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ULTRASTRUCTURE OF SENSORY UNITS ON THE FIRST ANTENNAE OF CALANOID COPEPODS

by

YOLANDA BARRIENTOS CHACON DE AVENDANO

Thesis submitted to the School of Graduate Studies and Research of the University of Ottawa in partial fulfillment of the requirements for the degree of Master of Science in Biology.

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DEDICATORY

Dedico esta tesis a mi madre Irene y a mis nonos, Ambrosio y Francisca de quienes he aprendido las mas solidas, humanas y sabias verdades de la vida. Su mistica estara por siempre en nuestras generaciones.

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ABSTRACT

The morphology of the first antennae and its associated sensory receptors was studied in both herbivorous and omnivorous calanoid copepod species, using scanning and transmission electron microscopic techniques.

In most calanoid copepods, the common types of sensory hairs (sensillae trichodea and basiconica) are present on the first articulated antennae. Species-specific differences, however, include distributional patterns, frequency of occurrence, and specific morphological features (tip angles, basal diameters, annulation) of each type of sensor.

The copepods studied have evolved a specific organization of the sensory structures on their first antennae that may be related to the ecological role of the animal. These sensory structures appear to be more diverse in marine than in the estuarine or fresh-water species.

In two marine species studied, _Calanus finmarchicus_ and _Centropages furcatus_, there is a triangular arrangement of two or three types of sensory hairs per segment; this is also present in two fresh-water species, _Skistodiaptomus or-_

egonensis and *Leptodiaptomus minutus*. However, the latter species has a less continuous pattern and three different sensory hairs (annulated and unannulated trichodea and basiconica hairs) form the arrangement in the ninth and twelfth segments.

In contrast, the estuarine species *Acartia longiremis*, *A. grani* and *A. discaudata* lack the triangular arrangement, with only two sensory hairs per segment. *Eucalanus pileatus* a marine calanoid, also lacks the triangular patterns but two or three annulated sensory hairs are present per segment. Acartiidae species have a unique plumose sensory hair 240 μm long and, the lowest number of potential chemoreceptors (aesthetasc) per individual. *E. pileatus* has also a unique compound seta formed by two elongated segments. The basal segment of this seta bears abundant opposed setules.

Additionally, *C. finmarchicus* displayed the highest diversity of sensory structures (total of 10), including basiconica and trichodea sensory hairs, microhairs, and spiny-like structures. The ultrastructure of the distal, penultimate and antepenultimate plumose setae resemble that of typical mechanoreceptors (modified ciliary structures). The ultrastructure of the basiconica sensory hair resembles that of typical contact chemoreceptors. The main cellular components of the first antennae are also described.

RESUME

La morphologie de la première paire d'antennes et de leurs récepteurs sensoriels fut étudiée sur des espèces de copépodes calanoides herbivores et carnivores, à l'aide de techniques microscopiques électroniques de balayage et de transmission.

Chez la plupart des copépodes calanoides, les types communs de soies sensorielles (sensille trichodea et basiconique) sont présents sur les premières antennes articulées. Toutefois, des différences spécifiques aux espèces comprennent les patterns de distribution, la fréquence à laquelle elles sont présents et des caractéristiques morphologiques spécifiques (angle des extrémités, diamètre de base, annelation) pour chaque type de "sensor".

Les spécimens étudiés ont évolués, sur leurs premières paires d'antennes, une organisation spécifique de leurs structures sensorielles qui peut être liée au rôle écologique de l'animal. Ces structures sensorielles semblent être plus diverses chez les espèces marines que chez les espèces provenant d'estuaries ou d'eaux douces.

Chez deux espèces marines étudiées, *Calanus finmarchicus* et *Centropages furcatus*, il y a un arrangement triangulaire de deux ou trois types de soies sensorielles par segment; ceci est aussi présent chez deux espèces d'eaux douces, *Skistodiaptomus oregonensis* et *Leptodiaptomus minutus*. Toutefois, cette dernière espèce possède un pattern discontinu et troies soies sensorielles différentes (des soies trichodea et basiconiques, annelées et non-annelées) forment toujours un arrangement sur le neuvième et douzième segment.

Par contre, les espèces d'estuaires *Acartia longiremis*, *A. grani* et *A. discaudata* n'ont pas d'arrangement triangulaire, ne possèdant que deux soies sensorielles par segment. *Eucalanus pileatus*, un calanoide marin, ne possède pas ce pattern triangulaire bien qu'il possède deux ou trois soies sensorielles annelées par segment. Les espèces Arcatides ont une soie sensorielle plumeuse unique de 240 µm de long et le nombre le plus faible de chimiorécepteurs potentiels (aesthétasc) par individu. *E. pileatus* possède aussi une soie composée unique, formée de deux segments allongés. Le segment basal de cette soie porte un grand nombre de "setule" opposées.

Additionellement, *C. finmarchicus* possède la diversité de structures sensorielles la plus élevée (total de 10), incluant des soies sensorielles basiconiques et trichodea, des

soies microscopiques et des structures en forme d'épines. L'ultrastructure des soies plumeuses distales, penultièmes et antepenultièmes ressemble a celle de mecanorecepteurs typiques (structures ciliairés modifiees). L'ultrastructure des soies sensorielles basiconiques ressemble a celle de chimiorecepteurs de contact typiques, les composantes cellulaires principales de la première paire d'antennes sont décrites.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Section I

INTRODUCTION

Ecological and behavioural studies of crustaceans show that they react to a diversity of stimuli from the physical, chemical, and biological components of their environments. Aspects such as vertical and horizontal distributions, feeding, breeding, and social behaviour require that the animals can monitor their surroundings. Such monitoring and interpretation imply the presence of a variety of sense organs in addition to eyes, antennal statocysts, and mouthpart receptors. Crustaceans have been shown to react to many types of stimuli (Waterman, 1961; Laverack, 1968, 1975; Katona, 1973; Strickler 1975; Fuzessery & Childress, 1976). The information that the animal probably obtains about its surroundings can be divided into three categories: The first type of information deals with the general characteristics of the environment: such as temperature, salinity, pressure, and the planes of polarization of downwelling light. The second type deals with events close to the animal which are monitored through sense organs by touch and taste, as well as those which detect the movements of the animal relative to the force of gravity. The third type of information is from events taking place at some distance from the animal which are monitored through pressure wave receptors for detecting sound, chemoreceptors for detecting pheromones, and mechanoreceptors for detecting hydrodynamic disturbances (Mauchline, 1977).

It is known that the integument of crustaceans bears numerous sensory organs such as sensory receptors or sensillae and integumental glands. The sensory receptors are innervated by one or several sensory neurons and generally two accessory cells. These accessory cells may be outgrowth structures in the form of a hair, a cone, a peg, or ingrowth structures such as pits or plate organs with sensory cell bodies located underneath (Laverack, 1968). Sensory neurons are of ciliary and non-ciliary types (Ong, 1969). The first one is associated with the presence of mechanoreceptors and the second one is associated with chemoreceptors. There are two types of ciliary structures in receptor cell: I- Cilia which occur at the stimulus site in some kinds of mechanoreceptors and which are structurally very similar to the motile cilia. Mechanoreceptors of this type appear in vibration receptors of ctenophores (Horridge, 1965a) and equilibrium receptors of cephalopods (Barber, 1968). This type of receptor was called epithelial-cell type by Thurm (1968). II- Modified ciliary structures which lie distant from the stimulus site, occuring in both mechano-, chemo- and photoreceptors, are called the bipolar-cell type. Mechanoreceptors of this type appear in the hair plate receptors of the honey bee (Thurm, 1964, 1965); scolopidial sensillum (Gray, 1960); arthropod chemoreceptor (Hayes, 1976; Laverack and Ardill 1965; Slifer and Sekhon 1963, 1964).

Zooplankters are very well equipped with olfactory sensors. These enable them to recognize food concentrations (Bainbridge, 1953), the quality of food (Fryer, 1957) and of the environment, to recognize mates by pheromones (Katona, 1973), and also to sense and avoid predators (Strickler, 1973, 1975a,b). Information available about hair sensillae and integumental gland distribution on crustaceans come from mapping studies. In these studies, animals are treated with hot potassium hydroxide in order to destroy most of the integumentary sensillae and glands and only holes or pores remain where they have been. Under these conditions, pores can be mapped and located exactly. Despite the destruction of the whole sensillae, this method constitutes the only procedure to establish patterns and distribution of hair sensillae on the specimen's integument for the purpose of defining intraspecific traits. Fleminger (1973) mapped the distribution of the sensillae and glands in species of the genus _Eucalanus_. Each species of this genus has a specific distributional pattern. In general, the species-specific differences appear to be shaped by character displacement. Strickler (1975) mapped the distribution of sensilla on the body of *Macrocyclops albidus*. Mauchline and Ballantyne (1975) mapped similar structures in several species of amphipods. They found very little variation in the pattern of distribution of integumental glands in individuals of the same species. Mauchline (1977) found that in copepods, pores are distributed in the integument in patterns that form "signatures" even among species of the same family. He found that among members of the Megacalanidae family, specifically in *Megacalanus* spp., there is a sensory structure different from the *Bathycalanus* and *Bradycalanus* spp. examined. This sensory structure consists of a sub-integumental sac with finger-like extentions to the pores.

The mapping studies cannot however, reveal any information about the type of sensory structure present. Consequently, ultrastructural work is required for such purposes. Ong (1969) found two types of sensory neurons in the mandible, second antennae, labrum, and maxillipeds of the brackish water calanoid copepod *Gladioferences pectinatus*. Strickler and Bal (1973), working with the apical setae of *Cyclops scutifer*, reported the existence of ciliary types of neurons or mechanoreceptors in its first antennae. Friedman and Strickler (1975) described the nature of chemoreceptors on the mandibular palps of *Diaptomus minutus*. Eloffson (1971) described the ultrastructure of the paired nerves, previously called frontal organs or x- organs in copepods.

These pairs of nerves run from the brain to the anterior tip of the animal. They have been found to contain the dendrites of three types of morphologically different sensory neurons. Similarities in the morphology of these components to other presumed chemosensory organs in the Arthropoda suggest that they are chemoreceptors.

Copepods lack a visual system and the cyclopidian eye shows a rather primitive structure limited in its capacity for temporal and spatial resolution (Strickler, in press). For this reason, the first antennae are considered to be the main sensory site for the animal (Strickler, 1973; Griffiths and Frost, 1976). This structure has an abundant number of setae and associated sensory structures which are not all mechanoreceptors (Fig. 1). If the sensory structures on the first antennae are not all mechanoreceptors, then what exactly are these other types? Further, are the mechanoreceptive structures found in the raptorial species Cyclops scutifer similar to those ones present in herbivoures copepods?.

The first antennae constitute pair one of the pre-oral appendages. Among the copepod group it is uniramous, annulated and of variable length. As a result, differences in the first antennae have been used as species- specific indicators among copepod species (Brehm and Zederbarier, 1906;

Haempel, 1918; Gurney, 1931; Hartman, 1971). Classically, systematic information has been recorded in terms of morphological characters related to sexually modified structures or details in the setation, spination, and segmentation of body and appendages. However, the first antennae show themselves to be of great value as an evolutionary indicator. For instance, change in the position of the geniculate segment to the left from the right in the marine copepod P. abdominale as in other calanoids, allowed Gurney (1931) to argue that geniculation of both antennae represents an ancestral form. Antennal cyclomorphosis in E. gracilis leads to a much pronounced spinuous process on the twenty-third segment of the geniculated antennae. Gurney (1931) described how E. pusillus had a reduced antennal process. The important point is that these two species are sympatric. Therefore, they have evolved to be in the one case always with a pronounced twenty-third joint in the right male antennule, slightly larger, and more fertile, and in the other either cyclomorphic or with a reduced process, smaller, and less fertile.

The first antenna has regenerative properties (Conover and Paffenhofer, personal communication). In natural conditions after an attack by a predator, the first antenna may be regenerated completely. However, this regeneration may lead to changes in the setal arrangement, depending on the stage of development of the animal. For instance in C. *finmarchicus*, if the breakage occurs during early copepodite stages the terminal segment of the first antennae will bear more long hairs than a normal animal (Conover, personal communication), and it will lack the two long plumose sensillae which are characteristic of the genus (Fig. 2).

The first antennae play several roles in the behavior of these zooplankters (Strickler, 1975; Blades, 1977, 1979) mainly used for orientation of the animal in the water column, as a grasping device during mating performances or as a complex-sensory site for predatory feeding.

Swimming Activities: The first use of the first antennae are as a balancing device for swimming (Lowndes,1935). Most of the planktonic copepods are floating organisms. Rising and falling movements are linked to specific limbs, the role of the first antenna is basic to avoid sinking once the motion of the limbs is stopped (Kaestner, 1970). If the first antennae are removed, the animal will no longer remain vertical with the anterior end uppermost but in many cases they will rise and fall with the anterior end down (Lowndes, 1935). During swimming, C. *finmarchicus* stretches out the first antennae to keep a vertical position and they act as balancers. The body often hangs diagonally, with the ventral surface up. Friction, increased by the numerous setae, is so great that the copepod sinks only very slowly (Kaestern, 1970).

Mating Activities: The first antennae are used as a mechanical and sensory device for mating behavior during precopulation (Kaester, 1970; Katona, 1973, 1975; Blades, 1977, 1979). In many calanoid males the first antennae are modified on one side into a grasping structure. However, in most harpacticoids and cyclopoids, they are geniculate on both sides for holding females (Kaestner, 1970; Rose, 1933). In addition to the antennal geniculation present on the males of Centropages typicus, there are specific structures such as modified rows of teeth and the presence of two hinges adjoining segment 18 . The fusion of segment 19 to 21 enables the first antenna to fold back upon itself (Blades, 1977). In C. typicus, mating seemed to be continued as long as sensory annulated and unannulated bristles of the antennae were stimulated (Blades, 1977). Numerous aesthetasc are present in adults of both sexes. These aesthetasc are sexually dimorphic; being much larger in the male than in the female (Schneider, 1969). Furthermore, intraspecific mating encounters has been suggested to be controlled by a pheromone produced by the adult female (Griffiths and Frost, 1976), and the first antennae have been considered as the major site for chemoreception in male copepods.

Predator-Prey Interactions: The first antennae play a fundamental role in the predator-prey interactions of this group of zooplankters (Strickler, 1975; Gerritsen, 1977; Landry, 1980). Zooplankters can detect small hydromechanical disturbances and respond by moving away (Strickler, 1974;Gerritsen, 1977). All the escape reactions occur as a response to signals in the form of water displacement. The reception of these signals is dependent on the size, shape, and speed of the detecting animal (Strickler, 1975). Predators can recognize prey at a distance presumably using mechanoreceptors which are specialized to differentiate between signals from predators or prey. On the other hand, chemoreception may operate at a very close distance. For instance, during filter feeding, Eucalanus pileatus is able to sense an alga from up to a distance of two body lengths (500 um) away and by using its mouthparts is able to change the direction of the water current to draw the alga towards its mouth (Alcaraz et al., in press). It is not yet known, however, whether this activation of the mouthpart appendages is triggered by chemoreceptors which may be present on the first antennae.

Recently, Landry (1980) analysed the role of the first antennae during feeding activities in Calanus pacificus, using amputated animals. He was able to show that there were no significant differences in the amount of phytoplankton taken in during feeding with respect to the controls. In predation experiments, however, removal of the first antennae of C. pacificus significantly reduced predatory feeding rates. The fact that predatory feeding is not completely reduced in the amputated specimens is an indication that sensing mechanisms on other parts of the body are involved.

Antennal Cleaning Activities: The first antennae seem to be related with cleaning activities of the mouthparts after feeding (Strickler et al., unpublished data). Using high speed cinematography, it was found while describing the feeding of certain calanoid copepods that there is a movement of the first antennae thought to be part of a cleaning activity after feeding. They found that both Eucalanus pileatus and Temora stylifera were able to clean their mouth appendages after feeding. The sequence involves two relatively fast smooth bendings of the antennae towards the animal's ventral area where the mouth appendages are located. A third bending of longer duration sweeps the antennae over each appendage and the respective setae.

There are reports of sensory organs, sensory hairs and other structures in or on the integuments of a variety of crustaceans (Waterman, 1961). A few studies on sense organs have been concerned with determining their structure and function. Most of this work has been carried out in larger crustaceans, and, in general, the sensillae are small and difficult to manipulate. Thus, insufficient information about the numbers, distribution and types of structures in the integument of those animals is available for an assessment of their importance.

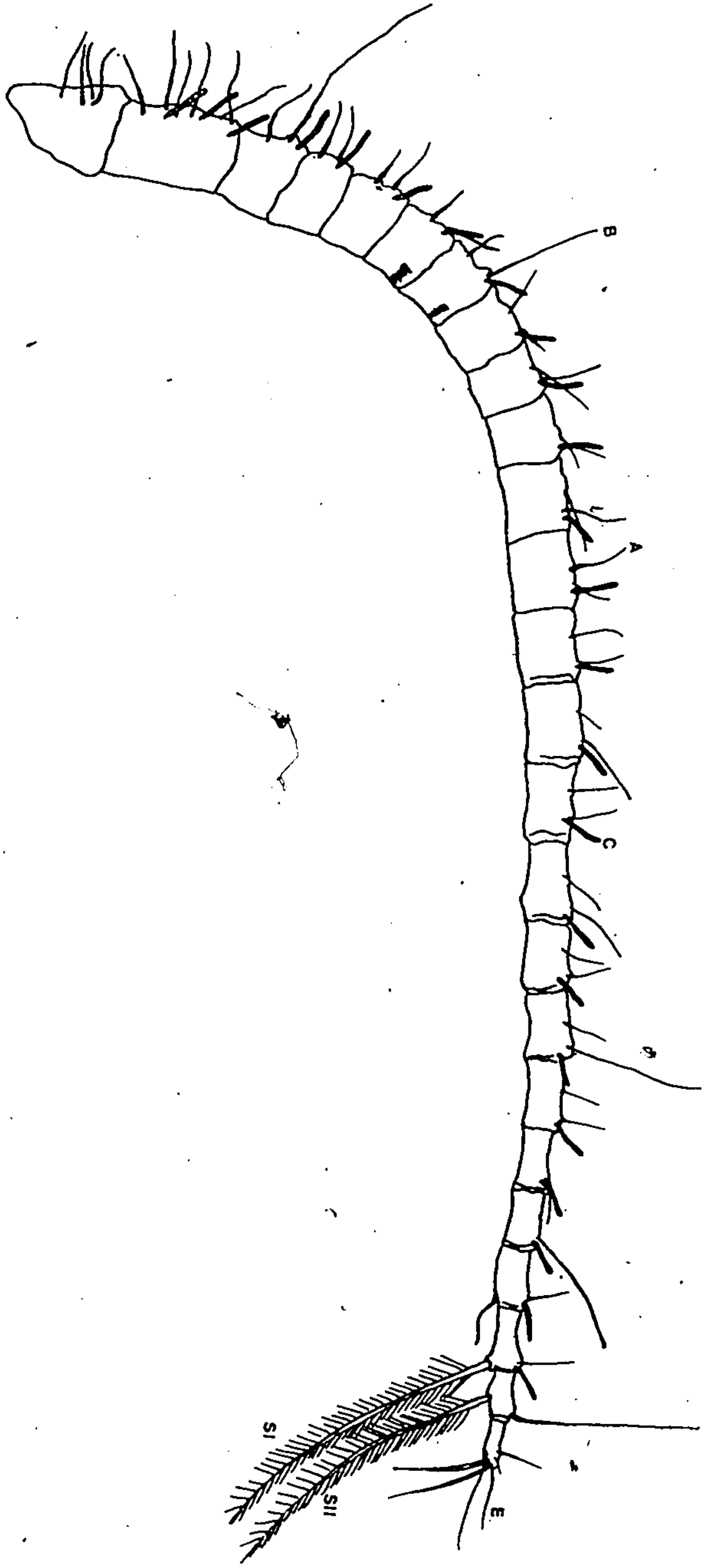
This thesis has four main objectives :

1. To determine through ultrastructural work the main types of sensory hairs present on the first antennae.
2. To establish the constancy of type and occurrence of the sensory structures present on the first antennae among the different genera studied.
3. To establish relationships between the occurrence of a particular sensor with the life habits of the species, particularly feeding habits.
4. To examine the diversity of the sensory structures among the genera studied which may indicate evolutionary trends, specifically species segregation and species specialization.

Adult females of the most representative families of the order Calanoida were used in the present study. They were chosen on the basis of their relatively abundance and their important rôle in the aquatic environments.

