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## Fine structure of the “button setae” in the deep-sea pelagic copepods of the genus *Euaugaptilus* (Calanoida: Augaptilidae)

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**Abstract** Many species of the carnivorous copepod family Augaptilidae, a primarily meso- and bathypelagic group, possess specialized “buttons” on the setae of their maxilla and maxilliped, which have been thought to be a simple cuticular outgrowth. The fine structure of the button setae in three species of *Euaugaptilus* was examined by light- and electron microscopy from samples collected in the eastern Indian Ocean and the subtropical western North Pacific. The buttons are arranged in two rows along the inner surface of the setae. There are differences in the shape, size, and arrangement of buttons among the three species, *Euaugaptilus laticeps*, *E. longimanus*, and *E. magnus*. The button setae have an elaborate internal structure consisting of “setal shaft”, “stalk”, “disc”, and “outer membrane”, with microtubule bundles in the setal lumen, but have no muscular tissues. The disc has only pin-point contact to the core of the stalk, but has connection over a wider area with the fibrous tissue surrounding the core, and the contact area between the stalk and the setal shaft is also small. These structures suggest that the disc will move freely on the apex of the core of the stalk and the stalk may be movable at its connection to the setal shaft. All these components of the button setae may function in concert to fit the surface of the discs firmly to the surface of a prey, and to absorb the energy generated by the struggling prey.

### Introduction

The calanoid copepods of the family Augaptilidae primarily inhabit the meso- and bathypelagic zones of the

world oceans (e.g. Matthews 1972; Mauchline 1998). On the basis of the mouthpart morphology and gut-content analysis, this family is considered a carnivorous group (Arashkevich 1969; Itoh 1970; Harding 1974). The family Augaptilidae consists of ten genera (see Mauchline 1998 for systematics), of which the genus *Euaugaptilus* encompasses the largest number of species (ca. 70), representing one of the species-richest single genera among all calanoid copepods. The distribution of *Euaugaptilus* spp. is restricted mostly to the lower meso- and bathypelagic zones, where they occur in low abundance (e.g. Roe 1972b; Madhupratap and Haridas 1990; Padmavati et al. 1998) and sympatrically with many congeneric species (e.g. 25 species from the Canary Islands, Roe 1972a; 31 species from the Izu region, Tanaka and Omori 1974).

Many species of the augaptilid genera (7 species in *Augaptilus*, 3 species in *Centraugaptilus* and 58 species in *Euaugaptilus*, after Matthews 1972; Tanaka and Omori 1974; Park 1993) have setae on the maxilla and maxilliped carrying a stalked, sucker-like structure (see Fig. 1), instead of the normal setules, which have been variously termed “buttons” (Krishnaswamy et al. 1967), “cup-shaped appendages” (Matthews 1972), “hooked spinules” (Park 1993), “mushroom-like bodies” (Arashkevich 1969) or “disques pédicellés” (Sars 1925). This button appears to be restricted to the above species within the Calanoida. The degree of development of the buttons varies considerably within the family (Boxshall 1985). The high species diversity, the low population density, and the development of the button setae in Augaptilidae suggest a specialization in their food habit in the resource-limited deep sea, which would be an interesting topic to elucidate speciation and resource partitioning in pelagic communities.

The buttons of *Centraugaptilus horridus* were examined by Krishnaswamy et al. (1967), who reported a total absence of cellular structures in the button. They assumed that the buttons are present to increase active feeding-surface area. In addition, Boxshall (1985) assumed that the buttons act as buffers, absorbing some of

