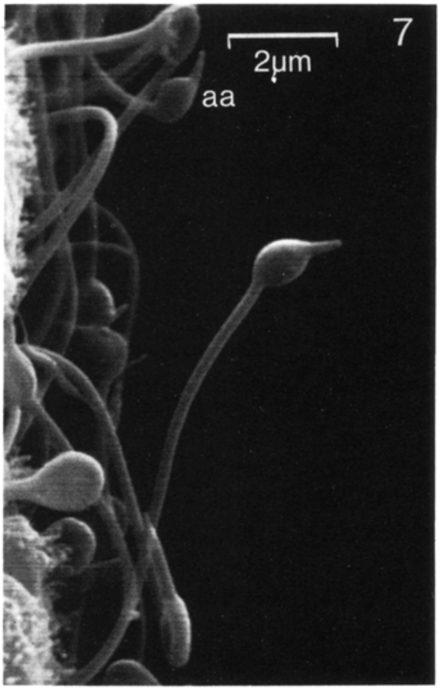
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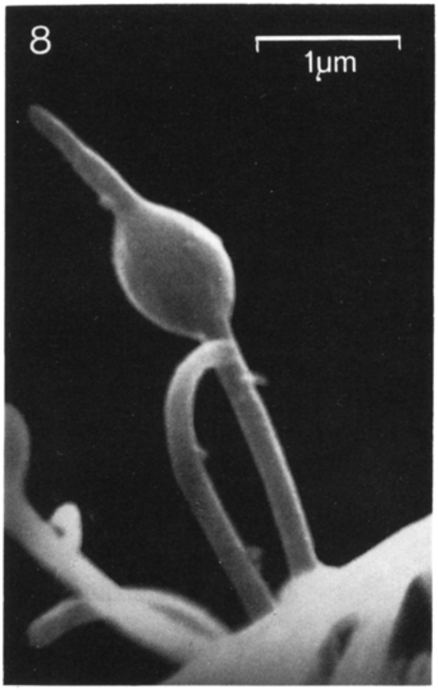
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in diameter (Fig. 16). Rarely there are spatulate cilia amongst those on the lip. The lip cilia are fewer per unit area than those of the body of the shield; and the cells that bear them have numerous short microvilli on their surfaces. These microvilli, although short, are longer than those on the cell surfaces of the spatulate cilia bearing cells.

The main body of the cephalic shield is covered with densely packed cilia, the majority of which are spatulate (Fig. 15). The cilia are shorter than the other cilia on the zooid with the exception of the short cilia associated with the lip cilia. The spatulae are most frequently associated with the distal ends of the cilia. Amongst these spatulate cilia, there are a small proportion of the usual cylindrical cilia. In the cephalic shield as in the tentacles, the blebs in many situations appear to be within the ciliary membrane and can occur at any position along the shaft of the cilium, from near to its origin to its distal tip. The distal tips of several of the cilia have long tapering ends about 1.2 μm long. These portions of the shaft often appear dirty with lots of small particles attached to the surface (Figs. 6, 11). These particles may well be the remains of the larger blebs. Fewer similar particles are sometimes seen along the regular shafts of the cilia. This separation of cilia type between the main body of the cephalic shield and its lip presumably indicates a specialisation of function and a different function for the two parts. It is probable that while the main body of the shield is involved in tube building the end of the shield may well have an additional tactile function.

The Stalk

The muscular stalk is only sparsely ciliated (Fig. 17). The cilia are of the usual cylindrical type. These cilia are much longer than those on other regions of the zooid. It is very rare to find paddle-like endings of large swellings of the shafts. However, there are smaller swellings along the lengths of the shafts and the direction of the shaft usually changes abruptly at each swelling. The cilia usually arise singly and widely spaced but an occasional clump of cilia

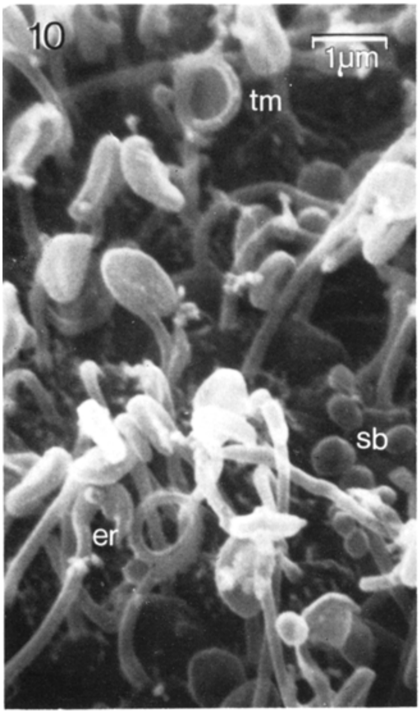
Fig. 10. Details of some cilia from the central region of the cephalic shield. Several sorts of ciliary endings are seen as well as an empty complete revolution of the ciliary shaft. On the surface of the underlying cephalic shield cells a patch of spherical bodies are visible

