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RESEARCH ARTICLE

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The morphology of the chemosensory aesthetasc-like setae used during settlement of cypris larvae in the parasitic barnacle *Sacculina carcini* (Cirripedia: Rhizocephala)

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Abstract Rhizocephalans of the suborder Kentrogonida are parasitic barnacles whose female cypris larvae must locate a suitable host organism (a decapod crustacean), while the male cypris larvae must find a host containing a virgin female. Some of the sensory structures assumed to be involved in this behaviour are the aesthetasc-like setae found on antennules of the cyprids, of which the females possess one and the males two. To verify the aesthetasc nature of these setae we examined their morphology and innervation in the cyprids of the "model" kentrogonid rhizocephalan, *Sacculina carcini*, using SEM and TEM. No structural differences were found between the two types of aesthetasc-like setae, and their ultrastructure strongly indicates them as being aesthetascs. They have an exceedingly delicate cuticle, 20–50 nm thick, and the lumen contained essentially only very fine ciliary branches of which many were in close contact with the cuticle. No sheath cells were seen in the setal lumen. The ciliary branches could be traced back through the fourth and third antennular segment. The bodies of the sensory cells were not located, but morphological evidence suggests that their inner dendritic segments are located in the second antennular segment, giving rise to cilia that evolve into sheath-wrapped ciliary bundles. All these characteristics support their role as aesthetascs and olfactory organs, while the absence of these traits in the so-called terminal aesthetasc invalidates its previous description as an aesthetasc altogether, although it may still be a chemosensory seta.

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Introduction

The Cirripedia Rhizocephala is a group of specialised crustaceans, which has adapted to a sessile and parasitic form of life as adults. Since the adult organism cannot change its locale, the task of finding a suitable habitat falls on the free-swimming larva, known as the cyprid and characteristic for all Cirripedia. The rhizocephalan larvae have separate sexes, each of which performs a separate task at settlement: the female cyprid locates a suitable host organism and infects it, while the male cyprid must find a suitable host already infected with a virgin female parasite (Ritchie and Høeg 1981; Høeg 1987a). The cyprids use a number of cues in order to locate their settlement targets, most importantly chemical signals emanating from the host (Høeg and Ritchie 1985; Høeg 1991; Boone et al. 2003). It has been shown that cyprids of *Heterosaccus dollfusi*, another rhizocephalan species, are capable of actively and effectively locating their host in still water and in flow using distance-chemoreception of waterborne metabolites of its host, the brachyuran crab *Charybdis longicollis* (Pasternak et al. 2004). The major chemosensory organs of the rhizocephalan cyprids are thought to be the lattice organs, situated dorsally on the carapace, and aesthetasc-like setae, attached to the penultimate and ultimate segments of the antennule. Aesthetascs represent a morphologically distinct type of crustacean seta, characterised by a specialised thin cuticle permeable to dissolved substances (Derby et al. 1997) and branched outer dendritic segments (sensory

cilia) that lead to extremely high numbers of ciliary branches per seta (Hallberg et al. 1997). Their morphology correlates with their function as extremely sensitive olfactory setae, with response thresholds in the picomolar range (Thompson and Ache 1980; Derby 1989; Derby et al. 1994). These unimodal chemoreceptors, lacking an associated scolopale, are believed to serve in long-distance food, sex and host detection during complex search behaviours (Ache 1982).

The lattice organs represent heavily modified putative chemosensory setae and have been studied extensively (Jensen et al. 1994a, 1994b; Høeg et al. 1998; Kolbasov et al. 1999; Høeg and Kolbasov 2002; Rybakov et al. 2002, 2003), but the putative aesthetascs have thus far not been given the same close attention. Earlier studies (Walker 1985; Glenner et al. 1989; Moyse et al. 1995; Walker and Lester 2000) described the external morphology of these setae, and Glenner et al. (1989) suggested them to be aesthetascs. In the sub-order Kentrogonida, both male and female cyprids possess on the fourth antennular segment a sub-terminal aesthetasc (STA) and what has been described as a terminal aesthetasc (TA), while the male cyprids also possess an additional, large aesthetasc (LA) on the third antennular segment. We have adopted this terminology here, and it was the goal of our study to add additional morphological evidence to the possible aesthetasc and olfactory nature of these setae. Observations were carried out by scanning (SEM) and transmission (TEM) electron microscopy, thus setting the stage for future experiments on the specific function of these setae. A comparison has been made between the ultrastructure of the three different types of suggested aesthetascs. We chose to use the "model" rhizocephalan *Sacculina carcini*, because it has been the subject of most seminal studies concerning the Rhizocephala.

