

Ultrastructure of the mucous feeding filter of the house of the appendicularian *Oikopleura vanhoeffeni*

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ABSTRACT: Transmission electron microscopy was used to investigate the pore size and fiber diameter of the feeding filter of the house of *Oikopleura vanhoeffeni*. Quantitative information on the ultrastructure of the filter is necessary to investigate particle retention efficiency and fluid mechanics of feeding. Specimens were collected by hand from April to July of 1983 and 1984 in Logy Bay, Conception Bay, and Bay Bulls, Newfoundland. The feeding filter consisted of a rectangular array of 3 types of fibers: smooth, nodulated, and microfibrils. There were nodes at points where nodulated fibers and microfibrils crossed. The distance separating smooth fibers was variable (1 to 12 μm). All 3 types of fibers formed branches. Mean pore size of the filter was 1.04 ± 0.26 ($n=223$) \times 0.22 ± 0.04 ($n=502$; \pm SD). Smooth and nodulated fibers were about 40 nm in diameter, and microfibrils about 12 nm. The % open area (porosity) of the feeding filter was 91%. The large surface area and high porosity of the feeding filter allow *O. vanhoeffeni* to maintain a high volume flow per unit time while concentrating food with a mucous net of small pore size.

INTRODUCTION

The oikopleurid appendicularians are gelatinous suspension feeders that concentrate and collect phytoplankton food using a complex system of mucopolysaccharide filters known as the 'house'. A general description of the structure and function of the house of several appendicularian species was presented by Alldredge (1977). The animal draws water into the house through bilateral incurrent filters of coarse mucous mesh with sinusoidal beats of its muscular tail. Suspended food particles are concentrated by the mucous mesh of the feeding filter (Jørgensen 1984b). The resulting concentrated food suspension passes to the animal's mouth through a short buccal tube. A third mucous net filter inside the pharynx collects the food particles. The pharyngeal filter with food particles enmeshed is wound into a cord at the esophagus and ingested. The feeding filter has a large surface area (Körner 1952) and occupies a large portion of the house, yet the mechanism by which it concentrates food particles is unknown (Alldredge 1977). Moreover, the fluid mechanics of this elaborate system of mucous filters has not been described.

It appears that mucous-net suspension feeders collect food particles by a sieving mechanism (Jørgensen 1984a). To describe and quantify the feeding mechanism, filtration rate, and fluid mechanics of a suspension feeder, the fluid medium, food particles, and filter must be characterized (Rubenstein & Koehl 1977). Much is known about the physical characteristics of seawater and suspended food particles (i.e. phytoplankton and detritus), but little is known about the physical characteristics of mucous-net filters. To describe the fluid mechanical characteristics of a filter the values of at least 3 variables must be determined (Jørgensen 1984a): (1) flow velocity at the filter surface; (2) retention efficiency of the filter; (3) pressure drop across the filter, which depends on filter resistance. The value of all of these variables depends in part on the pore size and fiber diameter of the mucous filter.

Flood (1981) found that the feeding filters of *Oikopleura dioica* and *Oikopleura albicans* were made of fine, evenly spaced longitudinal fibers crossed at right angles by thicker transverse fibers. The fibers were described as being uniform and non-branching, and as forming a regular, rectangular array. However, oblique 'subfilaments' were observed coursing between trans-

verse fibers, and less frequently 'lattice faults' were observed in the fine, longitudinal fibers. Electron-dense nodes were observed at points where longitudinal and transverse fibers crossed. Some of the longitudinal fibers of *O. albicans* were thickened. The mean pore size of the feeding filter of *O. albicans* was $0.92 \times 0.19 \mu\text{m}$, and that of *O. dioica* was $0.98 \times 0.15 \mu\text{m}$.

Oikopleura vanhoffeni is one of the largest oikopleurids, with an adult trunk length $>6 \text{ mm}$. It is abundant in Newfoundland coastal waters throughout the year (Udvardy 1954, Davis 1982). The pore size of the incurrent filters of *O. vanhoffeni* is the largest yet reported for any oikopleurid species ($\bar{X} = 169 \times 88 \mu\text{m}$), enabling it to ingest long chains of pennate diatoms and spinous cells (Deibel & Turner 1985). Is the pore size of the feeding filter of *O. vanhoffeni* also larger than that of smaller oikopleurid species? How much variation in pore size exists within and between houses? In this paper we report transmission electron microscopic observations of the ultrastructure of the feeding filter of the house of *Oikopleura vanhoffeni*.