Fig. 11. A juxta terminal drip on a cilium suggesting that the major part of the content of a large swelling has somehow been discharged

Fig. 12. The cilia in the mouth region showing asymmetric swelling as 90° bends in the ciliary shafts, some containing spherical enlargements and others without them. The distal fragments become narrower abruptly. One swelling has a large particle attached to its surface

Fig. 13. Another possibly partially discharged terminal swelling that has lost less of its content than the cilium in Figure 11. The adjacent ciliary terminals have long tapers and tiny terminal blebs

Fig. 14. Two mid shaft swellings are apparently full and one apparently discharged tapered end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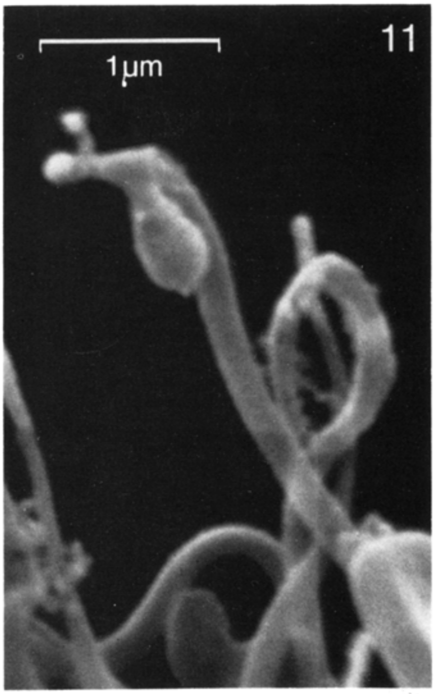
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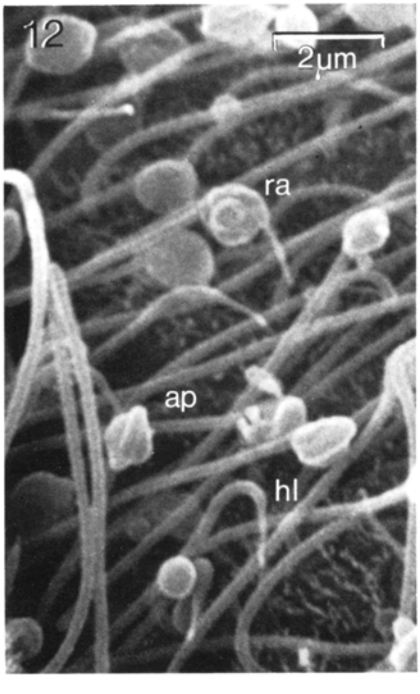
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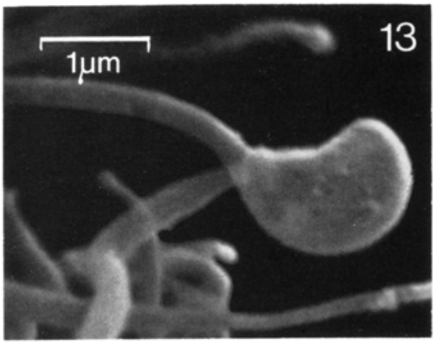
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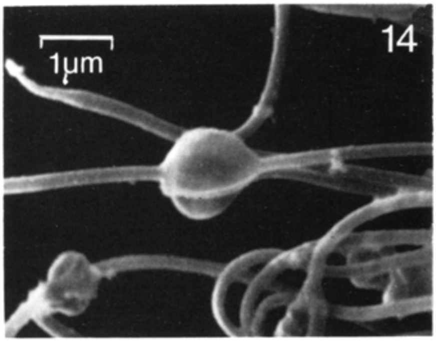