Materials and methods

Cypris larvae of *Sacculina carcini* were cultured at the Station Biologique, Roscoff, France, as described by Høeg (1984, 1987b). Larvae were fixed in 2.5% glutaraldehyde in 0.1 M sodium cacodylate buffer at pH 7.4, postfixed in 1% osmium tetroxide in the same buffer, dehydrated and embedded in TAAB 812 epon resin. More than five cyprids of each sex were sectioned semiserially and mounted on 70 or 50 mesh grids. Since we relied on material used in past studies (Høeg 1987a, 1987b) when employing this technique, we were prevented from tracing the sensory cells in complete detail, as would be possible using serial sections on slot grids. The sections were photographed, and the images were digitised by scanning negatives or positives. Specimens for SEM were examined and digitally photographed in a JEOL 840 microscope. Some photographs were digitally retouched for background clarity and uniformity.

Results

General antennular morphology

Walker (1985) gave an account of the number, position and general external morphology of the aesthetascs in cyprids of *Sacculina carcini*; we provide only those observations needed in order to appreciate the internal structure. The antennules of cirripede cyprids consist of four segments, with the setae found principally on the two distalmost (Moyse et al. 1995; Lagersson and Høeg 2002). Male cyprids carry two aesthetascs, a large one (the LA) on the third antennular segment and a smaller one sited sub-terminally (the STA) on the fourth antennular segment (Figs. 1A, B, 2B). The uniquely male LA sits ventro-laterally on the third antennular segment, also called the attachment organ, close to and a little proximal to the insertion of the fourth antennular segment (Fig. 1B). Both the fourth segment and the LA originate outside the attachment disc, which is covered with microcuticular projections or "villi". The LA extends posteriorly for more than half the length of the cylindrically shaped second antennular segment (Fig. 1B). Females possess the STA on the fourth antennular segment, but lack the third segmental LA altogether (Figs. 1C, 2A). The STA in both males and females emanates from a small ledge situated sub-terminally on the cylindrical fourth segment. Apically, this segment additionally carries four terminal setae (TS) (Fig. 1B, C, E). Two of the TS are somewhat sac shaped in the basal part. In females, one of them is reminiscent of a tiny "terminal aesthetasc" (Fig. 1C, TS1), whilst, in males, the homologous seta has a conspicuous short projection not seen in females (Fig. 1E, arrow). The other sac-shaped seta extends into a long and narrow apical part in both males and females.

Morphology of the putative aesthetascs

Aside from size, we found no external or internal differences between the putative aesthetascs, either between the LA and STA in males or between the STA of females and males. The aesthetascs are clothed by an exceedingly thin cuticle, which is 20–50 nm in thickness (Figs. 2C, 3B). Distally the thin aesthetasc cuticle is a continuation of the epicuticle of the remaining appendage, while the underlying procuticle ends abruptly in the proximal part of the setae (Fig. 3A). Externally, the aesthetascs have a smooth surface, but both the STA and LA have a conspicuous depression near the tip (Fig. 1D). This structure could not be identified with TEM, whence we assume that it is a purely cuticular feature and not a functional pore in the intermoult cyprid; it could be a moulting pore. At their basal part, the aesthetascs are reinforced by a socket of much thicker (ca. 0.5 μm) cuticle (Figs. 2C, 3A), and even the pliable arthrodial cuticle connecting the socket with the segment proper is

