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Ciliate feeding: effect of food presence or absence on occurrence of striae in tintinnids

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ABSTRACT: Tintinnid ciliates have been shown to be important components of many marine food webs, and several studies have been conducted to quantify their ingestion rates. The actual mechanism they use for prey capture, however, is not yet known. Extrosomes, membrane bound extrusible bodies subpellicularly located, are common in the ciliated Protozoa, and have diverse functions. Many species of tintinnid have been found to possess striae: cytoplasmic, capsule (extrosome) containing evaginations associated with the oral membranelles. To begin to test the hypothesis that the striae and the associated capsules are involved in prey capture, *Stenosemella oliva* and several species of the genus *Tintinnopsis* were used. Tintinnids were field collected and divided into 2 groups, one which was fed, the other unfed for about 20 h, in a series of experiments. Subsequent scanning electron microscopic examinations revealed numerous striae associated with the oral membranelles of the fed group, while the unfed group exhibited a paucity of these structures. Large sac-like bodies were observed in one well-fed individual. It is suggested that the striae and associated capsules may be used to capture prey.

INTRODUCTION

Ciliates are a major component of many marine, estuarine and freshwater planktonic and benthic communities (Vitiello 1964, Fenchel 1969, Hartwig 1973, Sorokin 1977, Heinbokel & Beers 1979, Beers et al. 1980, Hargraves 1981, Pace & Orcutt 1981, Capriulo & Carpenter 1983) and serve as a food source for many larger zooplankton including copepods and juvenile fish (LeBrasseur & Kennedy 1972, Voronina & Sukhanova 1976, Capriulo & Ninivaggi 1982, Robertson 1983, Turner & Anderson 1983, Stoecker & Govoni 1984, Stoecker & Sanders 1985) and foraminiferans (Hemleben et al. 1977). Tintinnid ciliates (class Spirotrichea, order Choreotrichida, suborder Tintinnina; Small & Lynn 1985) often dominate plankton communities (Gold & Morales 1975, Hargraves 1981, Capriulo & Carpenter 1983, Capriulo & Dexter unpubl.) and remove significant quantities of algae as well as heterotrophic biomass from many marine ecosystems (Heinbokel & Beers 1979, Capriulo & Carpenter 1980, 1983, Rassoulzadegan & Etienne 1981, Landry & Hassett 1982). Additionally, certain tintinnids, such as *Favella* sp., selectively feed on dinoflagellates including those responsible for toxic red tides (Stoecker et al. 1981).

Recent findings suggest that at least in certain environments tintinnid community ingestion rates are equal to those of the copepod community (Capriulo & Carpenter 1983). The feeding impact of these ciliates coupled with their short generation times, high abundances and high gross growth efficiencies clearly highlights this group as a major component of the planktonic (as well as the benthic) food web (Vitiello 1964, Fenchel 1969, Rassoulzadegan 1978, Hargraves 1981, Capriulo 1982, Capriulo & Carpenter 1983).

Despite the realization that ciliates are major players in aquatic microbial food webs, quantification of their feeding rates is rare. Ingestion and clearance rates for tintinnids have been reported by several workers (Spittler 1973, Blackbourn 1974, Heinbokel 1978a, b, Rassoulzadegan 1978, Rassoulzadegan & Etienne 1981, Stoecker et al. 1981, Capriulo 1982, Capriulo & Carpenter 1983), all of whom demonstrated that these ciliates were capable of selective feeding. The mechanism(s) by which food is actually captured and subsequently eaten by the tintinnids, however, remains unknown. Many ciliates use a specialized method of obtaining food which involves directly contacting prey items. This predatory mode of feeding requires production of special organelles known as extrosomes which are defined by Corliss (1979) as membrane-bound extrusible bodies usually sub-pellicularly located. Tintinnids have been found to pos-

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sess what appear to be extrusible bodies known as capsules. Their capsules are contained within striae which are cytoplasmic evaginations associated with the adoral membranelles (Entz 1929, Laval 1971, 1972, Gold 1979, Laval-Peuto et al. 1979). These striae have been found to contain numerous capsules (Laval 1971, Gold 1979, Laval-Peuto et al. 1979). The capsules show the same general organizational pattern in all species. They are grossly spherical in appearance, show a conical anterior pole distinct from a rounded posterior pole and the contents are electron dense and finely granular (Laval 1971, Gold 1979, Laval-Peuto et al. 1979). Laval-Peuto et al. (1979) also found that the capsules in *Tintinnopsis parva* exhibited distinct orientation in a cell with the anterior pole always oriented towards the cell membrane, and noted that the striae are just one of several structures by which the capsules are positioned in proximity to the adoral membranes. Capsules with a polar appearance have also been found in *Parafavella gigantea* and *Favella ehrenbergii* (Hedin 1975).