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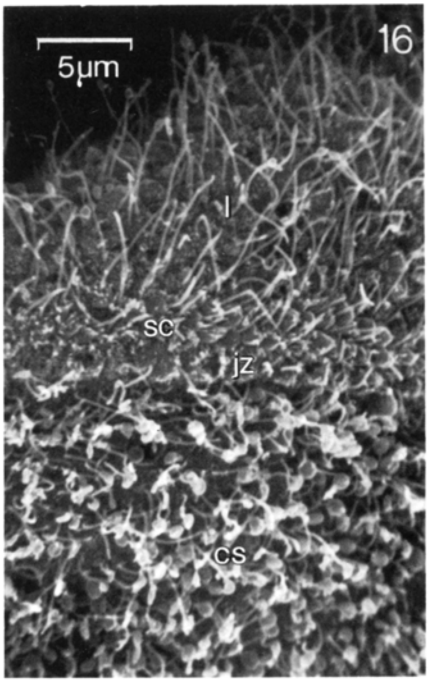
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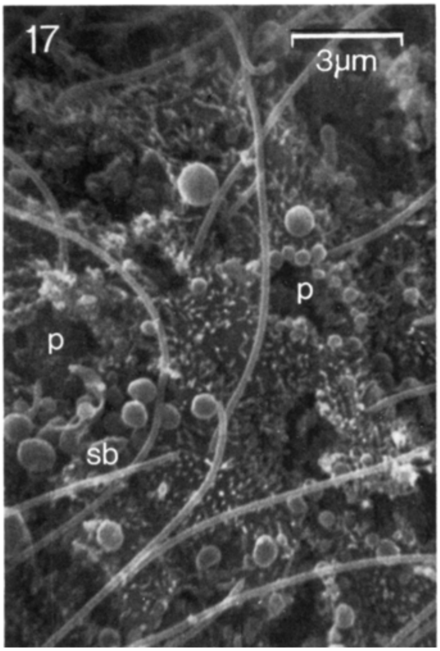
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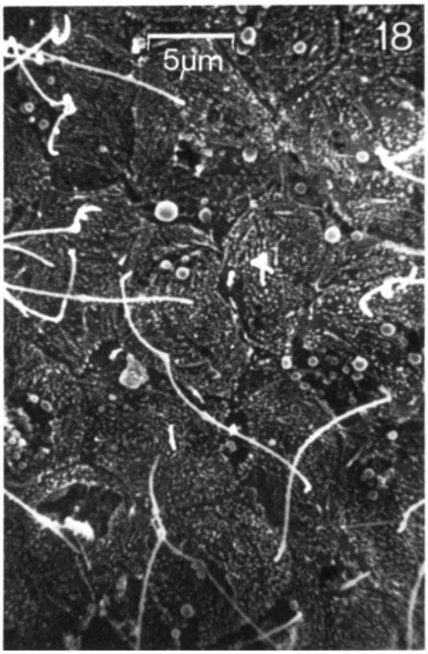
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is seen. The cilia bearing surface is confined to one half of the circumference. The surface of the stalk has a scattering of small blebs amongst these cilia, apparently attached to the cell surface upon its covering of microvilli. These spherical bodies of the same dimensions are some of the blebs associated with the ciliary shafts. It is attractive to suggest that these blebs are associated in some way with the ciliary swellings and their functions. There are holes in the surface of part of the body and stalk and around these holes there appears to be a concentration of spherical bodies. It is tempting to speculate that these particles are secreted by glands and we are observing them around the orifices of the glands before they are transported by the cilia.