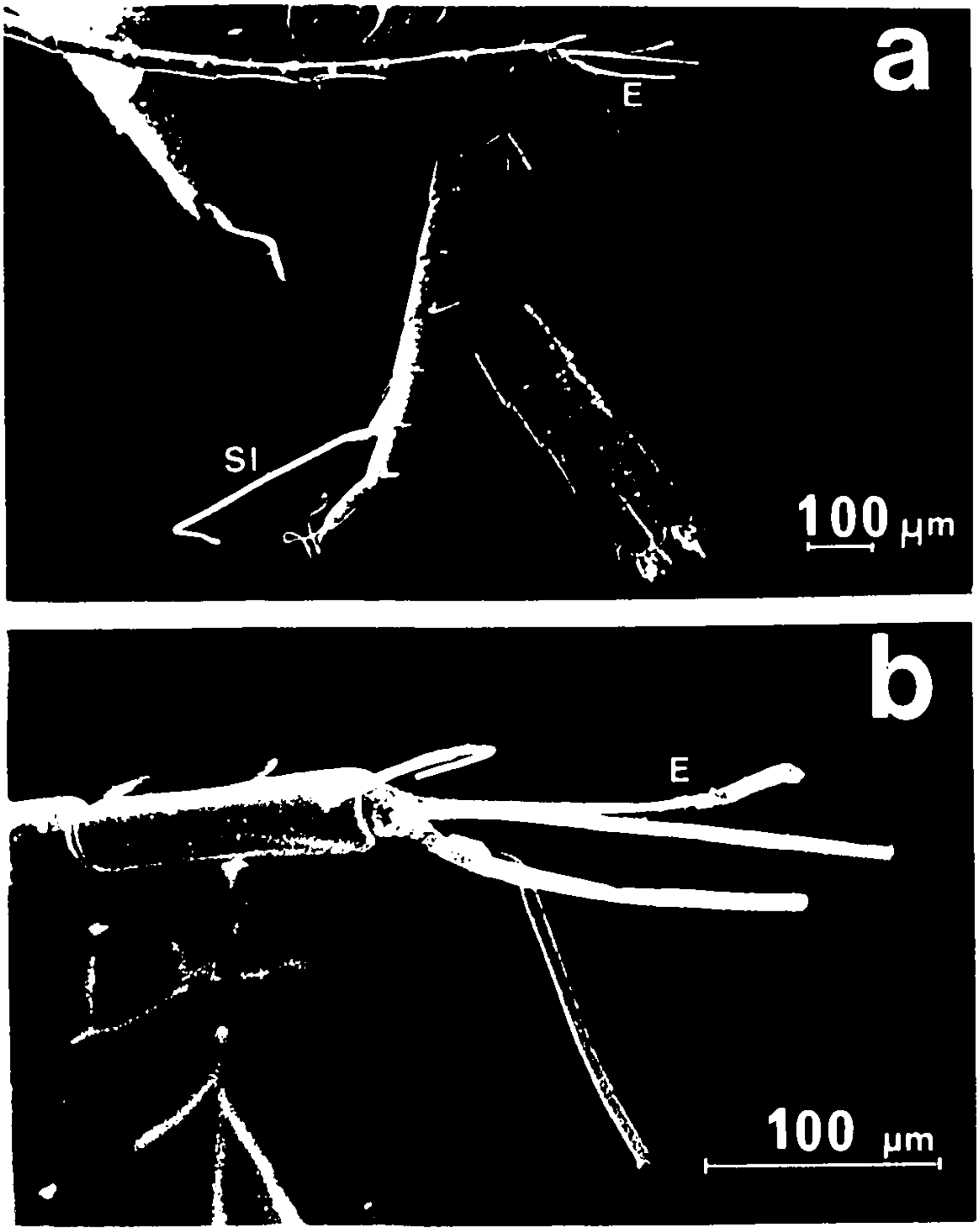
General morphological features showing segmental shapes and position of the main types of sensory hairs.
C-type hairs or aesthetacs dotted.
A, B, C, E = types of sensory hairs
SI, SII = long plumose setae

Figure 1: Schematic first antennae of typical female *Calanus pacificus*, Brodsky. X 300.


B
A
C
D
SI
SII
E

(a) Normal setal arrangement of the same area on the left antennae distal end, showing the plumose setae (b) Setal arrangement of the same area on the right antenna lacking the long plumose setae characteristic of the genus and showing the distal e-type hairs in higher number than the left antenna.
SI= long and plumose setae
E = e-type sensory hair

Figure 2: <u>Calanus</u> <u>finmarchicus</u> showing the uneven setal pattern on the distal end of the right antenna .


a
E
SI
100 µm
b
E
100 µm

Section II

MATERIALS AND METHODS

2.1 A- FIELD COLLECTION

Animals were collected with a 250 um plankton net. Vertical tows were done from 80 m depth to the surface. The net surface opening was 1/8 m² and the bottle 1 L capacity. Zooplankters were placed in plastic jars of 3 L capacity. The containers were completly filled up with water and a plastic film was placed over the water to prevent air bubbles. This was done to avoid specimens being trapped at the water-air interface. Animals were kept in low densities, at no more than twenty, in each container to avoid overcrowding. Water from the field was always filtered. This aspect was considered important because an excess of large particles could accumulate on the surface of the animal. The animals examined are from several sources. Many were collected from the Atlantic east coast between latitude 35 and 45° N. For instance, C. finmarchicus were obtained from the Halifax port, Nova Scotia, Canada; Acartia longiremis were collected at the St. Laurence gulf, east coast Canada. Centropages furcatus and Eucalanus pileatus were collected at the southeastern shelf of U.S.A. Some species are absent or rare in the N.E. Atlantic and so some of them have been obtained from other seas, e.g. the Mediterranean sea, as is the case for _A. grani_ and _A. discaudata_. Fresh-water species, _Skistodiaptomus oregonensis_ and _Leptodiaptomus minutus_ were collected from Meach lake, Ottawa area, Canada.

2.2 B - LABORATORY PROCEDURES:

2.2.1 Specimen handling

Animals were placed into glass beakers and selected according to sex, stage of development, and condition of body and appendages. Special care was given to antennal condition; specimens with broken antennae or setae were discarded. Wide pipets were used to avoid mechanical damage to the hairs. In order to standarize the study, only adult females were used, since sexual dimorphism of calanoid copepods occurs in the first antennae.

2.2.1.1 Scanning Electron Microscopy

For this preparation, I followed the procedures of Friedman (1977) and Hayat (1974, 1978); with some modifications, especially when dealing with marine calanoid copepods.

The animals were heat-narcotized. For SEM observations of the first antennae and associated structures, animals should keep body and appendages streched out after regular fixation. Therefore, heat-narcotization was used to avoid distress in the animal during fixation. No more than four animals were placed in a small petri dish and it was left on the top of a 50 ml beaker containing 25 ml of warm water (50 °C). The animals should not receive these warm vapors for more than 10 sec. The animals are very sensitive to the temperature changes and they can easily get overheated. In this case, the animal bends the appendages towards the body and it has to be discarded for this purpose. When the animals started decreasing swimming movements and the first antennae streched out from the body, they were ready to be transferred to the fixative. Steady animals are ~~easy to~~ handle and final checks can be done if it is necessary. The heat-narcotized animals were immersed in a 2% v/v glutaraldehyde solution buffered with 0.1 M sodium cacodylate for 1 h at 20°C (pH 7.2). Marine samples were fixed with 2% v/v glutaraldehyde solution buffered with filtered seawater. The specimens were washed three times with filtered sea water for 15 min. each and transferred through decreasing concentrations of filtered seawater to eliminate salts (100%, 75%, 50%, 25%, and distilled water) for 10 min. each. The specimens were post-fixed in 1% osmium tetroxide in 0.1 M sodium cacodylate buffer, washed three times in the same buffer for 15 min. each. The specimens were rapidly dehydrated in ascending concentrations of ethanol to 100% absolute ethanol and a graded ethanol-acetone series to 100% pure acetone. Two changes were done with 100% pure acetone for 10 min. each. Specimens were dried in liquid CO_2 using a critical point drying apparatus (Sandri PTV-3, Tousimins Research Corporation, Rockville, Maryland, USA). They were then mounted directly on SEM aluminum stubs using a thin film of conducting silver paint, and coated with 100% pure gold using a coating unit (Model 12 E6/1258 from Edwards High Vacuum Ltd, Crawley, Sussex, Uk). Specimens were examined in an scanning electron microscope (AMR 1000, Advanced Metal Research, Bedford, Massachusetts, USA) and photographically recorded on film either using Kodak, Plus-X Pan or Polaroid 4x5 land film.

2.2.1.2 Transmission Electron Microscopy

The animals were fixed at 20°C for 1 h in 2% glutaraldehyde with 0.1 M sodium cacodylate, pH 7.2. They were washed three times in 0.1 M sodium cacodylate for 15 min each and postfixed in 1% osmium tetroxide with 0.1 M sodium cacodylate pH 7.2 at 7°C. The specimens were washed again with the buffer and transferred through decreasing concentrations of filtered sea water, terminating in 100% distilled water. Dehydration was done using a graded acetone series ending up in 100% pure acetone. The last two changes were each for 10 min. at room temperature. Specimens were embedded in Spurr's hard resin mixture (Spurr,1969) which was polymerized at 60°C for 24 h. Thick and thin sections were cut on an ultramicrotome (Sorvall Porter Blum MT-2B, Sorvall Inc, Normalk, Connecticut, USA) with glass and diamond knife (Dupont), stained for 7 min. with uranyl acetate (Watson, 1958), followed by 5 min. with lead citrate (Reynolds, 1963), and examined with an electron microscope (EM6B Associated Electrical Industries Ltd, Harlow, Essex, UK). Thick sections for light microscopy were stained with 1% toluidine blue according to Rudeberg (1967).

Section III

RESULTS

All the morphological features and measurements were taken from scanning electron micrographs. Information on cephalothorax length, number of segments and habitat of occurrence for the species studied is given in Table 1. Sensory hairs were categorized into five groups: a, b, c, d, and e-types respectively, on the basis of the total length, base diameter, and the external features, such as annulation, shape and tip angles. Information on total length and base diameter is given in Table 2. In some scanning elcectron micrographs these hairs are identified with the same letters but capitalized. The other features mentioned are explained in the text. Observations will be reported first for the marine species, then the estuarine and lastly the fresh-water species. In this study many specimens were examined because results are directly dependant on the quality of fixation procedures. For this reason, the obtained data for Eucalanus pileatus, (Table 2) is incomplete because specimens were previously fixed in a 2% formaline solution and as a result sensory hairs were not clearly identified. For EM procedures, the sample must be alive for the respective treatment. The sample size, for the SEM studies was 10 well prepared specimens and two for TEM analysis.

TABLE 1

Cephalothorax dimensions, Number of antennal segments, and habitat of the species studied.

Species	Cephalothorax. length (mm)	Number of segments	Habitat
Calanus fimarchicus	3.2	25	Marine
Centropages furcatus	1.28	25	Marine
Eucalanus pileatus	1.83	25	Marine
Acartia longiremis	0.95	19	Brackish
A. grani	1.04	19	Brackish
A. discaudata	1.04	19	Brackish
Skistodiaptomus oregonensis	0.93	25	Fresh-water
Leptodiaptomus minutus	0.68	25	Fresh-water

TABLE 2

Comparative dimensions of the sensory hairs for the species studied.

Genus & Species	a*		b*		c*		d**		e**	
	L	B	L	B	L	B	L	B	L	B
Calanus finmarchicus	126	7	373	17	120	7	-	-	220	6
Centropages furcatus	60	3	75	7	30	3	-	-	-	-
Fucalanus pileatus	?		?		?		144	6	380	25
Acartia longiremis	30	4	—	—	60	3	220	8	300	20
A. grani	35	2	—	—	32	2	90	8	260	10
A. discaudata	25	3	—	—	28	2	60	5	190	10
Skistodiaptomus oregonensis	35	5	—	—	30	2	133	6	233	7
Leptodiaptomus minutus	36	2	—	—	24	2	—	—	198	10

L = Total length (um)
B = Basal diameter (um)
* = Single hairs
**= Compound hairs

3.1 MARINE SPECIES

3.1.0.3 *Calanus finmarchicus*, Gurnner 1765

The external surface of the first antennae display ten different types of sensory hairs which occur in different positions. The second proximal segment bears the highest number of sensory hairs (hair sensillae types) per segment, with a total of nine. In the subsequent segments sensory hairs are uniformly distributed, numbering three per segment (Fig. 4 arrow). However, this setal pattern of three hairs per segment, changes in the twenty-third and twenty-fourth segments where two long setae are present (SI and SII). These long setae consist of ninety annuli and bear a pair of opposing articulated setules on every second annulus. These setules are only seen by light microscopy observations since they disappear after SEM treatment, probably as a result of mechanical damage during drying routines. The innnervation of these long setae on the first antennae make the penultimate and antepenultimate segments wider than the preceding ones at their distal end (Fig. 4). This feature is also observed in the basal segments, after which the segments keep a regular shape and size. This gives a symmetrical appearance to the whole structure.

Calanus finmarchicus possesses three types of unannulated hairs called a-, b-, and c-types in this study (Table 2). One pair of a-type sensory hairs occurs on each article, with the exception of the third, seventh, fourteenth, eighteenth, twenty first and twenty fourth articles. In those, one b-type sensory hair replaces each a-type (Fig. 5a). These two sensory hairs have thick walls, taper gradually, and end in a pointed tip.

The third unannulated sensory hair is a c-type. These are found singly on each article and are situated at the latero-ventral side of each segment, just beside the distal a-type. The a-, b-, and c-type sensory hairs form an isosceles triangular pattern where c- and either a- or b-type sensory hairs are located at the bases (Fig.5a). The apical position is always occupied by an a-type hair. They are thin walled, nearly cylindrical for the first one third of their length, ending in a round tip with a group of three pores (Fig. 5b,c;11). Transmission electron micrographs reveal that the ciliary dendrites branch within the hair lumen until the tip. The following description is made for this species because of the unique occurrence of the particular structure.

Micro-hairs or ring-hairs: This name was given to a particular group of hairs located between the second and the eighth segment. One group is 5 to 7 um long, with a diameter of 3 um at the base. The hairs occur in patches of ten rows and are positioned behind the apical a-type sensory hair of the triangular configuration (Fig.6b,c). These ring hairs form a dense covering around the ventral and dorsal surface of each article. After the fifth segment they begin to decrease in density, disappearing completely after the eighth segment. In transmission electron micrographs, these microhairs show a thin outer tube separated by a space from a thick inner tube. These structures are empty of any cellular component (Fig. 7a,b).

Spine-like structures: These are present on the ventral and lateral surfaces of segments thirteen to nineteen (Fig.8a). These structures have a broad base (2 to 5 um in diameter), taper to a pointed end, and range in length from 3 to 8 um. They are arranged in rows of fifteen to twenty spines (Fig. 8,c,d). There is a second group of related structures located at the inner edge of the first seven basal segments. These spine-like structures are of similar length and are always located at the proximal part of the articulated segments. This is an important feature from the mechanical point of view. Electron micrographs show that the cuticle around the joints is highly sclerotized (Fig. 7b).

The first antennae of C. finmarchicus are also equipped with striated muscle (Fig. 7c,d) The antennal musculature is organized into bundles. In transverse sections, these fibres are grouped together to form hexagonal patterns. In longitudinal sections the musculature shows the typical striation of skeletal muscle in which the "A" and "I" bands can be distinguished clearly. Prominent mitochondria are present lying between individual muscle fibres (Fig. 7c, 12a). H and Z lines can be observed limiting the sarcomere. Lateral fibres seem to attach one article to the next (Fig. 9a,b,c).

3.1.0.4 Innervation

The sensory innervations of the "long and feathered" terminal setae were studied in detail. Basically, they contain two sensory neurons with a well-developed ciliary apparatus with basal bodies and a 9+0 pattern of microtubules in the ciliary base. The sensory cilium terminates in a canal several microns away from the base of the setae. The dendrites at their distal region present an accumulation of microtubules forming a tubular body. . The presence of this tubular body can be easily recognized even in light micrographs. There are neither pores on the surface of these sensillae, which dismisses any olfactory function (Slifer, 1959), nor are there single openings at the tip, which are a basic character of contact chemoreceptors (Slifer, 1959; 1970). No cellular organelles are present within the long setae; only neurotubules and vesicles are found to occupy almost the whole hair lumen. At the basal body, the structure resembles that of a classical scolopidium (Howse, 1968; Corbiere, 1969). These scolopidia possess two dendrites and the scolopale cells form a thick cylinder of dense material which form no separate rods. This is a dense and granular material which contains many microtubules. The cytoplasm of the scolopale cell contains numerous mitochondria. The thickness of the scolopale reaches its maximum dimensions along the proximal region and start shrinking beyond the ciliary basal body region. The scolopale cells form desmosome-like junctions (JL) at all the points of contact with the tubular sheath cells (Fig. 10d), of which there are three contacting the scolopale cell and lying between it and the nearest wall of the antennae. At the very proximal segment of the dendrites, the scolopale cells appear aggregated and they connect the dendrites with their enveloping cells (Fig.10d). They have abundant microtubules and scattered mitochondria.

The sensory innervation of the a- and b-type hairs shows the presence of two bipolar neurons. The ciliary segment of the dendrite which contains neurotubules is surrounded by the scopale matrix at the basal body region and at the base of the hair. In general, there is no difference between the innervating neurons and associated structures of the a-, b-type and the long feathered (SI and SII) sensory hairs.

Sensory hairs c-type do not have the scolopale matrix associated with the base of the setae (Fig. 11c). At this level, the innervating dendrites start branching within the hair lumen (Fig. 11 a,c,d). Each branch differs in the number of microtubules present and it is assumed that the number of microtubules per dendrite increases distally. Some dendrites show less than nine microtubule doublets found at the cilium. It seems that the dendrites terminates within the hair lumen at different distances. This branching of the dendrites will allow them to contact the exterior environment through setal pores.

The nerve cells of all the sensillae could not be morphologically distinguished from each other; the nerve cell typically has a large nucleus, sends an axon proximally and a dendrite distally. Groups of axons, as well as single myelinated and unmyelinated types of axons, are present. Neurotubules are abundant around unmyelinated axons, but randomly distributed (Fig. 12 a,b,c).

The distal segment of the first antenna bears a group of six nonsocketed, annulated e-type sensory hairs. They have a defined band of microtubules (tubular body) extending from the distal segment into the hair sensilla. This band narrows at the junction point, after which the band expands until it reaches the tip of the hair, where it occupies one third of the whole annulus. No evidence of typical basal body structures has been found in the dendrites innervating the setae (Fig. 13a). The setal cuticle shows a fibrous network in contrast to the normal laminated chitin around the basal portion of the setae (Fig. 13b). Inside the setae, only vesicles, mitochondria and neurotubules are present.

3.1.0.5 Centropages furcatus, Kroyer 1849

Centropages furcatus, shares the triangular arrangement of sensory hairs a, b, and c-type per article with Calanus finmarchicus. However, antennal articles are less symmetrical and two "horn-like projections" at the fourth segment gives the first antennae a completely different appearance (Fig. 14). These structures are 12 um long and have a diameter of 15 um at the base (Fig. 15, arrow). No hairs or pores are present on the surface of these structures. The distal article of the first antennae bears four e-type sensory hairs.

3.1.0.6 Eucalanus pileatus, Dana 1848

This species differs completely from the two marine species reported before in its setal arrangement and type (Fig. 16a,b). There are three sensory hairs only in the fourth, seventh and fourteenth segments. Each hair bends once at the middle point of its length (Fig. 16c), with opposed setules of 12 um length. E. pileatus bears a different type of annulated hair sensillae. These hairs have two segments with a broad base and bear abundant setules along their length (Fig. 17b). In Fig. 17a, it can be seen how the distribution of hairs and their joints maintain a line which could allow a great flexibility, for instance, to water displacements. Each even numbered segment bears one e-type hair. This pattern changes in the twenty second segment and twenty fifth segments with two and four e-type hairs respectively.

3.2 ESTUARINE SPECIES

The three estuarine species studied were: Acartia longiremis, Lilljeborg.1853. (Fig. 18) A. grani, Sars.1904. (Fig. 20) A. discaudata, Giesbrecht.1881. (Fig. 22). In the three species the first antennae consist of nineteen articles showing a high degree of asymmetry in their general morphology and the arrangement of the articles. This asymmetry is reflected mainly in constrictions and an irregular shape of the segments. There is a constant number of four hair sensillae at the second basal segment. The general pattern of hair sensillae distribution is two hairs per article (Fig. 24a). The most important morphological feature, however, only present in the Acartiidae family, is the presence along the whole surface of the first antennae of a specific e-type sensory hair (Fig. 24c). These hairs are very similar in length to the distal setae of _C. finmarchicus_ (Table 2) but _A. longiremis_ is 2-3 times smaller than _C. finmarchicus_. Additionally, these hairs have a well developed base (Fig. 24b,d) which allows them to be mobile. They resemble a feathered structure. Pairs of opposing setules are inserted along the seta main axis with an intersetular distance of 6 µm each. The setules vary in length from 4 µm at the base to 3 µm at the tip of the hair. These e-type hairs are distributed in number of one per article ending in five at the distal segment.

