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The structure of long distance (antennular) chemoreceptors in *Saduria entomon* (L.), Isopoda, and their role in feeding behaviour

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The morphology and fine structure of the antennular aesthetasc hairs of *Saduria entomon* were studied and described using transmission and scanning electron microscopy. The external structure of the aesthetascs of *Saduria* resembles the chemoreceptor structures of other aquatic crustaceans. The internal fine structure differs markedly from other chemoreceptor structures described among crustaceans.

The role of these antennular receptors in feeding behaviour was studied by behavioural tests in laboratory aquaria. After ablation of distal antennular segments accurate feeding orientation become random and sluggish. No recovery was observed after a four-week period.

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1. Introduction

Saduria entomon (L.) (Isopoda, Crustacea) is one of the most important bottom dwelling species of the Baltic Sea ecosystem. It is an important food source for many fish species, especially cod, *Gadus morrhua*, and flatfishes (*Pleuronectes platessa, P. flesus*) (Haahtela 1962, 1975). As an omnivorous scavenger, *Saduria* is an important cleaner in the benthic ecosystem. According to laboratory observations, *Saduria* is able to detect and capture *Daphnia*- and *Asellus*-species buried in the sediment, and it seems to be able to sense accurately both living and non-living organisms (Green 1957). This behaviour is most likely based on sensitive chemoreceptors. These presumed chemoreceptors in *Saduria entomon* are situated on the outer edge of the first antennae (antennules).

The antennular chemoreceptor structures of crustaceans were first described in 1860 by Leydig, who described them in *Asellus aquaticus* and *Astacus astacus*. Bell (1906) studied the sensitivity of different crustacean appendages to chemical substances and observed the sensitivity of antennae, mouthparts and chelipeds. Leydig's theory of the chemoreceptive ability of the antennule structures was first verified by Holmes and Homuth (1906) by ablating the antennules of *Carcinus maenas*. They observed that after antennule ablation *Carcinus* was capable of detecting bait only from a short distance.

Many other parts of crustaceans also possess chemoreceptive abilities: the walking legs (Shelton & Laverack 1970, Derby & Atema 1982), branchial chamber (Zimmer 1979) and the body surface in general (Hindley 1975). According to the behavioural experiments, these serve different functions in feeding behaviour (Eder & Atema 1978, Derby & Atema 1982).

The ultrastructure of the antennular chemoreceptors (aesthetascs) has been most fully described among *Decapod* crustaceans. In particular the structure of the aesthetascs of different lobster species has been thoroughly described by Laverack (1964) and Shelton & Laverack (1970). A few papers have been published about the aesthetasc structures of species in the order *Isopoda*. Nielsen & Strömberg (1973) described the internal and external fine structure of the aesthetascs of different *Cryptoniscina*-species, and Risler (1977) the terrestrial Isopod *Porcellio scaber*

and the antennular sense organs of *Idotea baltica* (Guse 1983).

In the study of chemoreceptor function most attention has been given to the order *Decapoda*, most likely because of its economical importance. Besides different lobster species (McLeese 1970, 1973, 1975; Devine & Atema 1982, Ache 1972, Fuzessery 1978, Shepheard 1974), *Carcinus maenas*, the common crustacean species of the coastal waters of Europe, has frequently been the subject of chemoreception studies (Case & Gwilliam 1961, Shelton & Mackie 1971, Fontaine et al. 1982). The most studied field is the role of chemoreception in feeding behaviour. The attractiviness of different chemical components in the food has also been rather intensively studied (Fuzessery & Childress 1975). These studies have been either a behavioural study in the aquarium (Ameyaw-Akumfi 1977) or a study performed in a special test maze, where the substance being studied is introduced in a water flow to form a concentration gradient (Shelton & Mackie 1971). Electrophysiological methodology is also used in experiments the aim of which is to try to discover more information concerning the function of aesthetasc structures (Ache et al. 1976, Fuzessery 1978, Hodgson 1958, Tazaki & Shigenaga 1974).

The object of this study was to describe the chemoreceptor structures situated on the first antennae of *Saduria entomon* from the point of view of both their surface structure and internal ultrastructure; and further to demonstrate their importance in feeding and orientation. The effect of unilateral antennule ablation was another aspect of interest. It was presumed that after a certain period following ablation the regeneration process would replace the missing antennules.