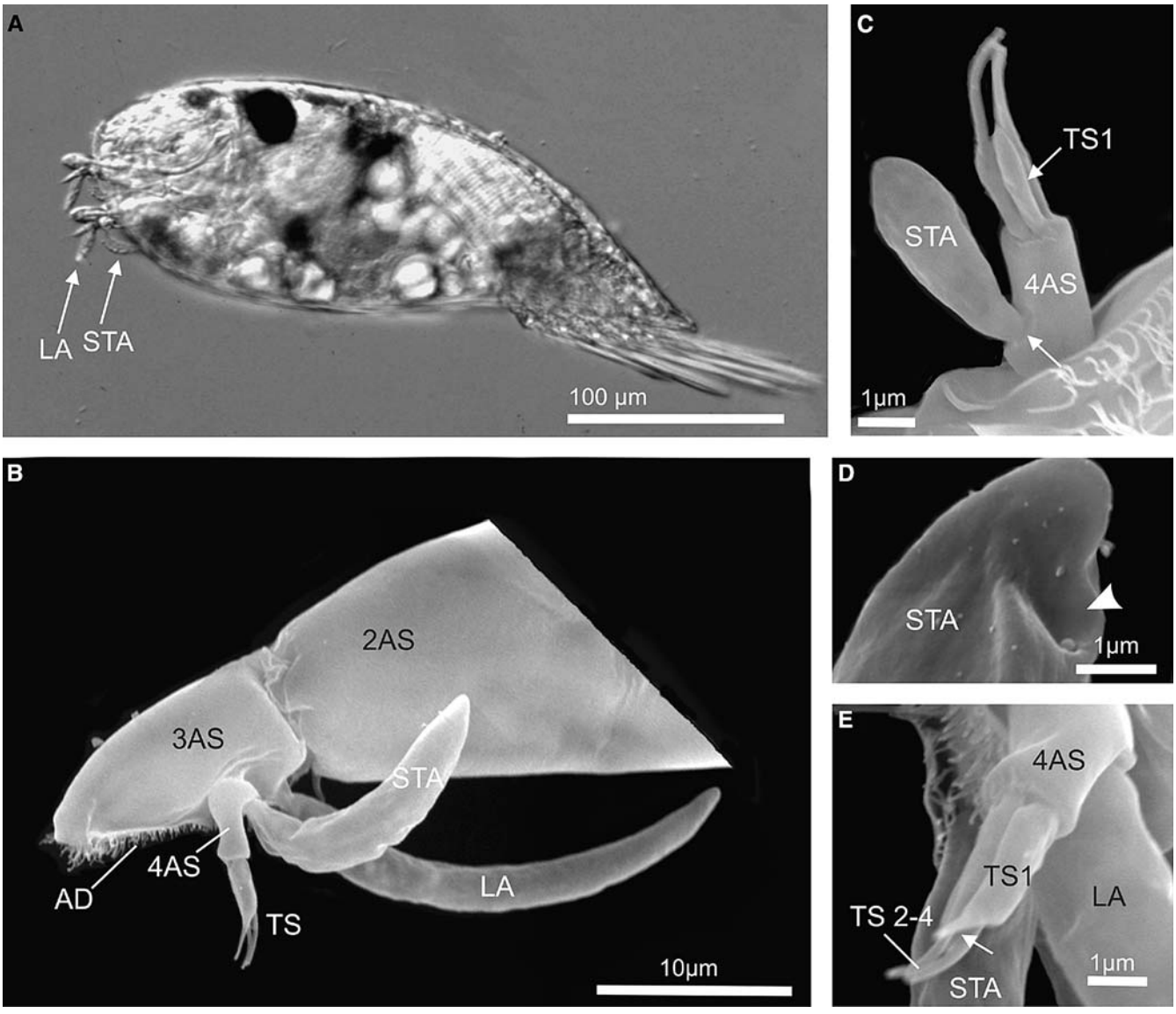


Fig. 1A–E *Sacculina carcini*. **A** Light microscopy photograph of a male cyprid of the parasitic barnacle *S. carcini* (Cirripedia: Rhizocephala), showing the arrangement of the aesthetascs (LA, STA) on antennules. **B–E** External morphology of the aesthetascs (SEM). **B** Male: second, third and fourth antennular segments (*2AS–4AS*). The large aesthetasc (*LA*) on the third segment is unique to males. The smaller aesthetasc sited sub-terminally (*STA*) on the fourth segment occurs in both males and females, but is relatively larger in males. **C** Female. The STA does not extend beyond the terminal setae (*TS*). **D** The pore-like depression (*arrowhead*) near the tip of the STA. **E** Male. One of the TS (*TS1*), with the swollen base terminating in a short, narrow part (*arrow*) (*AD* attachment disc)

several times thicker than in the distal part of the aesthetasc.

The interior of the aesthetasc contains only two elements: numerous tubular ciliary branches and a variable number of electron-dense bodies. The unsheathed ciliary branches enter the putative aesthetasc as a bundle through the narrow opening in the socket, and within the aesthetasc they occupy the central parts and extend immediately beneath the epicuticle all the way to the apex (Fig. 2C). The different-sized, electron-dense bodies also vary considerably in number. They are not an artefact, since we have also repeatedly seen them as small refracting bodies in light microscopic preparations of live cyprids. Except for a few specimens (Fig. 3D), neither these bodies nor the ciliary branches are very tightly packed, and the major part of the interior of the aesthetasc is a haemocoelic space (Fig. 2C).

Morphology of the terminal setae

None of the four terminal setae on the fourth segment has an internal structure resembling that described for the LA or the STA. All of them, including the two possessing a wide, sac-shaped basal part, possess a much thicker cuticle (100–200 nm), incorporating a procuticle layer, although still thin compared to cuticle thickness elsewhere in the antennule (Fig. 3E, F). One of the

sac-shaped setae seems to contain several sheath cells, and none of them contains a system of thin ciliary branches. Generally, they are more packed with cellular elements than are the aesthetascs.