A. grani and _A. discaudata_ have the same setal arrangement (Fig. 21,23). Both species have the same overall body length, but the hairs of _A. discaudata_ are half as long as those of _A. grani_. (Table 2). The three species have seven c-type hairs (aesthetasc) per antenna, in contrast to the twenty four found in _C. finmarchicus_.

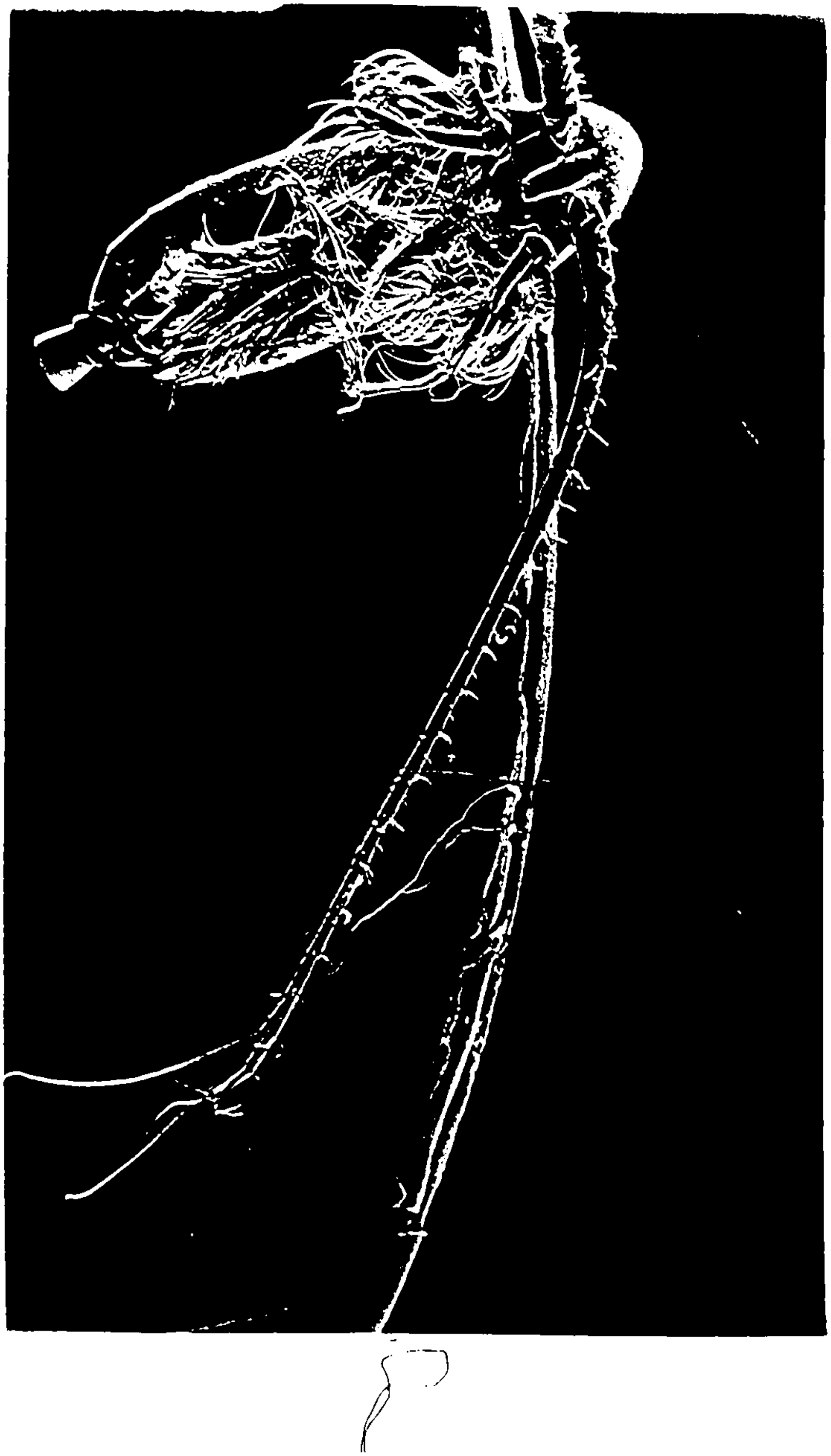
3.3 FRESH-WATER SPECIES

The two fresh-water species studied were _Skistodiaptomus oregonensis_ (Fig. 25) and _Leptodiaptomus minutus_, Lilljeborg, 1889 (Fig. 26). In both species first antennae are composed of twenty five articles. There is more symmetry in the article shape and arrangement along first antennae than in the Acartiidae species. Two constrictions, at the ninth and twelfth segments are shared by both diaptomid species (Fig. 26,28). Both species have four sensory hairs in the second basal segment and display a triangular configuration of the hair sensillae along first antennae, a character which is completely absent in the Acartiidae family.

S. oregonensis has a distribution of three hair sensillae per article. No b-type hairs are present, but an e-type hair replaces, in all the segments, the position of the b-type hair found in *C. finmarchicus*. Seventeen aesthetasc are present per antenna, and the last two distal articles bear two and five e-type sensory hairs.

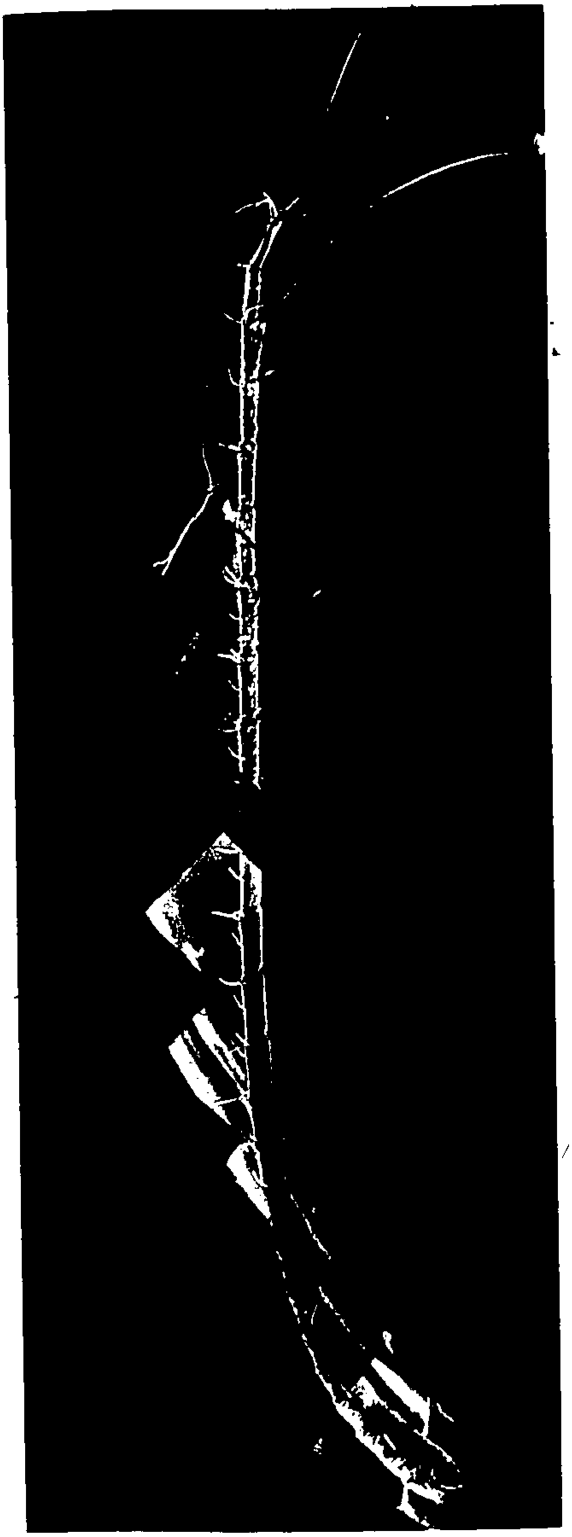
In contrast to *S. oregonensis*, *L. minutus* has a slightly different pattern of sensory hair distribution. Firstly, the three sensory hair/segment character is present only in the ninth and twelfth segments. The basic distributional pattern is the presence of one c- and e-type sensory hairs on each odd segment and one a-type on each even segment. In *L. minutus*, the triangular configuration of a-, c-, and e-type sensory hairs, is the same as that displayed by *S. oregonensis*. A total of eleven c-type (aesthetasc) are located along the first antennae and two and four e-type hairs are present in the last two distal articles.

Figure 3: General anterior ventral view of *Calanus finmarchicus* X 30.



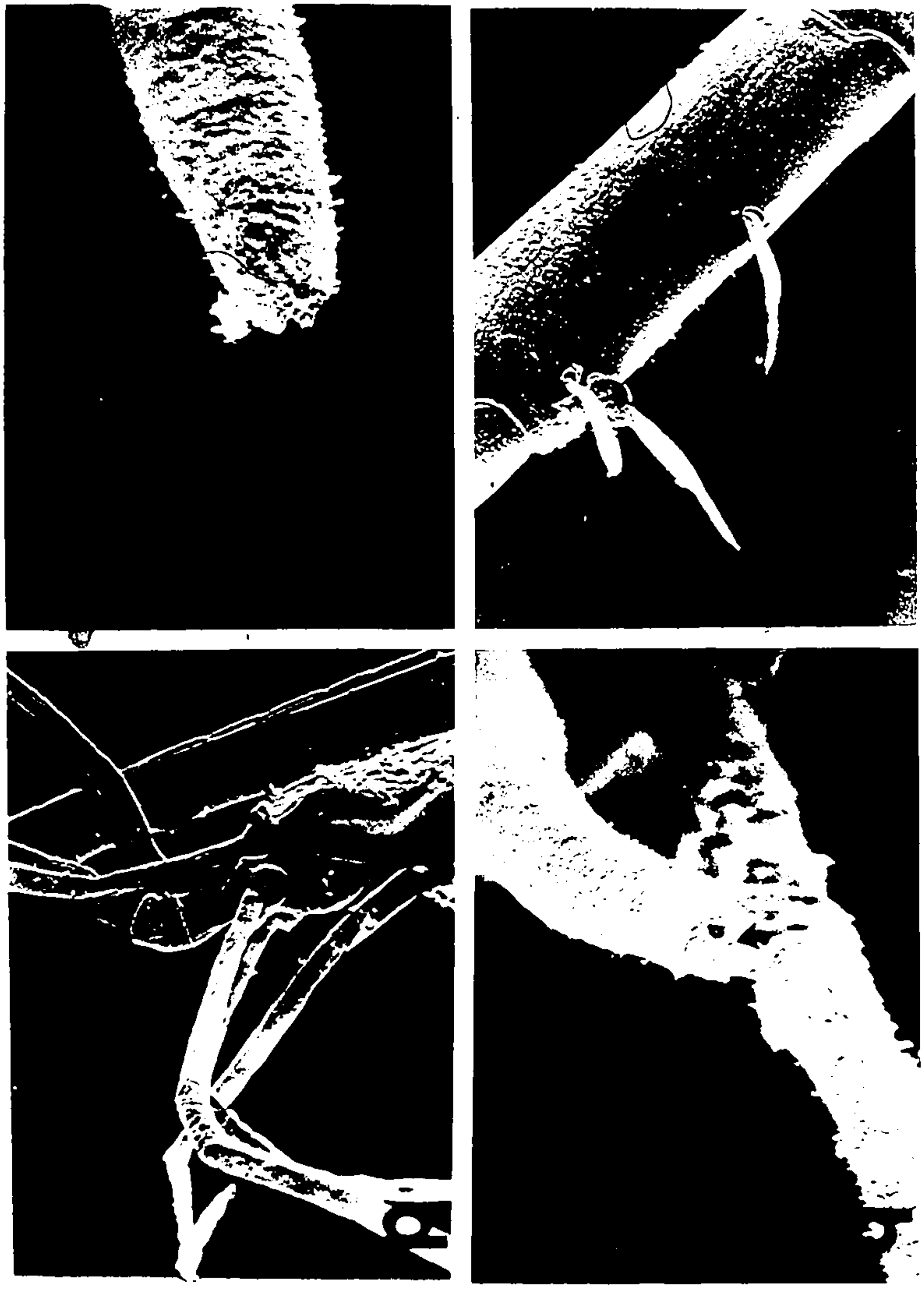
Second basal segment bears the maximun number of hairs (arrow);
A,B,C = Sensory hairs
Ch = Chaetica sensory hair
SI,SII= Long and plumose setae

Figure 4: *Calanus finmarchicus* anterior ventral view of the first antennae X 308.



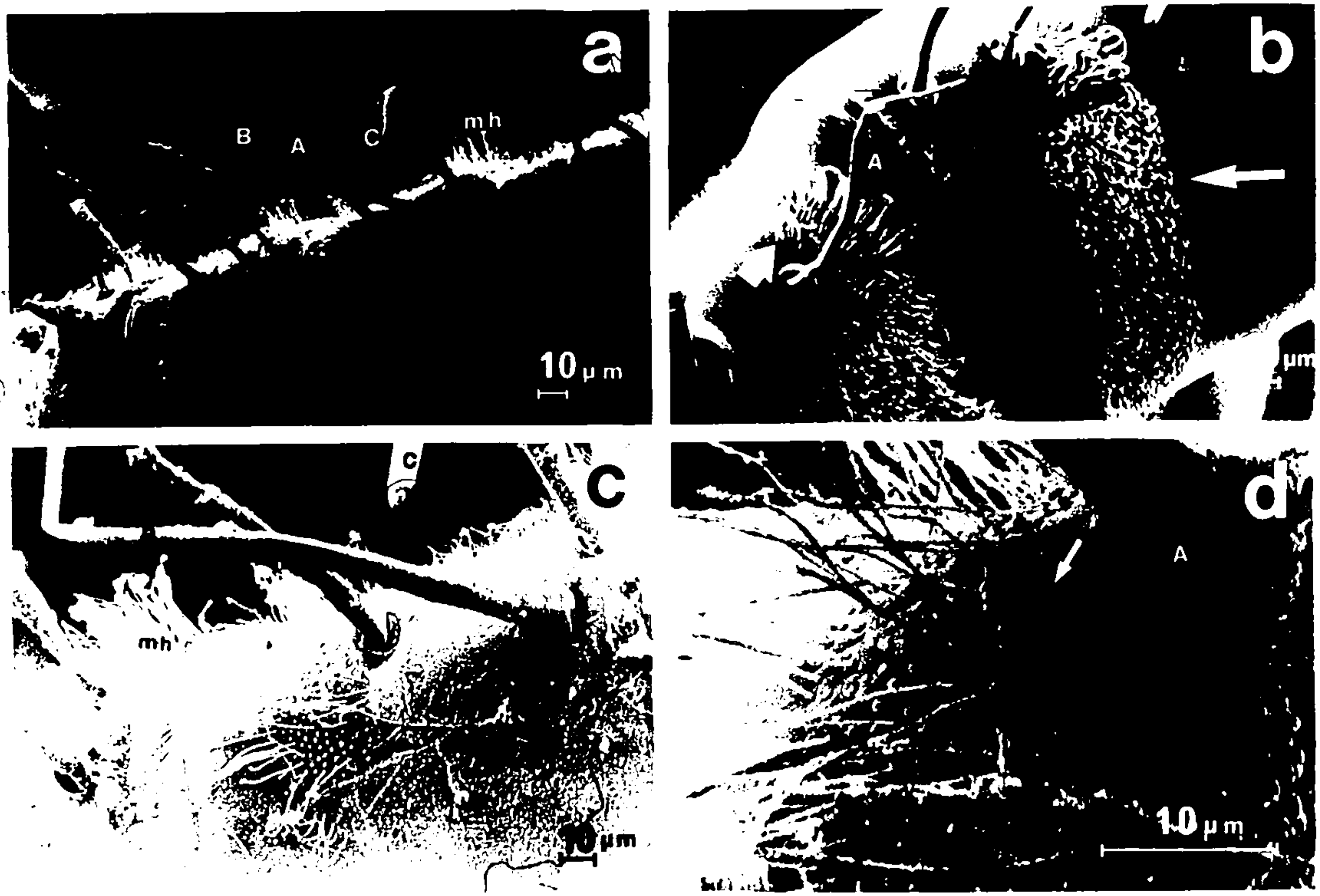
(a) Dorsal view of an article showing the triangular arrangement of the sensory hairs, (b) (c) An aesthetac close-up, arrows indicates the group of pores at the tip. (d) Distal setae
BSH = Basiconica (c-type sensory hair)
CH = Chaetica sensory hair
TSH = Trichodea (a, b-type sensory hair)
E = e-type sensory hair
SII = long plumose setae
p = apical pores

Figure 5: Main types of sensory hairs and their positions on the first antennae of *Calanus finmarchicus*.



(a) First basal segments showing the presence of microhairs or ring-like structures. (b) (c) Position of the microhairs surrounding the apical a-type hair (thick arrow).
(d) Details of the basal area of these hairs (thin arrow).
A,B,C = Sensory hair types
mh = Microhairs or ring hairs

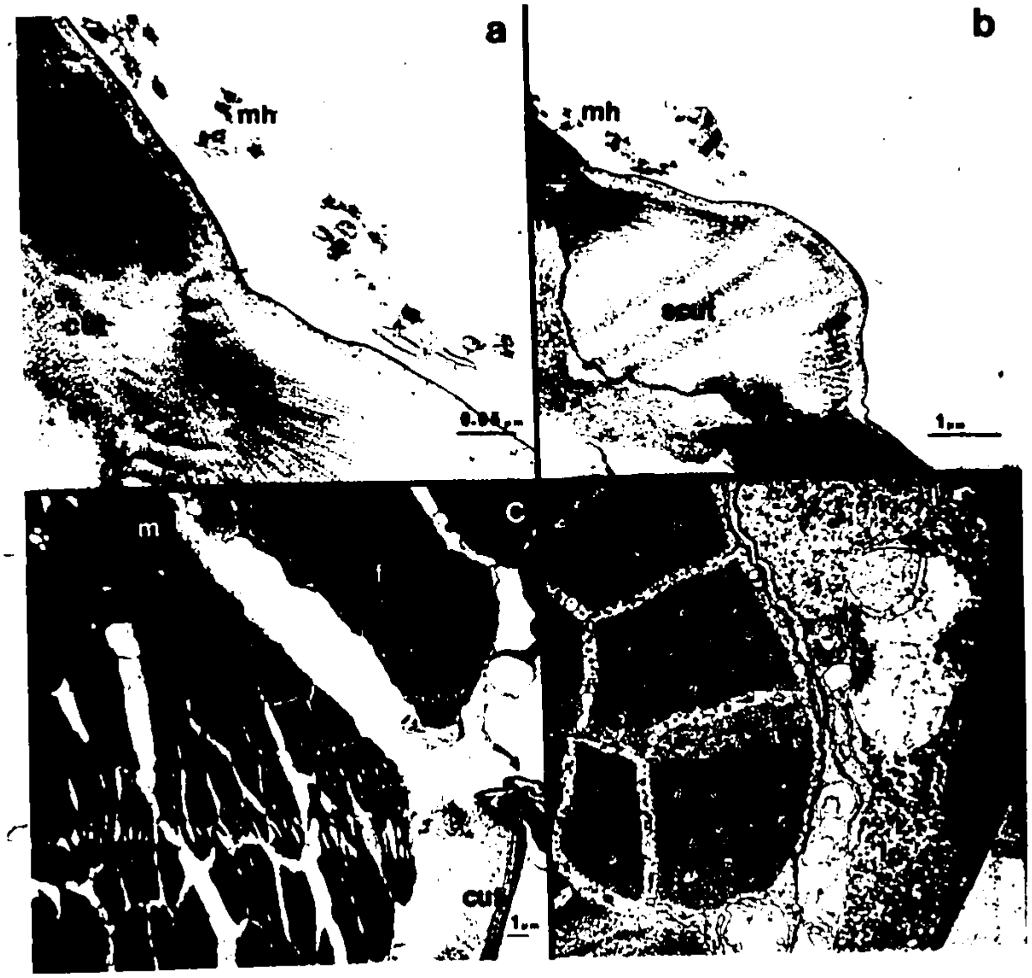
Figure 6: Micro-sensory hairs limiting the basal segments of the first antennae.


a
B
A
C
mh
10 µm
b
A
µm
c
c
mh
10 µm
d
A
10 µm

(a) Microhairs showing two tube like structures. (b) Joint between two segments showing the highly sclerotized cuticle at this point. (c) Reduction of the muscle fibre to narrow microfibres along the joining line (arrow). (d) Transverse section through a muscle bundle.

