Vol. 178: 101–107, 1999 | MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser | Published March 17

Ultrastructure of setae of the maxilliped of the marine planktonic copepod *Temora stylifera*

G.-A. Paffenhöfer*, P. A. Loyd

Skidaway Institute of Oceanography, 10 Ocean Science Circle, Savannah, Georgia 31411, USA

ABSTRACT: Copepodid stages and adult females of many calanoid copepods create feeding currents to obtain food. So far it has been uncertain whether food particles were perceived chemically or hydrodynamically or by both modes simultaneously. It was the goal of our study to determine the structures of potential sensors of setae on appendages of calanoids which are involved in the collection of food particles after these have been perceived at a distance from the gathering appendage(s). We report here on the ultrastructure of setae of the maxilliped of adult females of *Temora stylifera* Dana. This appendage not only contributes significantly to producing the feeding current, but also to gathering actively perceived food particles. Our results indicate that all setae of the female's maxilliped possess structures indicative of mechano- and chemosensors. Since setae of this mostly moving appendage are not still, distance perception of food particles is thought to occur by perceiving dissolved substances. Hydrodynamic sensors of the maxilliped are likely to be utilized when captured food particles have to be manipulated for ingestion or rejection.

KEY WORDS: Ultrastructure · Setae · Cephalic appendage · Marine planktonic copepod

INTRODUCTION

Planktonic copepods usually operate perpetually in the pelagic environment, where their life is largely governed by their ability to find food and avoid predators. Both functions require sensing in 3 dimensions, being followed by movements or no motion at all. To obtain food, a late juvenile or adult calanoid copepod utilizes all or some of its 6 pairs of cephalic appendages. Detailed observations revealed that copepodid stages and adult females of various calanoid species create a feeding current with their cephalic appendages by which water and particles therein are displaced towards the copepod (e.g. Strickler 1984, Paffenhöfer et al. 1996 and references therein). These particles are perceived individually and displaced by coordinated motions of various appendages towards the mouth, where they are perceived again, and then ingested or rejected (e.g. Paffenhöfer et al. 1982). It was hypothesized by way of a model that the feeding current and chemoperception would allow a calanoid to perceive a phytoplankton cell at a distance (Andrews 1983), leading to the previously described gathering process. Calculations by Legier-Visser et al. (1986) led these authors to suggest that perception of food particles by mechanosensors of the first antennae (A1) would be the main sensory process to obtain phytoplankton cells. Offering phytoplankton cells of 12 to ~30 µm width to late nauplii of *Eucalanus pileatus* revealed that here the A1 were not involved in the perception of food particles because the feeding current hardly touched the A1 (Paffenhöfer & Lewis 1989). Ultrastructure studies on late nauplii of *E. pileatus* revealed that at least 1 seta on its second antenna (A2) had the characteristics of a dually functional chemo- and mechanosensory sensillum (Bundy & Paffenhöfer 1997). Similarly, at lower food concentrations, copepodid stages and adult females of *E. pileatus*, perceived individual cells of the diatom *Thalassiosira*

*E-mail: paffenhofer@skio.peachnet.edu

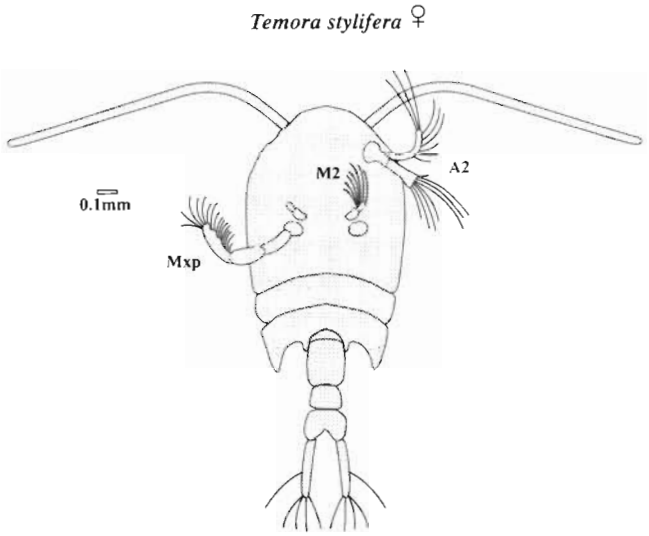


Fig. 1. *Temora stylifera* adult female. Second antenna (A2), second maxilla (M2) and maxilliped (Mxp) shown

weissflogii (11 µm width) prior to them reaching the tips of the setae of the A2 or the maxillipeds (Mxp, Paffenhöfer & Lewis 1990). The small size of these food particles and the perception of these cells at distances of repeatedly more than 1 mm from the tips of the setae led to the assumption that perception of a dissolved substance released by such a cell was the only possible distance perception. This supported the Andrews model (Andrews 1983). Earlier, Friedman & Strickler (1975) had described structures in setae of various mouthparts of the freshwater copepod *Diaptomus pallidus* which were thought to be indicative of chemo- but not of mechanoreceptor structures. Nishida & Ohtsuka (1997) thought that 2 types of setae on the Mxp of 2 species of mesopelagic copepods had chemosensory function.