A definitive function has not yet been ascribed to the striae or capsules found in tintinnids. Gold (1979) noted the abundance of capsules found inside the striae and the proximity of the striae to the oral area and proposed a mechanism whereby the capsules, protected only by the perilemma and cell membrane, rupture when brought in contact with prey organisms, subsequently releasing their contents to act upon the prey.

If, indeed, the striae are associated with tintinnid feeding, we hypothesize that food presence or absence would alter the numbers of striae in tintinnids, i.e. that the amount of food and the number of striae present would be functionally related. The research described here examines the relation between the presence or absence of food and the occurrence of striae in *Tintinnopsis* spp. and *Stenosemella oliva*.

MATERIALS AND METHODS

Several experiments were carried out, one on tintinnids collected from the surface waters of the New York Bight (NYB) and the others on tintinnids collected from the lower Hudson River Estuary at a station near the Tappan Zee Bridge (HRT). Tintinnids were collected by towing a 20 μm mesh, 0.25 m diameter plankton net through the surface water. Transportation of the water samples to the laboratory took only about 15 to 30 min, with no changes in temperature. Tintinnids were immediately micro-pipetted out of the water sample (about 1000 individuals) and transferred into either NYB or HRT filtered water. Following pipetting, the tintinnids were divided into 2 groups, one which was fed and the other unfed, and contained within separate 15 ml screw cap test tubes or small volume Petri dishes (about 15 ml size) at an initial concentration of about 70 cells ml^{-1}. Logarithmically growing cultures of one of 2 flagellated algae, *Isochrisis galbana* or *Dunaliella tertiolecta* (initial concentrations between approximately 10^3 and 10^5 ml^{-1}), were used as food for the NYB experiment and HRT experiments, respectively. All tubes were incubated in the dark (18 °C for HRT and 10 °C for NYB) for about 20 h. After this time actively swimming tintinnids from both groups were micropipetted out and fixed in Karnovsky's fixative (Karnovsky 1965, Gold 1980) in beem capsules, to be prepared for scanning microscopy. Fixation was followed by a 30 min rinsing in cacodylate buffer. Post fixation was carried out in 1 % osmium tetroxide in cacodylate buffer for 45 min followed by dehydration in a graded ethanol series, for 15 min in each. Tintinnids were then transferred into 1:1 ratio 100 % ethanol/100 % acetone, and then into 100 % acetone twice, for 15 min each. Transfer to anhydrous acetone prior to critical point drying in CO_2 was found to be beneficial (Bomar SPC-900/EX critical dryer was used for the HRT experiments and a Sorvall unit for the NYB). The entire process was carried out in beem capsules covered with 20 μm nitex screening on both top and bottom. The specimens were coated with gold/palladium for a total of 6 min at 9 V in a Hummer JR sputter coater. Coating was carried out in 30 s episodes followed by 90 s intervals for cooling, to prevent specimen burn. After a total of 2 min the sputter coater was turned off and air was admitted into the chamber, to prevent additional heating. Tintinnids were examined in a Super III A IAI scanning microscope (HRT) and a JSM-35U (JEOL, USA) scanning microscope (NYB).