It is surprising to find such long cilia on the muscular stalk, since the stalk during life is buried deep within the tubular coenecium and confined within its narrow channels. Presumably the main function of these cilia is to produce currents around the stalk and to move the fluid within the tube. The large number of swellings on the cell surfaces may be involved in the building of the thick tough black stolon that can surround the stalk for the major part of its length and may be long cilia are needed to plaster within such narrow confines.

The Body

The body is sparsely ciliated with cilia of very similar form to those of the stalk. These cilia are long and thin. The shafts typically have a regular cylindrical profile without terminal clubs of paddles. There are odd profiles along the shaft but they are tiny compared with those of the cephalic shield and do not have the smooth outline. Rather, they are slight irregular ovoid bulges not much more than 0.4 µm wide at their maximum diameter, and about 0.75 µm long. The direction of the shaft often changes as it traverses the swellings. Occasionally, there are terminal swellings. These swellings are much smaller than those of the shield and tentacles. The surfaces of the cells that bear the cilia are sparsely covered with microvilli and radiating across their surfaces there are a few fold-like ridges, the functions of which are not known. So far no particular regions of the body have been studied in detail, but the cilia around the mouth and anus are much more densely packed than those covering the rest of the body.

Fig. 15. Survey micrograph from the central region of the cephalic shield of *Rhabdopleura* showing the density of cilia and the mixture of cilia with and without terminal swellings

Fig. 16. A part of the junction between the encircling lip and the body of the cephalic shield. The contrast between the long, mainly regular cilia of the lip and the short spatulate cilia of the major part of the shield is well shown. There appears to be a row of cobblestone-like cell surfaces that help to delineate the junction

Fig. 17. Cilia on the stalk of *Rhabdopleura*. These cilia usually have regularly cylindrical shafts, but the cells have many spherical particles on their surfaces. These particles are associated with holes in the cell surfaces that may be glandular apertures

Fig. 18. A long cilium from the body of the zooid of *Rhabdopleura* showing several small swellings of the shaft along its length. The body, like the stalk, is only sparsely ciliated but with relatively very long cilia

Discussion

There are several observations that suggest that material is transported in two ways; either within the ciliary membrane, or along the outside of the ciliary shaft. There is evidence that the intracellularly transported particles become incorporated in the coenecium because broken off ends of cilia containing the swellings with about 1 μm of proximal shaft have been seen adhering to the outer surface of the coenecium. The idea that this is indeed a transport mechanism is supported by the observation of swellings at all positions along the lengths of the shafts, suggesting stages in movement along them. It is tempting to suppose that the reason why most swellings are found within the distal 1–2 μm of the shaft is that they have reached the end of the shaft and are being stored there ready for use. This would indeed illustrate an extreme case of intracellular transport.

The transport of materials within cells and along cellular processes is well established. Transport along the lengths of such relatively enormous extensions of the cell membrane as axons are becoming well understood. Transport along the length of a cilium should not present any unique problems, although its narrow transverse shaft dimensions may be thought to be a constraint. The filaments within a cilium could well act as material guides in a similar way to neurotubules and neurofilaments. Microtubules have a well known role in the intracellular translocation of organelles such as chromosomes and melanin granules. Schmitt (1968) suggested that in axons vesicles might be translocated along axons sliding along the surfaces of microtubules. Microtubules with side arms are the fundamental components of the axoneme and these tubules that are undoubtedly involved in generating force for cilia or flagellar movement may well prove both the guides and the source of the force that moves the material along the ciliary shaft.

The distension of the cell membrane over the ciliary shaft could represent a package of material being transported along the length of the shaft or specific storage areas. These swellings could either be broken off in packets and then deposited upon the substrate, or secreted somehow by rupture of the ciliary membrane. The ends of some cilia are known to break off. Afzelius (1969) has observed the anterior cilium of *Ceratium* breaking up into small beads, so there is in some cilia at least, a mechanism to break the shaft. T.E.M. sections of these enlargements do not show any electron dense contents of the swelling other than the usual 9 + 2 filaments. This could be interpreted either that the transported materials were not electron dense, or had been removed during processing. The idea that these enlargements are a dynamic transport mechanism depends upon the interpretation of a series of static micrographs. It may be that these swellings are permanent features in the ciliary membrane, and are inert discs that are manipulated by the ciliary shaft to act as spatulae. Such an alternative interpretation does not satisfactorily explain those swellings that are not at the distal tip of the cilium.

Secondly, some of the spherical swellings appear as if they are stuck to the ciliary surface and are independent of the ciliary membrane. These bodies may either be the surface spherical bodies being transported from the cell surfaces to the coenecium, or they may represent material attached to the cilium from some other source. These particles somehow stick to the surface but are moved along it proximal to distal. It is possible that the cilia adjacent to the one to which the body is attached act in some way to push it along the shaft towards the distal tip.

Most of these juxta-ciliary blebs are partially surrounded by a curve of the associated ciliary shaft. The curves of the ciliary shafts that surround the blebs must have a definite structural change, for it is possible to observe cilia with the correct ciliary curve to enclose the bleb, but the bleb is missing, suggesting that it has been deposited or become removed or dislodged during preparation. Cilia do bend along their shafts when they beat, and a modification of such a bending mechanism could easily provide a means of moving the spherical particle along the shaft. The stalk is the region where it is easiest to find evidence for this hypothesis. Here it is possible to see the spherical bodies accumulated around the apertures of glands. These swellings are of approximately the same dimensions as the enlargements of the cilia, suggesting that somehow they get picked up from the cell surface in a loop of cilium and transferred in that way. However the stalk is an odd source of material to be incorporated in the outside of the coenecium, and it is more likely that material from this particular source gets deposited upon the inside, during thickening of the tube and in making the stolon or dormant bud capsules (Dilly, 1975). It is probable that in other regions of the zooid the source of the particles is obscured by the density of the cilia.