Our assumptions of distance chemoperception of phytoplankton cells larger than 10 µm ESD (equivalent spherical diameter) by *Eucalanus pileatus* and similarly sized calanoids required proof. This led to the decision to investigate the ultrastructure of setae of those appendages which were the main participants in particle perception and gathering, i.e. the A2 and Mxp. The goal of this particular study was to determine whether some of the Mxp setae of female *Temora stylifera* possessed structures which could be considered of chemosensory and/or mechanosensory function. Our initial focus has been on the Mxp because they were responsible for 65% of all phytoplankton cell perceptions of adult females of *E. pileatus* (Paffenhöfer & Lewis 1990), and perceived and gathered almost all cells by adult females of the small calanoid *Paracalanus quasimodo* (Paffenhöfer unpubl. results). The nomenclature utilized throughout this paper is that used by Schmidt & Gnatzy (1984) and Weatherby et al. (1994).

MATERIAL AND METHODS

The taxon investigated in our studies was adult females of the calanoid copepod *Temora stylifera* Dana which occurs abundantly in subtropical and tropical regions of the Atlantic Ocean (Fleminger & Hülsemann 1973). *T. stylifera* is found on the southeastern continental shelf of the USA throughout most of the year. Females collected in late June/early July 1996 were maintained briefly in the laboratory and inspected for damage prior to fixation. To prevent major distortions of the cephalic appendages, the copepods were anesthetized in a magnesium chloride solution (3.5%) and then processed in the following manner, which is quite similar to the protocol used by Weatherby et al. (1994).

Initial fixation was for 30 min in 4% glutaraldehyde in 0.1 M sodium cacodylate buffer and 0.35 M sucrose. Decalcification occurred for 30 min in 2% sodium EDTA, which was followed by 30 min in 4% glutaraldehyde in 0.1 M sodium cacodylate, and 3 washes in 0.1 M cacodylate. The copepods were postfixed for 60 min in 1% osmium tetroxide (buffered), washed in 0.1 M cacodylate, which was followed by dehydration from 30 to 100% ethanol, propylene oxide and embedded in EPON 812.

90 nm thick sections were obtained with a Sorvall MT2-B ultramicrotome which was followed by staining with uranyl acetate and lead citrate. A JEOL 100 transmission electron microscope was made available at the Laboratory for Advanced Ultrastructure Research at the University of Georgia, Athens, USA.

RESULTS

The Mxp of *Temora stylifera* copepodid stages and adults are uniramous as compared with the second antennae which are biramous (Fig. 1). We identified 16 setae on the distal part of the Mxp which ranged in length from nearly 80 to about 220 µm. All setae were sectioned from near the tip to near the insertion into the Mxp. They all showed similar horizontal and cross-sectional organization from the distal to the proximal end (Fig. 2). The 10 seta cross-sections of Fig. 3 are intended to provide a general view of sensory structures of a seta of 1 of the 5 distal segments of the Mxp of a female *T. stylifera*. To optimally illustrate the setae's characteristics, we chose those micrographs which most clearly represent the setae's inner structure. Therefore, micrographs from different setae

