J. Cell Sci. 9, 569–579 (1971)
Printed in Great Britain

ULTRASTRUCTURE OF PSEUDOCILIA IN *TETRASPORA LUBRICA* (ROTH) AG.

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SUMMARY

The flagella-like, but immobile, pseudocilia of the unicellular green alga, *Tetraspora lubrica*, have been characterized ultrastructurally and compared with the true flagella of the motile green alga, *Chlamydomonas*. The basal body and transitional regions of the 2 organelle systems are basically similar. Most of the marked differences occur in the pseudocilium proper, and a few important dissimilarities are found in the cytoplasmic portions of the apparatus. The major differences are: (1) 4 instead of 2 proximal striated fibres in the pseudociliary apparatus; (2) a proximal-to-distal progressive decrease in subfibre number from 9 doublet fibres to a solitary fibre in the pseudocilium proper; (3) loss of interconnexions among the subfibres in the pseudocilium proper and a concomitant disorientation of those subfibres; (4) absence of major arms (dynein) on the A subfibre of peripheral doublets; (5) absence of the central pair of fibres. These and other differences are discussed with regard to their possible roles in loss of motility. Additional ultrastructural details – interconnexions between cytoplasmic microtubules and basal body subfibres of pseudocilia and flagella – are described and discussed in terms of their possible roles in the regulation of flagellar movement in motile organisms.

INTRODUCTION

Although similar morphologically to the unicellular green alga *Chlamydomonas*, cells of *Tetraspora* are non-motile, often embedded in a gelatinous matrix and are characterized especially by the presence of pseudocilia – flagella-like, but immobile, organelles that extend anteriorly through the matrix.

Modified cilia or flagella (those deviating from the typical 9+2 fibre configuration) are common in many kinds of animal cells (Dahl, 1963; Lom & Corliss, 1968; Phillips, 1969), but in plants they have been reported thus far only for diatom sperm (Manton & von Stosch, 1966), haptonema of some golden-brown algae (Manton, 1967), certain paralysed mutants of *Chlamydomonas* (Randall *et al.* 1967), and several members of the *Tetrasporaceae* (Lembi & Herndon, 1966; Wujek, 1968).

Investigations of atypical or non-functional organelles may provide insights into the structural bases for function, when the impaired organelles are compared with normal, functional organelles and the differences noted. Thus, comparison of the pseudociliary apparatus of *Tetraspora* with the flagellar apparatus of *Chlamydomonas* seems especially appropriate since there are gross similarities in cellular morphology and in structure of flagella and pseudocilia at the light-microscopic level. There are

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also possible evolutionary relationships between the organisms and thus between the 2 organelles, as suggested by the existence of other unicellular green algae with intermediary characteristics – e.g. *Tetrasporidium* is embedded in a gelatinous matrix, but retains true flagella (Fott, Nováková & Kalina, 1965). The flagellar apparatus of *Chlamydomonas* has been described recently by Ringo (1967*a*) and can serve as a model with which the pseudociliary apparatus of *Tetraspora* can be compared.

MATERIALS AND METHODS

Culture techniques

Axenic cultures of *Tetraspora lubrica* (Roth) Ag. were grown in Bold's modified Bristol's medium (BBM) (Bischoff & Bold, 1963) without $NaNO_3$ in 125-ml, cotton-stoppered flasks on an Eberbach reciprocating shaker and were regulated on a 16–8 h, diurnal cycle, with a light intensity of 150 ft.c. (515 lx) and a temperature of about 21 °C. Illumination was provided by 40-W cool-white fluorescent lamps.