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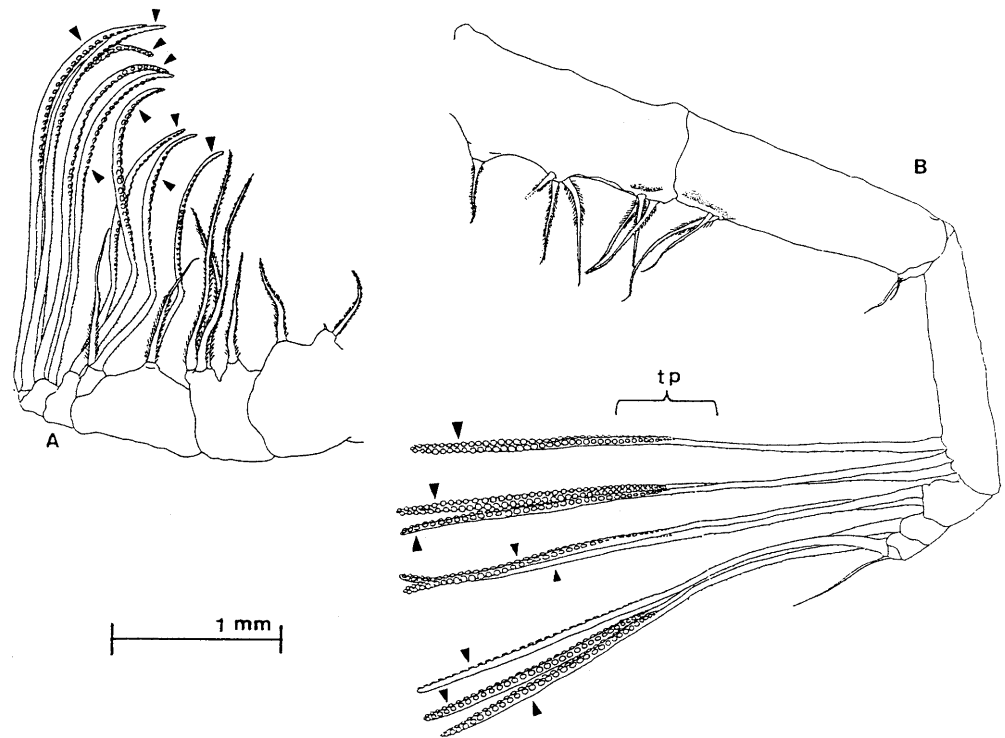
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**Fig. 1** *Euaugaptilus longimanus* female. **A** Maxilla. **B** Maxilliped. Arrangement of button setae (arrowheads) and transitional part (*tp*) are indicated



the energy generated by the struggling prey, thereby protecting the seta. Except for *C. horridus*, however, little is known on the gross morphology and the internal structure of “button setae” (i.e. the setae carrying the buttons). The present study examines the external and internal ultrastructure of the button setae in three species of the genus *Euaugaptilus*, and discusses their possible function.

## Materials and methods

Plankton samples were collected from the eastern Indian Ocean (4°56'S; 86°60'E) in January 1977 and in the subtropical western North Pacific (14°01'–23°52'N; 142°01'–146°59'E) from May to June 1998, during cruises of the R.V. “Hakuho-Maru” of the Ocean Research Institute, University of Tokyo.

In the eastern Indian Ocean, an opening-closing ORI-net (mesh size: 1 mm, Omori 1965) was towed horizontally in a 500 to 650 m depth layer. The samples were immediately fixed and preserved in 10% formalin/seawater solution buffered with sodium tetraborate. Adult females of *Euaugaptilus laticeps*, *E. longimanus*, and *E. magnus* were then sorted from the preserved samples, and their maxillae and maxillipeds were removed from the body with dissecting needles. The number of buttons on the setae of these appendages were counted under a light microscope.

In the subtropical western North Pacific, an ORI-net (mesh size: 0.33 mm) or an Isaacs-Kidd midwater trawl (mesh size: 0.5 mm, Isaacs and Kidd 1953) were towed obliquely from ca. 1200 m depth to the surface. Immediately after capture, adult females of *Euaugaptilus* spp. were sorted from the original samples in cold sea water, and fixed in 2% glutaraldehyde and 2.5% paraformaldehyde buffered with 0.1 M Millonig's phosphate buffer (pH 7.4 at 4 °C). The maxillae and maxillipeds were then removed from the body with dissecting needles for better penetration of fixative and resin. These appendages were post-fixed in 1% OsO<sub>4</sub> in the same buffer at 4 °C and dehydrated through a graded ethanol series from 50 to