were selected without compromising the sequential arrangement of ultrastructures observed in all setae. The tip of a seta contains a pore with an opening of about 0.2 µm diameter (Fig. 3a). The first microtubules can be seen 5 µm from the pore opening and the first dendrite can be clearly identified 9 µm from the tip (Figs. 2 & 3b). Eighteen µm from the tip, 4 dendrites can be recognized (Fig. 3c). Forty µm from the tip, the 4 dendrites possess specific structures: 2 have exclusively translucent microtubules which are positioned at similar distances from each other, the other 2 have more microtubules per area, with a large number of the microtubules being electron-dense (Fig. 3d). The structures surrounding these 4 dendrites could be enveloping cells; here microtubules are arranged rather randomly, i.e. at widely varying distances from each other. Five µm more proximal, both of the dendrites with translucent microtubules and 1 with electron-dense microtubules maintain their diameter, whereas the other dendrite has widened (Fig. 2) and displays 9 electron-dense bands at its periphery (Fig. 3e). The smaller-diameter electron-dense dendrite has begun to form very short bands at its periphery. About 6 µm further proximal, both of the electron-dense dendrites show typical 9+0 cilium-like structures (Fig. 3f), one of them forming outer dense bodies (looking like a pinwheel; Weatherby & Lenz 1993), the other a circlet (Weatherby & Lenz 