2. Materials and methods

The animals used in this study were collected with a bottom trawl from the sea (salinity 6 ‰) near the Tvärminne zoological station at a depth of 35 metres. The animals were kept in 100 litre glass aquaria provided with continuously flowing brackish water at 10°C. The animals were kept in an aquarium for at least one week prior to the experiments. Individuals which had been stored for longer than one month were not used. The specimens were fed twice a week with frozen and melted fish meat.

For scanning and transmission electron microscopical study the antennules were amputated and fixed in glutaraldehyde - phosphate buffer solution. Before fixation the animals were allowed to swim in water containing tensid in order to clean the antennules of bacteria and other epiphytes. The ultrasonic method was also used for cleaning. However, it was impossible to remove the epiphytic material entirely by these means without damaging the chemoreceptor structures themselves. The material intended for the scanning electron microscope (SEM) was then dehydrated in an ethanol series, followed by air-drying at room temperature. The antennules were glued to a copper chuck and sputtercoated with gold/palladium. A JEOL ISM 35-C scanning electron was used.

Whole antennulae were fixed for transmission electron microscopical (TEM) study in 3% glutaraldehyde-phosphate buffer (pH 7.2) solution. They were rinsed in the phosphate buffer solution and post-fixed in osmium tetroxide (1.5 % OsO_4). Material was rinsed and dehydrated in an ethanol series and then embedded in Epoxy resin. Sections were cut with a Porter-Blum MT-1 ultramicrotome and stained in uranylacetate and leadcitrate. The sections were examined and photographed using a Zeiss electron microscope (100 kv).

Dye penetration experiments were used to gain information about the function and permeability of these antennular structures. Vital dye (Methyl blue) was added around the detached antennule kept in brackish water and dye penetration in the aesthetascs was followed under a light microscope.

Before the behavioural experiments the distal two segments of the antennules were ablated (bi- and unilaterally). The animals were tested after a one-week recovery period and the results were compared with those from the intact animals. Both groups were starved for three days before the tests, and kept in continuously flowing brackish water in order to clean the antennules from possible impurities.

Animals used in the experiments were 3-4 cm in size. To avoid possible pheromone effects between females and males only males were used. Animals in a moult stage were not utilised. Observations were made in 53 × 53 cm persplex aquaria at a water temperature of 10°C, using stagnant water of 20 cm depth. The behaviour of animals after being offered bait (a piece of frozen and melted cod) in the aquarium was recorded by photographing the situation after 0.5, 1, 2, 5 and 10 minutes. Tests were performed under normal artificial illumination.

3. Results

3.1. The location and number of aesthetascs

The aesthetasc hairs and their accessory hairs in *Saduria* are located in tufts on the outer edge of the distal segment of the antennule (Fig. 1A). Their location and structure is shown diagrammatically in Fig. 2. They were first discovered and described by Kovalevskij (1864), who called them Leydig's tubules and assumed them to function in *Saduria entomon* as olfactory receptors. These receptors are grouped in pairs accompanied by three accessory hairs of unknown function (Fig. 1B). The length of the aesthetasc hairs varies between 150-300 μm, depending on