Innervation of the putative aesthetascs

Only the outer dendritic segments of the sensory cells enter the LA and the STA, and here they are already extensively and perhaps even fully branched. Additional branching does occur within the aesthetascs, but it is only very rarely seen on the sections (Fig. 3C, inset). We have followed the ciliary branches from the STA and LA into the fourth and third antennular segments. These segments contain no other inner dendritic segments than those from sensory cells that clearly connect with non-aesthetasc setae. The distal part of the second antennular segment is filled with sensory cells innervating setae on the third and fourth segments and glands exiting on the attachment disc (see also Høeg 1987b; Moyse et al. 1995). Distally, in the second segment, we found ciliary branches that in size and morphology correspond to those entering the aesthetascs, but, due to the semiserial nature of our material, we were unable to follow them unambiguously, and so their cell bodies were not found. One such very conspicuous bundle of branches, 4–6 μm across and wrapped in a single sheath cell, is seen in a cross-section of a male cyprid, distally in the second antennular segment, below the large unicellular gland unique to male cyprids (Fig. 2D, E). Future studies must decide if these connect with one of the aesthetascs and how many cells and cilia serve each of them. The number of cells and cilia cannot be large, due to the space restrictions in the second antennular segment, and could well be only one cell per aesthetasc-like seta. No scolopale was seen in connection with these sensory cells.

Discussion

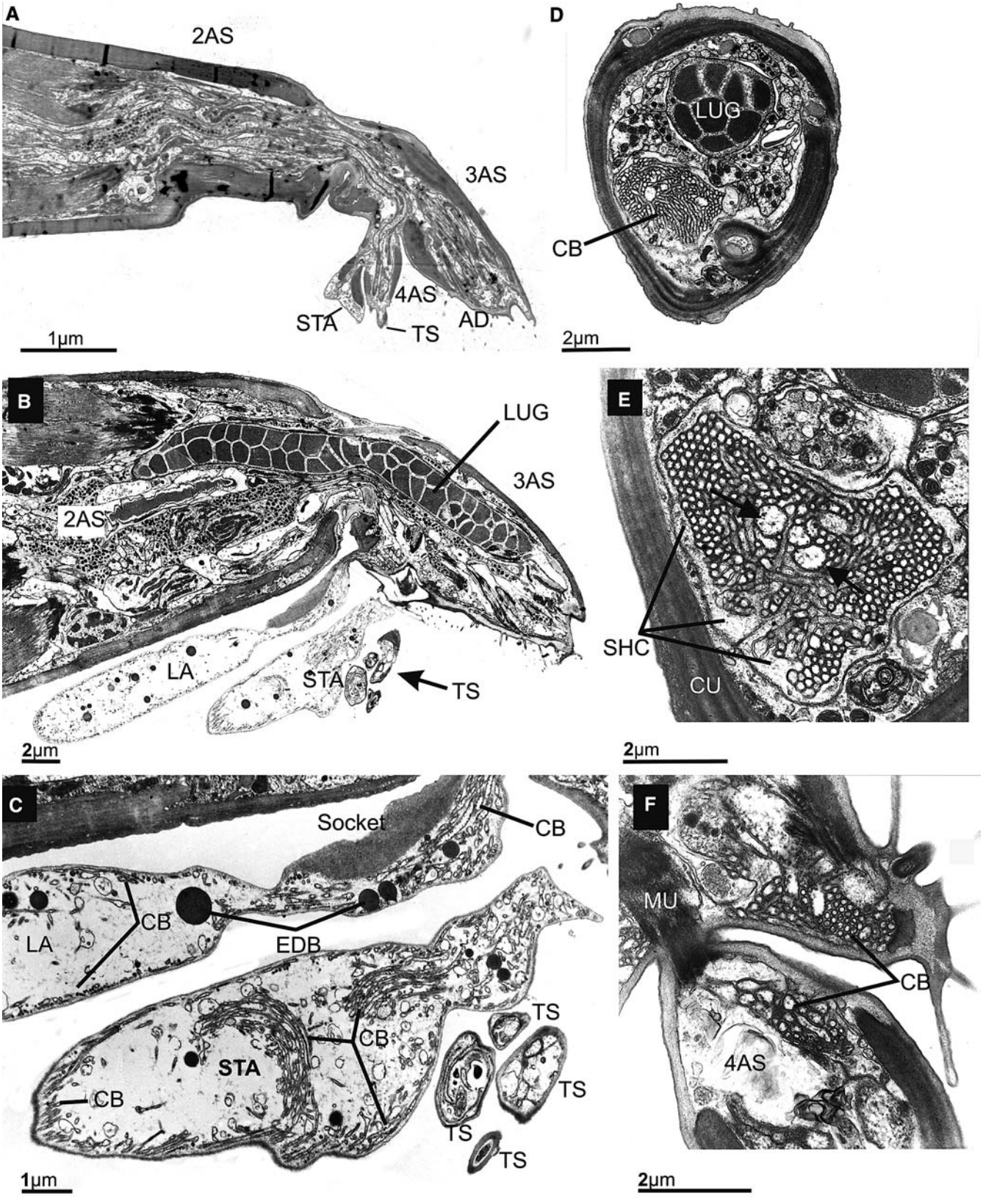
The present study of *Sacculina carcini* allows, for the first time for any barnacle species, an analysis of the ultrastructure of aesthetascs in cypris larvae. The large aesthetasc (LA) found in males only and the smaller aesthetasc (STA) situated sub-terminally on the fourth segment in both sexes conform to the aesthetasc concept. They possess an exceedingly thin cuticle, contain numerous ciliary branches representing highly branched outer dendritic segments, and they display neither sheath cells nor are they associated with a scolopale. The multiplication of ciliary branches presumably leads to an enlargement in the number of chemical receptor sites and, thus, to an increase in sensitivity (Heimann 1984). This is especially true when a large number of these branches are situated just on the inner side of the cuticle of the sac-shaped aesthetasc, as found in this study. Chemosensors other than aesthetascs have at times a cuticular pore, where the cilia gain direct contact with the exterior (Hipeau-Jacquotte 1986; Elofsson and Hessler 1994; Garm et al. 2003). Aesthetascs normally lack such a pore, and the chemical signal instead diffuses across the exceedingly thin cuticle which is of a porous nature (Derby et al. 1997). The cuticle in aesthetascs of cyprids of *S. carcini*, being < 50 nm across, must rank among the thinnest yet seen in any crustacean seta. All these data indicate that the STA and LA are indeed true olfactory aesthetascs, as suggested by Glenner et al. (1989), and, since cyprids do not feed and therefore do not need to detect food, it strongly suggests that these setae are used in substratum detection.