MATERIALS AND METHODS

Oikopleura vanhoffeni was collected from April to July 1983 and 1984 in Logy Bay, Conception Bay, and Bay Bulls, Newfoundland. Using SCUBA, we collected individuals by hand in 500 ml glass jars. During transport, jars containing appendicularians were held in a seawater bath at ambient sea-surface temperature. Within 90 min of collection the jars were placed in a flowing seawater bath in the laboratory. The temperature of the bath was within 2°C of the water temperature where the animals were collected. No artificial particles or stains were added to the naturally occurring food suspension.

Each house was fixed for 2 h in ice-cold 2% glutaral-

dehyde with 0.1M Sorensen's phosphate buffer (pH 7.2), washed in ice-cold phosphate buffer for 1 h, and post-fixed for 1 h in cold phosphate-buffered 1% OsO_4 (pH 7.2). The osmolality of the fixatives and rinse solution was adjusted to $1000 \text{ mOsmol kg}^{-1}$ by the addition of sucrose (Maser et al. 1967). Houses then were taken through a graded ethanol series to 70% ethanol.

For transmission electron microscopy (TEM), houses were transferred to a Petri dish and examined under a Zeiss stereomicroscope equipped with dark field base and fiber optic light source. Small portions of the feeding filter (Fig. 1) were removed while suspended in droplets of 70% ethanol and placed on Formvar coated, carbon-stabilized, 300-mesh copper grids. The preparations were air-dried on filter paper in clean Petri dishes. Samples were viewed with a Zeiss EM 109 electron microscope operated at an accelerating voltage of 50 kV.

For measurements of pore size and fiber diameter the highest quality area of each photomicrograph was preselected by choosing flat preparations and sharp images. When a large area of a particular photomicrograph was of high quality, we secondarily selected by eye enough of the area to sample the full range of pore size or fiber diameter. Because of differences in scale, rarely could both pore length and width be measured on the same photomicrograph. Thus, all measurements were reduced to mean values for each house.

The % open area (i.e. porosity) of the feeding filter mesh was calculated using a modification of the standard equation for the porosity of square-meshed plankton nets (Anonymous 1968).

$$\langle LW / [(L + n)(W + m)] \rangle \cdot 100\%$$

Where L = pore length (μm); W = pore width (μm); n = diameter of the nodulated fiber (μm); m = diameter of the microfiber (μm). (See 'Results' for the definitions of fiber types).

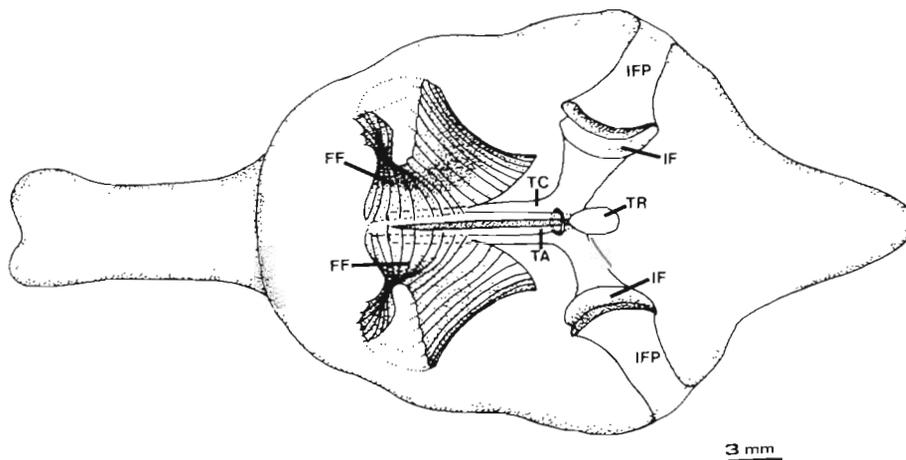


Fig. 1. *Oikopleura vanhoffeni*. Dorsal view of a specimen inside its house. Drawing made from a photograph taken of a living specimen in an aquarium. Samples for electron microscopy were taken from the feeding filter (FF). Note that the tail enters the tail chamber through a small opening in the chamber's wall. IF; incurrent filter; IFP; incurrent filter passageway; TA; tail; TC; tail chamber; TR; trunk