1993) which is a structure just distal from a basal body. According to Schmidt & Gnatzy (1984) these structures are part of the ciliary segment close to the ciliary base. One of the 2 dendrites with translucent microtubules has now widened (Figs. 2 & 3f), and the other narrowed. Nearly 6 µm proximal, one of the dendrites with cilium structure (Fig. 3g) maintains its configuration (pinwheel) whereas the other (arrow) is now proximal to the basal body, i.e. part of the inner dendrite segments, now representing a ciliary rootlet (Schmidt & Gnatzy 1984, their Fig. 3). Proximal from there, we were not able to identify any structures which we could relate clearly to these 2 cilium-like sensors.

More proximal, we found 2 or 3 dendrites with translucent microtubules in each of the setae. One of these dendrites increases in diameter (Fig. 2), with the number of microtubules hardly changing. The micrographs in Fig. 3h,i,j are from the same seta and show the sequence of formation of a putative chemosensory basal body. Approximately 35 µm farther proximal, a few of the translucent microtubules have formed doublets (Fig. 3h), the number of which increases 8 µm proximal (Fig. 3i). This dendrite then narrows, resulting about 4 µm proximal in a cilium-like structure (Figs. 2 & 3j). Here 9 doublets are connected by electron-dense material and are longitudinally apparent

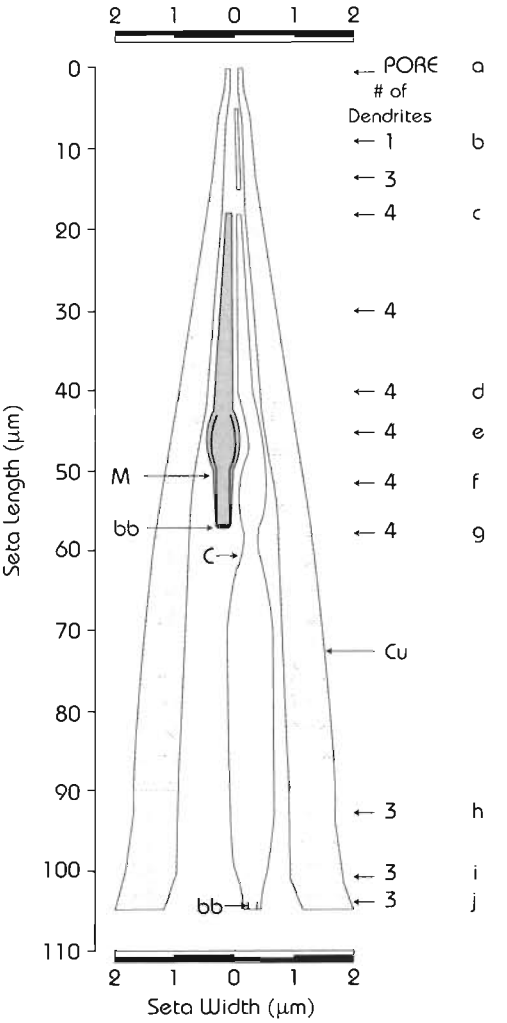
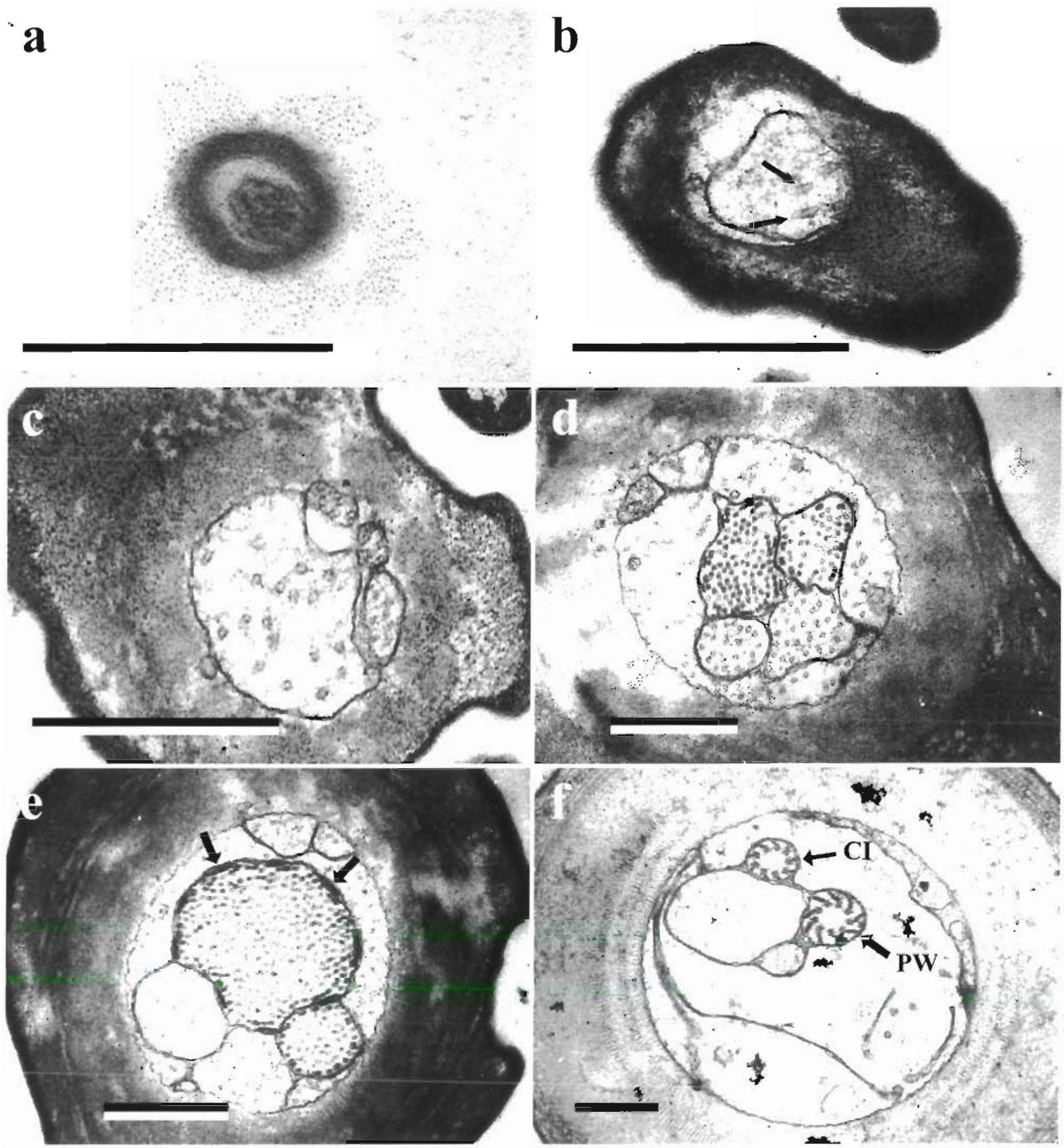