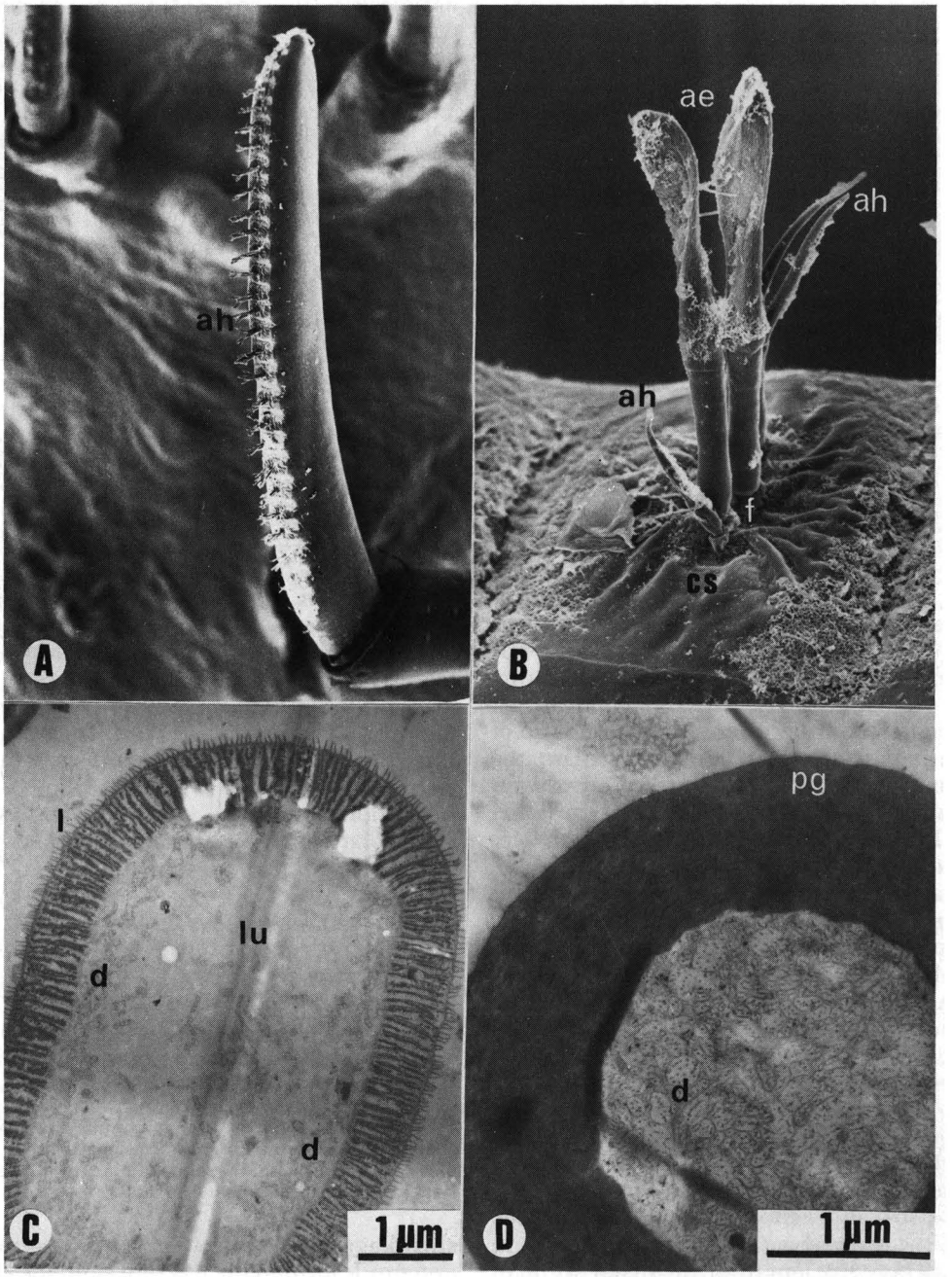

Fig. 1. — A. The first antennae (antennules) of *Saduria entomon*. On the outer edge of the most distal segment there are about 30 pairs of aesthetasc hairs (ah) accompanied by accessory hairs. 90×. Scanning electron microscope (SEM). — B. Two aesthetasc hairs (ae) accompanied by three accessory hairs (ah) (two long, one short). The cuticle forms a fossa (f) around the hairs. The distal part of the aesthetasc and the cuticular swellings (cs) have shrunken and collapsed during the drying of the preparation, but the proximal part has maintained its original structure. A dense microbe layer covers the surface of the distal part. 1400×. SEM. — C. Section through the distal part of the aesthetasc hair. Bare dendritic branches (d) are seen in the lumen (lu) of the hair. The wall is loose and striated in structure and carries cuticular ridges (l) of 0.2 µm on the outer surface. Transmission electron microscope. Bar 1 µm. — D. Section through the proximal part of the aesthetasc hair. Dendrites (d) are tightly packed in the lumen of the hair. The wall is thick, layered, and contains pigment granules (pg). TEM. Bar 1 µm.