RESULTS

Measurements of feeding filter pore size and fiber diameter could be made on 32 transmission electron micrographs from 6 houses (a total of 80 houses were examined). Of the 5 specimens that produced these 6 houses (2 houses were produced by the same individual), 3 could be measured while alive. These 3 animals had trunk lengths of 1.55 to 2.50 mm, tail lengths of 7.50 to 8.75 mm, and were of maturity Stages III and IV (after Shiga 1976: Stage V is a spawning adult).

The feeding filter of *Oikopleura vanhoeffeni* was composed of an array of mucous fibers arranged in a

rectangular pattern (Fig. 2a). Three types of fibers could be defined by differences in diameter and appearance. Since we were not certain of the orientation of these fibers in relation to the geometry of the feeding filter, we chose to name them in accordance with their appearance. These were microfibers, nodulated fibers, and smooth fibers (Fig. 2a, b). The smooth fibers were parallel to the microfibers and occurred on a variable spatial scale (Fig. 2a). The nodulated fibers were perpendicular to the smooth fibers and microfibers and had a node at every intersection with a microfiber (Fig. 2a, b). There were no nodes without an associated microfiber. With a few exceptions (Fig. 2b),

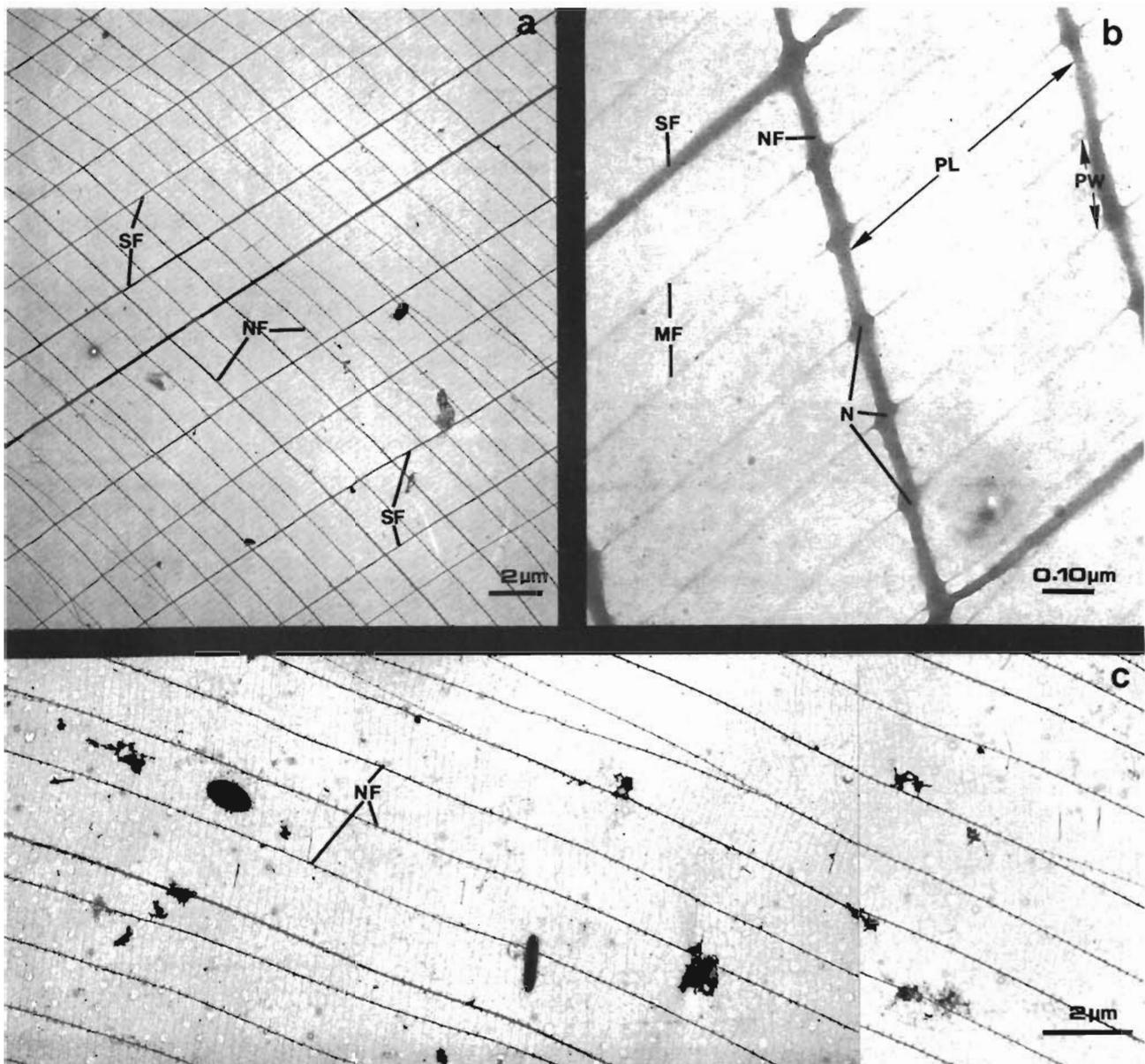


Fig. 2. *Oikopleura vanhoeffeni*. Transmission electron micrographs of feeding filter mesh showing spatial orientation of mucous fibers, the 3 types of fibers, and pore length (PL) and width (PW). In (c), note the absence of smooth fibers in this area of the filter. MF: microfiber; N: node; NF: nodulated fiber; SF: smooth fiber