Fig. 2. Schematic longitudinal view of a seta of the maxilliped of a female *Temora stylifera*. C = putative chemosensory dendrite; M = putative mechanosensory dendrite; Cu = cuticle; bb = basal body; letters a through j refer to cross-sections shown in Fig. 3a–j; # of dendrites: number of sensory cells identified in cross-sections at each arrow's location

for ~2 µm. Farther proximal we could not identify structures relating to this feature.

Comparing all 16 setae, we found that 7 setae had 1, and 9 setae 2 dendrites with dense microtubules. These were almost always accompanied by 2 dendrites with translucent microtubules which are arranged at similar distance (Fig. 3d). Thus, a sensory cell had probably 2+1 or 2+2 (Fig. 3d,e) (translucent + electron-dense) dendrites, with the remaining dendrite-like structures most likely being enveloping cells. Basal bodies with translucent doublets were always proximal (26 to 95 µm) to circlets formed by electron-dense microtubules. Basal bodies from electron-dense microtubules appear to extend ~1 µm, and those from translucent ones ~2 µm, longitudinally.



DISCUSSION

Ultrastructure observations

Our goal was to investigate the ultrastructure of cephalic appendages of calanoid copepods other than the first antennae to find evidence for chemo- and/or mechanosensory structures therein. Some of the structures which were observed resemble those found in a seta of assumed dual-function in the first antennae of a calanoid copepod (Weatherby et al. 1994), in sensory structures of the shore crab *Carcinus maenas* (Schmidt & Gnatzy 1984) and in bimodal setae of the crayfish *Austropotamobius torrentium* (Altner et al. 1983, Derby 1989). A comparison with ultrastructures of Mxp setae of 2 mesopelagic copepods (Nishida & Ohtsuka 1997) was excluded because morphology and location of those setae (on the Mxp's coxa) clearly

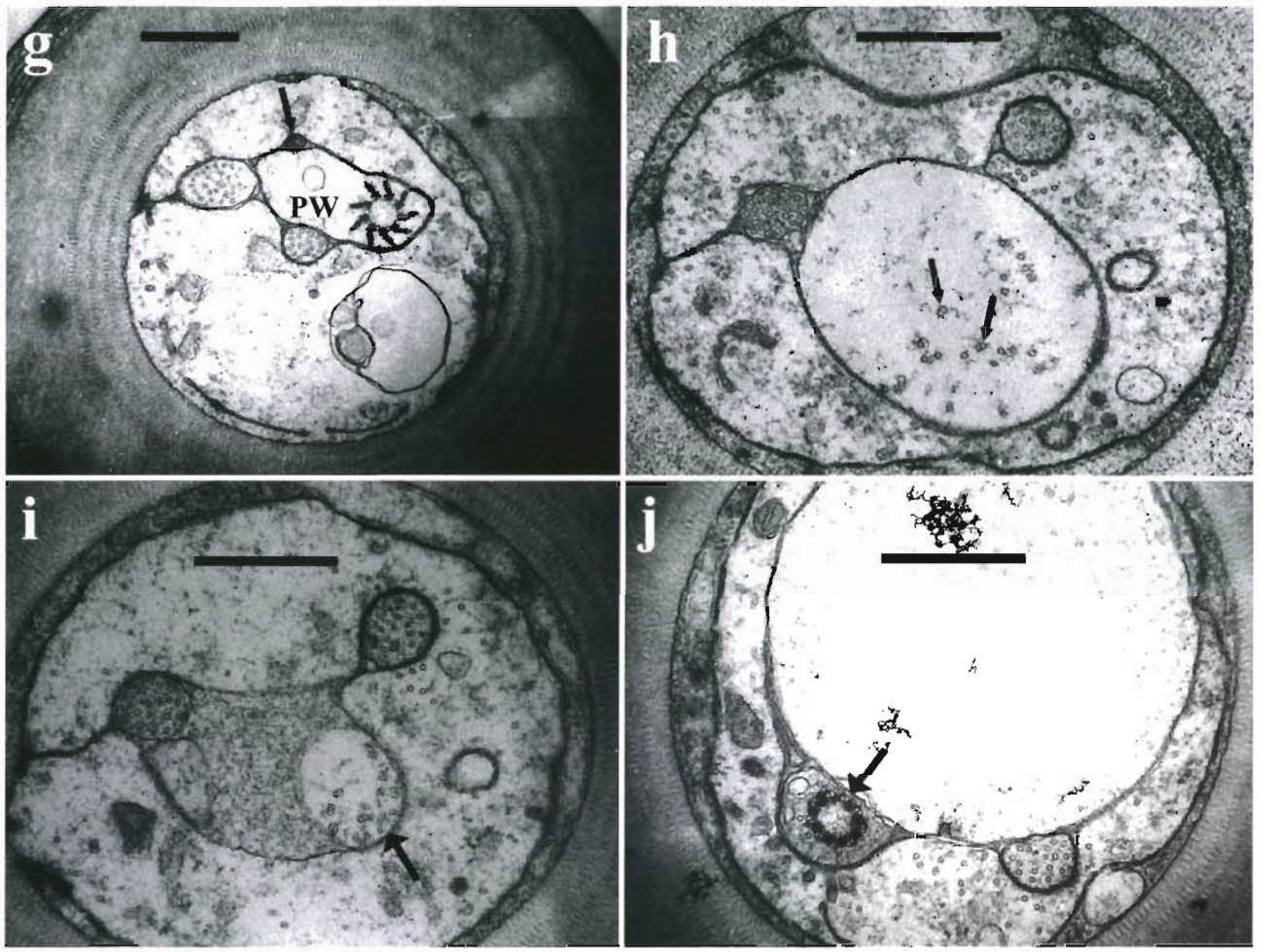


Fig. 3. (facing page and above) *Temora stylifera*. Cross-sections from the tip of a seta to near its insertion into the maxilliped. (a) Pore at tip of seta, including substance within pore; seta completely round; (b) seta's cross-section now elongated, showing 1 dendrite with 2 microtubules (arrows); (c) 18 µm from its tip, seta now has 4 dendrites; (d) 40 µm from the tip, the seta has 4 dendrites, 2 of which have a larger number of microtubules which are mostly darker, and 2 of which have fewer microtubules which are translucent at similar distances from each other; (e) 3 of the 4 dendrites maintain their diameter, while the fourth has widened, increased its number of microtubules, and formed 9 electron-dense bands at its periphery (arrows) which originate from merging of microtubules; (f) both dendrites with dense microtubules now show cilium-like structures forming a pinwheel (PW) and circlet (CI); (g) 6 µm proximal, the circlet appears as a ciliary rootlet (arrow) and the number of translucent microtubules in the 2 respective dendrites has hardly changed; (h) ~35 µm proximal, the microtubules in 1 of the dendrites begin to form doublets (arrows); (i) doublets have increased in number (arrow); (j) doublets have formed a basal body (arrow) and are connected to electron-dense material. Bars = 0.5 µm