RESULTS

Scanning electron microscope (SEM) examination of fed *Tintinnopsis beroidea* from NYB revealed numerous striae associated with the adoral membranelles (Fig. 1 & 2). Few striae could be found in the unfed group (Fig. 3). Three follow-up experiments carried out on several species of the genus *Tintinnopsis* from HRT resulted in similar findings. Numerous striae were found associated with the oral membranelles of the fed groups (Fig. 4 to 10) while the unfed organisms consistently exhibited a paucity of these structures (Fig. 11 to 15). In some cases tintinnids from the unfed group were almost completely devoid of any striae (Fig. 12). In those unfed individuals where striae were found they typically were observed close to the base of the membranelles (Fig. 13, 14 & 15), and in lesser amounts, as compared to the fed individuals where the striae were stretched out over the entire length of the

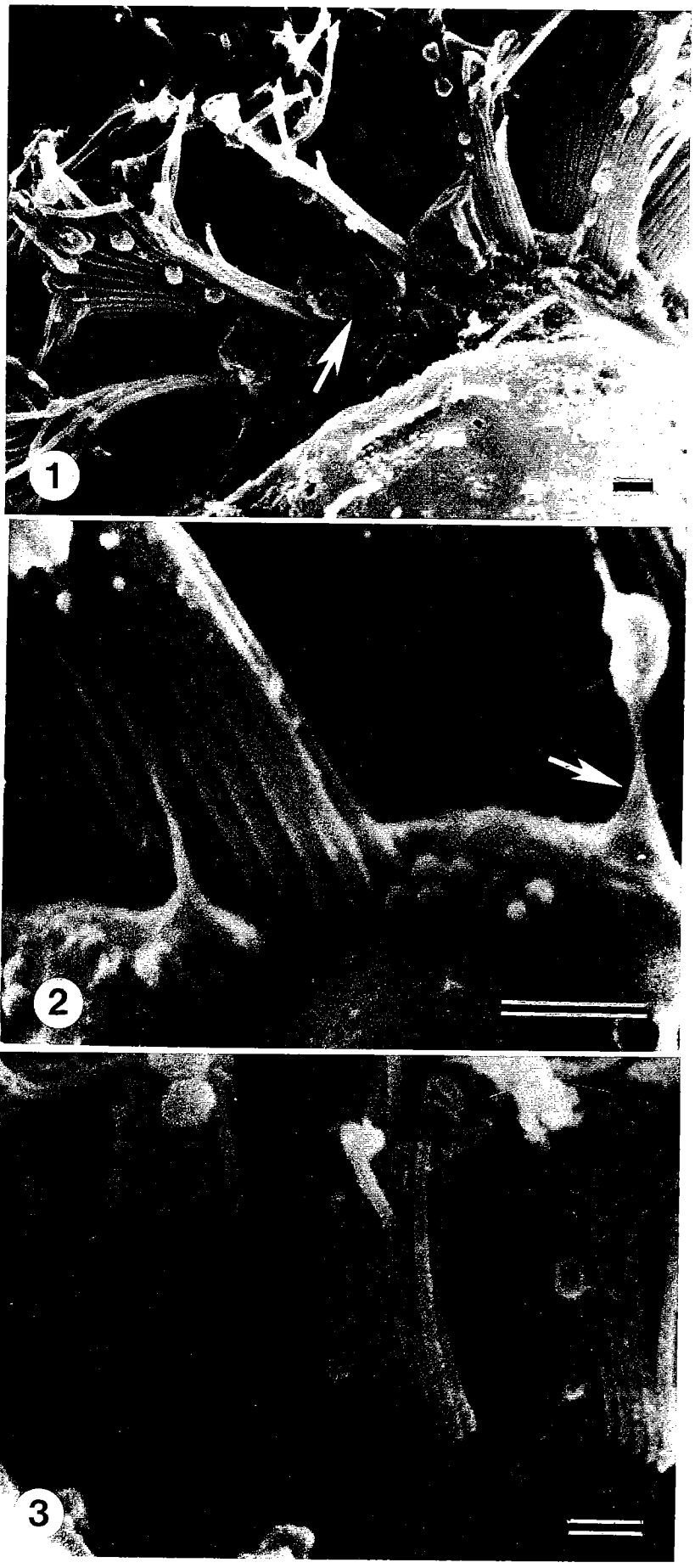
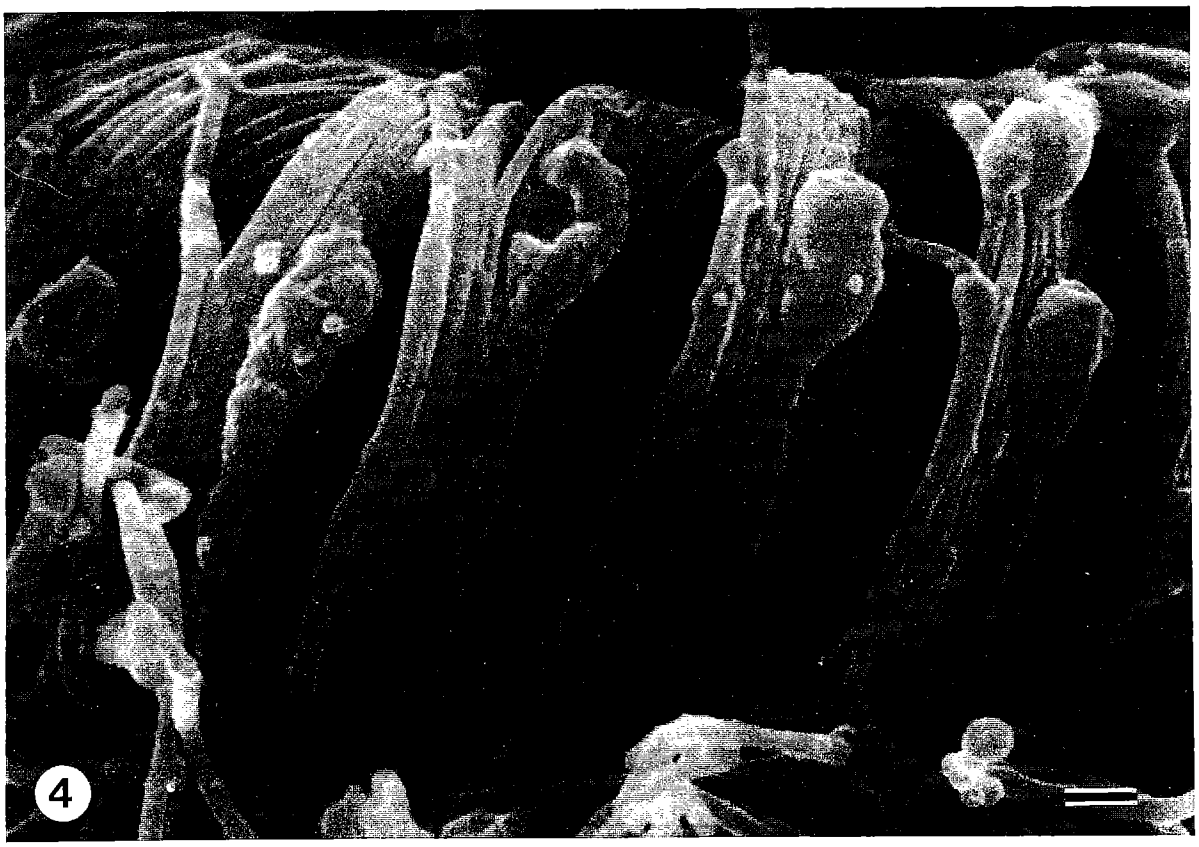