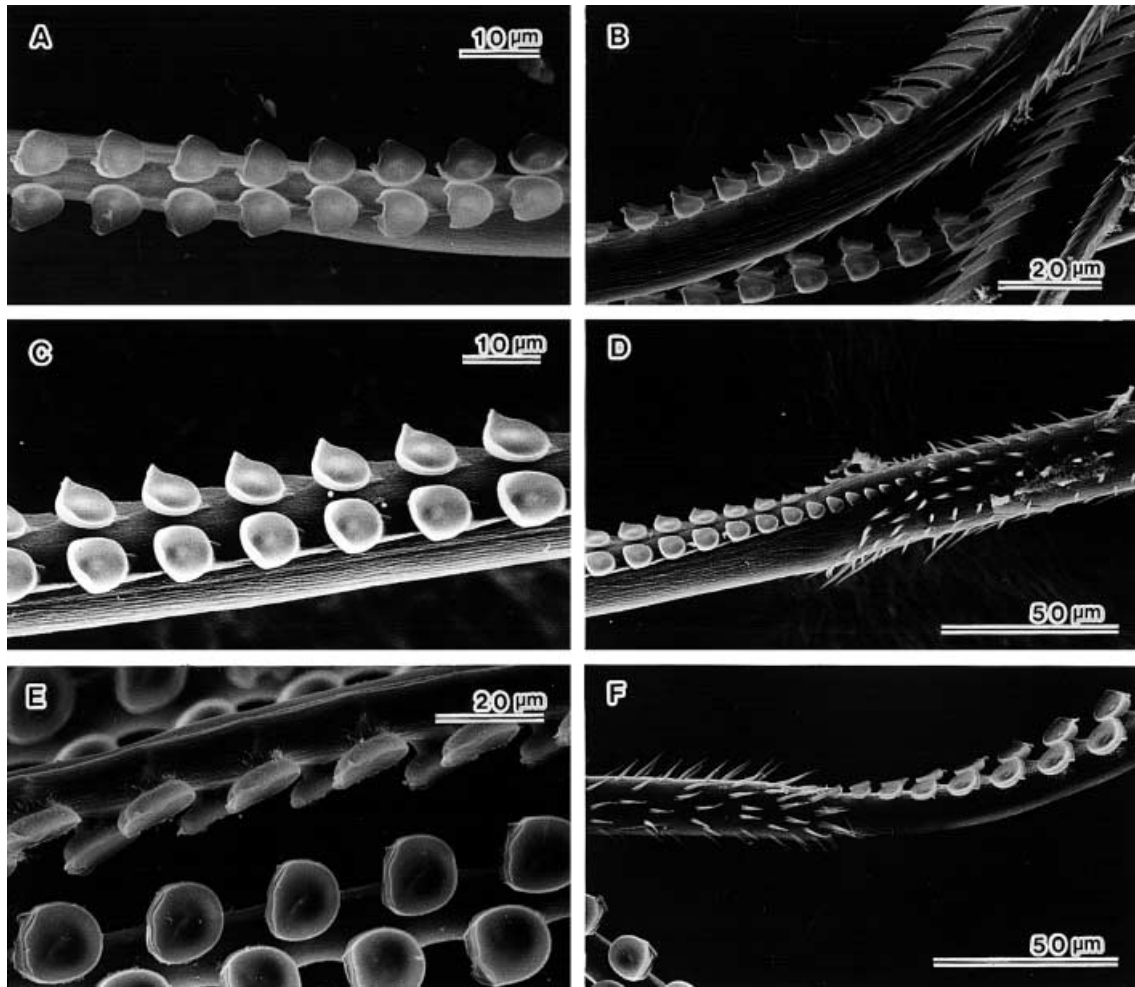
100%. For scanning electron microscopy (SEM) the appendages of *E. laticeps*, *E. longimanus*, and *E. magnus* were critical-point dried, coated with gold, and examined with an Akashi Alpha-25A SEM at an accelerating voltage of 15 kV. For transmission electron microscopy (TEM) the appendages of *E. longimanus* and *E. magnus*, fixed and dehydrated as for SEM, were embedded in Epon-812 resin. Ultrathin sections were stained with uranyl acetate and lead citrate, then examined with a Hitachi H-7100 TEM at an accelerating voltage of 100 kV.

## Results

### External morphology

In the three species examined, the buttons (hereafter referred to as “discs”, see following subsection) are arranged in two rows along the inner surface of the button setae (Figs. 1, 2). The shape and diameter of the discs, and the arrangement of the button setae are shown in Fig. 2 and Table 1. There are differences in the shape, size, and arrangement between the discs on the homologous appendages of the three species, while no marked differences were detected between the discs on the maxilla and maxilliped within each species.