differed from the setae at the distal segments of the Mxp.

Beginning with the most distal part of the seta shown (Figs. 2 & 3a) an apical pore is considered characteristic of a seta with dual/bimodal function, i.e. mechano- and chemosensory capability (e.g. Altner et al. 1983, Weatherby et al. 1994). Such setae of dual function possess dendrites with electron-dense and translucent microtubules (Fig. 3d,e) of which the former are considered indicative of mechanosensory and the latter of chemosensory function (Altner et al. 1983, Derby 1989). More proximally, the electron-dense microtubules form dense bands at the dendrite's periphery (Weatherby & Lenz 1993, their Fig. 3c) which eventually assume the configuration of a pinwheel (Bundy & Paffenhöfer 1997, their Fig. 3d) as also shown for *Temora stylifera* (Fig. 3f). Such pinwheel-like structures have been reported for other copepods (e.g. Kurbjeweit & Buchholz 1991, Gresty et al. 1993). These dense cilium-like structures (9+0) more proximally become less elongated, forming a circlet (Weatherby & Lenz 1993), and eventually become one dense structure, the basal body (Weatherby & Lenz 1993, Weatherby et al. 1994, their Fig. 3f).

Farther proximal we found only dendrites with a limited number of translucent microtubules (ranging from nearly 20 to 30), which eventually began to form doublets (Fig. 3h), as also shown by Schmidt & Gnatzy (1984) in their Type I and II dendrites, which, farther distal, form 9×2 ciliary segments (their Figs. 5d & 6d), and then basal bodies. The doublets are connected by an electron-dense material. The basal body found near the base of our seta (Figs. 2 & 3j) closely resembles that found by Schmidt & Gnatzy (1984) for their Type II dendrite, except that the proximal basal body found in each of several setae of the Mxp of a *Temora stylifera* female had a 9×2 configuration. Schmidt & Gnatzy (1984) ascribe their Type I dendrites (distal) a mechanosensory and their Type II dendrites (proximal) a chemosensory function. The ciliary segment of their Type I shows doublets, each of which consists of 1 electron-dense and 1 translucent microtubule, whereas the doublets of Type II possess 2 translucent microtubules each. Doublets in our proximal basal bodies had only translucent microtubules (Fig. 3j).

As compared to previous observations on putative mechanosensory structures in copepods and other crustaceans (e.g. Schmidt & Gnatzy 1984, Weatherby et al. 1994), none of the putative mechanosensory structures in any of the 16 setae of the Mxp had a scolopale, which is thought to have a stiffening function. However, we found scolopales around putative mechanosensory dendrites near the base of setae of the A1 of the copepodid stages of the calanoid *Eucalanus pileatus*. Whereas such setae on the A1 of copepods, especially at their tips, are rigid in order to perceive the slightest hydrodynamic forcing (e.g. Lenz & Yen 1993), setae on the A2 and the Mxp are flexible. They contribute to creating the feeding current and displacing perceived particles towards the copepod's median (see 'Discussion: function'). We could not detect rootlets other than the one shown in Fig. 3g proximal to both types of basal bodies. Weatherby et al. (1994) reported that ciliary rootlets were reduced in copepod dendrites.