Fig. 1 & 2. *Tintinnopsis beroidea*. Membranelles and associated striae under fed and unfed conditions. Fig. 1. Striae condition representative of the general findings for the fed individuals. Arrow indicates sac-like body discussed in the text. Fig. 2. Higher magnification of the striae of a fed individual. Arrow indicates apparent cytoplasmic origin of the striae. Scale bars = 1 μm

Fig. 3. *Tintinnopsis beroidea*. Micrograph representative of the best case of striae production in the unfed group. Other individuals were completely devoid of any recognizable striae. Scale bars = 1 μm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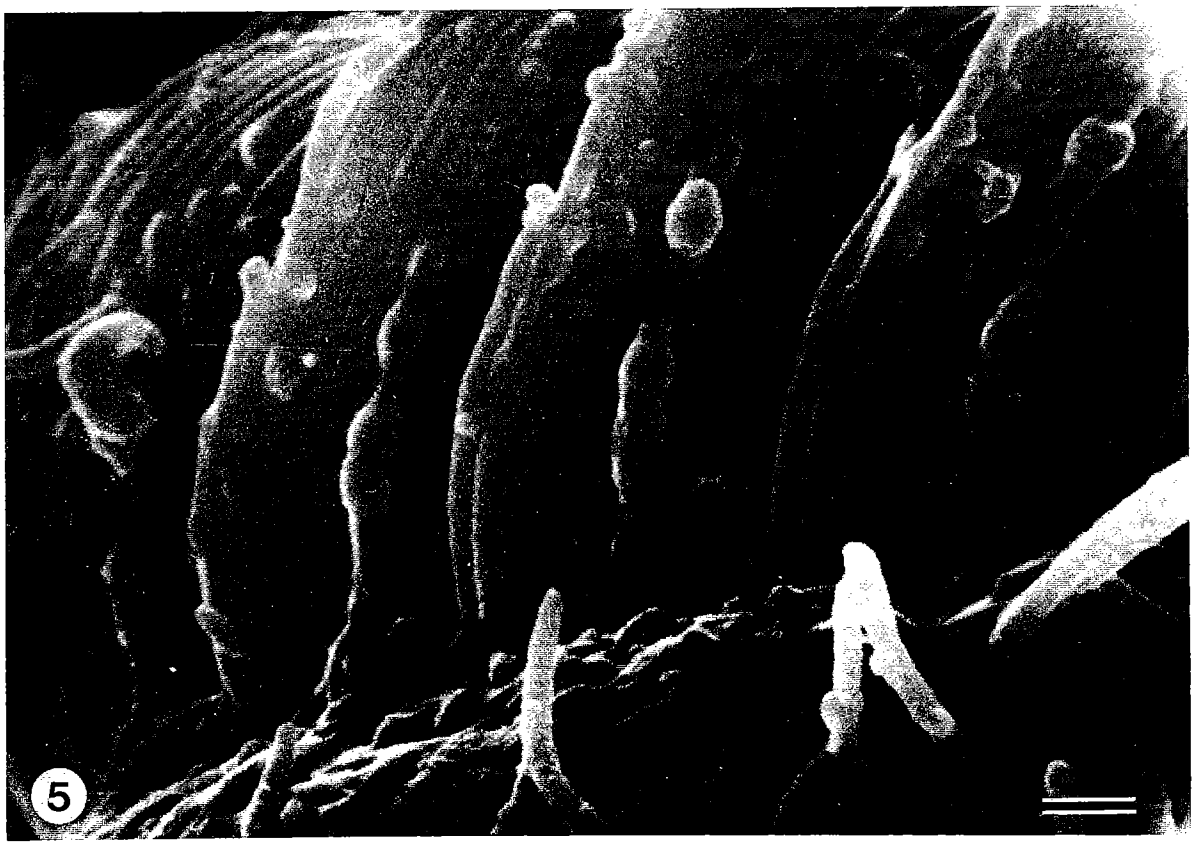