It is possible to find associated with a small number of each of the examples of the shaft enlargements smaller irregular particles 0.5–1 μm in diameter and apparently stuck to their surfaces. Rarely, similar such small particles are also found adhering to the uniform proximal shafts of cilia, but more frequently to the apparently discharged tapering distal tips of the tentacular cilia. Some of these small particles are probably the remnants of the transported material.

If these transport mechanisms exist then the source of the transported material is derived from at least two sources, one from within the cilia bearing cell and passed up the ciliary shaft, and in the other the material is first secreted onto the zooid surface from gland cells and then picked up by cilia.

The other function of the cilia on the tentacles is to assist in feeding. It is surprising that if the cilia trap prey then no recognisable animals or plants are seen amongst them. It is hard to believe that all the prey would be roughly spherical in shape and membrane bounded, unless of course it has become enclosed in a cell membrane vacuole. The cilia have been observed to beat in waves (Stebbing and Dilly, 1972) and perhaps the paddle-like extensions of the cilia set up more effective feeding currents. Although it is possible to observe currents in the water created by the tentacle cilia, and this may be one way of wafting food particles towards the mouth, it is also possible that the paddles are sticky. If they were sticky, then the enlargement of the shaft would present a greater surface area upon which material might become trapped. In support of this idea, tiny particles are frequently seen adhering to the surfaces of the enlargements, but the mode of transport from cilium to cilium would need explanation.

Whether the ends can also act as minute spatulae in the way suggested by Tamarin et al. (1974) and plaster secretions onto the forming coenecium is not known, but seems likely. If it could be shown that not only the cephalic disc but also the tentacles were involved in making the coenecium then this would considerably extend the surface area of the zooid that is involved in tube building. This would add support for the idea that the tubes are built by the zooid hanging out of the tube and adding material to the outside, and extrapolating from *Rhabdopleura* to the graptolites would suggest an alternative to Urbanek's (1976) idea that the tube in graptolites is secreted by a membrane that covers the tube. Several hypothetical reconstructions of the graptolite zooid have suggested that it has a lophophore and a cephalic shield. Recently Crowther (personal communication) has observed a bandaging effect in the walls of several graptolite thecae, and it is tempting to suggest that these bandage-like strips each represent one secretory effort of the cephalic shield-lophophore complex. If we can involve the lophophore as well as the cephalic disc that both have spatulate cilia in tube secretion, both in *Rhabdopleura* and the graptolites, then we have a much more convincing mass of tissue involved in tube construction and can probably avoid the need to speculate that there is also a tube secreting membrane outside the graptolite theca.

The idea that the paddles are in some way associated with a sticky material is provoked by Tamarin's observation of similar cilia in the byssus attachment secreting area of *Mytilus*. In *Rhabdopleura* the repent part of the coenecium is well stuck to *glycymeris* shells and my observations of similar cilia on *spirorbis* which also secretes a tube that is well stuck down to substrate (Dilly unpublished) suggest that it may be that many glueing secretions are handled by spatulate cilia.

It is known that the tube-making worm *Owenia* revolves in the tube, and the setae of the gland-bearing segments act as brushes for applying the secretion to the wall as it flows from the duct openings. Maybe the cephalic shield acts as a mould in which the secretion hardens, while the spatulate cilia mould the material to shape. A similar moulding technique is known from *Sabella* (Nicol, 1930).

In *Rhabdopleura* the spatulate endings of the cilia would be more efficient at plastering the sticky secretions onto the coenecium than would the usual cylindrical shafts of the more common types. Whether the blebs themselves contain the sticky material or are merely passive is not known. These cilia have been observed to beat with a metachronal wave during feeding, and when the tentacles are extended free into the water above the erect tube (Dilly, 1972). The activity of the cilia has not been observed during tube building, but it is of interest to speculate that the metachronal wave organisation may be replaced with a much more random type of beat such as has been observed in the specialised cilia of the distal depression in *Mytilus* (Tamarin et al., 1974). T.E.M. sections close to the surface of the zooid tentacle show that the central pair of tubules are arranged with their axes in the same general direction and not randomly as in *Mytilus*. The neurociliary control needed to superimpose a random movement upon these specialised cilia must be quite different from that required for the more usual rhythmic activity, and if such random movements can be observed in *Rhabdopleura* then it may be that further study of its neurociliary control mechanisms will add significant understanding to our knowledge of the nervous and other control of ciliary activity.

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Accepted January 17, 1977