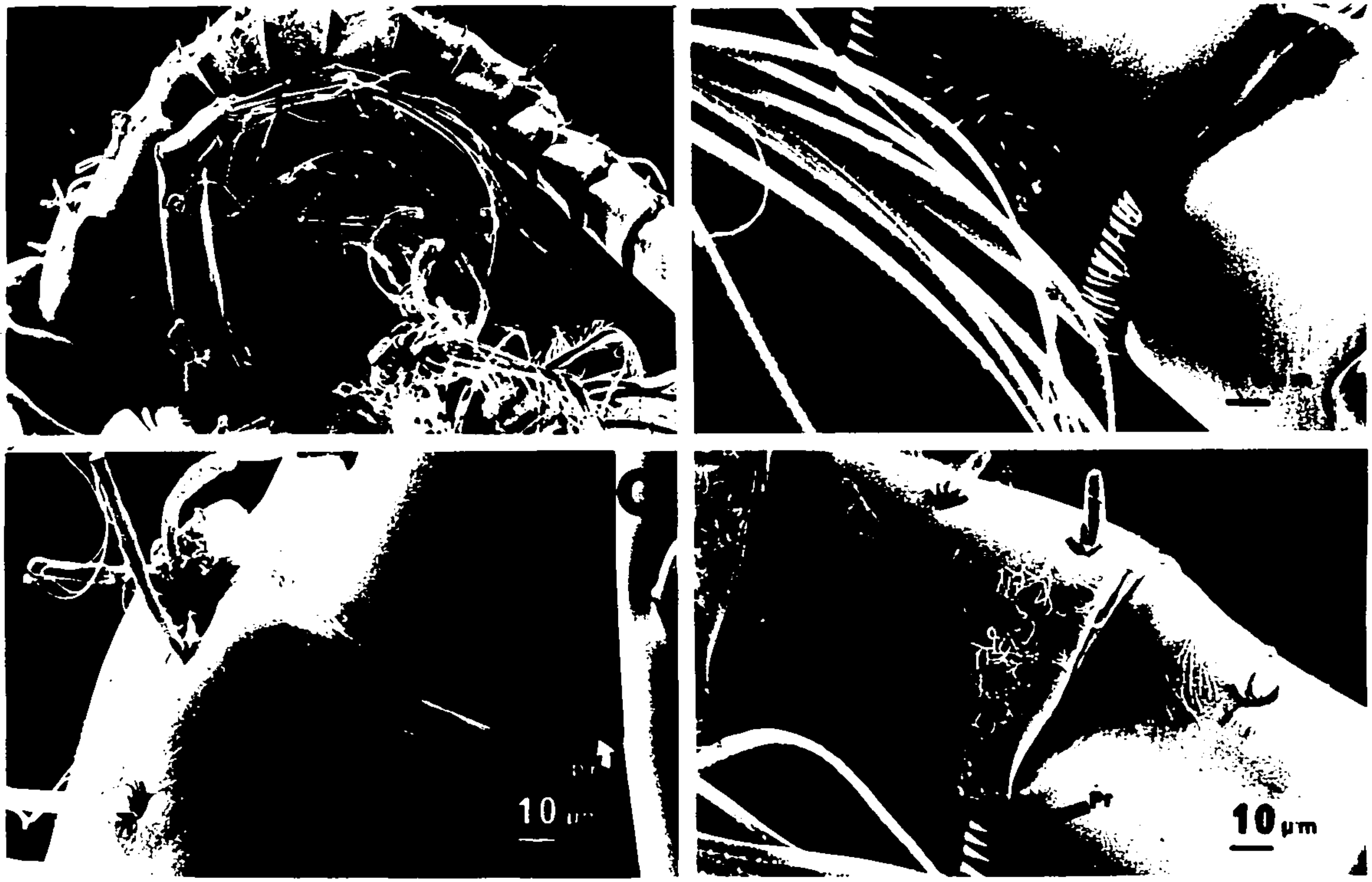
cut = cuticle
f = muscle fibre
lp = electron-dense granules
m = mitochondria
tt = intra-fibrillar tubules

Figure 7: Ultrastructural features of microhairs and cuticle joints.


a
mh
0.05 µm
b
mh
scut
1µm
c
m
f
cut
1µm

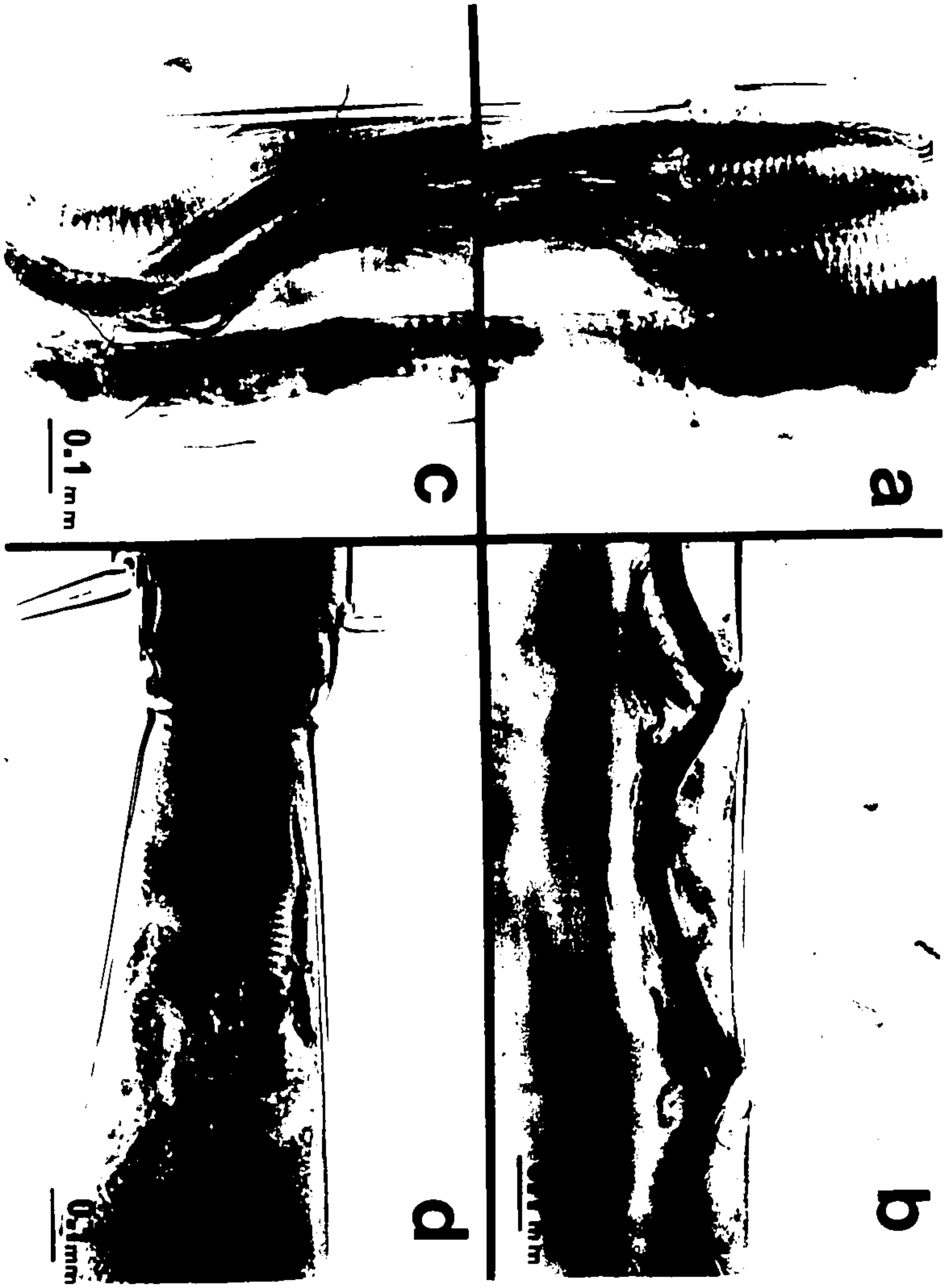
(a) Basal segments showing the spine-like structures. (b) (c) (d) Position of the proprioceptors at the edge of each segment (arrows).
pr = proprioceptors

Figure 8: External features and position of spiny-like structures or proprioceptors in *Calanus finmarchicus*.


Pr
10 µm
Pr
10 µm

(a) (c) Show the position of the central and lateral fibres.
(b) Lateral fibres of muscles connecting each article.
(d) End of the central fibre of striated muscles at the 24 segment.
cb = central muscle fibres
pb = lateral or peripheral muscle fibres
S24 = twenty fourth segment
mb = muscle bundle

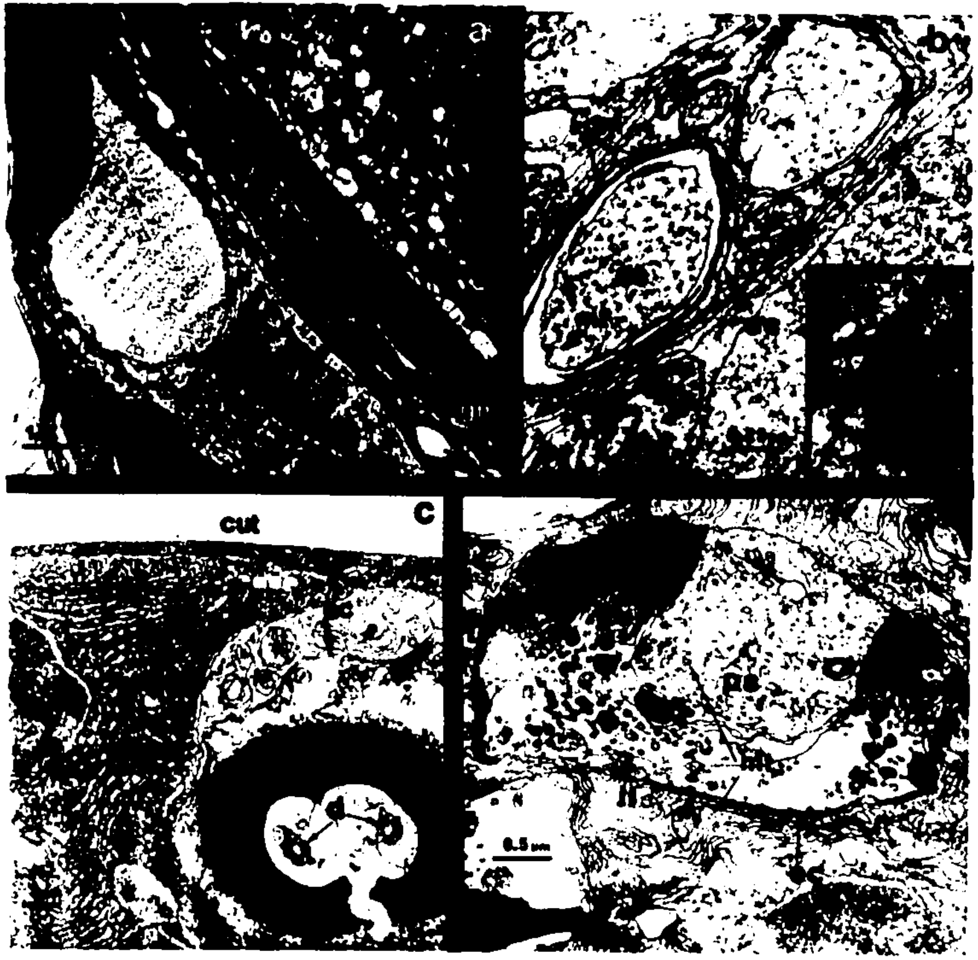
Figure 9: Light micrographs of the muscle fibres within first antennae after osmium tetroxide postfixation.


a
b
c
d
0.1 mm
0.1 mm
0.1 mm

(a) Transverse section through dendrites just below shaft hair. only two dendrites are visible. (b) The two dendrites at the apical region of the ciliary segment showing microtubule singlets and the scolopale granular matrix. (c) Cross section through the the scolopidium showing the two dendrites with the scolopale matrix. (d) Section of the scolopidium at the very proximal segment showing the scolopale cell joints with the tubular sheath cells.

cut = cuticle
d = dendrites
ec = enveloping cells
ds = dendrites distal segment
gm = electron dense matrix or dendritic sheath
JI = membranal junctions between the scolopale and enveloping cells
mt = microtubules
n = nucleus
ps = dendrites proximal segment
scp = scolopale matrix
Th = trichogen cell

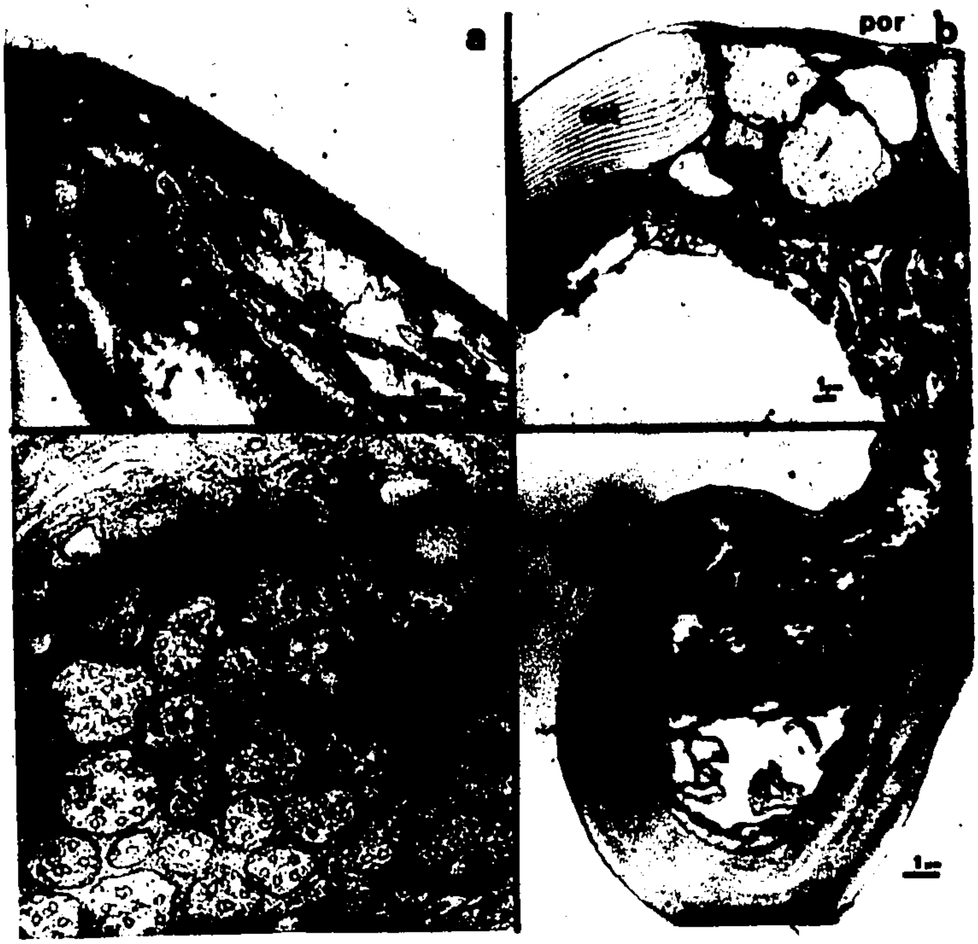
Figure 10: Cross section of the penultimate and antepenultimate long and plumose setae.


a
b
cut
c
0.5 µm

(a) (d) Longitudinal sections showing the ciliary branching of the dendrites within the lumen of the hair. (b) Three dendritic limiting pore (c) Cross section at the ciliary segment of the dendrites showing the microtubules singlets and the lack of the dense granular matrix surrounding the dendrites.

cut = cuticle
d = dendrites
por = pore

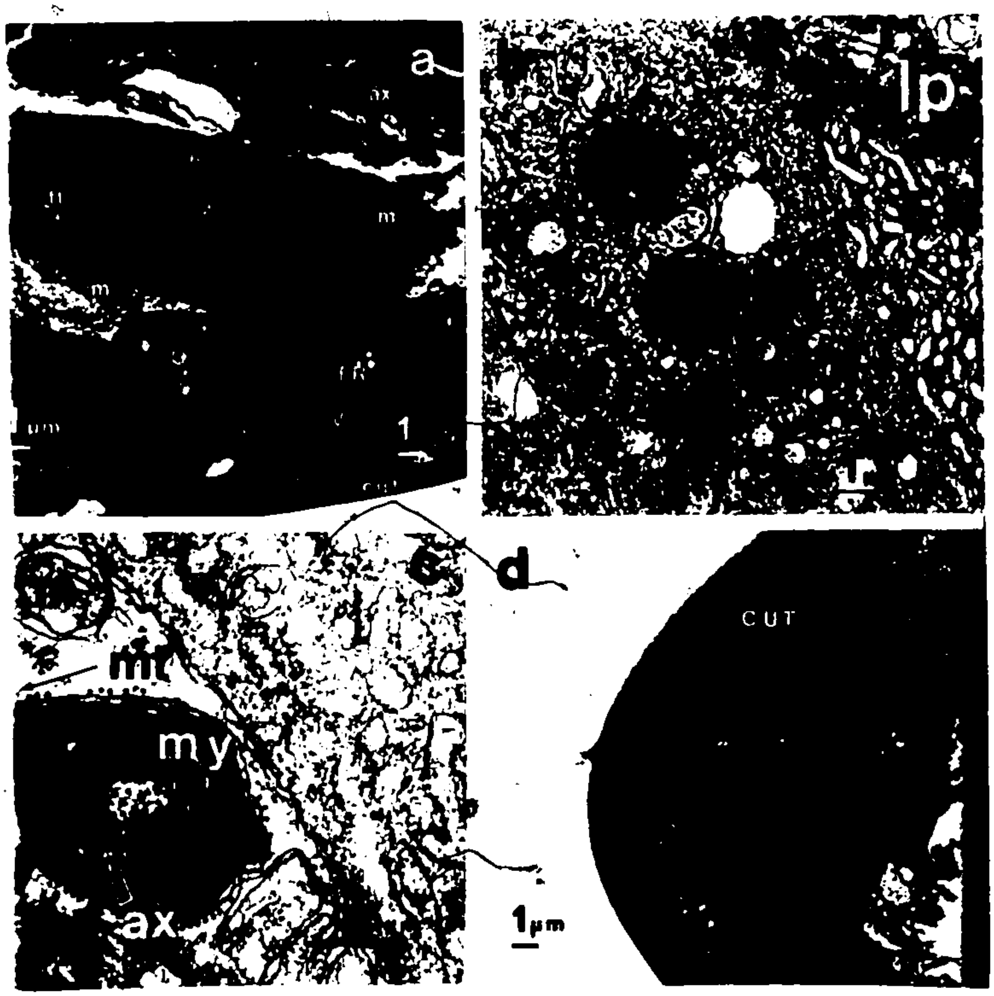
Figure 11: Ultrastructural features of the basiconica or aesthetac sensory hair.


a
por
b
1μ
1μ

(a) (b) Abundant number of large mitochondria surrounds the muscle bands , trichogen cells are present close to the cuticle containing large nucleus (c) Transverse section of a myelinated axon showing the central axon and surrounding microtubules. (d) Laminated pattern present in the cuticle.

cut = laminated cuticle
ax = axon
ER = endoplasmatic reticulum
G = Golgi apparatus
f = muscle fibrils
z = z line
h = h zone
m = mitochondria
mt = microtubules
my = myelinated axons
n = nucleus
tt = intra-fibrillar tubules
v = vacuoles
lp = electron dense granules

Figure 12: Main cellular components of the first antennae.


a
ax
m
m
m
1
μm
cut
lp
d
mt
my
ax
1μm
CUT

(a) Showing the continuous microtubule bundle. (b) Fibrous network (arrows) within the setal cuticle different from the laminated antennal cuticle and abundant neurotubules.

A1 = antennae main body
mt = microtubule bundle
nt = neurotubules
sw = setal wall

Figure 13: Longitudinal section of e-type setae of *Calanus finmarchicus* first antennae.