Electron microscopy

Cells were fixed in 2 % glutaraldehyde-2 % acrolein buffered with 0·05 M s-collidine, pH 7·4, for 1 h at room temperature, rinsed well in buffer, post-fixed in s-collidine-buffered OsO_4 (1 %) for 1 h at room temperature and left overnight in cold uranyl acetate (0·5 %, aqueous). Following dehydration in a graded series of ethanol and acetone, cells were embedded in a mixture of Epon and Araldite as described by Mollenhauer (1964). Sections were cut on a Sorvall MT-2 ultramicrotome, stained with uranyl acetate followed by lead citrate, and examined with a JEM-6C electron microscope.

OBSERVATIONS

The pseudociliary apparatus consists of the cytoplasmic (root) microtubule system, striated fibre system, basal body, transitional region, and pseudocilium proper (Fig. 1). Since the morphology of *Tetraspora* is similar to that of *Chlamydomonas*, the terminology used in the present investigation follows closely that used by Ringo in his study of *Chlamydomonas* (1967*a*).

Cytoplasmic (root) microtubule system

Four bands of microtubules, arranged in a cruciate manner, originate near the midpoint between the 2 basal bodies. In the area near the basal bodies, transverse sections of each band reveal a 3 over 1 configuration of microtubules (Fig. 2) similar to that reported in *Chlamydomonas*. As a band approaches the outermost portion of a basal body, 2 microtubules end abruptly (the bottom microtubule in the 3 over 1 pattern and the microtubule farthest from the basal body) leaving a 2-membered band (Fig. 2, inset). The microtubule closer to the basal body is designated microtubule 1; the microtubule farther from the basal body is designated microtubule 2.

Electron-dense interconnexions between basal bodies of pseudocilia and cytoplasmic microtubules have been described recently by Lembi & Walne (1969). Additional data on the sequence in which the interconnexions appear along the length of each microtubule band are now reported.

As the 2-membered band approaches the basal body, an arm-like projection

extends from microtubule 1 toward the basal body (Fig. 2, inset). The microtubule band subsequently passes over the proximal fibre, and at this point (Fig. 3) the projection from microtubule 1 plus a now-visible projection from microtubule 2 extend into the proximal fibre (Fig. 3).

As the band continues toward the midpoint between the 2 basal bodies, the distal striated fibre appears and only a portion of the proximal fibre remains in the plane of section (Fig. 4). At this point, the projection from microtubule 1, extending at a 45° angle, is no longer attached only to the proximal fibre but now inserts into the basal body subfibre at its juncture with the proximal fibre (Fig. 4). Even when the proximal fibre is no longer visible at all, the interconnexion between microtubule 1 and the basal body subfibre is still evident (Fig. 5). Only microtubule 1 retains its arm as the band continues below the distal fibre. The arm on microtubule 2 is evident only in those planes of section in which a major portion of the proximal fibre is also evident. Additional projections connect the 2 component microtubules to one another throughout the length of the 2-membered band (Figs. 2, inset, and 3, 5). At the very tip of the band, the 2 microtubules terminate, microtubule 2 ending first (Fig. 5, inset). Microtubule 1 retains its projection until it, too, ends beneath the distal striated fibre near the midpoint between the 2 basal bodies. No connexion has been observed linking the separate microtubule bands to one another.

Fibre system

The single distal striated fibre connecting the 2 basal bodies generally appears electron-opaque; however, in favourable sections, its striated nature is evident (Fig. 5, arrowheads). The same fibre in horizontal longitudinal section (Fig. 6) displays at least 3 definite striations of equal density (Fig. 6, arrowheads) and dimension. Examination of other micrographs reveals that at the region where it attaches to the basal body, the distal fibre is tripartite in outline. Each protuberance directly abuts 1 of 3 adjacent triplet fibres. No arm-like interconnexions have been observed between the basal body subfibres and the distal fibre.

Two other fibres, the proximal fibres, are attached to the lowermost end of each basal body (Fig. 7). Horizontal longitudinal sections (Fig. 7) of this region reveal that the 2 proximal fibres on 1 basal body are in close proximity to the corresponding 2 fibres of the other basal body; however, the matching fibres are not connected to one another as they are in *Chlamydomonas*.

