MICROTUBULE ARMS AND CYTOPLASMIC STREAMING AND MICROTUBULE BENDING AND STRETCHING OF INTERTUBULE LINKS IN THE FEEDING TENTACLE OF THE SUCTORIAN CILIATE TOKOPHYRA

J. B. TUCKER
From the Department of Zoology, The University, St. Andrews, Fife KY16 9TS, Scotland

ABSTRACT
Microtubules attached to the pellicle at the tips of tentacles pivot through about 140° on these attachments, splay apart, and bend along their longitudinal axes when feeding occurs. The tubules could be bending in response to pellicular contractions; active bending, sliding, or contraction of the tubules may not be involved. Intertubule links apparently prevent tubules from splaying apart at certain levels. These links are probably under tension during feeding. They stretch; they sometimes become half as thick and eight times as long as they are before feeding. Often, tubules joined together by these links also change in shape; they become slightly flattened and elliptical in cross section.

Cytoplasm from the ciliate Tetrahymena is drawn down a feeding tentacle inside an invagination of the Tokophrya cell membrane from the tentacle tip. The positions of arm-bearing microtubules around such invaginations indicate that arms are involved in moving invaginations along. The edges of the perforated Tetrahymena cell membrane are "sealed" to the cell membrane of Tokophrya around each feeding tentacle tip.

INTRODUCTION
Microtubules are often spatially associated with intracellular components which are being translocated from one cytoplasmic region to another. It has been suggested that armlike structures projecting from the walls of neurotubules may be involved in moving materials along nerve axons (Smith, 1971; Fernandez et al., 1971). Recently, the author pointed out that the microtubular cytopharyngeal portions of the feeding organelles of most ciliates are lined by rows of arm-bearing microtubules and suggested that it is these tubules in particular which may be most directly involved in drawing food materials into these organisms (Tucker, 1972). Simultaneously, and independently, Bardele (1972) came to a similar conclusion for the arm-bearing microtubules in suctorian tentacles. This study of Tokophrya tentacles provides further evidence for such involvement.

The organization of suctorian tentacles also merits special attention because they are the only microtubular organelles so far described for which microtubule bending, as well as marked changes in microtubule arrangement and packing, occurs, while cytoplasm streams in the vicinity of the tubules (Rudzinska, 1965, 1970; Batisse, 1967; Bardele and Grell, 1967; Bardele, 1972). Examination...
tion of these changes, which are probably not directly related to the flow of cytoplasm along tentacles, provides the first demonstrable instance of a situation where intertubule links stretch and change in shape. It has usually been assumed that the links which connect adjacent tubules in microtubule bundles are rigid skeletal elements which assist in maintaining the structural integrity of the arrays (Tucker, 1972) and help to define the rather precise positioning of tubules relative to each other during development (Tilney, 1971).

MATERIALS AND METHODS

The free-living freshwater suctorian *Tokophrya* was collected from mud and other detritus included in consignments of the freshwater oligochaete *Tubifex rivulorum* supplied by St. Martin's Aquaria, London. The main structural features of the species used closely resemble those of *Tokophrya infusionum* which has been described by other workers, particularly by Rudzinska and her colleagues (Rudzinska, 1965, 1967, 1970, 1973; Hascall and Rudzinska, 1970). There is no detailed systematic publication dealing with freshwater suctorians; the species to which the *Tokophrya* studied here belongs has not been ascertained.

Petri dishes lined with 2% (aqueous) agar and filled with glass-distilled water were allowed to stand at room temperature (21°C) for 5 days before suctorians were inoculated into them. The composition of the water changes during this period to that of a medium in which suctorians have been supplied to them. Feeding suctorians, adhered to the slip when it was lifted from the surface of a culture and containing large numbers of feeding organisms were collected by lightly agitating the watch glass when the watch glass was gently agitated. After washing for 12 h with a phosphate buffer (12 changes) the organisms were fixed with a solution of osmium tetroxide. After two washings with the buffer the clumps of organisms were embedded in 2% agar, dehydrated, and embedded in Araldite. Full details of this procedure have been described elsewhere (Tucker, 1967). Thin sections of portions of the clumps were stained with lead citrate and uranyl acetate before examination with a Siemens Elmiskop I. In addition, two micrographs are included which were obtained using a Philips EM 301 fitted with a goniometer tilting stage to show the advantages of section tilting for examination of microtubules. Sections cutting tubule bundles at angles greater than about 15° to a plane at right angles to the longitudinal axes of the tubules do not clearly reveal tubule arrangement and linkage (Fig. 1). If the angle is less than about 40°, tilting these sections through angles of up to 40° about the appropriate axis (Fig. 2) provides images of the same quality as those of microtubules originally cut in perfect cross section (compare Figs. 1, 2, 8). Sections cutting tubules at angles between 15° and 40° to planes at right angles to their longitudinal axes are at least ten times as numerous as perfect tubule bundle cross sections when pellets or clumps of cells are sectioned. I thank Mr. F. Sheldon (Philips Analytical Department, Pye Unicam Ltd., Cambridge, England) for providing instruction and facilities.