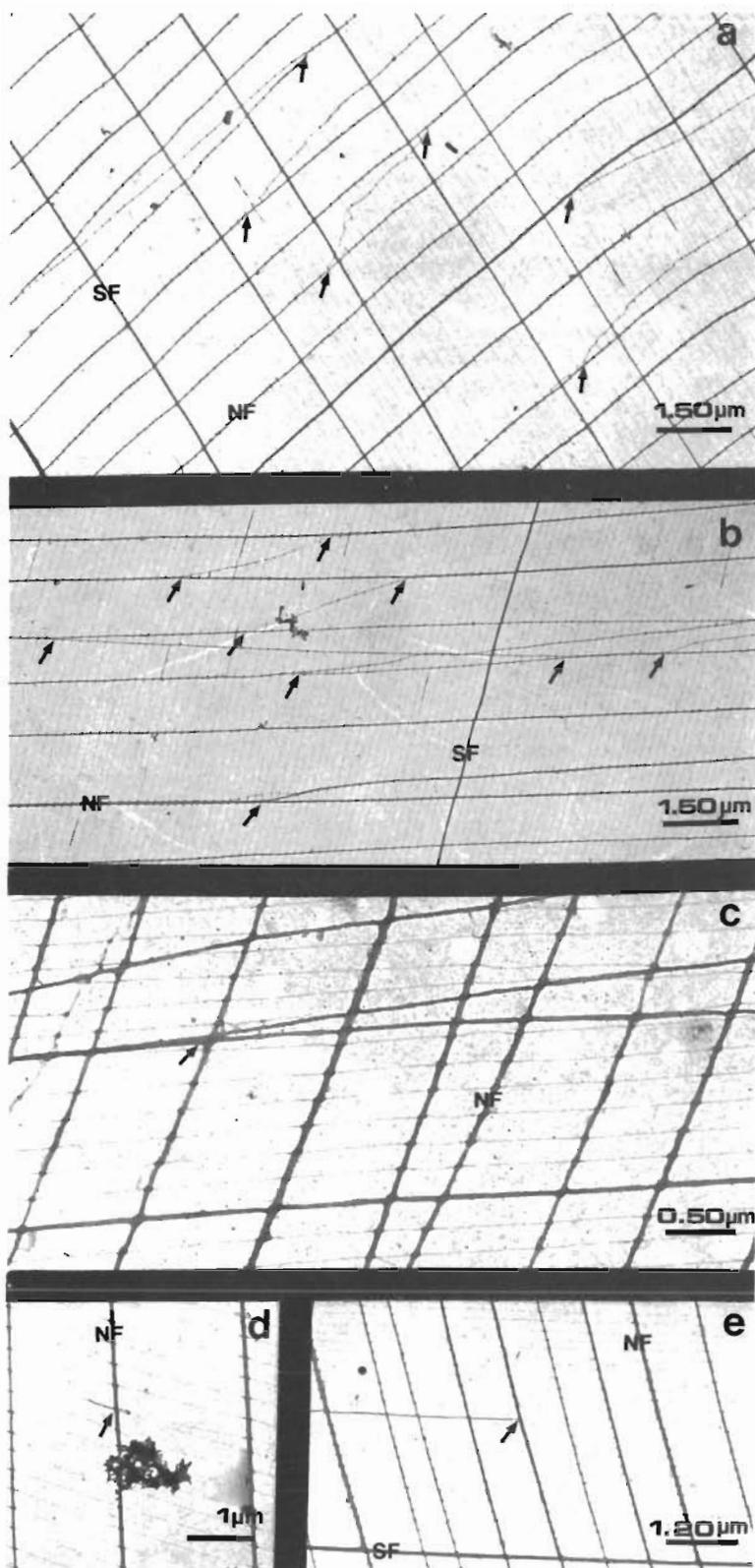


Fig. 3. *Oikopleura vanhoeffeni*. Transmission electron micrographs of feeding filter mesh showing the various types of branching fibers. (a) Branching points of nodulated fibers (arrows); (b) multiple branching of nodulated fibers (arrows); (c) branching point of a smooth fiber (arrow); (d) branching point of a microfiber (arrow); (e) smooth fiber branching into 2 microfibrils (arrow). NF: nodulated fiber; SF: smooth fiber

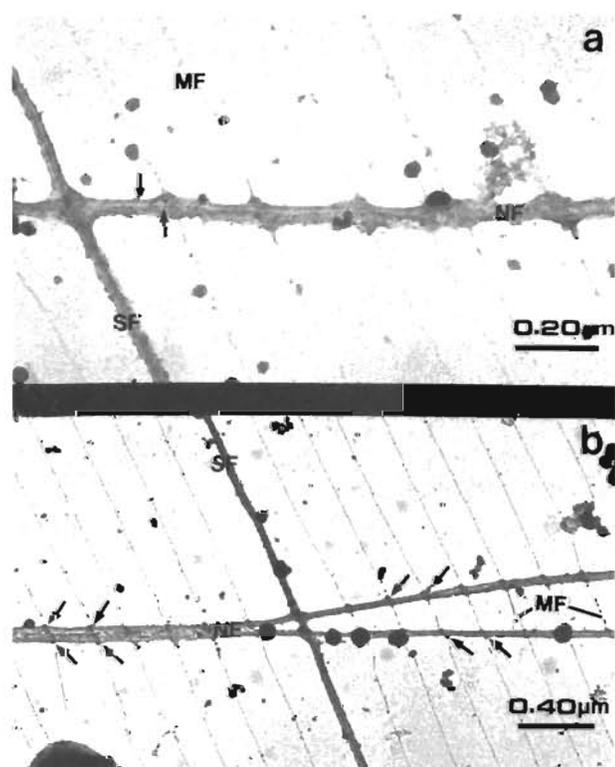


Fig. 4. *Oikopleura vanhoeffeni*. Transmission electron micrographs of nodulated fiber subunit structure (light and dark bands). (a) dark bands (arrows); (b) separate nodes (arrows). MF: microfiber; NF: nodulated fiber; SF: smooth fiber

there did not appear to be nodes where smooth fibers crossed nodulated fibers (Fig. 2a). The smooth fibers were extremely far apart in some areas of the feeding filter (Fig. 2c). The microfibers were of small diameter and seemed to be spaced evenly (Fig. 2a, b). The smooth fibers and microfibers correspond to 'longitudinal' fibers as defined by Flood (1981), and the nodulated fibers correspond to 'transverse' fibers as defined by Flood (1981). Preparation for scanning electron microscopy (SEM) destroyed most microfibers.