Most rhizocephalan cyprids carry four terminal setae on their fourth antennular segment. In females, one of these setae is sometimes bulbous and resembles an aesthetasc (Fig. 1C). This external similarity has caused some researchers to refer to it as the "terminal aesthetasc" (TA) (e.g. Glenner et al. 1989), but our TEM data reveal that this is not a true aesthetasc. The "TA" does not display numerous ciliary branches, and its cuticle is much thicker than that of the LA and STA. Other differences are the presence of sheath cells in the lumen of the "TA" and the electron-dense bodies in the STA and LA, which are not found in the "TA"; the composition and function of these structures is as yet unclear. This shows that the so-called TA is most probably not an aesthetasc at all. None of this changes the possibility that some or all of the terminal setae may have chemosensory properties.

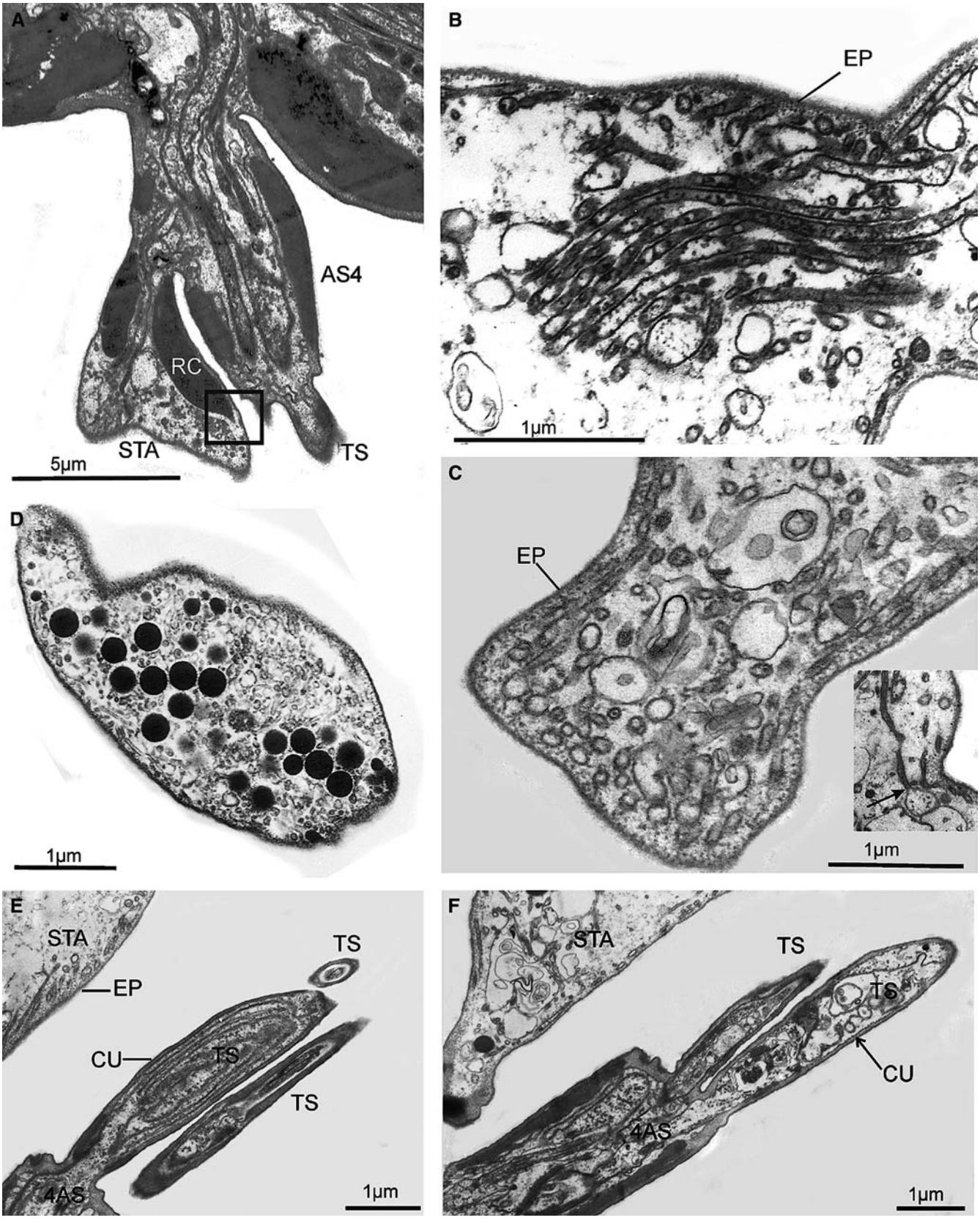
Sexual dimorphism and substratum selection

Rhizocephalan aesthetascs are confined to the cypris instar, the major function of which is to select a settlement target by reacting to chemical stimuli (Crisp 1985), so it is safe to assume that these chemoreceptors are used in substratum selection, as also discussed above. Female rhizocephalan cyprids must locate a suitable host species on which to settle and attempt infestation, leading to a

Fig. 2A–F *Sacculina carcini*. TEM of antennular aesthetascs. **A** Female; sagittal section through second, third and fourth antennular segments (*2AS–4AS*) showing the arrangement of the fourth antennular segment and the sub-terminal aesthetasc (*STA*). **B** Male: sagittal section through the antennule showing the large, male-specific aesthetasc (*LA*), the sub-terminal aesthetasc and the terminal setae (*TS*, in near cross-section). The large unicellular gland (*LUG*) is unique to male cyprids (see Høeg 1987a). **C** Male. Detail from specimen in panel B, showing the interior of the aesthetasc with ciliary branches (*CB*) and electron-dense bodies (*EDB*). Note that all the terminal setae have cuticle (*CU*) thicker than in the two aesthetascs. **D** Male. Cross-section of second antennular segment near articulation to the third segment showing the bundle of tightly packed ciliary branches that more distally enters the large aesthetasc. **E** Male. Detail from male specimen in panel C. Bundle of ciliary branches wrapped in a sheath cell (*SHC*). **F** Insertion of fourth antennular segment on the third and muscle (*MU*) operating the fourth segment. Cross-section of bundles of ciliary branches in both segments 3 and 4 (*AD* attachment disc)



new parasite (Fig. 4). Thus, in principle, every individual of the proper host species is a prospective substratum, although females do exhibit strong preferences in terms of host moulting cycle stage, preferring early postmoult animals (Glenner and Werner 1998). In contrast, male cyprids have an apparently much more daunting task. Not only must they locate a crab of the right species, but one that already hosts an external, female parasite in the



virgin state (Fig. 4; see Høeg 1984). This sex-specific difference in substratum location and specificity probably accounts for the cyprids' dissimilar chemosensory armament. The fourth segmental aesthetasc, common to cyprids of both sexes, could possibly be stimulated by the host animal itself, which is the settlement target in