Living organisms were photographed with Panatomic-X film (Eastman Kodak Co., Rochester, N. Y.) using a Carl Zeiss Universal microscope fitted with microflash and Nomarski interference-contrast attachments.

RESULTS

Resting Tentacles

A resting tentacle is one that is not engaged in feeding. Microtubules run along the entire length of each tentacle and project for several micrometers into the cell body beyond the base of the tentacle. A knob (k) is situated at the top of the shaft (s) of each tentacle (Fig. 3). Unlike the knobs of some other suctorians, each knob includes a region which is lined by the pellicular epiplastic layer where microtubules extend into the knob from the shaft, as well as a tip region which does not include tubules where only the cell membrane separates cytoplasm in the tentacle from the external medium (Fig. 5). Seven *microtubule rows* (r) surrounded by *outer tubules* (x) encircle the lumen of the tentacle (Fig. 8). Each row is a cytopharyngeal lamella (Tucker, 1968, 1972; Hitchen and Butler, 1973). The walls of adjacent row tubules are separated by distances of about 2 nm and often appear to be connected by fine links. In the shaft and cell body, *interrow links* (arrows)
sometimes join tubules at the juxtaposed ends of adjacent rows (Fig. 10). Arms (Fig. 13, arrows) project from the luminal surfaces of most of the row tubules. They are situated on the side of the luminal surface which is closest to the tubule in the same row which bears an interrow link on its luminal surface. Longitudinal sections of tentacles indicate that the projections which have an armlike appearance in cross sections of tentacles are stump-shaped "arms" rather than cross-sectional profiles of ridgelike structures (Fig. 9, arrows). A periodic arrangement of the arms has not been detected; the center-to-center spacing of the arms along a tubule seems to vary between about 18 and 27 nm. Arms have thicknesses of about 8 nm and their lengths vary between about 12 and 22 nm. This variation may be due to incomplete preservation of arms in some instances. Each outer tubule is usually jointed to a row tubule by an outer link (Fig. 11, arrows). Dense membrane-bounded vesicles are often situated in the tentacular lumen; they are particularly numerous in the knob and upper portions of the shaft (Fig. 8, v). Sometimes arms appear to contact them. It is not known whether the arms bind to the vesicles or are involved in establishing or maintaining their positions inside tentacles.

There are more outer tubules (about 34) in the knob than there are in the shaft of each tentacle (about 25). These tubules form part of a circular sleeve (Hitchen and Butler, 1973) (Fig. 13, c) which extends along the lower portion of the knob for at least 1 μm (Fig. 5). Adjacent outer tubules are joined by sleeve links (Fig. 14, arrows). Above the sleeve tubule rows and outer tubules are not joined by well-defined links passing circumferentially around the tubule bundle; in addition, outer tubules (x) follow markedly helical courses around the outer surfaces of the tubule rows (r) (Fig. 12). The tops of row tubules (r) contact a circular rim of dense material (arrow) which is situated around the top of the epiplastic layer (p) (Figs. 5, 18). The
tops of outer tubules are situated about 0.6 µm below the rim and do not appear to contact the epiplasm (Fig. 5).