Basal body and transitional region

These components of the pseudociliary apparatus appear to be identical to the respective structures in *Chlamydomonas*.

Pseudocilium proper

The lowermost region of the pseudocilium proper is characterized by the termination in the transitional region of the H-piece and the 9-pointed star. Transverse sections of this region demonstrate the appearance of fine interconnexions (hereafter

termed the minor arms), which are identical to those described by Allen (1968) in *Tetrahymena*, and which link adjacent doublet fibres to one another (Fig. 8, arrow). In decided contrast to *Chlamydomonas*, the central pair of fibres is lacking in *Tetraspora*.

Although the 9 peripheral doublet fibres may extend farther into the pseudocilium proper, the termination of some subfibres usually ensues just distal to the 9-pointed star. The sequence of termination begins with the loss of one subfibre from a doublet (Fig. 8, arrowheads) and continues with the loss of one subfibre from the adjacent doublet. This pattern of termination proceeds sequentially around the circle of doublets. Concomitant with the transition of doublets to single fibres is the loss of the circular orientation of fibres (Fig. 9). The disorientation of a fibre is accompanied by the loss of the minor arm which links it to the adjacent fibre (Fig. 8, line).

Transverse sections which show the pseudocilium proper just distal to the cell wall reveal that, in most instances, 9 single subfibres are present (Fig. 10). The arrangement is roughly that of 8 subfibres surrounding a central subfibre. As the more distal portions of the pseudocilium are examined, the subfibres gradually terminate, and the surrounding membrane contracts or draws in around the remaining subfibres (Figs. 11, 12). Transverse sections of a single subfibre per pseudocilium have been observed; presumably this configuration represents the tip of the pseudocilium. A specialized tip with an electron-dense plate separating the 2 remaining subfibres, as is found in *Chlamydomonas*, is not observed in *Tetraspora lubrica*.

Transverse sections of the pseudocilium proper show that the subfibres are composed of subunits typical of flagellar and ciliary subfibres (Phillips, 1966; Ringo, 1967*b*) (Fig. 8). Contrary to the situation found in the flagella and cilia proper of many organisms (Gibbons & Grimstone, 1960; Allen, 1968), the ATPase-containing arms (hereafter termed the major arms) which would extend from the A subfibres are not present. Longitudinal and transverse sections reveal very fine filaments which extend from the subfibres toward either the pseudociliary membrane or the other subfibres (Figs. 13, 14). These filaments, however, are not arranged in an orderly manner as they are in *Chlamydomonas* (Ringo, 1967*a*) in which filaments appear between the central and peripheral fibres and between the peripheral fibres and the flagellar membrane.

DISCUSSION

Variations of subfibre number are not common in flagella of plant cells, although a variety of subfibre patterns do occur in the cilia and flagella of many animal cells (Satir, 1962; Dahl, 1963; Lom & Corliss, 1968; Phillips, 1969). Most studies of modified cilia and flagella have dealt largely with descriptions of structure; only a few have provided information on the existence and/or function of the major and minor arms on the subfibres (Dahl, 1963; Boquist, 1968; Phillips, 1969; Kiefer, 1970). Those data, plus the present investigation, suggest that the presence of major and minor arms is integral to the orientation of the subfibres within the organelle.

Dahl (1963) discerned 2 fibre patterns in the cilia of the cerebral cortex of the rat

– a 9+0 pattern in which the 9 peripheral fibres retain their major arms, and an 8+1 arrangement, which originates from the shifting in position of 1 of the 9 peripheral fibres to a central position. He also reported the loss of major arms from all of the doublet fibres and suggested that the arms normally hold the fibres together in a ring and that loss of the major arms leads to the disorientation of fibres within the cilium.