In *Euaugaptilus laticeps* the discs are semicircular with more-or-less linear margins on the distal side of a seta (Fig. 2A). In the button setae the basal-most setules are replaced distally by triangular spines which form two rows on the middle part and change into buttons, arranged side-by-side, more distally (Fig. 2B). The diameter of the discs is ca. 6 μm throughout the seta, except on the terminal part, where it decreases to about half of that of the discs on the more basal part.



**Fig. 2** *Euaugaptilus laticeps* female (A, B), *E. magnus* female (C, D) and *E. longimanus* (E, F) female. SEM micrographs of button setae. The subterminal (A, C and E) and transitional (B, D and F) parts of a seta. Distal side to the left in A to E, to the right in F

In *Euaugaptilus magnus* the discs are semicircular as in *E. laticeps* (Fig. 2C). In the button setae the basal-most setules are replaced distally by small processes which form two rows on the middle part, and change into buttons arranged side-by-side (Fig. 2D). The diameter of the discs is ca. 7 µm, gradually decreasing distally to ca. 1.5 µm at the tip of the seta.

In *Euaugaptilus longimanus* the discs are circular, and sucker-like (Fig. 2E). In the button setae the basal-most setules are replaced distally by small buttons which form two rows on the middle part and gradually increase to

alternately arranged discs, ca. 14 µm in diameter, more distally (Fig. 2F). The diameter of the discs gradually decreases distally to ca. 9 µm at the tip of the seta.

The number of discs on a button seta and the total surface area of the discs of the three species are shown in Table 2. The total surface area of discs per copepod, calculated on the basis of the disc diameters in Table 1 and assuming a circular shape for all discs, is ca.  $1.5 \times 10^5$ ,  $3.4 \times 10^5$ , and  $3.7 \times 10^5$  µm<sup>2</sup>, in *E. laticeps*, *E. magnus*, and *E. longimanus*, respectively.

#### Internal ultrastructure

The button setae on the maxillae and maxillipeds of *Euaugaptilus magnus* and *E. longimanus* have basically

**Table 1** *Euaugaptilus* spp. Body length, disc shape, disc diameter, and arrangement of button setae

Species	No. inds examined	Body length (mm)	Disc shape	Approx. disc diameter (µm)	No. button setae on maxilla		No. button setae on maxilliped
					Endopod	Basis	Endopod
<i>E. laticeps</i>	6	7.0–7.1	Semicircular	6	7	0	7
<i>E. magnus</i>	6	7.3–7.7	Semicircular	7	9	1	7
<i>E. longimanus</i>	6	4.5–4.6	Circular	14	8	1	8

**Table 2** *Euaugaptilus* spp. Number and total surface area of discs. The total surface area of the discs over all setae was calculated on the basis of the disc diameters in Table 1 assuming a circular shape for all discs