**Feeding Tentacles**

When feeding commences the epiplasmic rim increases in diameter and moves downwards so that it is situated about 1.5 µm below the tip of the tentacle (compare Figs. 5, 6). Microtubules in the terminal knob bend along their longitudinal axes and splay apart at levels above the sleeve as their tips move outwards and downwards (Fig. 6). The tips of row tubules (r) are still attached to the epiplasmic rim (arrow) (Fig. 19) although they have pivoted through about 140° on this attachment (compare Figs. 5, 6, and 18, 19). The inverted tips of row tubules are more widely spaced (Fig. 21, r) than they are in resting tentacles. This is presumably because these tips are firmly embedded in the epiplasmic rim which has increased in diameter relative to its resting condition. The arm-bearing surfaces of the tubule rows are positioned close to the invaginating cell membrane at the top of the knob, as well as where they surround the lumen. The outer tubules are not positioned so closely against the invaginating membrane (Fig. 6). Some sections reveal that this membrane exhibits the three layers typical of a unit cell membrane. The tips of outer tubules are situated more distantly from the rim and the tips of adjacent tubule rows in feeding tentacles than they are in resting tentacles (compare Figs. 5, 6). Due to differences in their helical arrangement, these two types of tubules splay apart in a slightly different
FIGURE 5 Diagrammatic median longitudinal section of the knob of a resting tentacle with its tip towards the top of the page. Tubules have a helical arrangement (see text); tubules on opposite sides of the knob are not contained in a single plane although they have been drawn as if they are so contained. The sleeve is situated between the levels indicated by the arrows. The short black lines projecting from tubule rows show the arrangement of their arms. The thicknesses and lateral spacings of tentacular components have not always been accurately drawn to scale. The scale indicates the overall dimensions of the knob and the spacing of structures along its length.

fashion which results in their tips becoming more distantly separated: this rather complicated aspect of tubule rearrangement will be dealt with in more detail in a later paper.

The sleeve extends along the knob for at least 1 \( \mu m \) because in feeding tentacles outer tubules are joined by sleeve links from the level at which they splay apart to levels below the epiplasmic rim (Fig. 6). The sleeve may extend to levels somewhat lower than those indicated in Figs. 5 and 6. The sleeve (c) increases in diameter and its tubules become more widely spaced when feeding starts (compare Figs. 13, 17). The sleeve links are longer and thinner in feeding tentacles than they are in resting tentacles (compare Figs. 14-16). In resting tentacles sleeve links have lengths of about 9.5 \( \mu m \) and thicknesses of about 17 \( \mu m \). In feeding tentacles they have lengths of up to 76 \( \mu m \) and their thicknesses may decrease to 8 \( \mu m \). The tubules connected by these stretched links often exhibit elliptical cross-sectional profiles (Fig. 16). In some instances the appearance of these profiles is apparently not simply the result of oblique sectioning. The profiles of the walls of such tubules do not appear less dense at the ends of the ellipse as is usually the case when tubules are cut in oblique section. In addition, the tubules are slightly flattened. In the sleeve, outer tubules with circular cross-sectional profiles have diameters of about 24 \( \mu m \) but for elliptical tubules the minor axes of their elliptical profiles are sometimes as little as 20.5 \( \mu m \) and their major axes as much as 30 \( \mu m \). Some cross sections of the sleeves of feeding tentacles include both circular and elliptical tubules; micrographs of such sections have been used to compare tubule diameters to avoid errors introduced by changes in microscope magnification calibration. In addition, sleeve links do not all stretch to the same extent (Fig. 15). Tubules exhibiting the most extensive elliptical flattening are not always associated with the most highly stretched links. These observations indicate that resistance of individual links and tubules to the forces which induce the circumferential stretching of the sleeve may vary. Sections of resting tentacles show that all the outer tubules in the sleeve are joined to their neighbors by well-defined sleeve links (Fig. 13), but in feeding tentacles the stretched links sometimes appear to be incomplete and their densities vary considerably in a way which is not entirely correlated with variations in the amount of stretching (Fig. 17). These appearances may be because stretched links have become thinner so that there are larger spaces between them along the length of the sleeve and, consequently, there is a greater likelihood of only part of a link being included in a section than is the case for a resting tentacle. Alternatively, stretched links may be preserved less completely than resting links.