The scattered arrangement of doublet fibres within a modified cilium or flagellum is clearly discernible in the present study and in 2 other investigations (Boquist, 1968; Phillips, 1969), in which the doublet fibres either lack major arms or possess only 1 major arm. In the last 2 studies, the minor arms, apparently, are missing. Although the major arms are absent from the 9 ring-oriented fibres shown in Fig. 8, the minor arms are present between all but one pair of doublets in *Tetraspora*. Where the interconnexion is missing, 1 of the 2 doublets has lost its alignment in the ring. Thus, disorientation of peripheral fibres is probably not due to a loss of major arms as Dahl (1963) suspected but rather to the disruption of the minor arms. That the major arms (dynein) play no role in keeping the doublet tubules in a ring has also been suggested by the work of Gibbons (1967) and of Kiefer (1970). By his fractionation work, Gibbons has shown clearly that dynein could be removed from the axonemes and the doublets would still retain their circular configuration. Kiefer, in studying the degeneration of sterile sperm flagella in a *Drosophila* mutant, noted that the loss of interconnecting minor arms between doublet fibres was accompanied by the disorientation of the axonemal components.

Although major and minor arms are missing in *Tetraspora*, the presence of very fine filaments that appear to link subfibres to one another and to the flagellar or ciliary membrane has been noted in the present study. Examination of micrographs from other studies of modified cilia (Reese, 1965; Dickson, 1966), reveals the presence of similar filaments in other organisms as well. The filaments in *Tetraspora* may correspond to those located in comparable positions in the flagella of *Chlamydomonas* as described by Ringo (1967*a*) and to the radial links observed in unmodified cilia of several other organisms (Gibbons & Grimstone, 1960; André, 1961; Doolin & Birge, 1966). The filaments found in *Tetraspora* are not, however, arranged at regular intervals along the length of the subfibres; they are scattered and, in fact, often lacking in many longitudinal sections of the pseudocilium proper.

The present investigation has brought to light several structural modifications which may account for, or be related to, the loss of motility: absence of major arms on the A subfibre, absence of the central pair of fibres, progressive loss of minor arms and concomitant disorientation of peripheral subfibres, presence of interconnexions between cytoplasmic (root) microtubules and pseudociliary basal bodies, 4 (instead of 2) proximal striated fibres and a distal striated fibre with uniformly electron-dense band instead of a pattern of light and dark bands as in *Chlamydomonas*.

The reason for the loss of motility in *Tetraspora* and other organisms is not readily apparent, however, and most probably cannot be attributed to any one of the above-mentioned structural differences. Ultimately, interactions between complex genetic and environmental factors must be considered. In fact, some of the above

modifications may be ruled out as the single causal factor when the work of other investigators is considered. For example, Randall *et al.* (1967) showed that flagella of immobile mutants of *Chlamydomonas* display major arms on the A subfibres and also possess the amount of ATPase (dynein) common to normal flagella. Manton & von Stosch (1966) reported that flagella of actively motile diatom sperm lack the central pair of fibres. Thus, it appears that the presence or absence of major arms (dynein) and/or central fibres are not, in themselves, the determining factors in motility.

Interconnexions between root microtubules and basal bodies have been reported in *Tetraspora* (Lembi & Walne, 1969) and observed by us in *Chlamydomonas*. Similar projections – namely, the major arms which extend from the A subfibres in cilia and flagella (Gibbons & Rowe, 1965), the arms which extend from myosin filaments of muscle fibres (Huxley, 1969), and arms which connect adjacent spindle fibres (Wilson, 1969) – have been hypothesized to be sites of ATPase. It is also possible that the basal body-microtubule interconnexions may also be sites of ATPase localization. If so, their presence becomes highly significant in cellular motility. Although the interconnexions have been described for non-motile pseudocilia, these data might well be extrapolated for motile organisms, since similar projections have been observed in micrographs of motile flagella. Thus, in a manner not too different from that suggested by Huxley for muscle contraction (Huxley, 1969), flagellar contraction may be effected by some mechanism which induces a sliding force between adjacent microtubles and basal body subfibres. The interconnexions as ATPase, could serve as cross-bridges between the 2 and could somehow be involved in generating that force.