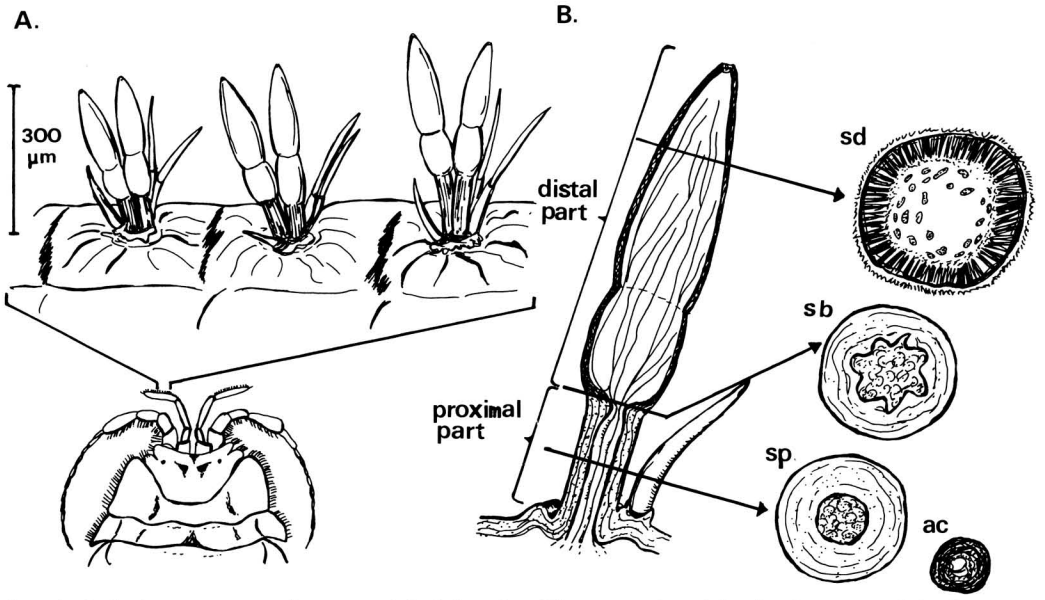

Fig. 2. — A. *Saduria entomon*, aesthetascs and their location. The outer edge of the distal segment of the first antennae (antennula). — B. The inner structure of the aesthetasc and accessory hair. Sections from different levels drawn and represented schematically, as seen under the transmission electron microscope. — sd = section from distal part of the aesthetasc, sb = section from the junction of distal and proximal parts, sp = section from the proximal part, ac = section from the accessory hair.

their location on the antennule and the size of the animal itself. The hairs located on the proximal part of the first segment are always somewhat smaller than the hairs on the distal part. The soft distal part of the aesthetasc makes up two-thirds of the total length of the organ and the hard proximal part the remaining one-third. In a *Saduria entomon* female 4 cm in length the length of the aesthetasc is normally 230 µm, while in a male of equivalent size it is 262 µm. The difference is statistically significant. There is no difference in the number of aesthetascs on males and females of equivalent size.

The number of aesthetasc hairs varies between one pair in 2 mm long *Saduria* taken from the marsupium and 30 pairs in a 7 cm long male. The increase in number of aesthetascs in conjunction with increases in the size of the animal as a whole can be seen in Fig. 3, where the length of the distal segment and the aesthetasc number is plotted against the length of the animal.

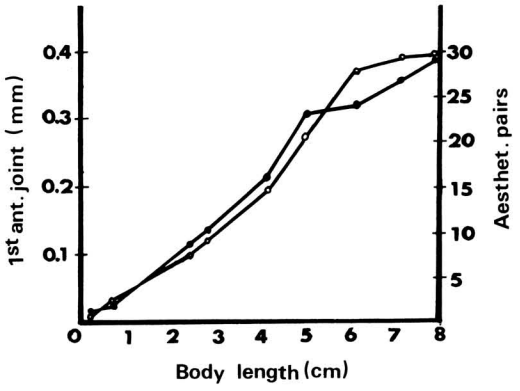

Fig. 3. The length of the first antennular segment (solid circles) and the number of aesthetasc pairs (open circles) plotted against the body length of a *Saduria* individual. Data measured from nine individuals.