In the shaft and cell body also, the lumen often has a greater diameter when it contains a membranous invagination than it has in resting tentacles. This is particularly the case at levels where relatively large organelles such as mitochondria are being ingested (Fig. 4). In these instances the
Tubule rows \((r)\) are spaced more or less evenly around the invagination with their inner arm-bearing surfaces close to its membrane (arrow) (Fig. 24). In some cases the arms appear to contact the membrane (Figs. 9, 20, arrows). Adjacent tubule rows are separated from each other by much greater distances than they are in resting tentacles and are apparently no longer joined by interrow links which must detach from tubules at one of their ends, break at some point, or become so attenuated that they have not been detected. Outer tubules \((x)\) are less regularly arranged than they are in resting tentacles (compare Figs. 8, 24). Most of them are not linked to row tubules but some of them still occasionally exhibit this attachment (Fig. 20, y). Sometimes outer tubules \((x)\) are positioned closely alongside the membrane of the invagination (arrow) (Fig. 24). However, in feeding tentacles where the invagination (arrow) has a diameter which is approximately the same as the lumen of a resting tentacle, most of the outer tubules \((x)\) have the same arrangement as they do in resting tentacles and are still joined to tubule rows \((r)\) by outer links (compare Figs. 2, 8). This raises the possibility that the proximity of outer tubules to the membranous invagination and the loss of linkage to tubule rows, apparent in some electron micrographs, maybe artifacts introduced by distortions occurring to a more marked extent in greatly distended portions of tentacles during fixation, rather than any active process which is involved in the propulsion of prey cytoplasm down tentacles. Outer tubules are also arranged irregularly, and are not linked to tubule rows, in flattened resting tentacles which have apparently shrunken laterally during preparation for electron microscopy.

No differences in the dimensions or orientations of arms correlated with the feeding or resting states of tentacles have been detected. Throughout ingestion, dense vesicles situated outside the lumen between the outer surfaces of the tubule rows and the pellicle, move upwards at about the same speed as prey cytoplasm travels down the lumen (speeds of up to \(20 \mu m \text{ s}^{-1}\) have been observed).

The shafts of some tentacles prepared for electron microscopy contain intraluminal membrane-bounded structures which have diameters which are considerably less than that of a resting tentacle lumen. Whenever such narrow membrane-bounded structures occur in tentacles, they are always situated in the lumen and tubule rows are always packed closely around them in configurations which are distinctly different from those found in tentacles which lack such a structure, including tentacles in which some of the tubule rows have apparently been displaced and have moved towards the center of the tentacle because tentacles have shrunk and flattened during preparation for microscopy. These configurations are
**FIGURE 7** Part of the shaft of a feeding tentacle in cross section. Tubule rows are clustered around the membranous invagination (arrow). × 240,000.

**FIGURE 8** Part of the shaft of a resting tentacle cut in cross section about 5 μm below the bottom of the terminal knob. The lumen of the tentacle contains dense vesicles (v) and is surrounded by tubule rows (r) and outer tubules (x). × 175,000.

**FIGURE 9** Longitudinal section of part of the shaft of a feeding tentacle. The arms projecting from a row tubule (r) appear to contact the membranous invagination (h) at the points arrowed. × 333,000.

**FIGURE 10** Cross section of part of the shaft of a resting tentacle. Links (arrows) connect tubules at the ends of adjacent tubule rows. × 283,000.

**FIGURE 11** Cross section of part of the shaft of a resting tentacle. Outer links (arrows) connect outer tubules to the tubule row which is towards the bottom of the figure. × 375,000.
such that at least part of each tubule row is usually positioned close to the membrane-bounded structure (arrow) which would not have been the case had the rows not become more closely packed together (Fig. 7). Sequences of sections show that such membranous structures, which have roughly circular profiles when tentacles are cut transversely, are not spherical or spheroidal vesicles. The possibility that they represent part of long (several micrometers) vesicles has not been eliminated. The membrane-bounded structures may represent unusually narrow membranous invaginations of feeding tentacles, because dense vesicles (v) are often present outside the lumen in the shafts of tentacles containing such membranous structures (Fig. 25) as is commonly the case for feeding tentacles with larger membranous invaginations containing recognizable Tetrahymena organelles. Dense vesicles are rarely situated outside the lumen in the shafts of resting tentacles. Sections were also obtained of a tentacle in which the membranous invagination appears to have forked into two or three very slender invaginations (arrows); here the tubule rows are separated into two groups so that their arms are positioned closer to the invaginations than would have been the case had this grouping not occurred (Fig. 25).