The available biochemical data on these structures are too sparse at present to permit more extensive speculation on their specific roles in motility; the same may be said for the proximal and distal striated fibres. Loss of the minor arms, together with disorganization of subfibres may be the critical factors in loss of motility. To our knowledge, there are no reports of motile cells, plant or animal, which exhibit disordered arrays of subfibres in cilia or flagella. On the other hand, some immobile flagella do exhibit well ordered substructure (Randall *et al.* 1967). Thus, we must reiterate that loss of motility is probably not a consequence of a single causal factor.

This investigation was supported in part by an NDEA TITLE IV Predoctoral Fellowship to the senior author and by a University of Tennessee Faculty Research Grant and a University of Tennessee Biomedical Sciences Support Grant No. 1101R-01 to the junior author.

Contribution No. 354 from the Department of Botany, The University of Tennessee, Knoxville.

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(*Received* 1 *October* 1970—*Revised* 8 *January* 1971)

Fig. 1. Two pseudocilia (*ps*) extend anteriorly in a V-shaped manner through openings in the cell wall (*cw*). Other visible components of the pseudociliary apparatus are the transitional region (*tr*), characterized by the H-piece (arrow), the basal body (*bb*), and the distal striated fibre (*df*). × 24500.

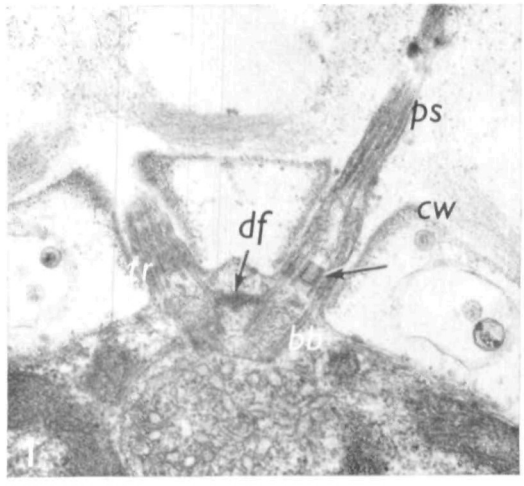
Figs. 2–5. Electron micrographs of the microtubule band in the region of the pseudociliary basal bodies of *Tetraspora lubrica*.

Fig. 2. A 3 over 1 configuration of microtubules is evident when the microtubule band (*mb*) is in the area near the pseudocilium. Note pseudociliary sheath (arrow). × 130000. Inset: At a point slightly closer to the basal body than in Fig. 2, 2 of the microtubules have terminated, leaving 2 microtubules per band. Note the electron-dense plate above the microtubules and the projection (arrow) which extends from microtubule 1. The microtubules are also connected to one another. × 180000.

Fig. 3. Longitudinal section through a basal body (*bb*) and transitional region (*tr*) of a pseudocilium. A portion of the proximal striated fibre (*pf*), seen in longitudinal section, is connected to 2 microtubules of a band by prominent arms (arrowheads). Interconnexions between the proximal fibre and a subfibre of the pseudociliary basal body are shown (arrow). Note the dense striations of the proximal fibre. × 105000.

Fig. 4. Longitudinal section through a pseudociliary basal body at a point closer to the midpoint between the 2 basal bodies than in Fig. 3. Portions of the distal (*df*) and proximal (*pf*) striated fibres are seen in longitudinal section. A prominent arm extends at an angle of about 45° from the upper microtubule and appears to insert (arrow) at the coarctation of the proximal fibre and basal body subfibre. (*bb*, basal body; *tr*, transitional region.) × 103500.