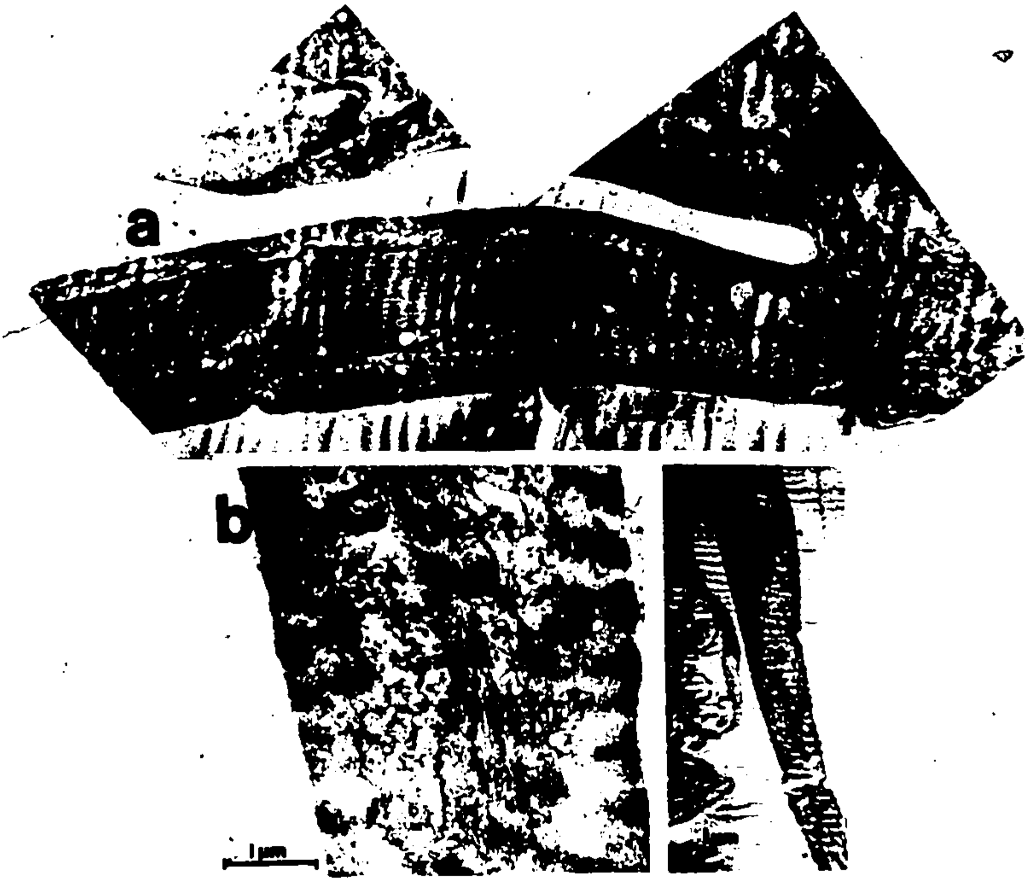
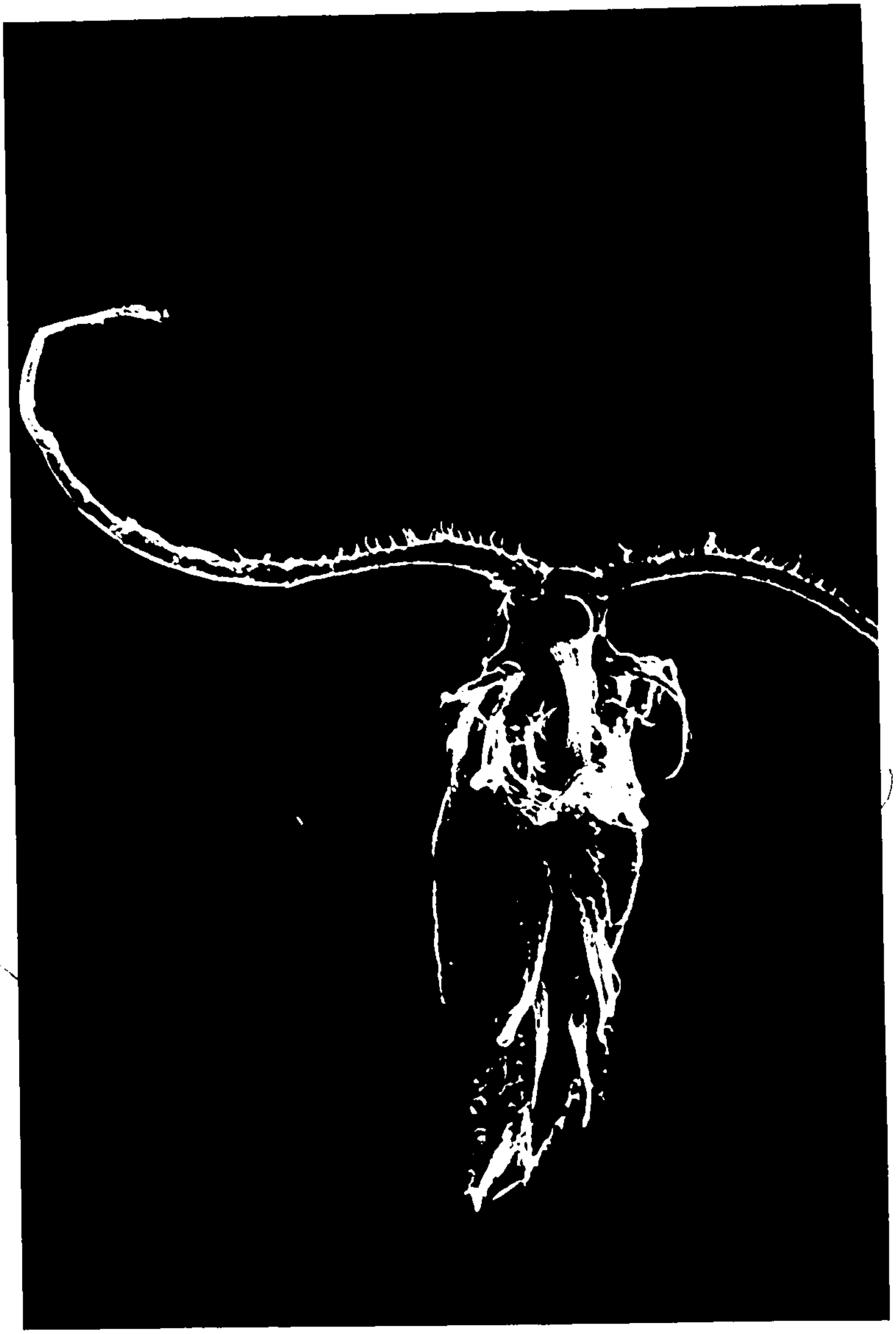
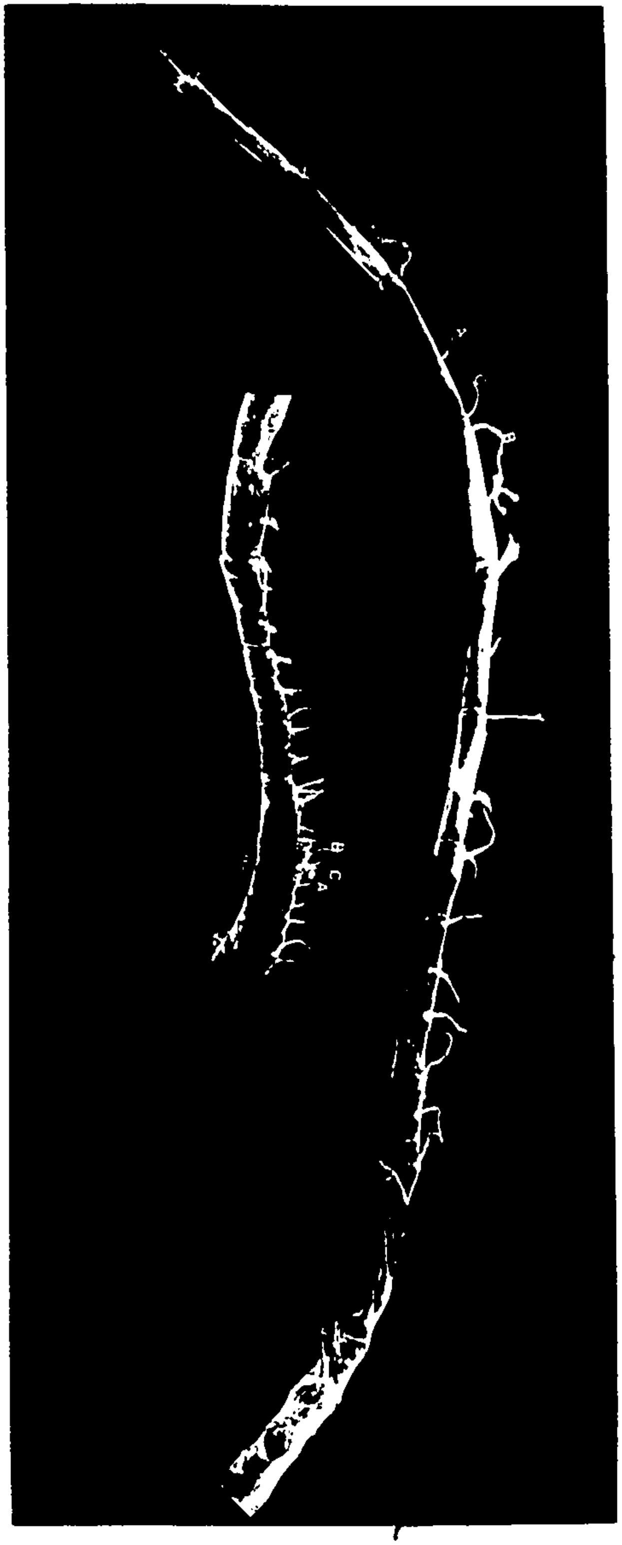

a
b
1 μm

Figure 14: General anterior ventral view of <u>Centropages furcatus</u> X 52.



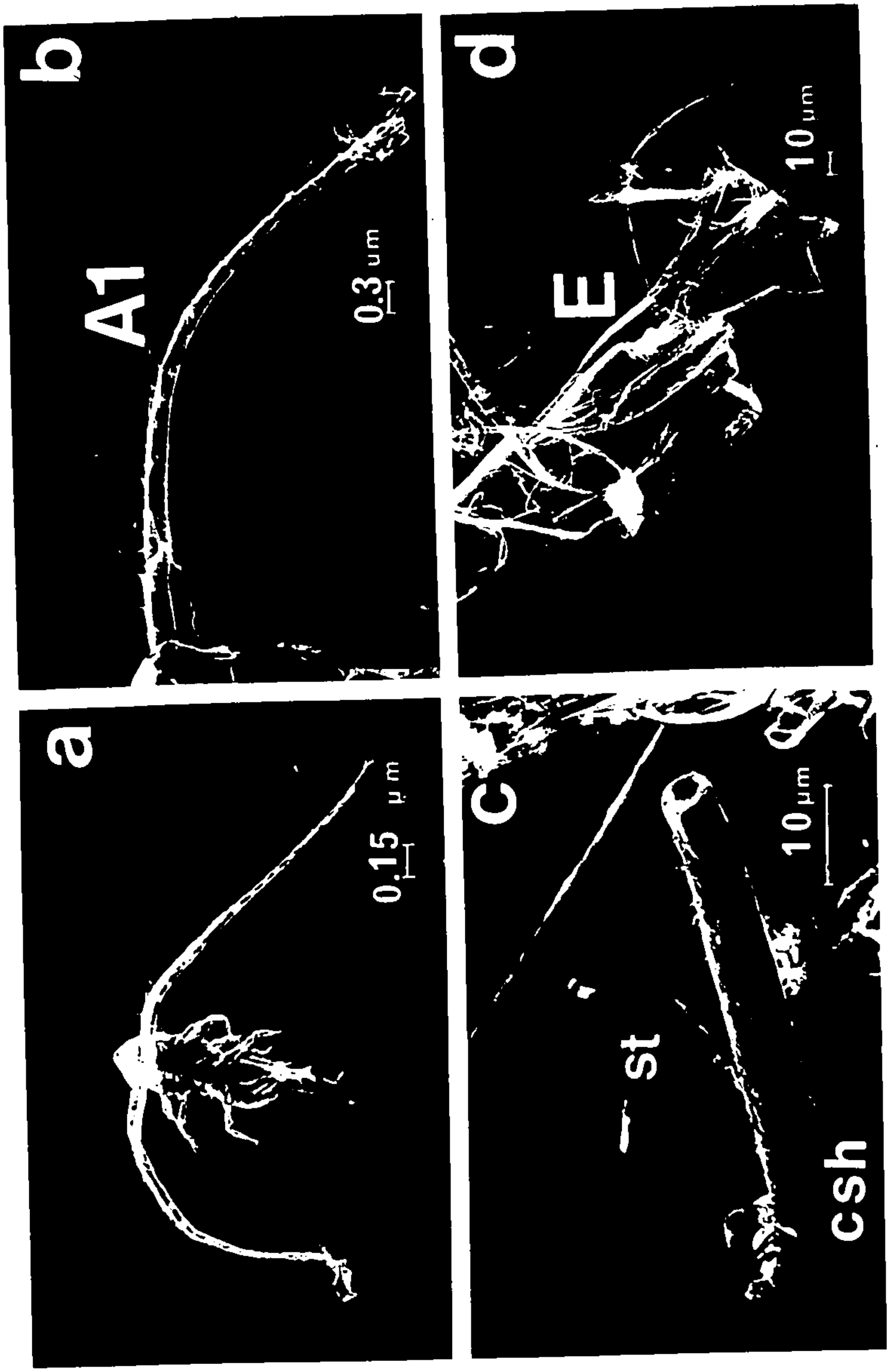
(a) Shows the triangular arrangement of the a, b, and c-type setae. The horn-like structure is apparent at the third basal segment (arrow).
A,B,C = Types of sensory hairs

Figure 15: General view of *Centropages furcatus* first antennae X 1200.


B
C
A

(a) Body general ventral view. (b) First antenna dorsal view showing the position of the sensory hairs. (c) C ompound sensory hair showing the position of the setules. (d) Distal e-type sensory hairs.
A1 = first antennae
E = type sensory hair
csh = compound sensory hair
ST = setules

Figure 16: Main morphological features of <u>Eucalanus pileatus</u>.


a
0.15 μm
b
A1
0.3 um
c
st
csh
10 μm
d
E
10 um

(a) General view of the first antenna showing the long feathered e-type hairs and terminal plumose setae, bending line of the compound setae (arrows). (b) High magnification of a compound setae and basal setules. (c) Complete view of the specimen.

CSH = compound setae
E = type sensory hair
SI = long and plumose terminal setae
ST = setules

Figure 17: Light micrographs of main morphological features of *Eucalanus pileatus* first antennae.

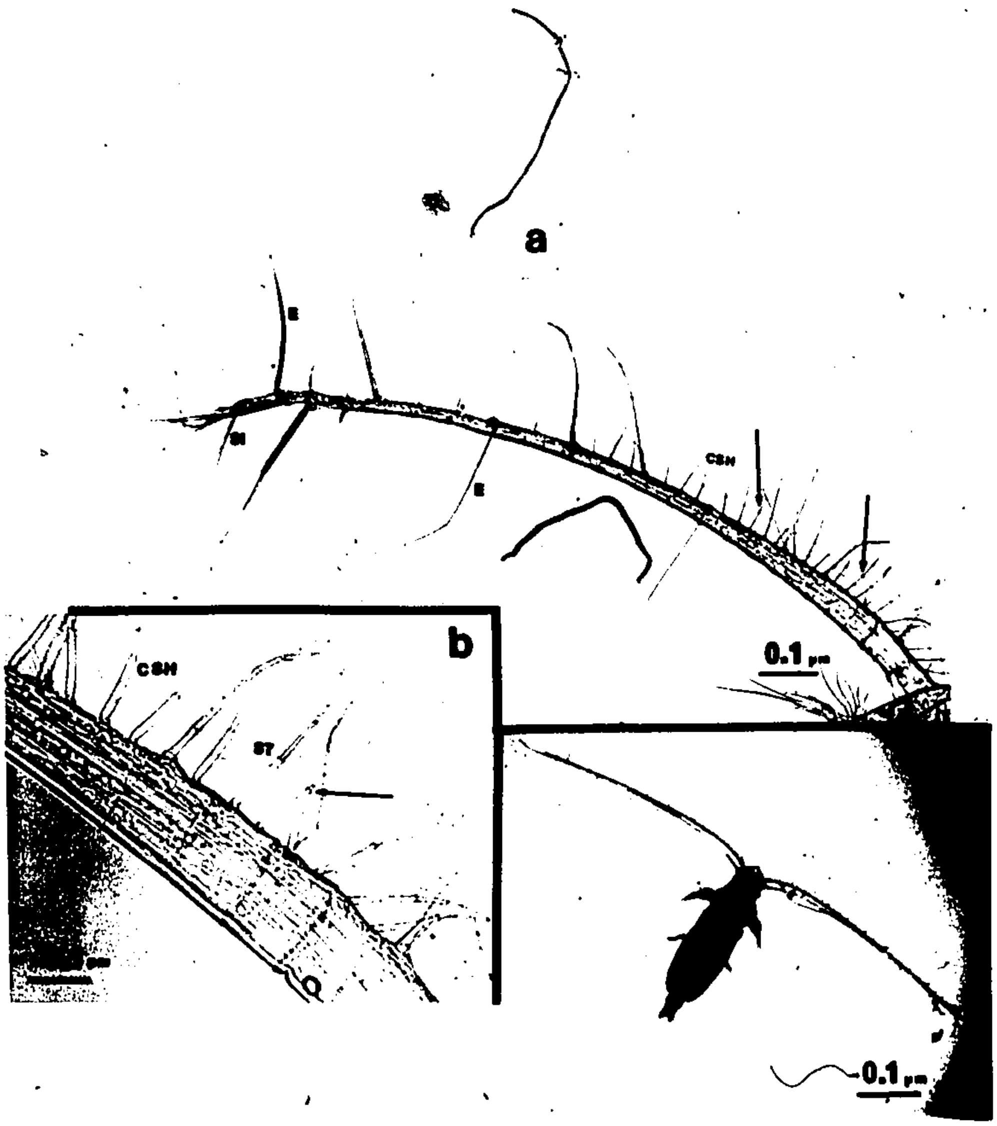
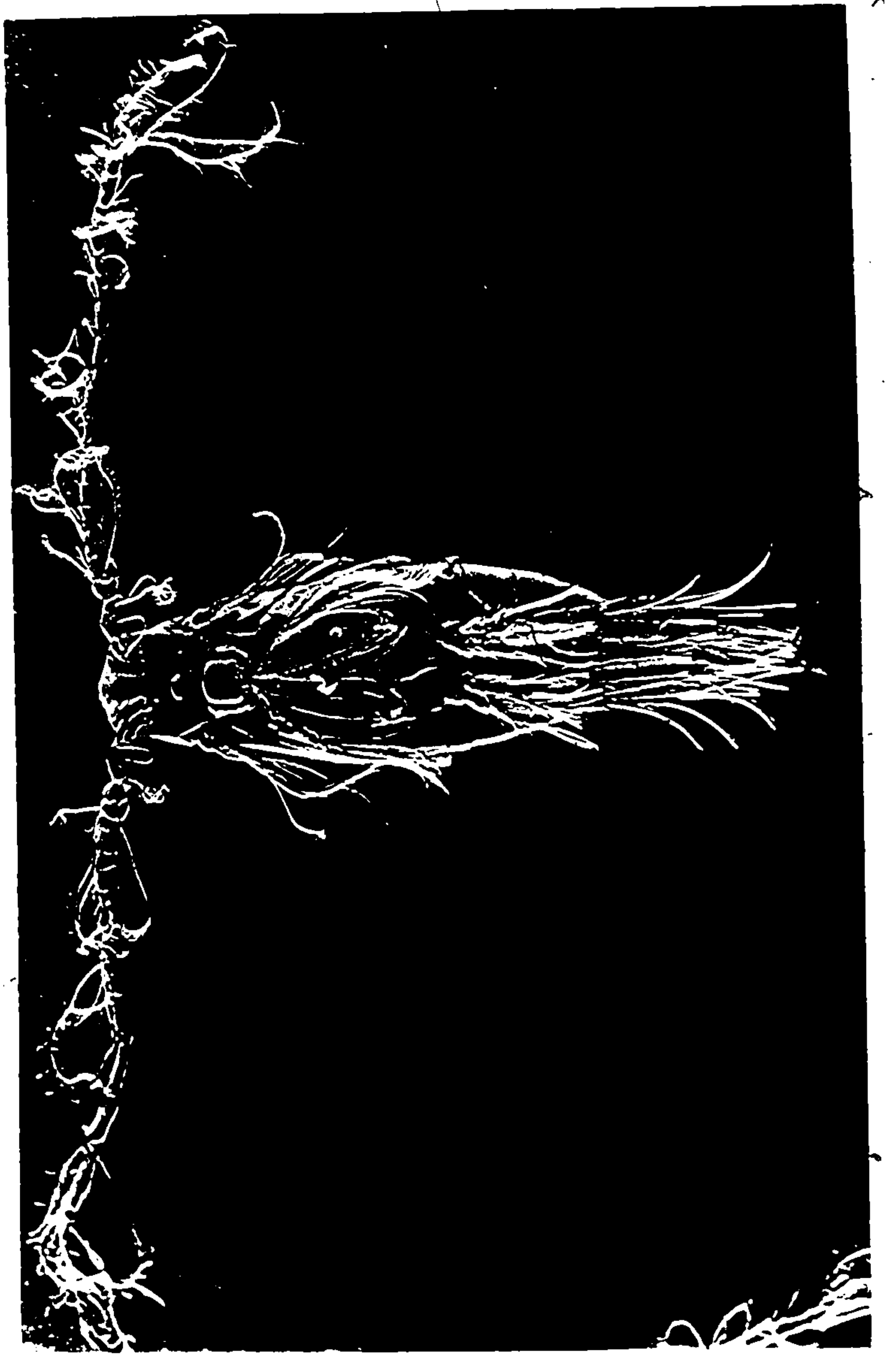

a
E
SI
E
CSN
0.1 µm
b
CSN
ST
0.1 µm

Figure 18: General view of *Acartia longiremis* X 76.