When a tentacle tip penetrates Tetrahymena, the edges of the roughly circular perforation in the cell membrane of Tetrahymena are closely applied around the cell membrane of the tentacle near the bottom of the knob. In this region the unit cell membranes of the two organisms are apparently tightly sealed together (Fig. 6) so that cytoplasm does not escape from the perforated Tetrahymena into the external medium. Sections through this membrane seal reveal that it is composed of at least five layers, three dense ones are separated by two much less densely stained layers (Fig. 23). The central dense layer is twice as thick as the two outer ones, and in some sections consists of two dense layers separated by a less dense layer (Fig. 22, arrows).

DISCUSSION

Propulsion of the Membranous Invagination and Prey Cytoplasm

Are the elements responsible for the propulsion of prey cytoplasm down tentacles located inside tentacles? If they are not, then presumably materials must be drawn down tentacles because there is a lower hydrostatic pressure inside the cell body of the suctorian than there is in the body of the prey and at the tentacle tip (Kitching, 1952; Hull, 1961). The upward movement of vesicles at the periphery of tentacles indicates that such pressure gradients are not present and hence the propulsive elements are probably located inside tentacles. Upward vesicle movement also indicates that streams of cytoplasm are not propelled because of a peristaltic action produced by coordinated undulations of the microtubules (Rudzinska, 1967), since such action would drive intra- and extraluminal cytoplasm in the same direction.

Does the membranous invagination move down the tentacle throughout ingestion, or does it represent a stationary tube for passage of prey cytoplasm after its initial invagination (incorporating new membrane at its bottom as food vacuoles pinch off)? The cytopharynx of Nassula is lined by arm-bearing tubule rows (Tucker, 1968). Throughout ingestion a membranous invagination moves down the cytopharynx at the same speed as the food materials it contains (unpublished observation).

In the discussion which follows I shall assume that the invagination moves downwards and that certain actively contractile elements are located inside the tentacle. Such elements must be anchored to relatively rigid structures if they promote the type of unidirectional cytoplasmic stream which sometimes passes down a tentacle for periods of a minute or more. If the contractile elements are not anchored they will simply shorten towards their midpoints and cytoplasm in their vicinity will move in two opposite directions towards such points rather than stream in a single direction. Bundles of linked microtubules in the cytopharynges of other ciliates are definitely fairly rigid structures (Tucker, 1968, 1972). In a feeding tentacle, the tubule rows are usually closer to the invagination than the outer tubules, which often have tubule rows situated between them and the invagination. The arms on the tubule rows, which are usually situated within at least a few nanometers of the moving invagination, may represent the anchor points considered above. If contractile elements are bound to the arms in a polarized fashion, contraction of such elements could set up a region of active shear along the luminal surfaces of the rows which drives the invagination down the tentacle. Arms have been found attached to tubule rows at all levels; they are not confined to the tip regions of tentacles as claimed for Dendrocometes.
The arms may not be just anchor points, but themselves represent all, or part, of the contractile elements. The dimensions of the arms (about 22 x 8 nm) more closely resemble those of the inner dynein arms of cilia and flagella (about 20 x 9 nm) than those of the heavy meromyosin S, cross-bridge units of striated muscle (approximately 15 x 4 nm).

It has been suggested that tubule rows slide up and down and that their arms bind to the membranous invagination during downward sliding (Bardele, 1972). The contact between arms and the invagination apparent in some micrographs may only indicate that the invagination, which is often swollen with prey cytoplasm, is sometimes pressed against the arms rather than that it is bound to them. In feeding *Choanophrya* tentacles, the tubule rows are sometimes arranged in such a way that only a few of the arms can effect such binding (Hitchen and Butler, 1973). This is always the case in the feeding cytopharynx of *Nassula* where highly gelated cytoplasm situated between the invagination and the arm streams downwards at the same speed as the invagination and its food contents (unpublished observation). In a suctorian tentacle, a thin layer of luminal cytoplasm may be actively propelled downwards alongside the arm-bearing surfaces of the tubule rows and draw the invagination down with it. The extraluminal movement of vesicles may be an indication of an upflow of cytoplasm to replace that driven down the lumen. A bidirectional flow of tentacular cytoplasm has also been proposed by Canella (1957). If an active shearing process takes place along the arm-bearing surfaces of the tubule rows, movement of the invagination will be facilitated if the rows are positioned closely around it. The rather marked rearrangement of rows so that they group around what appear to be unusually narrow invaginations maybe for the purposes of accomplishing such proximity. The overlapping arrangement of tubule rows illustrated in Fig. 7 does not place most of the arms in positions where they can bind to the invagination but it does situate them closer to the invagination than they would have been had the rows not overlapped so extensively. However it has not been established that such tentacles are actually feeding. The arrangements of their tubule rows to some extent resemble those around narrow constrictions in the invaginations of feeding *Ryncheta* tentacles (Hitchen and Butler, 1974), but they also resemble those around vesicles apparently resulting from the break up of the invagination in post-feeding tentacles of *Choanophrya* (E. T. Hitchen, personal communication).