All 3 types of fibers of the feeding filter had many branches. These branches probably correspond to the oblique subfilaments and lattice faults of Flood (1981). Some areas of the feeding filter had few branched fibers (Fig. 2c), while other areas had many (Fig. 3a, b). Branching of the nodulated fibers seemed to be most common (Fig. 3a, b), although branching smooth fibers (Fig. 3c) and microfibers (Fig. 3d) were observed. Occasionally a smooth fiber split into 2 microfibers (Fig. 3e). Branches were usually of lesser diameter than were the fibers from which they arose. Complex patterns resulted from branches joining other fibers (Fig. 3b).

Light and dark bands ran longitudinally within the nodulated fibers, suggesting that they were composed

of a type of subunit (Fig. 4a, b). When a nodulated fiber split, nodes were present on each branch before the branches were entirely separated (Fig. 4b). Also, microfibers were present between the branches immediately upon their separation (Fig. 4b). This evidence, and a detailed examination of the appearance and pattern of branching fibers (Fig. 3), indicated that all 3 types of fibers may be composed of subunits.

Pore size of the feeding filter mesh depends on the separation between neighboring microfibers and nodulated fibers. Pore length was defined as the distance between nodulated fibers and pore width as the distance between microfibers (Fig. 2b). Within each house mean pore length varied little (Table 1: coefficient of variation 11 to 19%). Examination of the 95% confidence intervals and coefficients of variation show that mean pore length varied more between different houses than within each house (coefficient of variation of the grand mean was 25%: Table 1). However, much of the between House variability was due to the large mean pore length of House # 1.

Table 1. *Oikopleura vanhoeffeni*. Mean (\pm 95% confidence interval) pore length and pore width of the feeding filter mesh. n: number of individual measurements of pore length or width taken from a series of photomicrographs for each house

House	Mean pore length (μm) [n] Range	Coefficient of variation of mean pore length (%)	Mean pore width (μm) [n] Range	Coefficient of variation of mean pore width (%)
1	1.73 \pm 0.11 [14] 1.40 – 2.16	11	0.24 \pm 0.01 [14] 0.18 – 0.28	10
2	0.85 \pm 0.10 [6] 0.65 – 1.00	13	0.20 \pm 0.01 [22] 0.13 – 0.26	18
3	0.98 \pm 0.04 [114] 0.59 – 1.52	18	0.27 \pm 0.01 [138] 0.15 – 0.38	16
4a	1.02 \pm 0.04 [83] 0.51 – 1.63	19	0.20 \pm 0.004 [216] 0.10 – 0.25	13
4b	NA	NA	0.22 \pm 0.004 [72] 0.19 – 0.26	6
5	1.07 \pm 0.12 [6] 0.98 – 1.33	13	0.23 \pm 0.006 [40] 0.20 – 0.27	8
Mean	1.04 \pm 0.04 [223] 0.51 – 2.16	25	0.22 \pm 0.004 [502] 0.10 – 0.38	18
NA Data not available				

Mean pore width was as uniform as mean pore length (Table 1: coefficient of variation 6 to 18%). Mean pore width of all feeding filters was similar, ranging from 0.20 to 0.27 μm (Table 1). There was as much variability in mean pore width within each house as there was between different houses. The pore-width to pore-length ratio of the mesh of these feeding filters had a range of 0.16 to 0.28.

The distance between smooth fibers was variable (coefficient of variation 25 to 71%: Table 2). Generally there was greater variability in the mean distance between smooth fibers between different houses rather than within each house.

The mean diameter of smooth fibers and nodulated fibers was similar (Table 3). In the single case in which it was possible to make accurate measurements of microfibre diameter, the mean diameter was 12.2 ± 2.1 nm ($\pm 95\%$ confidence interval; $n = 9$; data not shown). Therefore, each smooth and nodulated fiber may have consisted of 3 to 4 subunits each equal to the diameter of a single microfibre. Using the mean nodulated fiber diameter of 45 nm (Table 3), and the mean microfibre diameter of 12.2 nm, the % open area of the feeding filter mesh of the 5 houses for which both mean pore length and width could be calculated (Table 1) was 89 to 93%.