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Fig. 3A–F *Sacculina carcini*. TEM of antennular aesthetascs. **A** Female. Detail from specimen in Fig. 2A, showing the origin of the sub-terminal aesthetasc (*STA*) and one of the terminal setae (*TS*) on the fourth segment. Note the collar of reinforcing cuticle (*RC*) is close to the narrow connection between the aesthetasc and the fourth segment. *Framed area* indicates that the distal part of the aesthetasc cuticle represents only the epicuticle. **B** Detail from an aesthetasc, showing the thin epicuticle (*EP*) and the mostly longitudinally arranged ciliary branches. **C** Aesthetasc, showing the ciliary branches mostly in cross-section. *Inset* indicates branching cilia (*arrow*). **D** Region of an aesthetasc unusually tightly packed with electron-dense bodies. **E** Sagittal section of three terminal setae, all cuticles (*CU*) much thicker than in the sub-terminal aesthetasc. **F** Another section from same specimen as in panel E, showing that the second, swollen terminal seta also has a much thicker cuticle than an aesthetasc (*4AS* fourth antennular segment)

females and could be an initial attractant in males, although they never directly contact the crab, but only the female parasite (Høeg and Ritchie 1985; Glenner et al. 1989; Høeg 1991). The third segmental, male-specific aesthetasc may be specifically stimulated by metabolites released by the juvenile female parasite (Høeg 1991), thus possessing the ability to identify virgin externae (Clare et al. 1993). Indeed, male kentrogonid cyprids may be among the most superb "sniffers" in nature. Høeg (1987a) showed that they need but a few minutes to both locate a host with a virgin parasite and place themselves accurately at the mantle aperture of the externa. The lack of structural differences between the large and sub-terminal aesthetascs does not speak against this hypothesis, since it is well established that the specificity of chemosensory setae rests on the level of receptor proteins.

Aesthetascs in other cirripedes and other Thecostraca

Aesthetascs are found in cyprids of all species of the rhizocephalan sub-order Kentrogonida, which is by far the most species-rich. In other Cirripedia (orders Acro-