The tips of row tubules seem to be permanently attached to the epiplastic rim. If rows slide back and forth during feeding (Bardele, 1972), the epiplasma near the rim must be repeatedly stretched and/or moved up and down, unless the sliding is accommodated by changes in the curvature of the bent portions of the tubules.

**Tubule Bending and Link Stretching**

The outward and downward bending of tubules in the knob may not involve any active bending,
FIGURE 18 Longitudinal section of part of the tip of the knob of a resting tentacle. The tentacle tip is towards the top of the figure. The tip of a tubule row (r) is attached to the rim (arrow) positioned at the top of the pellicular epiplastic layer (p) which lies just inside the cell membrane (u). x 166,000.

FIGURE 19 Longitudinal section of part of the knob of a feeding tentacle. The tentacle tip is towards the top of the figure. The tip of a tubule row (r) has pivoted on the rim (arrow) at the top of the epiplastic layer (p). The cell membrane (u) is also shown. x 125,000.

FIGURE 20 Cross section of part of the shaft of a feeding tentacle. One of the outer tubules is connected to a row tubule by an outer link (y). Some of the arms projecting from the tubule row appear to contact the membranous invagination at the points arrowed. x 333,000.

FIGURE 21 This cross section of part of the knob of a feeding tentacle passes through the knob at a slightly higher level to the left of the figure, where it cuts through part of the epiplastic rim (arrow), than it does towards the right where the tips of five tubules of a tubule row (r) are sectioned just above the level at which they contact the rim. x 92,000.

FIGURE 22 Cross section of part of the knob of a feeding tentacle; the membrane seal is sectioned in a plane at right angles to the planes of the membranes. There appear to be two closely apposed unit membranes at the point arrowed. x 396,000.

FIGURE 23 A section of the membrane seal similar to that shown in Fig. 22. The profile of the thick central dense layer of the seal does not exhibit a tripartite composition along most of its length. x 396,000.

sliding, or shortening of the tubules themselves, or of elements bound along the lengths of the tubules. The tops of the tubule rows may splay apart, and push the outer tubules which are arranged around them to new positions, because their tips are attached to the epiplastic rim which pulls them downwards and outwards as the rim moves downwards away from the tentacle tip (compare Figs. 5,
If this suggestion is correct, it indicates that contractile elements are included in, or bound to, the tentacular epiplastic layer. Such elements may also be responsible for the shortening of tentacles which occurs during feeding. The long microtubule bundle may have considerable inertia, so that contraction of the epiplastic pulls the tops of tubule rows outwards and downwards, as well as shortening the tentacle and pulling the tubule bundle further into the cell body.

Sleeves or "manchettes" are situated near the bottoms of the knobs of several other suctorian species (Bardele, 1972) and the sleeve of Choanophrya stretches during feeding (Hitchen and Butler, 1973). In Tokophrya, the sleeve represents the highest level in the tentacle where tubules are joined by well-defined links running circumferentially around the tubule bundle, links connecting tubules in the same row excepted. Correlated with this, tubules only splay apart from levels above the top of the sleeve (Fig. 6). The role of the sleeve is apparently to prevent such splaying from occurring at levels below it. At the start of feeding it increases in diameter as sleeve links stretch and the tubules they connect sometimes apparently become flattened and elliptical in cross section. Presumably stretching takes place because tubule rows press outwards against the sleeve when they splay apart at higher levels and setup a tension around its circumference. The possibility that tubules in the sleeve are always circular in living organisms, but become elliptical when fixed under tension because their walls are weakened by the action of the fixative, cannot be discounted. The
FIGURE 25 Cross section of the shaft of a feeding tentacle. Tubule rows are grouped around the membranous invagination (arrows) and two dense vesicles (v) are situated near the periphery of the tentacle. The pellicular epiplasmic layer (p) is positioned just inside the cell membrane (u). x 166,000.

links may resist stretching elastically and provide a restoring force so that the sleeve returns to its original diameter at the end of feeding.