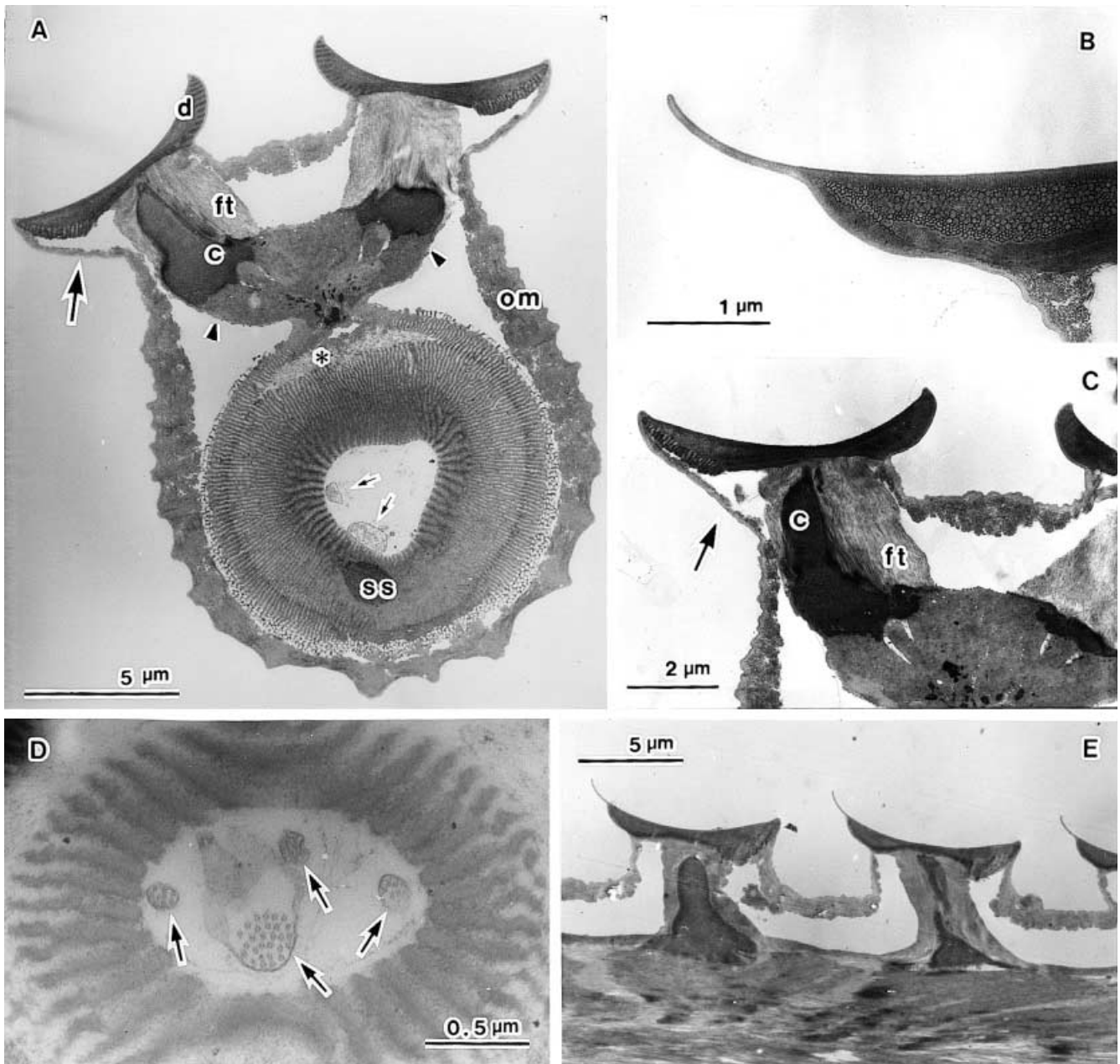
Species	No. of discs seta <sup>-1</sup> (median):		Total surface area of discs copepod <sup>-1</sup> ( $\mu\text{m}^2$ )
	<i>n</i> Maxilla	<i>n</i> Maxilliped	
<i>E. laticeps</i>	19 140–223 (186)	13 132–230 (194)	$1.5 \times 10^5$
<i>E. magnus</i>	13 244–294 (258)	13 212–368 (266)	$3.4 \times 10^5$
<i>E. longimanus</i>	20 58–72 (64)	24 70–90 (78)	$3.7 \times 10^5$