3.2. General appearance of aesthetasc

After removal of the antennulae from the aquatic environment there is an obvious shrinkage of both the cuticula of the antennule around the receptors and the chemoreceptors themselves, as can be seen in Fig. 1B. This may be due to the diminishing of the internal hemolymphic pressure after detachment of the antennule. It appears that hemolymphic pressure together with the supporting external medium confer the rigidity necessary to maintain the diffuse and soft chemoreceptor structures. The aesthetasc hair

seems to be divided into two parts differing in their general appearance. The proximal part (about one-third of the total length) has a smooth external appearance. In contrast to the distal part and the cuticular fossa around the aesthetasc, this does not shrink during the drying of the preparation. It is cylindrical in form and has a practically constant diameter along its entire length. The distal two-thirds of the aesthetasc are longitudinally striated on the outer surface. This portion is also cylindrical in form, is thickest near the middle and becomes narrower towards the apex of the hair. Due to the heavy microbial growth on the aesthetasc surface it is not possible to see the ultrastructure of the apex of the hair. Under the light microscope a crease can be seen in the middle of the distal part of the aesthetasc.

Both light and scanning electron microscopical observations revealed a heavy microbe layer growing on the distal part of the aesthetasc. On the apex of the hair there are some filamentous non-chlorophyllous microbes growing in tufts (Fig. 4). Most likely these are filamentous bacteria or fungal hyphae. This microbial contamination is of about the same intensity through the year and is present on the other surfaces of *Saduria* as well. Keeping stocks of animals in aquaria appears to increase contamination, but microbial epiphytes are obviously a part of the normal flora in the natural conditions obtaining on the bottom.

The accessory hairs are narrow and smooth, with a node in the middle part of the hair. They are obviously rigid in structure, because they do not shrink in air. The distal segment of the antennule is rigid except on the cuticular swellings, on which hair tufts are situated. The cuticula forms a fossa around the base of the hair tuft, which is made up of aesthetasc and accessory hairs.

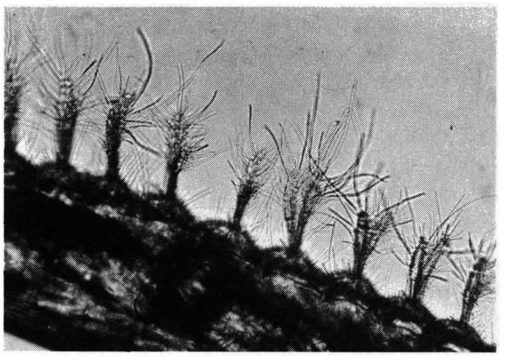

Fig. 4. Aesthetascs of *Saduria entomon* photographed under the light microscope. On the apex of the hairs a tuft of filamentous bacteria or fungal hyphae is growing. 600×.

3.3. Internal structure of the aesthetasc

The cuticular wall of the proximal part is thick (0.8–1 μm) and contains small pigment granules. The diameter of the proximal part is 3–4 μm. The wall is formed of layers and there are no pores through it. The lumen consists of tightly packed bare dendritic branches.

The wall of the distal part is loose and striated in appearance (Fig. 1C). Its diameter varies between 7–10 μm and its thickness is about 1 μm. The wall is formed of two layers: an outer layer with cuticular ridges, which increase the surface area of the chemoreceptors, and an inner layer formed by the cuticular projections with narrow passages between them.

In the lumen bare dendritic branches are located among an opaque, non-cellular medium. Close to the wall there is a narrow layer of granules. The thick wall of the proximal part is creased at the junction of the distal and proximal parts. At this place the wall is thick and the lumen very narrow, with tightly packed dendritic branches (Fig. 1D). The accessory hairs appear very simple in internal structure. The wall is thick and a hollow central cavity is striated by supporting filaments.

The permeability of the hair wall was studied using the in vitro dye as a permeating substance. Permeation of the dye was observed under the light microscope. It was observed how the very tip of the distal part became stained first. Then the colour slowly (taking about 1–2 minutes) moved down towards the proximal part. Finally, the dye became concentrated in the upper part of the proximal hair region, where it formed a narrow, diffuse belt. The wall appears to be more permeable at the apex or else there exists a pore through which the permeating substance rapidly passes into the lumen of the hair. Tightly packed dendrites in the proximal part obviously prevent the dye from penetrating further into the antennule itself.