I thank Dr. R. D. Butler for critically reading the manuscript and Mr. J. B. Mackie for undertaking some of the electron microscopy.

Support from Science Research Council (United Kingdom) grant no. B/SR/88418 is acknowledged.

Received for publication 19 November 1973, and in revised form 21 February 1974.

REFERENCES

BARDELE, C. F. 1972. A microtubule model for ingestion and transport in the suctorian tentacle. Z. Zellforsch. Mikrosk. Anat. 126:116.

BARDELE, C. F., and K. G. GRELL. 1967. Electronenmikroskopische Beobachtungen zur Nahrungsaufnahme bei dem Suktor Acineteta tuberosa Ehrenberg. Z. Zellforsch. Mikrosk. Anat. 80:108.

BATISSE, A. 1967. Données nouvelles sur la structure et le fonctionnement des ventouses tentaculaires des Acinétiens. C. R. Hebd. Séances Acad. Sci. Ser. D Sci. Nat. 265:1056.

CANELLA, M. F. 1957. Studi e ricerche sui Tentaculiferi nel quadro della Biologia generale. Ann. Univ. Ferrara Sez. III Biol. Anim. 1:259.

FERNANDEZ, H. L., P. R. BURTON, and F. E. SAMSON. 1971. Axoplasmic transport in the crayfish nerve cord. The role of fibrillar constituents of neurons. J. Cell Biol. 51:176.

HASCALL, G. K., and M. A. RUDZINSKA. 1970. Metamorphosis in Tokohrya infusionum: an electron microscope study. J. Protozool. 17:311.

HITCHEN, E. T., and R. D. BUTLER. 1973. Ultrastructural studies of the commensal suctorian, Chondophrya infundibulifera Hartog. 1. Tentacle structure, movement and feeding. Z. Zellforsch. Mikrosk. Anat. 144:37.

HITCHEN, E. T., and R. D. BUTLER. 1974. The ultrastructure and function of the tentacle in Rhyncheta cyclopum Zenker (Ciliata, Suctorida). J. Ultrastruct. Res. 46:279.

HULL, R. W. 1961. Studies on suctorian protozoa: the
mechanism of ingestion of prey cytoplasm. *J. Protozool.* **8**:351.

**Kitching, J. A.** 1952. Observations on the mechanism of feeding in the suctorian *Podophrya*. *J. Exp. Biol.* **29**:225.

**Rudzinska, M. A.** 1965. The fine structure and function of the tentacle in *Tokophrya infusionum*. *J. Cell Biol.* **25**:459.

**Rudzinska, M. A.** 1967. Ultrastructures involved in the feeding mechanism of suctoria. *Trans. N. Y. Acad. Sci.* **29**:512.

**Rudzinska, M. A.** 1970. The mechanism of food intake in *Tokophrya infusionum* and ultrastructural changes in food vacuoles during digestion. *J. Protozool.* **17**:626.

**Rudzinska, M. A.** 1973. Do Suctoria really feed by suction? *Bioscience.* **23**:87.

**Smith, D. S.** 1971. On the significance of cross-bridges between microtubules and synaptic vesicles. *Philos. Trans. R. Soc. Ser. B Biol. Sci.* **261**:395.

**Tilney, L. G.** 1971. How microtubule patterns are generated. The relative importance of nucleation and bridging of microtubules in the formation of the axoneme of *Raphidiophrys*. *J. Cell Biol.* **51**:837.

**Tucker, J. B.** 1967. Changes in nuclear structure during binary fission in the ciliate *Nassula*. *J. Cell Sci.* **2**:481.

**Tucker, J. B.** 1968. Fine structure and function of the cytopharyngeal basket in the ciliate *Nassula*. *J. Cell Sci.* **3**:493.

**Tucker, J. B.** 1972. Microtubule-arms and propulsion of food particles inside a large feeding organelle in the ciliate *Phascolodon vorticella*. *J. Cell Sci.* **10**:883.