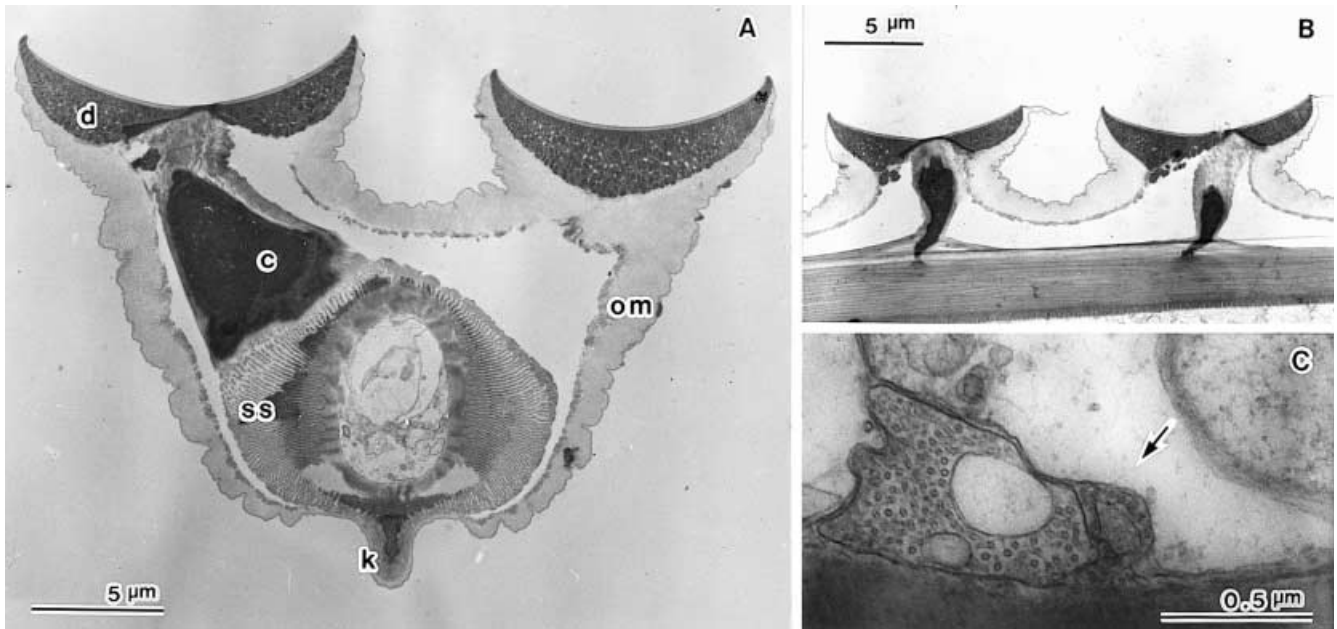
similar components: “the setal shaft”, “the stalk”, “the disc”, and “the outer membrane” surrounding all the other components except the outer surface of the disc which is exposed to the environment (Figs. 3A,

4A). There are no muscular tissues within the button setae.

In a cross section, the setal shaft is circular in *Euaugaptilus magnus* (Fig. 3A), while it is depressed in

**Fig. 3** *Euaugaptilus magnus* female. TEM micrographs of a button seta. The subterminal (A, B, C and E) and terminal (D) part of seta. **A** Cross section of seta on the maxilliped, containing setal shaft (ss), disc (d), stalk (arrowheads), outer membrane (om), and electron-sparse tissue (asterisk); stalk consists of electron-dense core (c) and more sparse fibrous tissue (ft); setal lumen containing microtubule bundles (small arrows). The outer membrane is loose (large arrow). **B** Longitudinal section of disc of a seta on the maxilliped. **C** Cross section containing core (c) and fibrous tissue (ft) of stalk of a seta on the maxilliped. The outer membrane is stretched (arrow). **D** Cross section of setal lumen of a seta on the maxilla containing microtubule bundles (arrows). **E** Longitudinal section of a seta on the maxilliped; distal side to the left





**Fig. 4** *Euaugaptilus longimanus* female. TEM micrographs of a button seta. **A** Cross section of subterminal part of seta on the maxilla, containing setal shaft (*ss*), disc (*d*), core of stalk (*c*), and outer membrane (*om*). A keel (*k*) is on the outer side of shaft. **B** Longitudinal section of subterminal part of a seta on the maxilliped; distal side to the right. **C** Cross section of setal lumen of terminal part of a seta on the maxilla containing microtubule bundle (*arrow*)

*E. longimanus* (Fig. 4A). The setal lumen is surrounded by several distinct layers. In *E. magnus*, the shaft consists of two layers: the inner layer occupies much of the shaft and consists of radially branching laminae (ca. 3.7 µm thick) running parallel to the long axis of the shaft; the outer layer is much thinner (ca. 0.4 µm) and consists of a porous tissue (Fig. 3A). On the inner side of the shaft, at the attachment to the stalk, there is a space within the inner layer filled with an electron-sparse tissue (Fig. 3A). In *E. longimanus*, there is a keel on the outer side of a shaft along the long axis; there appear to be at least two layers in the shaft, as in *E. magnus*, but the outer layer is not porous and has a more dense appearance (Fig. 4A). In both species there are microtubule bundles in the setal lumen (Figs. 3A, D, 4A, C).