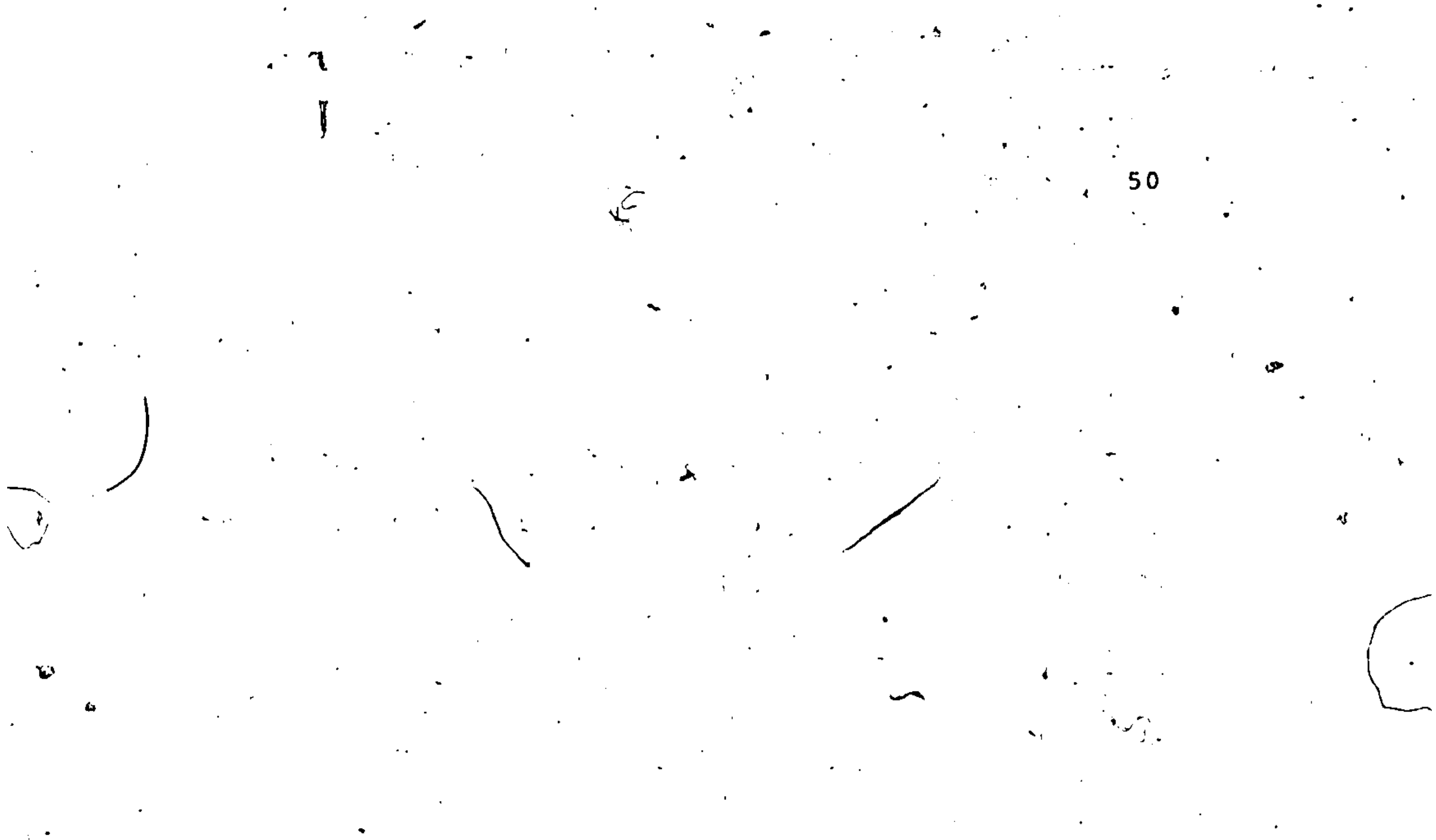
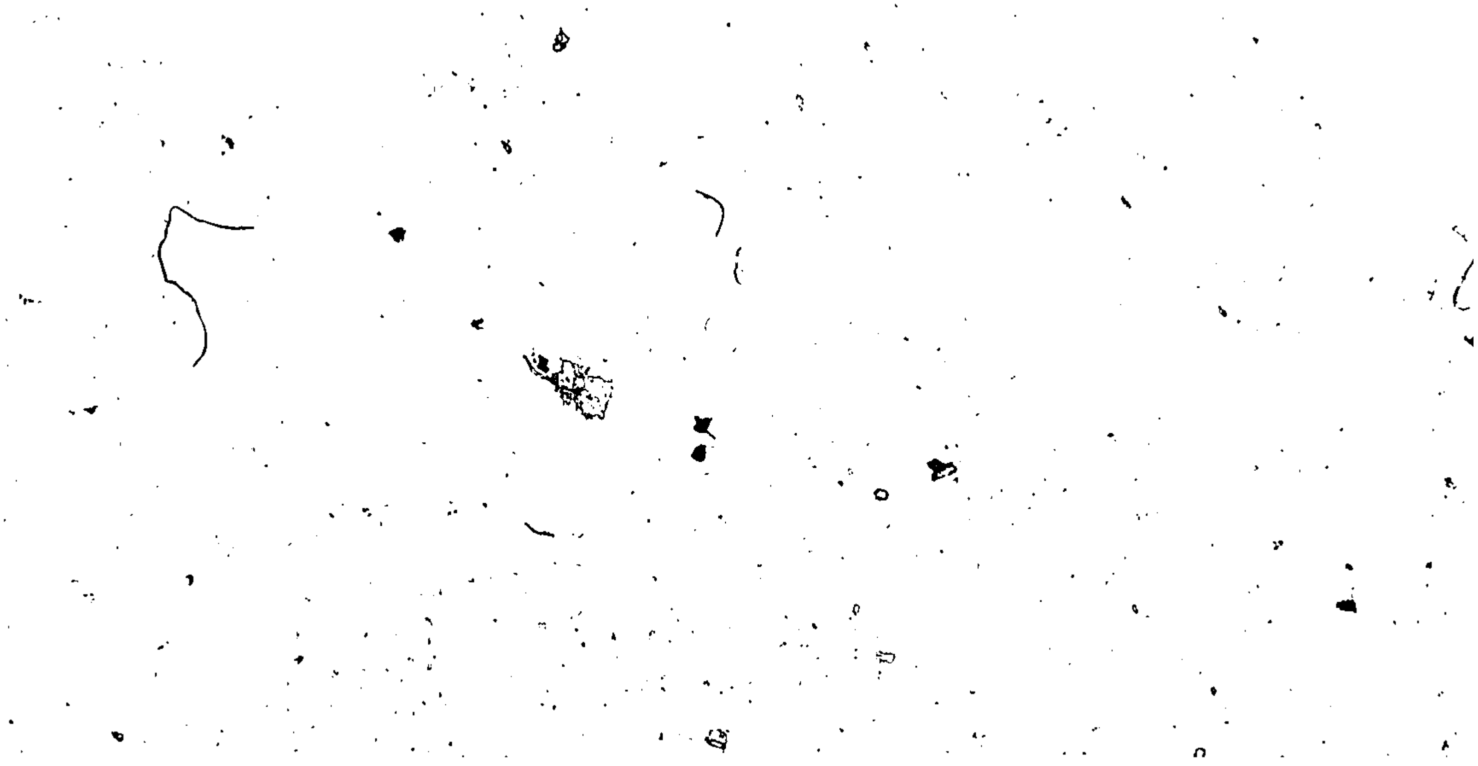


Figure 19: General view of *Acartia longiremis* first antennae.



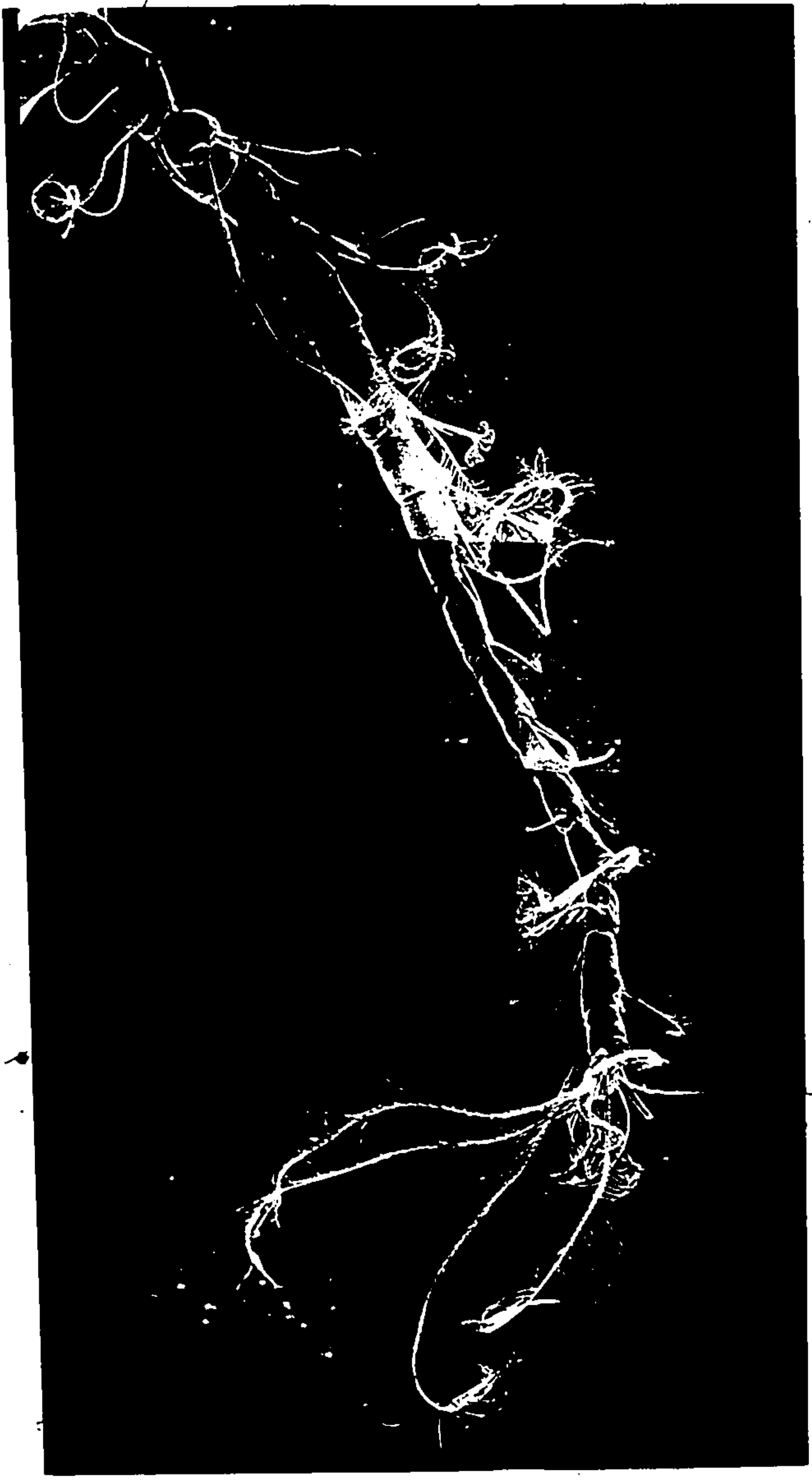


Figure 20: General view of *Acartia grani*.

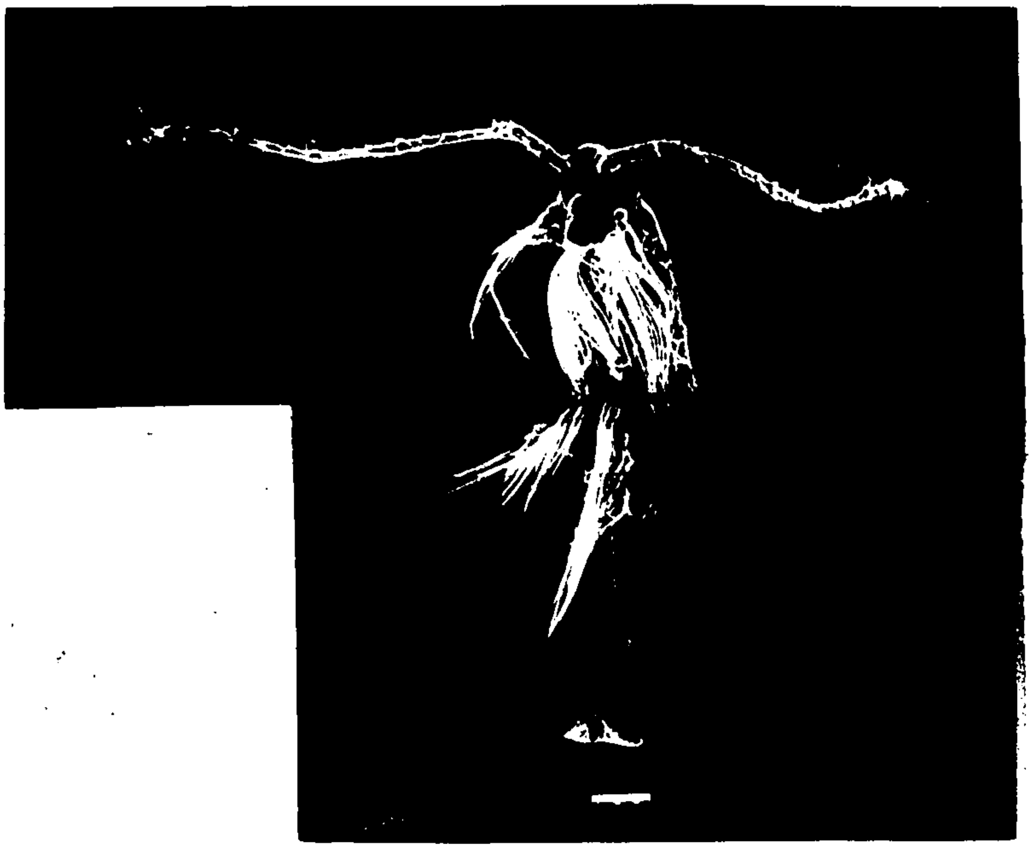
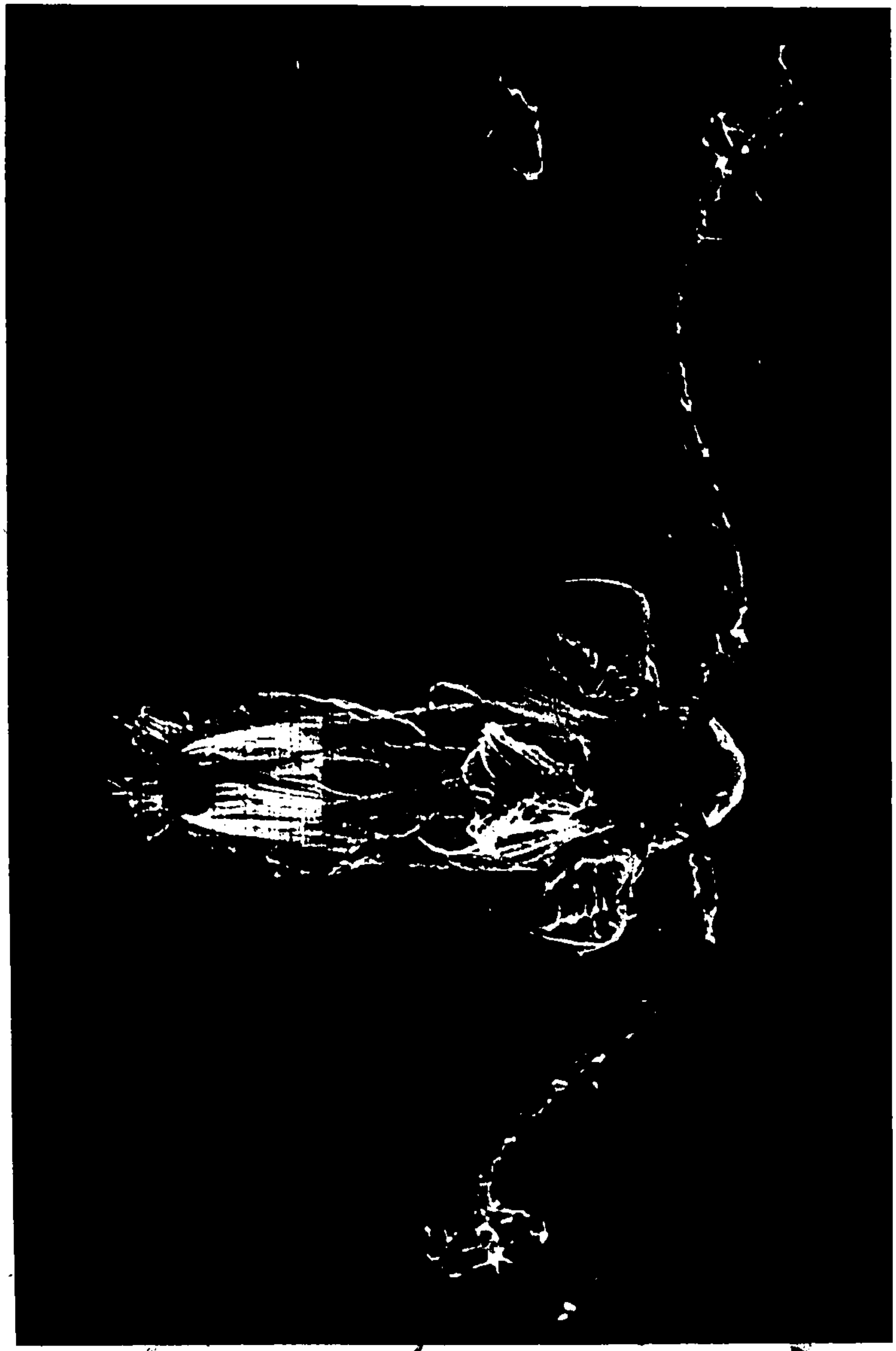


Figure 21: General view of *Acartia grani* first antennae X 1080.

Figure 22: General view of *Acartia discaudata* X 66.



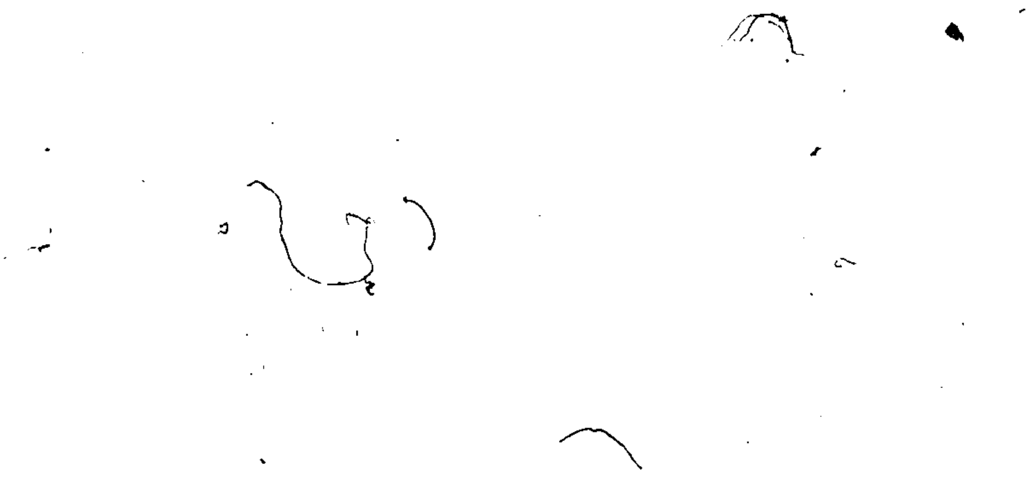
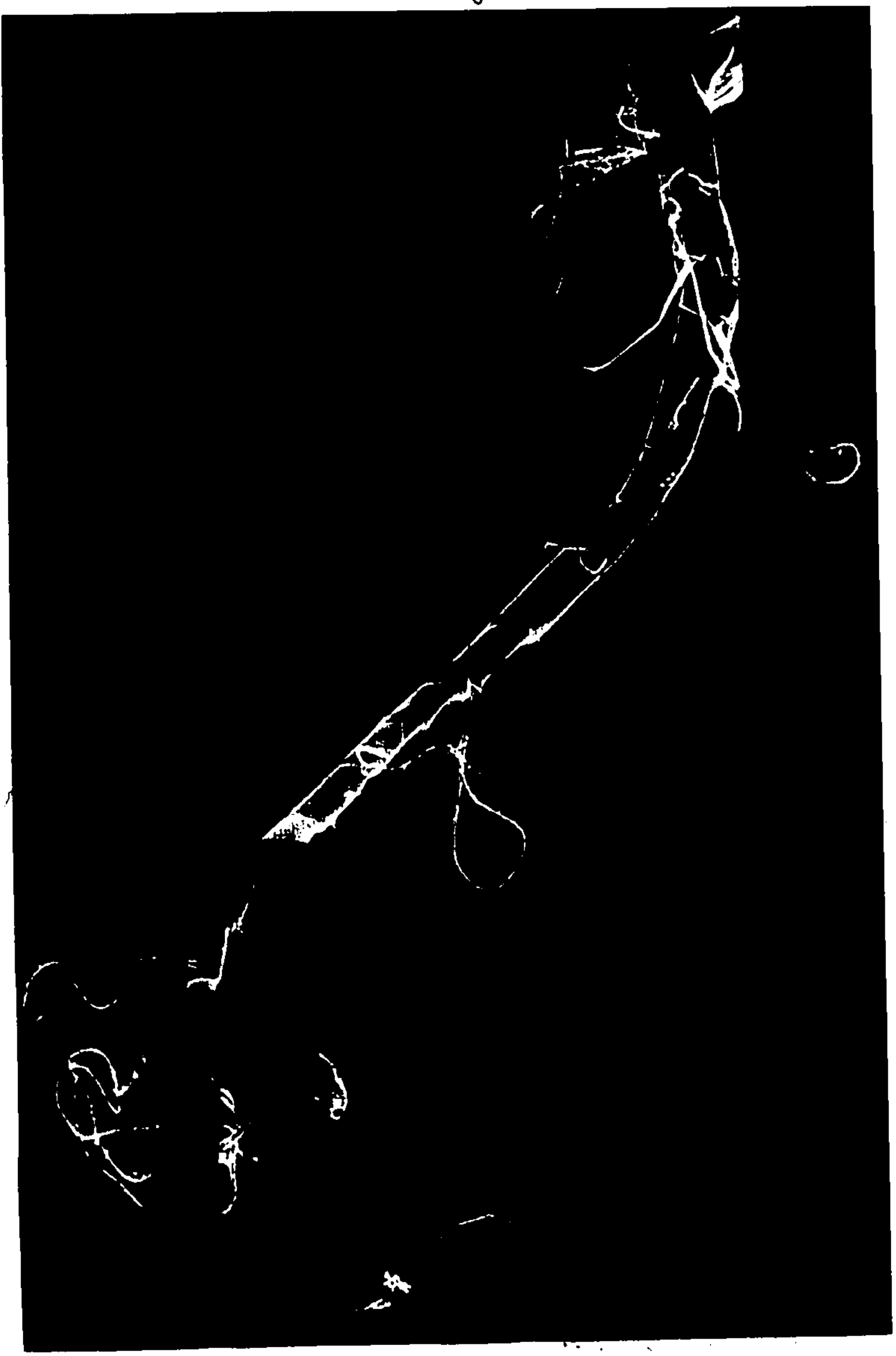


Figure 23: General view of Acartia discaudata first antennae X 1080.