Function

As all of the 16 setae of the Mxp of *Temora stylifera* had similar longitudinal and cross-sectional structures, we can assume, using evidence from other authors (e.g. Altner et al. 1983, Weatherby et al. 1994), that all of these setae have dual function, i.e. chemo- and mechanosensory. Uniporous sensilla of insects usually have 3 to 6 neurons, of which 1 is of mechanosensory function (Zacharuk 1980), and have gustatory chemoperception through the apical pore. As calanoid copepods' Mxp, together with the A2, move back and forth at 10 to 80 Hz (Price et al. 1983, Paffenhöfer & Lewis 1990) they create a feeding current whose velocity reaches 4 to 8 mm s^{-1} at the copepod. The tips of these setae continuously move through the oncoming water and thus encounter large volumes per unit time. Single molecules, having been released by potential food particles such as diatoms, dinoflagellates and heterotrophic protozoa, and preceding the particle, could encounter 1 or several pores and be perceived (Andrews 1983). The rapid perception of such a signal would allow the respective copepod to capture within less than 0.1 s the particle (associated with the perceived chemical compounds) which traveled at ~5 mm s^{-1} (Paffenhöfer & Lewis 1990). Mechanoperception of a particle of 11 µm diameter at a distance of ~500 µm from the tips of the flexible setae is unlikely. It has been proposed that chemoreceptors in dual-function setae had low chemosensory sensitivities and that excitant substances could not quickly reach the respective chemosensory dendrites (Lenz et al. 1996). This interpretation may be applicable for certain setae of dual function on the A1 which, e.g., could perceive molecules in a trail produced by a female. However, nearly instantaneous perception of signals produced by (1) predators, triggering the A1 mechanosensors, and (2) rapidly traveling food particles is of utmost importance to avoid being eaten, and to obtain sufficient food in an environment of food scarcity. The observation that odorant-binding molecules (proteins) at the pore at the tip of a bimodal seta possess cavities which can be readily occupied by specific molecules (Tegoni et al. 1996) could probably be applied to dual-function setae of copepods. With at least 1 dendrite being within microns of the pore opening and its mucus (Figs. 2 & 3a, see also Zacharuk 1980 for insects), rapid signal transmission by ion current change to the axon via microtubules could be envisioned as a possibility.

The function of the putative mechanosensors in the Mxp's setae is assumed to be that of contact receptors. The bending setae of the Mxp, and of other moving appendages, should not possess the same high sensitivity as the rigid setae at the tips of the A1, i.e. they should not be able to perceive minute hydrodynamic displacements. However, they would be sensitive to larger particles which are captured and displaced to the mouth, where they are positioned for ingestion by the setae of the mandibles (nauplii, Paffenhöfer & Lewis 1989) or those of the first maxillae (Paffenhöfer et al. 1982). In case of rejection at the mouth, mechanoperception of the respective particle(s) would have to be occurring by sensors in the setae of participating appendages (Mxp, second maxillae).

CONCLUSION

Examination of the ultrastructure of the 16 setae of the maxilliped of a female *Temora stylifera* revealed general structural similarity of all 16 setae (Figs. 2 & 3). By comparison with sensory ultrastructures of setae of other crustaceans, including copepods, we hypothesize that each of these 16 setae has dual function, i.e. mechano- as well as chemoperception. We also hypothesize that each of these setae has identical function, i.e. perception of chemical compounds released by approaching food particles to trigger gathering and capture of such potential food particles, plus participation in a possible rejection of a captured particle (e.g. Paffenhöfer et al. 1982). The high motion frequency of the Mxp and the A2, being near 40 Hz for adult females of *T. stylifera*, makes it much more probable to perceive an approaching food particle via chemosensory than stationary setae on the A1 of copepods which swim at velocities of ~0.5 mm s^{-1}, especially when the feeding current does not touch the A1. If all 32 setae of the 2 Mxp are able to perceive chemical compounds of approaching phytoplankton cells, the probability that each approaching cell could be perceived in a feeding current should be probable, especially when food concentrations are extremely low (Paffenhöfer & Lewis 1990). We realize that confirmation of our assumptions on the function of the respective dendrites most likely cannot be achieved until physiological evidence has been obtained.

Acknowledgements. This research was supported by a grant from the National Science Foundation (OCE 94 15791). Tina Weatherby Carvalho (University of Hawaii at Manoa), Cathy Kelloes and Mark Farmer (University of Georgia) guided us with numerous suggestions and protocols. Without their contributions, we could not have succeeded. Tina Carvalho and Petra Lenz provided constructive comments on an early draft of this manuscript. Vicki Patrick typed the manuscript and Suzanne McIntosh drew the figures. We gratefully acknowledge their support and that of the National Science Foundation.