The stalk consists of an electron-dense “core” and a more sparse fibrous tissue surrounding the core (Figs. 3A, C, E, 4A, B). The core is pointed distally and appears to have contact with the central inner surface of a disc (Fig. 3C). In *Euaugaptilus magnus* the stalk is U-shaped, the base of the “U” being fused to the setal shaft, and supports two discs (Fig. 3A). The base of the U-shaped stalk extends along the length of a seta, thus interconnecting the stalks supporting different pairs of discs (Fig. 3A, E). In *E. longimanus* the stalks are columnar and not interconnected, and each column supports one disc (Fig. 4A, B).

The disc has a smooth and slightly concave surface. The tissue of a disc shows an electron-dense, particulate appearance (Fig. 3B). The thickness of a disc is minimal

at the margin to the distal side of a shaft (ca. 70 and 80 nm in *Euaugaptilus magnus* and *E. longimanus*, respectively) and intermediate at the center (ca. 250 and 200 nm), and is maximal in the medial region (ca. 1.0 and 2.6 µm) (Figs. 3, 4).

The outer membrane consists of an electron-sparse tissue with irregularly undulated surface and is 0.2 to 1.0 µm thick in *Euaugaptilus magnus* (Fig. 3A, C, E) and 0.5 to 3.0 µm thick in *E. longimanus* (Fig. 4A, B). This membrane covers all components of the setae except the outer surface of the disc, connects all discs at the brim, and leaves spaces between the membrane itself and all other components (Figs. 3A, C, E, 4A, B).

## Discussion

### Comparative morphology

The present observations demonstrated that the button setae have an elaborate structure consisting of several components, each presumed to have a distinct mechanical role, and that there are distinct structural differences in the button setae between species.

The button setae exist not only on the appendages in adult females but also in adult males and immature copepodid stages (Sewell 1947; Matsuura unpublished data). Hence, the button setae may be involved in feeding rather than in mating behavior. In some species of the genus *Euaugaptilus* numerous small buttons exist on the setae of the arthrite of the maxillule, being arranged radially in many rows (Sewell 1947). Boxshall (1985) termed the seta “stud seta”, suggesting that it is involved in manipulating and transferring the prey from the maxillae and maxillipeds to the mandibles. In *E. laticeps* and *E. magnus* the stud setae exist on the precoxal arthrite of the maxillule, and the basal endite

and the first endopod segment of the maxillae (Matsuura unpublished data).

Matthews (1972) distinguished the degrees of development in the buttons as: "absent", "poorly developed", and "well developed". The buttons of *Euaugaptilus longimanus* were ranked as well developed, while those of *E. laticeps* and *E. magnus* were poorly developed. The present observation is consistent with Matthews' (1972) results, demonstrating that discs are much larger in *E. longimanus* than in *E. laticeps* and *E. magnus* (Table 1). The estimated total surface area of discs per copepod was similar between *E. longimanus* and *E. magnus*, while in *E. laticeps* it was about half that found in the other two species. The size and number of the discs of *E. laticeps* are similar to those in *E. magnus*, but the number of button setae is smaller. The number of discs of *E. longimanus* is very small compared with that of the other two species, but the estimated total surface area of discs per copepod was, despite the smallest body length, the largest among the three species, because this species has discs of larger size. This difference in estimated total surface area of discs per copepod may be related to some differences in feeding behavior among species, a hypothesis which awaits further study.

In the button setae, there were differences in the transition from normal setules to buttons among the three species examined. In *Euaugaptilus laticeps*, especially, the button seta shows a gradual transition, from setules to serrate spines, which change into buttons. Sewell (1947) has commented on the transition in button setae in various members of the genus *Euaugaptilus*, and Boxshall (1985: Fig. 47) showed the transition in the genus *Centraugaptilus*. Hence, the buttons appear to be modified setules, originating from the integument (see also Krishnaswamy et al. 1967; Boxshall 1985). The species in the genus *Arietellus* have setae on the maxillae and maxillipeds carrying specific processes, a row of flattened platelets each terminating in a short spine (Sewell 1947; Ohtsuka et al. 1994). This specific process appears to be a modified setule, similar to the buttons in the Augaptilidae, but its structure and function are still unknown.