(a) (b) Asymmetric basal segment and article constrictions (c) Details of the abundant number of setules present in the e-type hairs and Position of an aesthetac. (d) High magnification of the socket-like base of the e-type hairs.

A1 = first antennae
C = aesthetacs or c-type sensory hair
E = e-type sensory hair
SB = socket-like base

Figure 24: Morphological details of the *Acartia longiremis* first antennae.

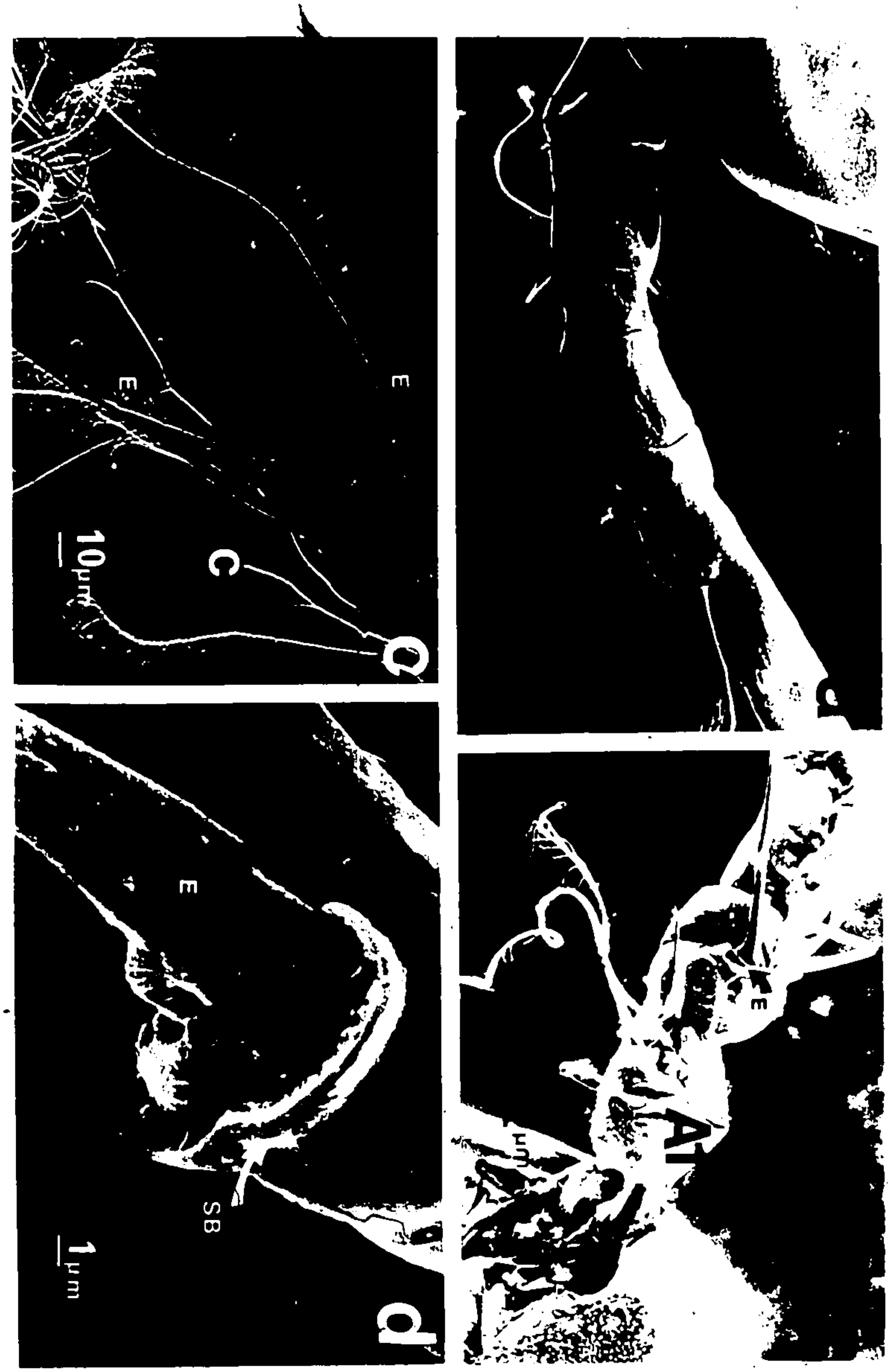

E
E
C
10 µm
c
E
SB
1 µm
d
a
E
A1

Figure 25: General view of *Skistodiaptomus oregonensis* X 153.

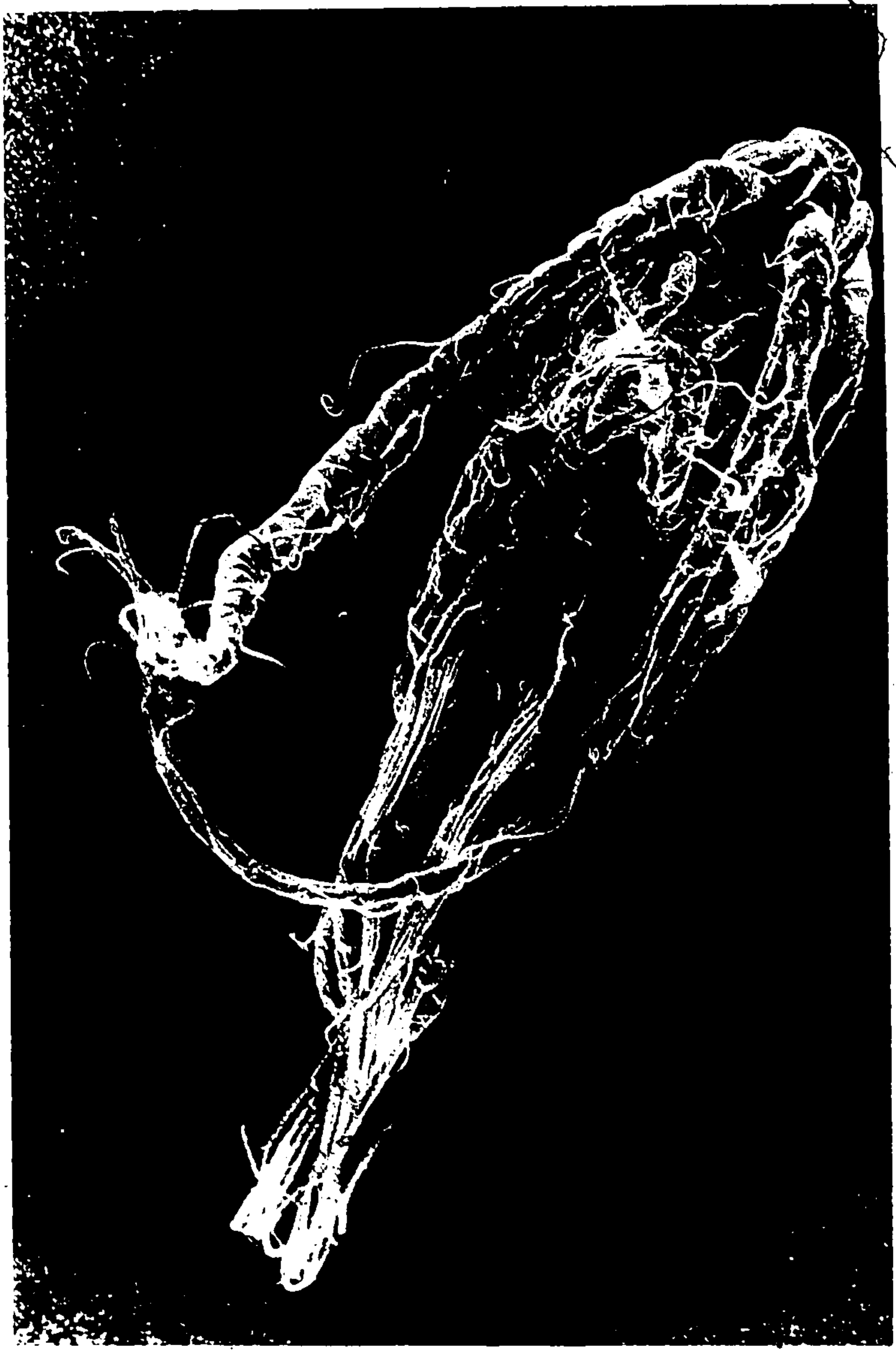


Figure 26: General view of <u>Skistodiaptomus</u> <u>oregonensis</u> first antennae X 960.

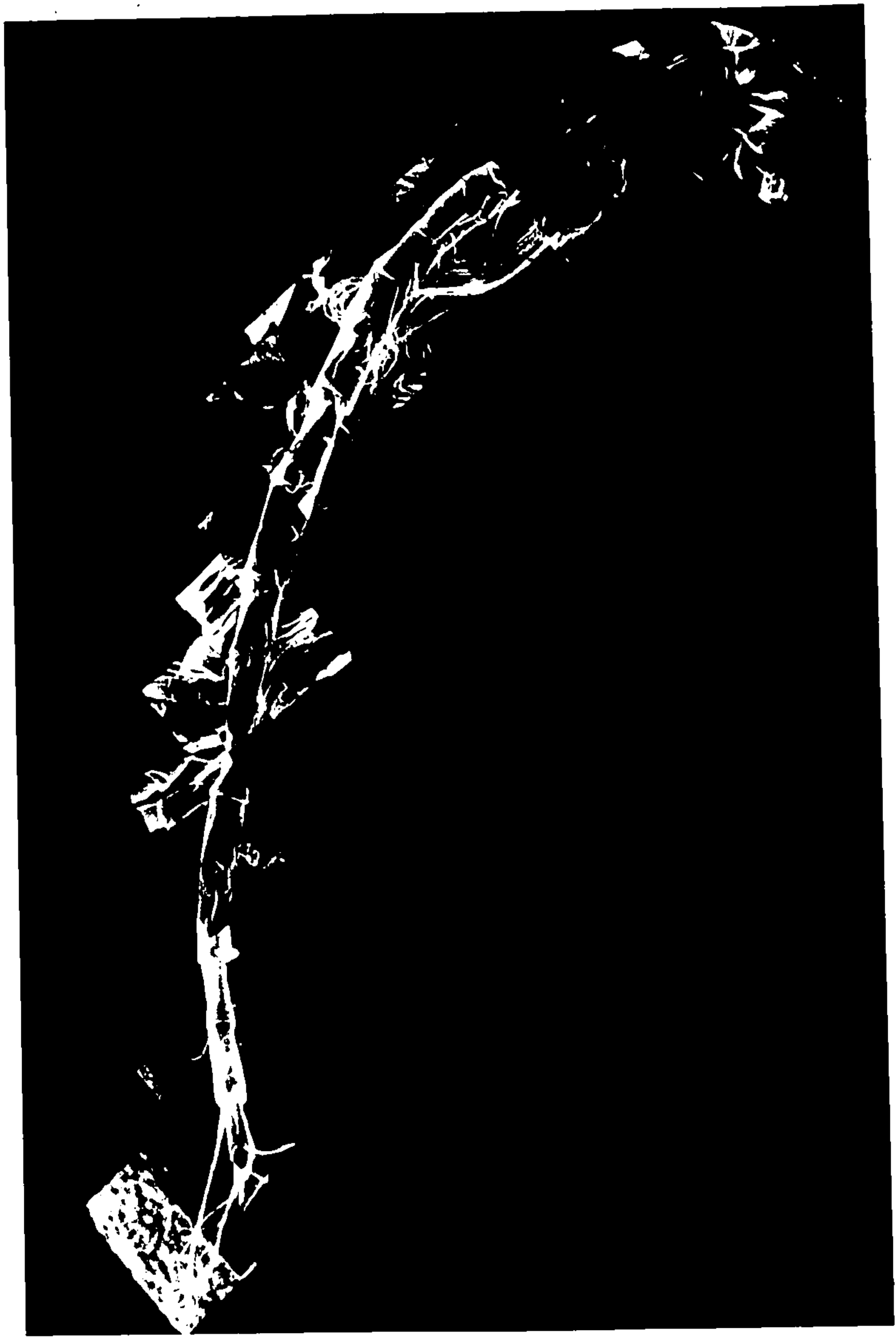


Figure 27: General view of *Leptodiaptomus minutus* x 84.

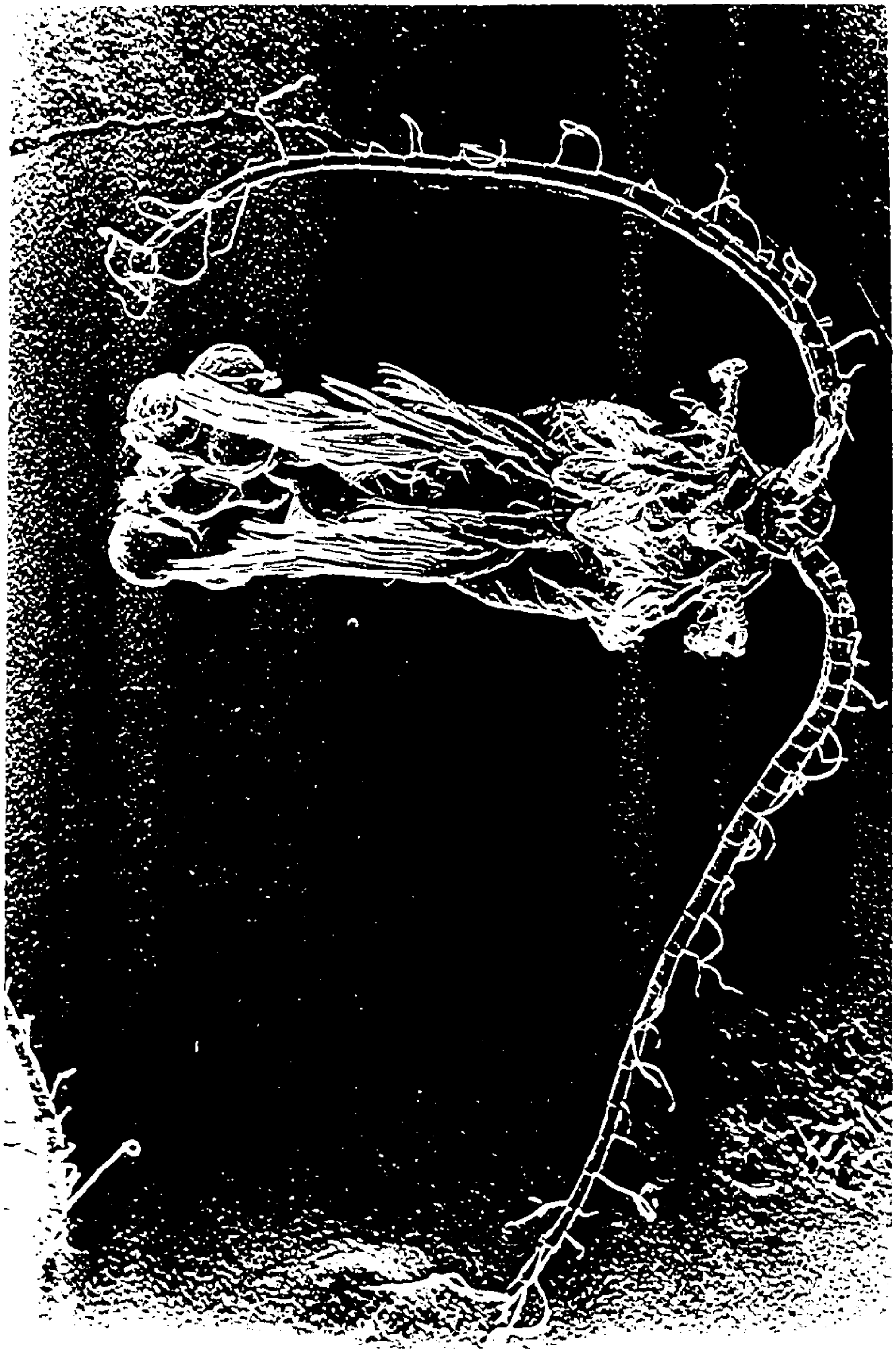
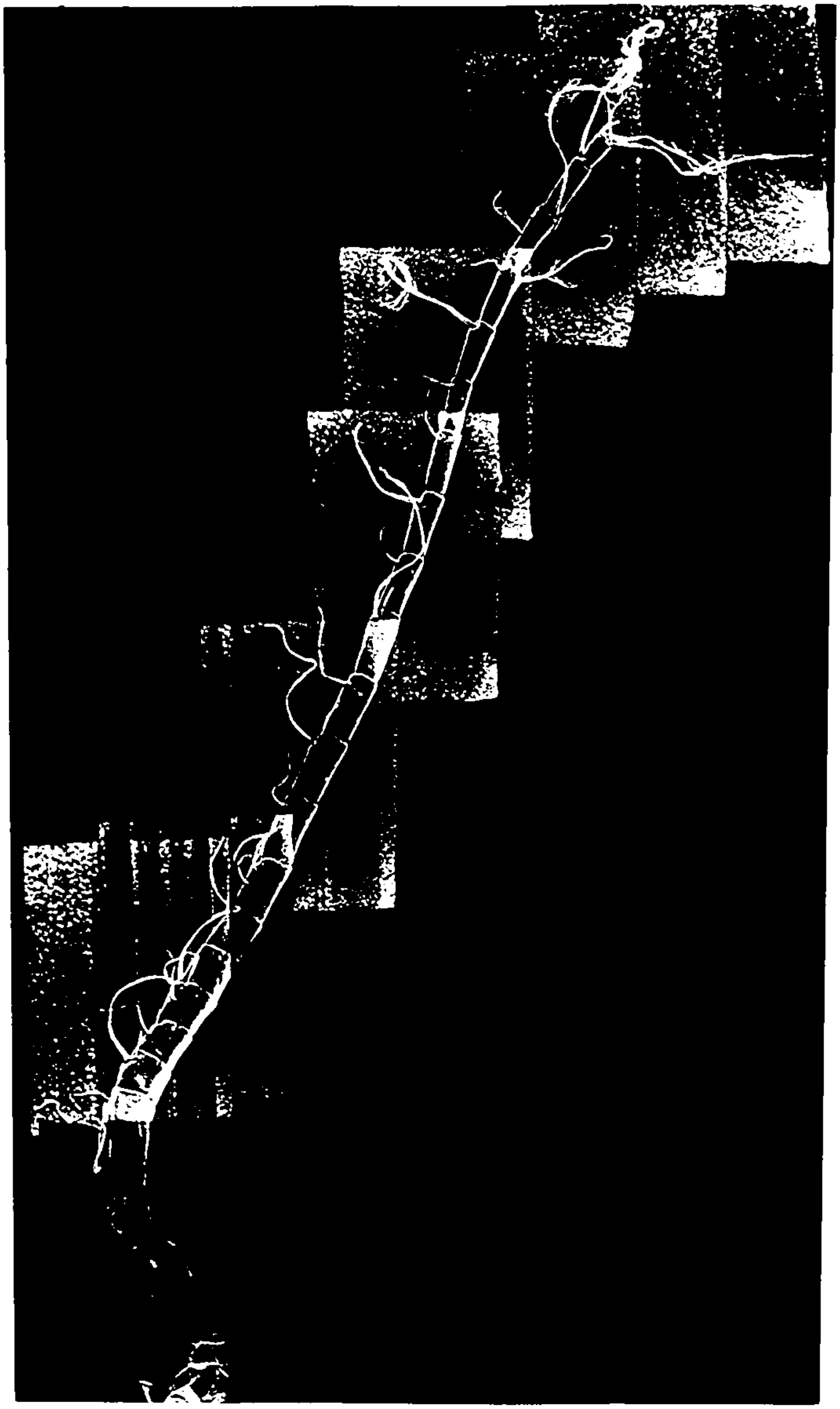


Figure 28: General view of *Leptodiaptomus minutus* first antennae X 560.