Fig. 5. Longitudinal section through the basal body (*bb*), transitional region (*tr*), and distal striated fibre (*df*). The proximal striated fibre is just out of the plane of section. Note the prominent arm (arrow) which connects the microtubule to the basal body subfibre, and the striated nature (arrowheads) of the distal striated fibre. × 200000. Inset: longitudinal section through the basal body (*bb*), and distal fibre (*df*) at a point very near the midpoint between the 2 basal bodies. Only 1 microtubule and projection arm are present. The end wall of the second microtubule is visible (arrow). × 111000.



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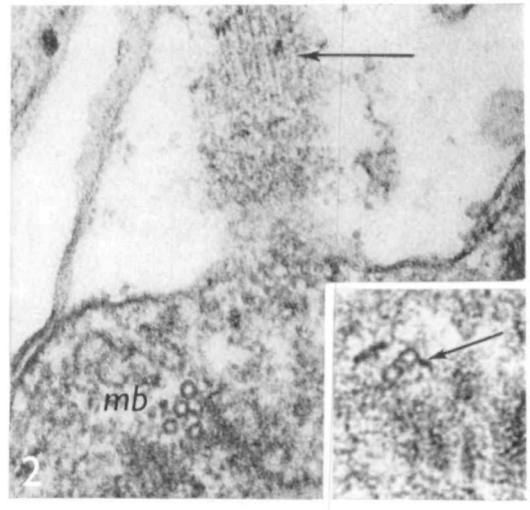

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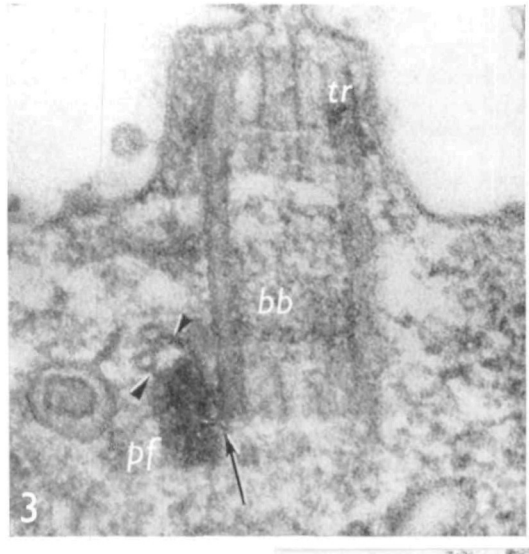

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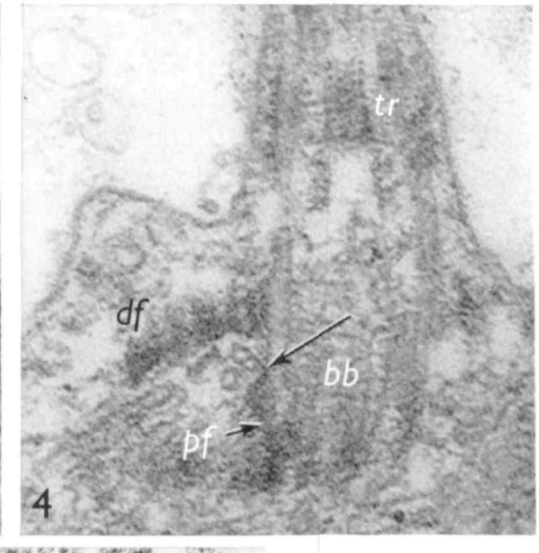

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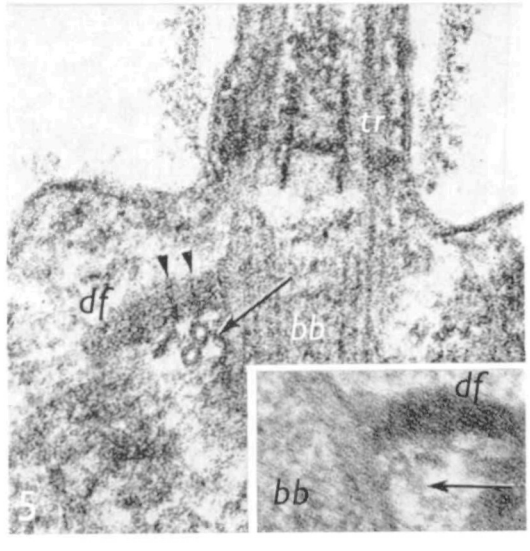

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Figs. 6, 7. Electron micrographs of the distal and proximal striated fibres of *T. lubrica*.