LITERATURE CITED

Altner I, Hatt H, Altner H (1983) Structural properties of bimodal chemo- and mechanosensitive setae on the pereiopod chelae of the crayfish *Austropotamobius torrentium*. Cell Tissue Res 228:357–374

Andrews JC (1983) Deformation of the active space in the low Reynolds number feeding current of calanoid copepods. Can J Fish Aquat Sci 40:1293–1302

Bundy MH, Paffenhöfer GA (1997) The innervation of the setae on the appendages of the nauplius of *Eucalanus pileatus* Giesbrecht. Mar Freshw Behav Physiol 30:195–207

Derby CD (1989) Physiology of sensory neurons in morphologically identified cuticular sensilla of crustaceans. In: Felgenhauer BE, Watling L, Thistle AB (eds) Functional morphology of feeding and grooming in Crustacea. AA Balkema, Rotterdam/Brookfield, p 27–47

Fleminger A, Hülsemann K (1973) Relationship of Indian Ocean epiplanktonic calanoids to the World Oceans. In: Zeitzschel B (ed) The biology of the Indian Ocean. Springer-Verlag, Berlin, p 339–347

Friedman MM, Strickler JR (1975) Chemoreceptors and feeding in calanoid copepods (Arthropoda: Crustacea). Proc Natl Acad Sci USA 72:4185–4188

Gresty KA, Boxshall GA, Nagasawa K (1993) Antennulary sensors of the infective copepodid larva of the salmon louse, *Lepeophtheirus salmonis* (Copepods: Caligidae). In: Boxhall GA, Defaye D (eds) Pathogens of wild and farmed fish-sea lice. Ellis, Horwood, New York, p 83–98

Kurbjeweit F, Buchholz C (1991) Structures and suspected functions of antennular sensilla and pores of three Arctic copepods (*Calanus glacialis, Metridia longa, Pareuchaeta norvegica*). Meeresforsch 33:168–182

Legier-Visser MF, Mitchell JG, Okubo A, Fuhrman JA (1986) Mechanoreception in calanoid copepods—a mechanism for prey detection. Mar Biol 90:529–535

Lenz PH, Yen J (1993) Distal setal mechanoreceptors of the first antennae of marine copepods. Bull Mar Sci 53: 170–179

Lenz PH, Weatherby TM, Weber W, Wong KK (1996) Sensory specialization along the first antenna of a calanoid copepod, *Pleuromamma xiphias* (Crustacea). Mar Freshw Behav Physiol 27:355–363

Nishida S, Ohtsuka S (1997) Ultrastructure of the mouthpart sensory setae in mesopelagic copepods of the family Scolecitrichidae. Plankton Biol Ecol 44:81–90

Paffenhöfer GA, Lewis KD (1989) Feeding behavior of nauplii of the genus *Eucalanus* (Copepoda, Calanoida). Mar Ecol Prog Ser 57:129–136

Paffenhöfer GA, Lewis KD (1990) Perceptive performance and feeding behavior of calanoid copepods. J Plankton Res 12:933–946

Paffenhöfer GA, Strickler JR, Alcaraz M (1982) Suspension-feeding by herbivorous calanoid copepods: a cinematographic study. Mar Biol 67:193–199

Paffenhöfer GA, Strickler JR, Lewis KD, Richman S (1996) A comparative analysis of motion of and created by juvenile marine planktonic copepods (Crustacea: Copepoda). J Plankton Res 18:1699–1715

Price HJ, Paffenhöfer GA, Strickler JR (1983) Modes of cell capture in calanoid copepods. Limnol Oceanogr 28:116–123

Schmidt M, Gnatzy W (1984) Are the funnel-canal organs the 'campaniform sensilla' of the shore crab, *Carcinus maenas* (Decapoda, Crustacea)? II. Ultrastructure. Cell Tissue Res 237:81–93

Strickler JR (1984) Sticky water: a selective force in copepods evolution. In: Meyers DG, Strickler JR (eds) Trophic interactions within aquatic ecosystems. AAAS Selected Symposium 85, Westview Press, Boulder, CO, p 187–239

Tegoni M, Ramoni R, Bignetti E, Spinelli S, Cambillau C (1996) Domain swapping creates a 3-D putative combining site in bovine odorant binding protein dimer. Nat Struct Biol 3:863–867

Weatherby TM, Lenz PH (1993) Proliferation of microtubules from discrete electron-dense bodies in the ciliary dendritic portion of mechanosensory setae of copepod antennae. In: Bailey GW, Rieder CL (eds) Proc 51st Annual Meeting Microscopy Soc America. San Francisco Press, San Francisco, p 340–341

Weatherby TM, Wong KK, Lenz PH (1994) Fine structure of the distal sensor setae on the first antennae of *Pleuromamma xiphias* Giesbrecht (Copepoda). J Crustac Biol 14:670–685

Zacharuk RY (1980) Ultrastructure and function of insect chemosensilla. Annu Rev Entomol 25:27–47

Editorial responsibility: Evelyn and Barry Sherr (Contributing Editors), Corvallis, Oregon, USA

Submitted: July 9, 1998; Accepted: November 9, 1998
Proofs received from author(s): March 8, 1999