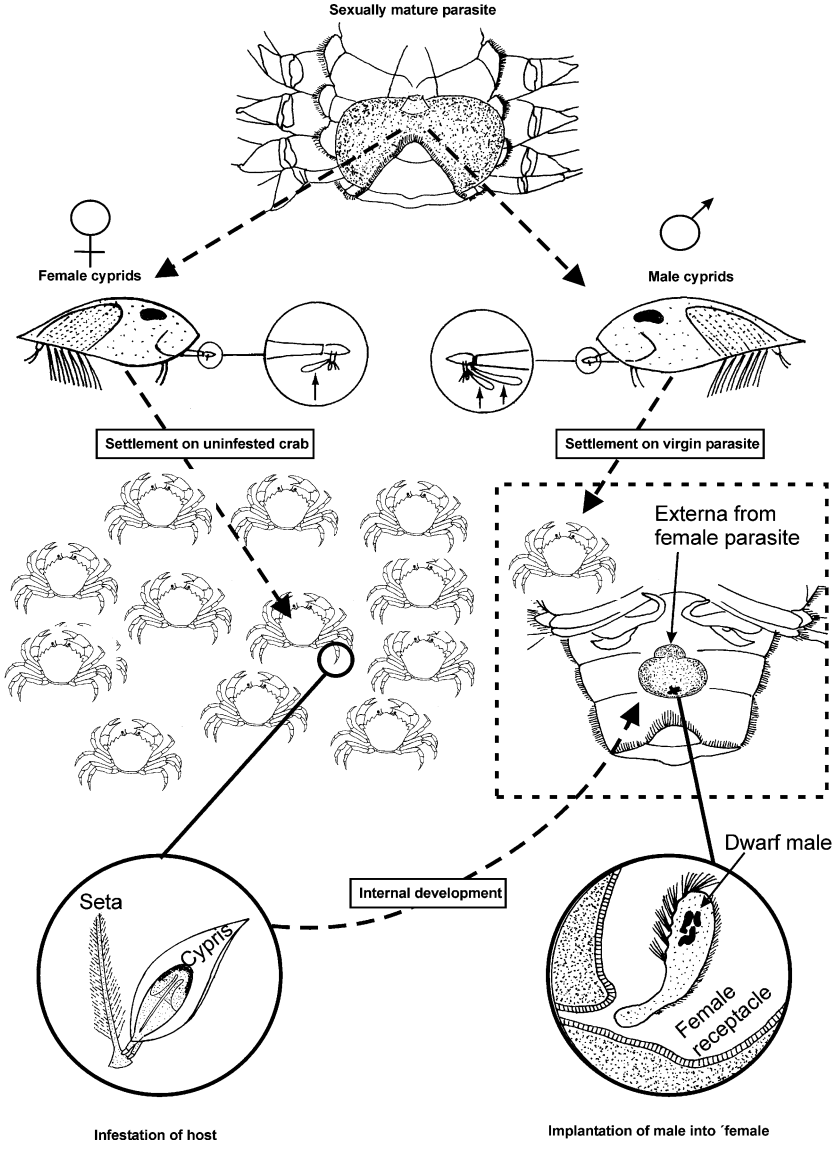

Fig. 4 *Sacculina carcini*. The rhizocephalan parasite *S. carcini* releases male and female larvae. In the terminal larval instar (the cyprid) males and females differ structurally and notably in the armament of antennular aesthetascs, males possessing two and females only one. Female larvae settle on crabs and can, in principle, infest any individual of the appropriate host species. In contrast, male larvae settle only on the tiny fraction of the crab population that carries an external parasite externa in the virgin state. They neither settle nor can they metamorphose on the host crab or on sexually maturing or fully mature parasites. The more extensive armament of chemosensory aesthetascs in males probably assists them in locating their rare target substratum. Settled female cyprids infest the host by means of a kentrogon stage, and after an internal phase they emerge as virgin externae. Settled males become implanted by means of a trichogon as dwarf males in the female parasite

thoracica and Thoracica), setae on the fourth antennular segment of cyprids have been suggested as being of the aesthetasc type, although the little existing TEM data do not support this, since all setae are associated with a scolopale (Gibson and Nott 1971; Lagersson et al. 2003). A sac-shaped seta situated terminally on the fourth segment seems to be the most obvious candidate (Blomsterberg et al. 2004), but the four sub-terminally sited setae in these cyprids have also been suggested as aesthetascs (Clare and Nott 1994).

The sub-class Cirripedia belongs to the monophylum Thecostraca, all of which have permanently sessile adults in the form of parasites or filter feeders. All thecostracans also possess a cypridoid larva, functioning as the settlement stage (Høeg et al. 2003), and they always attach by means of the antennules, which, at least in the many parasitic forms, seem to universally carry one or a few sac-shaped aesthetascs (Glenner et al. 1989; Grygier and Ito 1995; Kolbasov and Høeg 2003). The sister group of the Thecostraca is the Tantulocarida, a class of parasites in which all stages, including the settlement stage called the tantulus, have lost the antennules and, in fact, all cephalic appendages. Interestingly, a small group of aesthetascs is situated anterio-ventrally on the tantulus larva, marking the site of the otherwise totally lost antennules (Boxshall and Lincoln 1987). The presence of aesthetascs in the settling larval stages of these closely related taxa, all of which have sessile adults, testifies to the importance of these chemosensors for efficient location of substrata.