Fig. 6. Horizontal longitudinal section of the distal striated fibre. The 2 basal bodies (*bb*) are seen in oblique transverse sections. At least 3 of the dense bands (arrowheads) which comprise the distal fibre are evident. × 140000.

Fig. 7. Horizontal longitudinal section of the 4 proximal fibres (*pf*). Although in close proximity, the fibres of the adjacent basal bodies (*bb*) are not connected to one another. × 54000.

Fig. 8. The level of section is just distal to the 9-pointed star. Note the termination of 2 of the subfibres (arrowheads), the fine arms connecting all of the doublets but one to each other (arrows) and that where the interconnexion is missing, the doublet has lost its orientation in the ring (line). × 270000.

Fig. 9. Several of the subfibres have terminated in this section, which is distal to that shown in Fig. 8. Note the disorientation of the fibres and subfibres. The striated nature of the channel is evident. × 111000.

Figs. 10–14. Electron micrographs of the pseudocilium proper distal to the channel in *T. lubrica*.

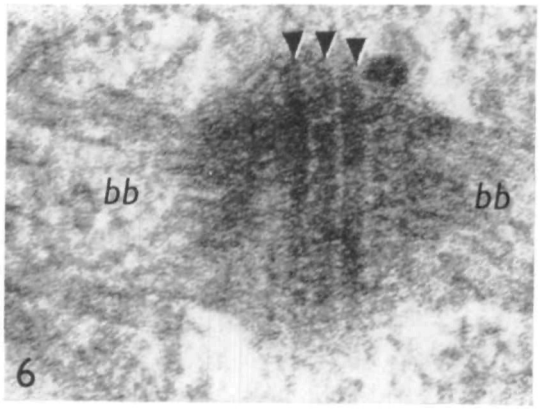
Fig. 10. Nine subfibres are present in the pseudocilium in a section just distal to the channel; 8 subfibres surround a central subfibre. × 105000.

Fig. 11. Seven subfibres are evident. The subunits of which the subfibre is comprised are evident. × 162000.

Fig. 12. Two pseudocilia, each with 4 subfibres, are shown. × 80000.

Fig. 13. Very fine arms (arrow) extend from the subfibres to the pseudociliary membrane. × 140000.