The internal structure of button setae in the two species of *Euaugaptilus* examined is similar to that of *Centraugaptilus horridus* in having the smooth, concave surface of a disc, the absence of muscle tissues, the laminar structure of the setal shaft, and the stalk containing a core of structureless, electron-opaque material (Krishnaswamy et al. 1967). However, the button setae of the present species have two other components, the microtubule bundles and the outer membrane, which were lacking in *C. horridus* examined by Krishnaswamy et al. (1967), who suggested that the button setae are not sensory on the basis of the absence of nerve endings. The presence of microtubule bundles in the setal lumen in the present species suggests a possibility for the button setae being sensory, while there appears to be no direct contact between the microtubules and the stalk, and the complete

structure of the sensory neurons has not yet been characterized. While these differences in setal structure between *C. horridus* and the present species may partly be attributable to specific or generic differences, the major cause for the differences seems to be the use of specimens preserved in formaldehyde, by Krishnaswamy et al. (1967), which often destructs structural details.

### Structure and function

In button setae, the disc and the core of the stalk consist of electron-dense tissues which are assumed to be harder than the other components. The disc has only pin-point contact to the core of the stalk, but has connection over a wider area with the fibrous, presumably elastic, electron-sparse tissue surrounding the core. Hence, the disc will move freely on the apex of the core of the stalk as a fulcrum in accordance with a relative angle of a prey surface (compare Fig. 3A and C). In *Euaugaptilus magnus* the base of the U-shaped stalk is attached to the outer surface of the setal shaft, while in *E. longimanus* the base of the columnar stalk is attached to the lateral side of a shaft. This difference in stalk structure may be related to the differences in disc diameter, disc arrangement, and the structure of the setal shaft in the two species. The columnar stalk in *E. longimanus* corresponds to the larger disc diameter (two times that of *E. magnus*), which necessitates the discs being arranged alternatively rather than side-by-side, the stalks being located further apart, the flattened setal shaft, and the presence of a keel for strengthening the flattened shaft. In both species, the contact area between the stalk and the setal shaft is small. Hence, the stalk may also be movable at its connection to the setal shaft. The spaces between each of the components are probably filled with body fluid. The movable disc and stalk, the fluid in the space, the multilayered and keel-supported shaft, and the outer membrane, which may be elastic, all may function in concert to fit the surface of the discs firmly to the surfaces of a prey, and to absorb the energy generated by the struggling prey, as suggested by Boxshall (1985). Despite lack of muscular tissue, the movable discs may be instrumental in holding a prey, by the shearing force of the surface.

The setal shaft in the two species of *Euaugaptilus* consists of radially branching laminae in a cross section. This remarkable laminal structure in the setal shaft has not been reported in the maxillae and maxillipeds of other copepods (see, e.g., TEMs in Nishida and Ohtsuka 1997; Paffenhöfer and Loyd 1999). The setal shaft in *Centraugaptilus horridus* has a laminal structure in the innermost setal wall (Krishnaswamy et al. 1967), but it is much thinner and occupies a much smaller part of the setal shaft than in the present species. It is unclear how the laminal structure in the setal shaft of *Euaugaptilus* spp. is involved in the function of the button setae.

The button setae of *Euaugaptilus* spp. are more slender and appear to be more flexible than the setae on

maxillae and maxillipeds of other carnivorous calanoid copepods belonging to such families as Candaciidae, Euchaetidae, Pontellidae, and Tortanidae, which have well-developed, stout setae (Wickstead 1962; Arashkevich 1969; Ohtsuka et al. 1987; Ohtsuka and Onbé 1989, 1991). The flexibility of the button setae thus appears to represent an energy-saving strategy in prey capture, by absorbing prey movement rather than powerfully grasping a prey, which is consistent with the ambush predatory mode suggested for the augaptilids on the basis of oxygen consumption rates and enzymatic activities (Thuesen et al. 1998).

The specialization and diversification of feeding appendages in the augaptilids, as described above, also suggest a specialization of prey for the family and among species, i.e., they might have exploited food resources that are not utilizable for other copepods, and might have further partitioned the resources by species-specific feeding strategies. The structure of the button setae suggests that the targeted prey organisms may have a relatively wide area of smooth surface on their integument, such as that found among copepods and gelatinous plankters. However, most augaptilid copepods with button setae previously examined had empty guts (Harding 1974; Matsuura unpublished data); only two specimens of *Euaugaptilus* were reported to contain only copepods as gut contents (Harding 1974). For a better understanding of the feeding strategies of augaptilid copepods, further studies on their feeding ecology, including analyses of gut contents and feeding behavior, are necessary.

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