Comparison to aesthetascs from other crustacean taxa

The most studied aesthetascs are those from decapod crustaceans. Their typical arrangement and morphological features include hundreds of closely spaced, hose-like setae that are devoid of pores and possess a thin cuticle. Each seta is innervated by 100–500 sensory cells that possess two outer dendritic segments each (Hallberg et al. 1997). The rhizocephalan aesthetascs differ in having a smooth cuticular surface without regional differentiation (Guse 1983), in their sac-like shape, and in occurring in small, fixed numbers. In this they resemble the aesthetascs known from relatively closely related Crustacea such as ascothoracidans, facetotectans and copepods (Perez-Losada et al. 2002). They also resemble aesthetascs from the more distantly related mysids (Johansson et al. 1996). Contrary to expectation for an aesthetasc, we did not observe microtubules within the ciliary branches in our material, but we ascribe that to a deficiency in the fixation method also observable in other organs. Such microtubules are visible in our unpublished micrographs of differently fixed aesthetascs from the rhizocephalan species *Peltogaster paguri*.

The arrangement of multiple aesthetascs on the lateral antennular filament in decapods has been correlated with antennular flicking behaviour (Snow 1973; Gomez and Atema 1996; Goldman and Koehl 2001). This behaviour has been described in different groups of decapods and is considered to be important for the acquisition of stimuli; owing to the viscosity of water, boundary layers are formed around the setae and hamper the diffusion of stimulus molecules to the setae. Flicking movements of the antennules reduce the thickness of the boundary layer and enable a renewal of the water volume trapped by the aesthetascs (Schmidt and Ache 1979; Goldman and Koehl 2001). Still, flicking of the antennules has been observed for some cypris larvae (Glenner, unpublished results), but the functional significance of this behaviour is unknown.

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