Section IV

DISCUSSION AND CONCLUSIONS

Mechanoreceptive structures have the same feature in common: that is, the nerve cell is stimulated by a mechanical deflection (Corbiere-Tichane, 1971). In mechanoreception there are two types of receptors involved: the tactile receptors, which are represented by the articulated setae and the proprioceptors which include campaniform sensilla and chordotonal organs (Corbiere-Tichane, 1971).

In most calanoid copepods studied here, there are basically two types of hair sensillae, sensilla trichodea (a-, b-, d-, e-type) and sensila basiconica (c-type). They resemble the types described by Fleminger (1973) for *Eucalanus* species. The sensory hairs studied here are long and articulated protuding from the cuticle (sensilla trichodea, basiconica and chaetica).

All the sensillae trichodea studied (a-, b-, d-, e-type sensory hairs) appear to be mechanoreceptors. The basis for this conclusion is the presence of a nerve scolopale matrix located at the base of the hair which articulates with the socket membrane of the setae (Borg and Norris, 1971; Corbiere-Tichane, 1971) and the ciliary portions of their dendrites. The tubular body present in the distal region of the dendrites is also characteristic of arthropod cuticular mechanoreceptors (McIver, 1975) but it has been found only in the antennal setae of the copepod *Cyclops scutifer* (Strickler and Bal, 1973), and in the trichodea sensillae studied here. For insect mechanoreceptors it is believed that the tubular body at the tip of the dendrite is involved in the transduction process and the compression of this body is the effective stimulus (Thurm, 1965; Chapman and Duckrow, 1975). This tubular body ends in a canal above the hair base; the canal also characterizes mechanoreceptors (Schneider and Steinbrecht, 1968). Also, the trichodea hairs are mounted on a flexible membrane and they have abundant setules which would make them more efficient in picking up nearby waterborne vibrations. The bases of the trichodea sensillae are surrounded by a ridge. Ball and Cowan (1977) suggested that this ridge might either have the effect of carrying water smoothly upward and past the setule base, or the gap between the ridge and the setule base may be sufficient to create an area of turbulent flow in front of the setule.

Thurm (1968) described similar trichodea structures in honey bees as being mechanoreceptors with modified ciliary process. The trichodea as well as the long (SI and SII) sensillae have the same basal body-like structures found by Strickler and Bal (1973) in the apical setae of Cyclops scutifer. However, at this level the whole structure resembles that of a basal scolopidium (Howse, 1968; Corbiere-Tichane, 1969). Chordotonal organs, in which scolopidia are contained, are the basic structures for the movement of body and appendages (Schneider and Steinbecht, 1968) or are sensitive to vibrations (Howse, 1968). Triple scolopidia are basic connponents of the Johnston's organ of Speophyes spp, a cave coleoptera, found to be extremely sensitive to vibrations (Corbiere-Tichane, 1975). Gewecke and Schlegel (1970) studied the response of this organ to vibrations, in the antennae of a blow fly, Calliphora erythrocephala. They found that the action potential always depended on the vibrational forces in the antennae and its angular position with respect to the antennal base or pedicel. In contrast, in this study, the scolopidium found in the sensory units of the first antennae differs from the above mentioned in having only two dendrites which form a tubular body apically. As seen in Figure 10d, the scolopidium is surrounded by enveloping cells (glial cells); abundant microtubules are close to the junctions (JI) with the scolopale cells and the tubular sheath cells. They may provide support and contribute to the functioning of the receptor. Moran et al., (1971) working in the fine structure of cockroach campaniform sensilla suggested that microtubules of the sensory process (modified cilium) play an important role in mechanoelectric transduction of this sensilla. On the basis of their ultrastructure, the mechanoreceptive units of the first antennae of the copepods studied here might be considered vibration receptors.

The other type of sensilla found on the antennae of calanoid copepods was the sensilla basiconica. These tube-like structures lack setules. The presence of eight to ten dendrites in this seta is unusual for an arthropod mechanoreceptor, since mechanoreceptors are generally characterized as having only one or two neurons innervating each setae (Slifer, 1970; McIver, 1975) while chemoreceptors have more. These sensory hairs have been called aesthetasc (Esterly, 1907; Slifer, 1961; Laverack, 1968). Grouped as chemoreceptors because of their dendritic branches (Slifer and Sekhon, 1965; Elofsson, 1971), they are externally exposed through pores in the cuticular wall of each seta. The number of pores in the setal wall was not determined, but they appear to be numerous on the distal one-third of the setae (Fig. 5b,c). A pore opening in the cuticular wall is spherical. The presence of three pores at the tip of the hair (Fig. 5c), and five dendritic branches may categorize them as chemoreceptive structures, of an olfactory type (Slifer, 1961). This type of seta also lacks the scolopale-nerve complex found consistently in mechanoreceptors (Borg and Norris, 1971). Griffiths and Frost (1976) reported in experimental studies of chemical communication in Calanus spp., that the antennae seem to accumulate dissolved organic matter at a higher rate than the rest of the body. Inspection of the autoradiographs indicates that there was uptake of labelled dissolved organic matter at points along the antennae which correspond to the location of aesthetacs. This also supports the hypothesis that aesthetacs are the antennal chemoreceptors. On the basis of the ultrastructural evidence presented in this study, no statement can be made on the types of chemicals to which the sensilla basiconica is sensitive. Further studies using electrophysiological procedures must be done to identify the specific properties.

The micro-hairs or ring-hairs reported here cannot be categorized as chemo- or mechanoreceptors. When the animal bends the antennae towards the body, these hairs are bordering the mouthpart area, it is unknown whether they are related to the removal of undesirable particles attached to the setal appendages after feeding. Ball and Cowan (1967) suggested that in sergid shrimps, the antennal microhairs (tuft hairs) may be used to trap small amounts of food. This food is then cleaned off the microhairs by the mouth parts and transferred into the mouth.

Spine-like structures has been also reported by Alcaraz (1977) in some Acartia species; Blades (1979) reported them as being epicuticular structures with no sensory function. In both cases, these spines were found on the genital segment of two species of female copepods. In contrast, there are sensory spines located in the chela of the male _Centropages typicus_ fifth leg that could possibly be stimulated as the chela grips the female urosome. Repeated stimulation of the spines may control the behavioural pattern during mating once the antennae have released their hold (Blades, 1977). In spite of lacking ultrastructural data to describe the characteristics of the second group of spine-like structures, it could be said from their position and appearance that they are ~~probably~~ related to identified proprioceptors (Laverack, 1968; Coberiere-Tichane, 1975; Barth, 1976). Similar structures were also located on segments of the metasome, swimming legs, and on the furca of _Macrocyclops albidus_ (Strickler, 1965). As was mentioned previously, proprioceptors are basic structures for bending, of the antennal flagellum and the antennal pedicel (Bromley _et al._, 1980).

The presence of muscle attachment sites is another factor to be considered in the bending of the antennae. It is known that bending forces can be set up by muscular contractions (Barth and Pickleman, 1975). The high degree of sclerotization of cuticle around the joints may be required for sliding. In those joints, forces are transferred from one segment to the next by the surface of articular condyles or hinges (Fig. 7b). The presence of sclerotization may then indicate that antennal segments can move, responding to their muscular attachments and proprioceptors present along the first antennae.

The sensory machinery of the first antennae is represented by the trichodea and basiconica sensillae. Characteristics of number, potential use, and arrangement of these two main types were used to establish the species-specific differences. These differences were interpreted in terms of species specializations which may reflect evolutionary or ecological trends.

Sympatric species may differ from each other, in order to avoid niche overlap, in several non-morphological characters relating to their physiology, ecology, and behavior (Mayr, 1965). Ecological incompatability has forced species to display spatial and temporal segregation (MacArthur, 1958; Hutchinson, 1959). Although this divergence may be at first strictly non- morphological, consisting of a different utilization of the available resources, it would be reinforced by selection of morphological differences in order to facilitate ecological divergence (Mayr, 1965). In copepods, differences in adult size have often been used as an effective parameter to express character displacement or segregation (Hutchinson, 1967; Sandercork, 1967). The main factors affecting size are temperature, salinity and food supply (Deevey, 1960). The coexistence of *A. clausi* and *A. margalefi* was not determined, however, by the factors affecting size (Alcaraz,1976). The length of the metasome and maxillipeds setae differed in their allometry, and the minimal particle size they were able to filter ranged from 9 to 15 um. An identical spacing of the first maxilliped setae implied strong competition between the two species. However, this competitive force was reduced by spatial segregation. According to the present data, *A. grani* and *A. discaudata* are closely related species which coexist in the same area. Both species have similar metasome length, but trichodea sensillae (e-type hairs) are almost double in length in *A. grani*, with respect to *A. discaudata* (Table 2). This difference might increase the sensory field of *A. grani* and could help the organisms to segregate in a particular habitat.

The diversity of sensory structures present in the marine calanoids, for example in *C. finmarchicus*, might indicate a certain degree of specialization to the habitat where the species occurs regularly. Lowndes (1933) pointed out that *C. finmarchicus* is considered to be the most successful of all the calanoid copepods, which is manifested by its dominance in the North Atlantic and North sea. His main argument was the diversity of limb movements. Additionally, I have found that this species bears the highest diversity of sensory structures on its first antennae, in a total of ten different types. This species success is possibly due to its ability to adapt to and survive adverse environmental conditions, like food scarcity. Survival can be enhanced by a sophisticated and diverse sensory apparatus. It would appear that the combined motor and sensory abilities of Calanus would better explain the success of this species. Although successful, the Calanidae have been considered as the most primitive family (Giesbrecht, 1892). It has been found that adults bear fused spines in the caudal armature, which is considered a primitive characteristic (Hanaoka, 1952). Adults are less dimorphic and have the fifth pair of legs more symmetrical than is usual in other copepods; adults also possess a large number of segments in the body. All the above features indicate primitiveness (Hanaoka, 1952). In addition, primitive traits are also apparent in the morphology of the nauplii, such as abundant setae on the mandibule and in the antennae (Heberer, 1932; Bjornberg, 1972). The Calanid species studied here is a specialized filter feeder according to Dahl (1956) who considers filter feeding a primitive process, and finds that the Calanidae have a morphologically simple arrangement of the appendages for filter feeding. For this reason they are restricted to planktonic life and to filter feeding. In brief, crustacean evolution probably consisted of sequential simplification, reduction, and specialization of structures (Sanders, 1963). If this proposal is accepted, *C. finmarchicus* has a sensorial arrangement in the first antennae to be considered the most primitive as compared to the Centropagidae, Eucalanidae, Acartiidae and Diaptomidae species. Therefore, the Acartiidae species represent probably the most recent group because of their simple and asymmetric sensorial arrangement.

From this study, however, it would appear that the number of setae is not as important as the complexity and arrangement of the setae. Therefore, it is not safe to establish "primitiveness" of a species by the number of sensory hairs present in its early or late stages. In order to establish which species is more primitive than another, information is required on the actual structure, distributional pattern, and frequency of occurrence of the sensors on the first antennae. Observing adult members of this group, I have found that most calanoid copepods have the same type of sensory hairs (sensillae trichodea and basiconica). The species-specific differences are established by the distributional pattern and frequency of occurrence of each sensilla on the first antennae.

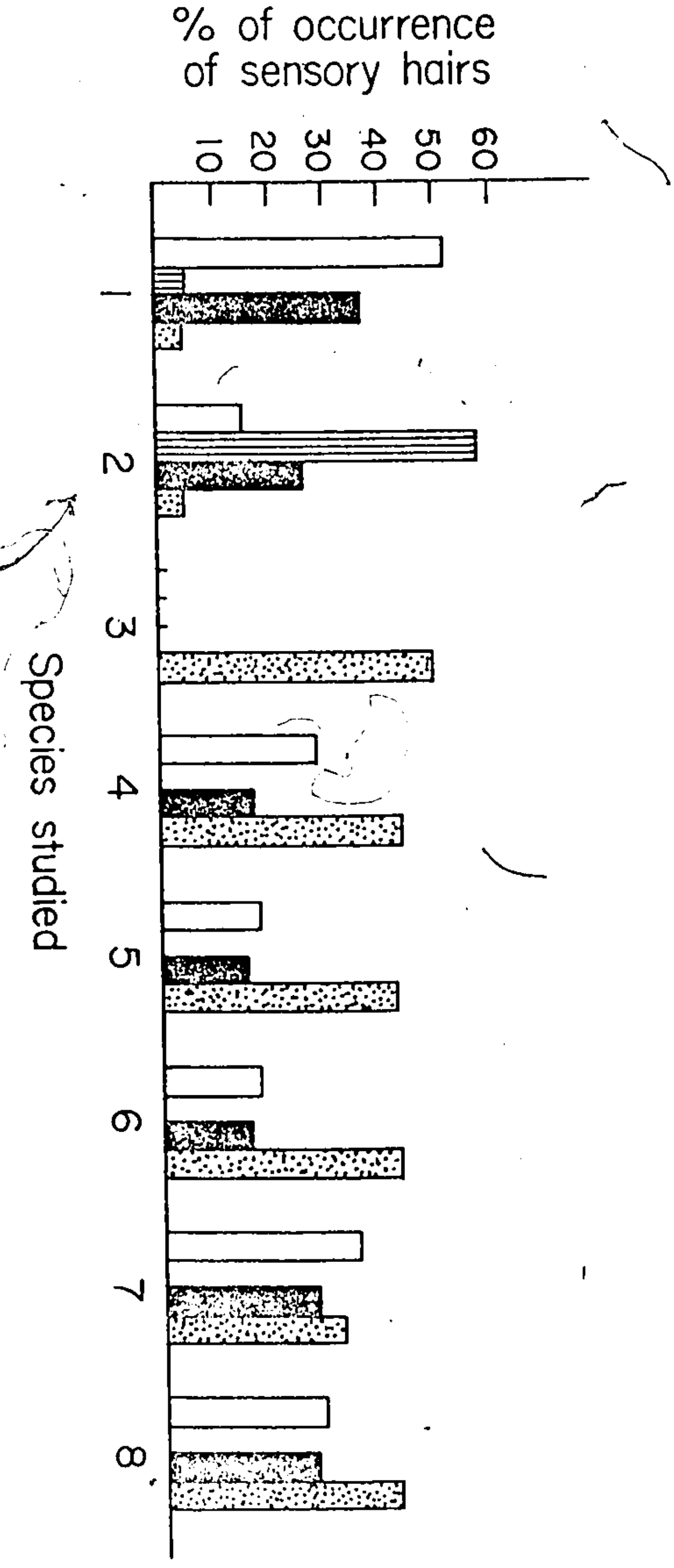
Marine and fresh-water calanoid copepods share a triangular arrangement of sensillae. In the marine species this is usually composed of two types of sensillae but in some instances they are composed of three types especially in the odd numbered segments. The triangular arrangement occurs on every segment but the last. The fresh-water species always possess three types of sensory hairs on each article where the triangular pattern is present. This pattern is present on each article for S. oregonensis but not for the closely related L. minutus. In contrast, Acartiidae lack completely the triangular arrangement, with a maximum of only two sensillae per article. Additionally, it is this group which possesses the maximum number of e-type sensory hairs (mechanoreceptors) and the lowest number of c-type (aesthetasc) sensory hairs. Is the low frequency of occurrence of aesthetasc in the Acartiidae significant with respect to the high frequency of occurrence of e-type sensory hairs? Might it be related to the feeding and predation habits of the animal? Late copepodid and adult Acartiidae are mainly omnivorous (Mullin, 1966) and, as such, a superior mechanoreception should help them in detecting and in capturing prey and large particles. If so, my data suggest basic differences between herbivorous and omnivorous species based on the way the sensors are organized on the first antennae.

In the present study I have found that omnivorous copepod species posses chemoreceptors and long mechanoreceptors in a proportion of 1:3 respectively (Fig. 29 Species 2,4,5,6). If the percentage of occurrence of each hair is calculated per antenna, then in omnivorous species the occurrence of aesthetasc is less than 18%, but the occurrence of e-type sensory hairs is 45% (Fig. 29, Species 2,4,5,6). The herbivorous species L. minutus has 43% occurrence of e-type sensory hairs but has a higher proportion (28%) of c-type sensory hairs. S. oregonensis shares the same proportion of c-type sensory hairs but with only 31% of e-type. The evolution of more mechanoreceptive sensors in L. minutus than in its closely related species S. oregonensis might be the result of predation pressure. The presence of more mechanoreceptive structures in this species could facilitate faster responses and make it less vulnerable to predation (Fig. 29, Species 8).

In general, the frequency of occurrence of the c-type sensory hairs may provide an important clue to establish a tentative division between obligate herbivorous and omnivorous calanoid copepods. Therefore, when the proportion of occurrences of c-type or basiconica sensory hairs is less than 18% of the total number of sensory hairs per antenna the species may be classified as omnivorous.

Trichodea sensory hair: a-type □; b-type ▥; e-type ▒.
Basiconica sensory hair:c-type ■.
Species studied: (1) *Calanus finmarchicus*; (2) *Centropages furcatus*; (3) *Eucalanus pileatus*; (4) *Acartia longiremis*; (5) *Acartia grani*; (6) *Acartia discaudata*; (7) *Skistodiaptomus oregonensis*; (8) *Leptodiaptomus minutus*.

Figure 29: Percentage of occurrence of trichodea and basiconica sensory hairs in the species studied.


% of occurrence of sensory hairs
10
20
30
40
50
60
1
2
3
4
5
6
7
8
Species studied

Carnivorous and omnivorous copepods must be able to detect and locate their prey at a distance (Mauchline, 1977). It seems that localization of prey could be done by specialized mechanoreceptors, e.g. a vibration sense. The presence of compound setae, similar to some of those described in amphipods (Mauchline & Ballantine, 1975) and considered to have a hydrodynamic function, has been found in the genus _Eucalanus_. From all the studied species, these hairs look similar to those present in _Epischura_ _lacustris_ and _Heterocope_ _borealis_ which are omnivorous fresh-water calanoid copepods (Barrientos, unpublished data). Additionally, the presence of setules in most of the trichodea sensory hairs might identify them as hydrodynamic receptors like those reported by Mauchline (1977). The seta with setules is a mechanoreceptor and occurs in decapods, mysids, amphipods, copepods, and other groups. It is most developed in decapods, being feather-like in _Palinurus_ _vulgaris_ (Vedel and Clarac, 1976), while moderately developed in the Calanidae, Acartiidae and and Eucalanidae species studied here, but relatively simple in form in amphipods (Mauchline and Ballantyne, 1975). These setae are more developed in the Acartiidae species than in any other group member studied here. They have similar characteristics to those which Mauchline (1977) describes as mechanoreceptors sensing water currents or pressure waves.

The present study has provided a description of the more common sensory hairs in calanoid copepods on the basis of their whole structure, and not by analysing the specimen integument after chemical digestion by potassium hydroxide as it has been traditionally described by several authors.

In conclusion, the sensory organization of the first antennae in calanoid copepods reveals many differences that may be related to specific evolutionary traits or ecological roles, such as food gathering activities. Mechanoreceptors and chemoreceptors are the dominant sensory structures in copepods. Further detailed work has to be carried out on the ultrastructure of each sensor in order to understand the sensory organization of the animal. Behavioural and field studies are also required to give a better understanding of the role of these structures in nature.

Finally, this study leaves a very important opening for further research. The well developed feather-like sensillae present in Acartia spp. constituted the most interesting structure reported in the present study. The ecological and adaptative implications of such a development for species living in a estuarine habitat deserves a careful examination.

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