Fig. 14. Longitudinal section of the pseudocilium proper. Fine arms (arrows) extend between subfibres. × 126000.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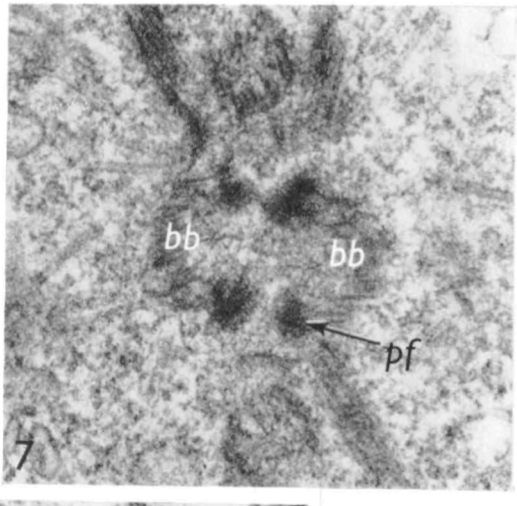
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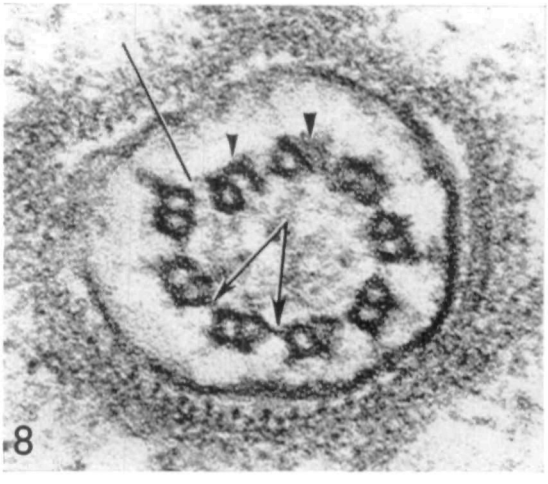
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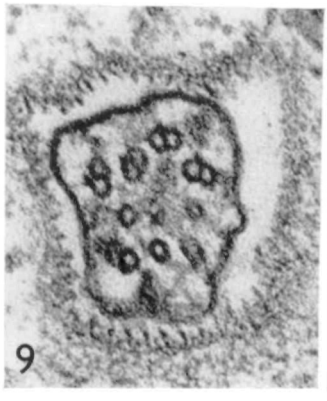
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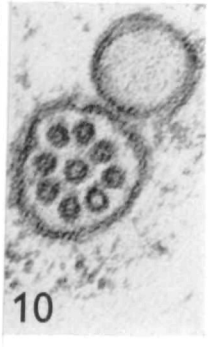
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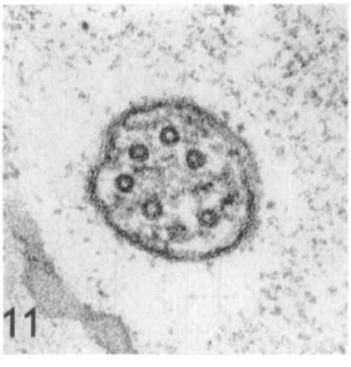
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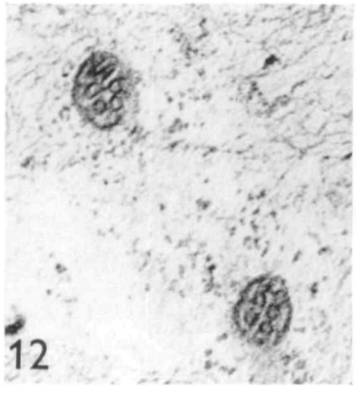
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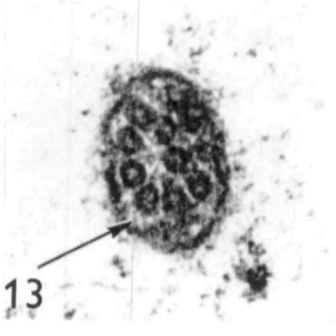
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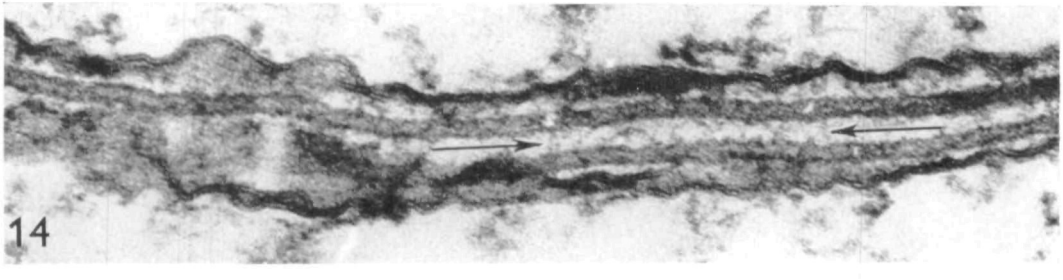
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