DISCUSSION

It is not possible to predict precisely the retention efficiency of mucous filters from pore sizes such as those determined in this study. There are 2 major artifacts which have been discussed by Flood (1978). First, the mucous net is distended or stretched by hydrostatic pressure when the animal feeds. This pressure cannot be simulated in mucus prepared for electron microscopy. Secondly, the mucous net probably shrinks due to dehydration during preparation for electron microscopy. The magnitude of these artifacts is difficult to determine. An alternative method is to estimate the pore size empirically by offering the animal a range of particle sizes and determining the

Table 2. *Oikopleura vanhoeffeni*. Mean ($\pm 95\%$ confidence interval) distance between 'smooth' fibers of the feeding filter mesh. 'n' is as defined in Table 1

House	Mean distance (μm)	n	Range (μm)	Coefficient of variation (%)
1	3.14 ± 1.16	6	1.37 – 4.26	35
3	2.24 ± 0.12	82	1.01 – 3.75	25
4a	4.51 ± 1.51	20	1.56 – 12.2	71
Mean	2.71 ± 0.32	108	1.01 – 12.2	63

Table 3. *Oikopleura vanhoeffeni*. Mean ($\pm 95\%$ confidence interval) diameter of smooth and nodulated fibers of the feeding filter mesh. 'n' is as defined in Table 1

House	Mean diameter (nm) [n]		Range (nm)	
	Smooth	Nodulated	Smooth	Nodulated
1	31 ± 3 [11]	38 ± 5 [13]	27 – 41	26 – 53
2	28 ± 10 [3]	28 ± 6 [5]	24 – 31	22 – 34
4b	NA	46 ± 5 [9]	NA	37 – 61
5	52 ± 3 [11]	56 ± 6 [16]	47 – 63	39 – 75
Mean	40 ± 5 (n = 25)	45 ± 4 (n = 43)	24 – 63	22 – 75
NA Data not available				

retention efficiency spectrum (Harbison & McAlister 1979). But direct interception, electrostatic attraction, and 'leakiness' will confound determination of the particle size of 100% retention, and thus will confound determination of the minimum pore size (Rubenstein & Koehl 1977, Flood & Fiala-Medioni 1981). A solution to this dilemma is to study the mucous mesh directly with TEM for its ultrastructural and fluid mechanical properties, and empirically by determining the retention efficiency spectrum for its ability to collect food particles of various sizes. This combination of techniques has not been applied to pelagic tunicates.

The ultrastructure of the feeding filter of *Oikopleura vanhoeffeni* is similar to that of *O. albicans* (Flood 1981). Both filters have 3 types of fibers, including a thickened smooth fiber about every 5th to 25th fine microfibre (Flood 1981). These thickened fibers may support the large mucous nets of *O. vanhoeffeni* and *O. albicans*. However, smooth fibers appear to be absent in *O. dioica* (Flood 1981), and their functional role is unknown.

The pore width of the feeding filter mesh of *Oikopleura vanhoeffeni* was slightly larger than that of all other oikopleurid species examined to date (Table 4). Perhaps larger oikopleurid species have a feeding filter mesh of greater pore width than smaller species. The pore width of the mesh of all oikopleurid feeding filters indicates that they will retain most free bacteria, and thus will make this food source available to be collected by the pharyngeal filter. The % open area of the feeding filter mesh of all oikopleurid species that have been examined is about 90% (Table 4). Also, the width-to-length ratio of the feeding filter mesh of all species is low (Table 4). Wallace & Malas (1976) have shown that in terms of material investment, an elongate, rectangular mesh with a small width-to-length ratio is the most economical way for an animal to trap small particles.