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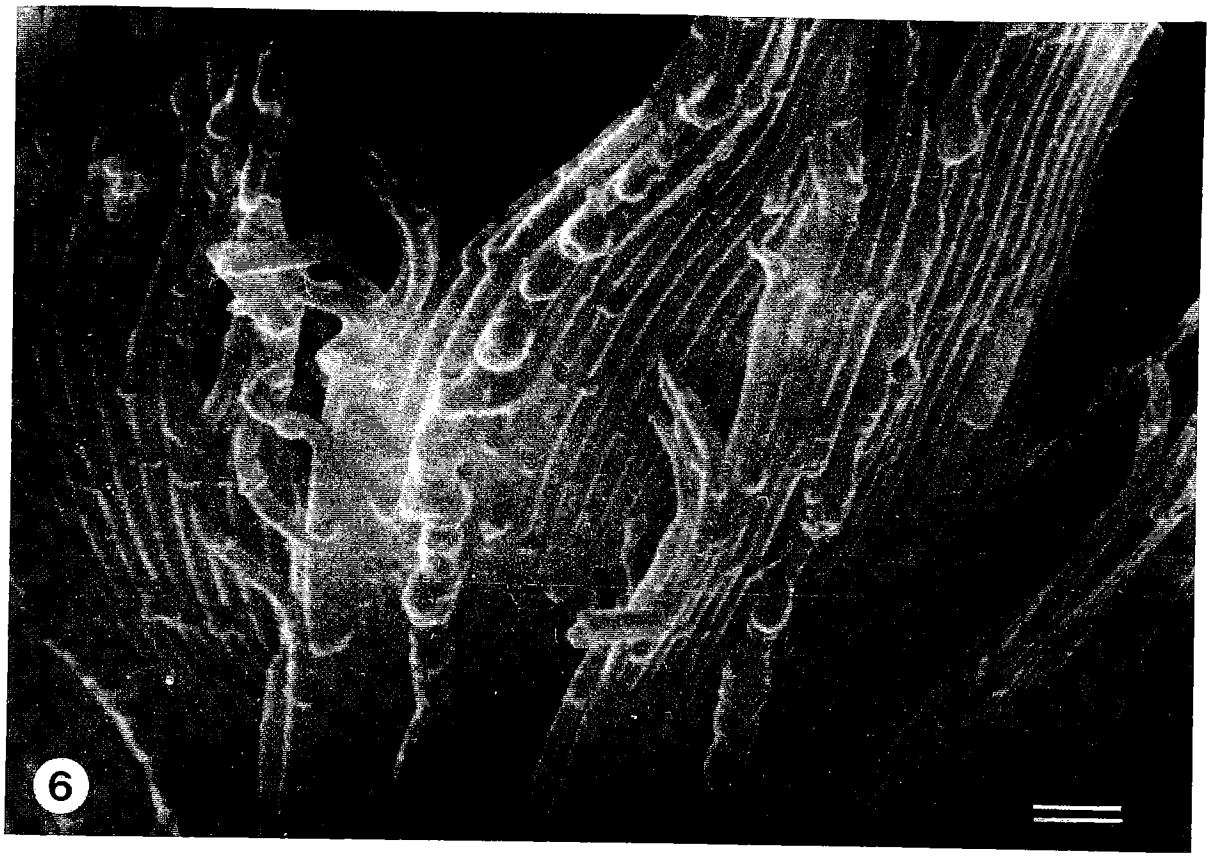
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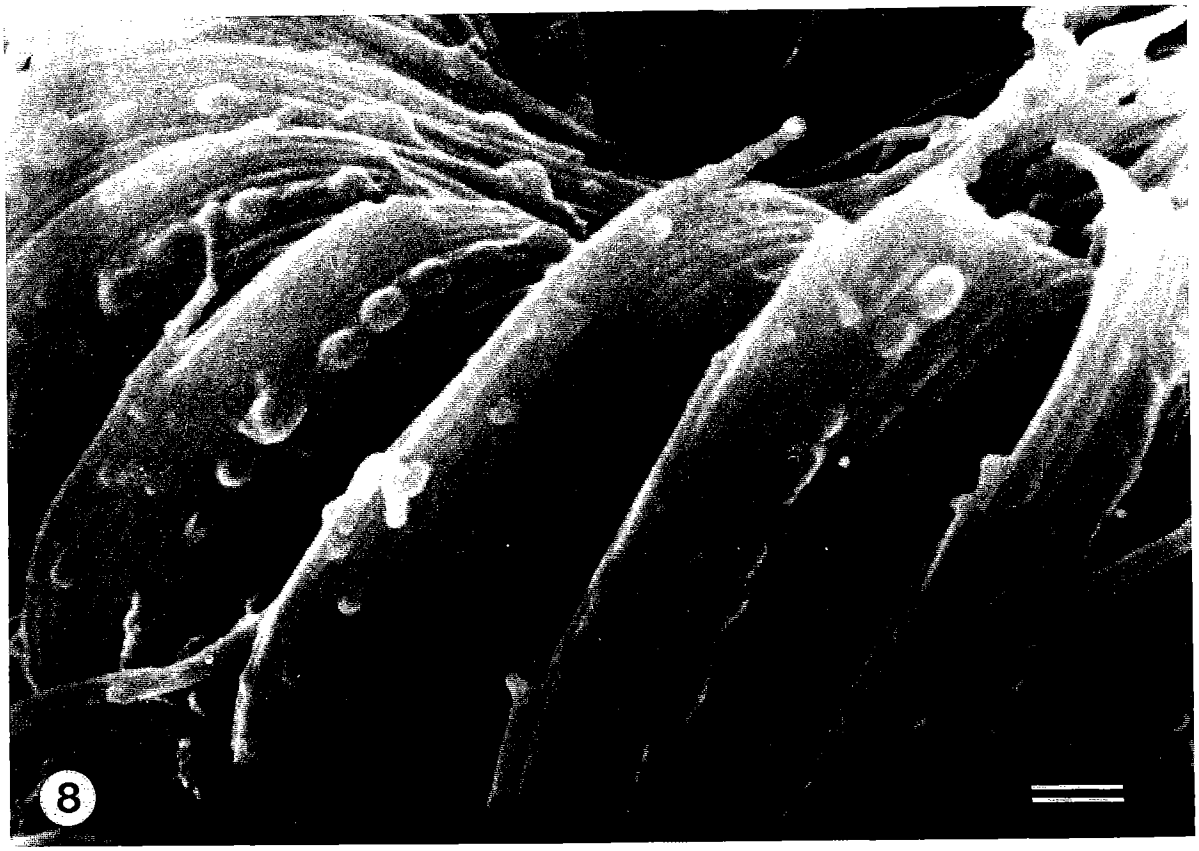
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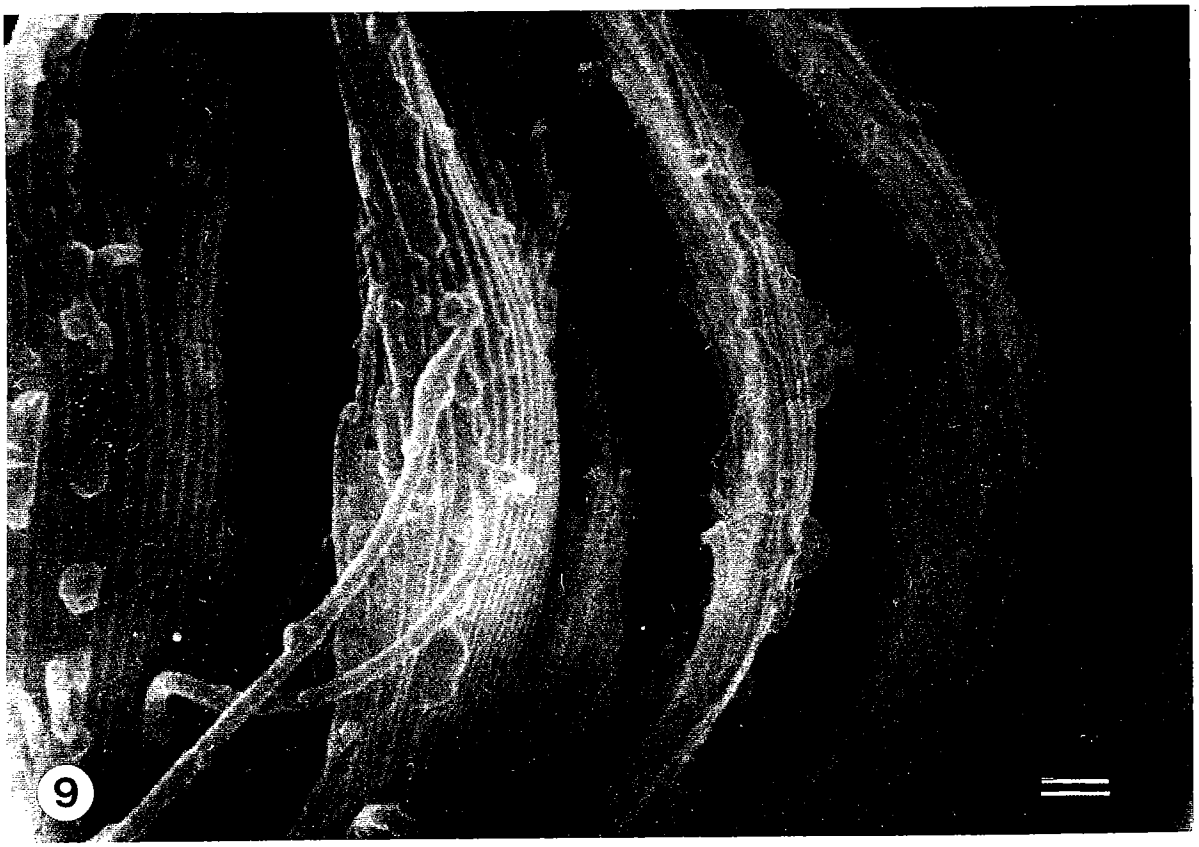
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