Rectangular arrangements of filter fibers are common in other suspension feeders, including ascidians

Table 4. *Oikopleura* spp. Comparative transmission electron micrograph data on the mucous mesh of feeding filters (mean \pm standard deviation). Figures in parentheses: number of observations pooled for each mean

Species	Mature trunk length (mm)	Pore length (μm)	Pore width (μm)	Width/length	Diameter (nm)			% open area	Source
					Smooth (longitudinal)	Nodulated (transverse)	Microfiber (longitudinal)		
<i>Oikopleura vanhoeffeni</i>	2.0–9.0*	1.04 \pm 0.26 (223)	0.22 \pm 0.04 (502)	0.22 \pm 0.04 (5)	40 \pm 12 (25)	45 \pm 14 (43)	12 \pm 2.7 (9)	91 \pm 1 (5)	Present study
<i>Oikopleura albicans</i>	3.0–5.0**	0.92 \pm 0.06	0.19 \pm 0.01	0.22	10–40	10–40	NA	~90	Flood 1981
<i>Oikopleura dioica</i>	0.5–1.0*	0.98 \pm 0.22	0.15 \pm 0.02	0.17	10–40	10–40	NA	~90	Flood 1981
<i>Oikopleura</i> sp.	NA	0.80	0.10	0.13	NA	NA	NA	NA	Fjordingstad (in Jørgensen 1966)

* Berrill (1950)
 ** Thompson (1948)
 NA Data not available

(Flood & Fiala-Medioni 1979, 1981), salps (Silver & Bruland 1981), trichoptera larvae (Wallace & Malas 1976), and chaetopterid worms (Flood 1981). The mucous nets of ascidians and salps are not similar in function or origin to the feeding filter of the house of *Oikopleura vanhoeffeni* (Flood & Fiala-Medioni 1981). The filters of ascidians and salps are pharyngeal nets produced by the endostyle, while the feeding filter of appendicularians is external and is produced by specialized epithelial cells on the animal's trunk. There have been a few observations of the pharyngeal filters of salps (Silver & Bruland 1981), but no measurements of the pharyngeal filter of an appendicularian. It is the pore size of the pharyngeal filter that determines the size composition of ingested particles (Jørgensen 1984b).

The feeding filter of *Oikopleura vanhoeffeni* has a complex pattern of branching fibers (Fig. 3). Although Flood (1981) described the feeding filter mesh of *O. albicans* and *O. dioica* as non-branching, he observed many oblique subfilaments connecting transverse fibers and a few lattice faults of longitudinal fibers. The fibers of *O. dioica* (Flood 1981) and *O. vanhoeffeni* (Fig. 4) seem to be composed of fibrous subunits which we believe form the branches. The feeding filter is spatially complex, with compound curves and recurves, and regular folds or ridges. Perhaps branching fibers are necessary to allow for changes in filter surface area to form complex shapes; there seem to be no branching fibers in the pharyngeal nets of ascidians (Flood & Fiala-Medioni 1979, 1981) which are unsupported conical or cylindrical nets of simple shape.

The feeding filter of oikopleurids may be adapted to the demands of concentrating food using a filter of small pore size. Because of fluid mechanical constraints, it is costly to have a filter that both is highly retentive (i.e. with a small pore size) and has a high

flow volume per unit time (Wallace & Merritt 1980). The energy needed to force water through the filter is simply too high. Oikopleurids use a feeding filter with a large surface area and high porosity to concentrate the food suspension. Concentration of food is achieved by excluding much of the incoming water. Consequently, the pharyngeal filter with a small surface area must sieve only a fraction of the total volume of water taken into the house (Jørgensen 1984b). The feeding filter allows oikopleurids to use a highly retentive pharyngeal filter while maintaining the ability to process large volumes of water per unit time. The incurrent filters protect the feeding filter from premature clogging due to large or spinous particles, enabling the house to be used longer before abandonment. The rate at which an oikopleurid abandons its houses will affect the retention efficiency of its feeding filter, because the longer a house is used the more the filter becomes loaded with particles. Loading decreases the pore size of the filter, increasing both its capture efficiency and resistance (Rubenstein & Koehl 1977, Wallace & Merritt 1980). By increasing the turnover rate of houses an animal will increase the time-averaged porosity of its feeding filter and will decrease mean filter resistance.

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