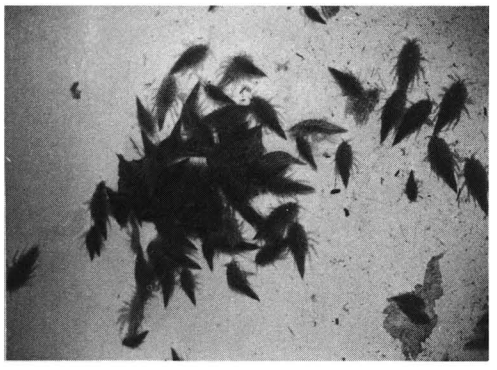

Fig. 5. Feeding behaviour of *Saduria entomon* in aquarium. Within two minutes after offering the bait it is totally covered by grasping Isopods.

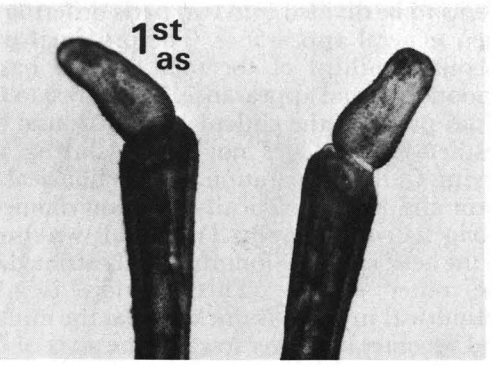

Fig. 6. The two distal segments of *Saduria entomon* after a 3-month regeneration period. The first segment has reached one-third of its original length. No aesthetasc structures can be seen. 100×. — 1st as = first antennular segment.

3.4. The role of antennules in feeding behaviour

The feeding behaviour of *Saduria entomon* is a rapid and violent action. During the activity period, if *Saduria* is not burrowed in the sediment, the animal moves randomly on the bottom or swims by flicking movements of the pleopods in a photoventral position (rheotactic movement). When the animal senses a food source, its movements become more rapid and oriented towards the source of stimulation. Movement towards the bait is not straightforward, rather it follows a zigzag course which finally leads to the food source. On reaching the bait, *Saduria* violently attacks it, accompanied by a rapid jerking of the cephalon. This reaction can be directed at another *Saduria* individual or a piece of cotton wool dipped in the fish extract. When a piece of fish is placed in an aquarium, within two minutes the bait is completely covered by swarming and feeding Isopoda (Fig. 5). During orientation the combing of the antennules by the gnathopods is sometimes observed.

When 1-2 distal segments of the antennules are ablated, the orientation is less intensive and more random and sluggish. Some animals are totally unable to locate the bait. A few individuals still manage to locate the bait by accident if they happen to walk over it, and they detect it by means of receptors on the mouthparts. If only one antennule is cut (unilateral ablation) the orientation behaviour is changed as dramatically as in the case of bilateral ablation. In observations made on animals ablated on the left or right side, it was noted that the animal passed the stimulus source mostly on the side of the remaining antennule. This kind of malfunction in tropotaxis was observed in about 80% of the animals ablated either on the left or on the right side.

Four weeks after antennule ablation feeding behaviour was tested again, but no recovery was observed. After three months the distal segment has partly regenerated (Fig. 6). Presumably the animal has by then gone through one moult cyclus. At this stage the antennule has attained about one-third of its final length, but no sensory hairs were seen on the outer edge of the distal segment.

Animals caught from the sea often bear antennules of unequal length. This is obviously a result of losing, and subsequent regeneration of, some segments of the antennule. It is quite usual for animals kept in aquaria to lose parts of their antennae or other appendages, mostly due to attack by other individuals in the abnormally dense population.

4. Discussion

4.1. Structure of the chemoreceptors

The chemoreceptor structures of terrestrial and aquatic crustaceans differ from each other in terms of both external morphology and wall structure (Chiradella et al. 1968). The aesthetascs of terrestrial crustaceans are well-defined, short, and possess a thick wall. This results from the need for a rigid supporting wall and the necessity of preventing the loss of

water from the receptor lumen. The aesthetasc hairs of *Saduria* resemble those of other aquatic crustaceans in being thin-walled, narrow and slender in form. The outer cuticular wall is thin and not able to give the necessary rigidity to maintain normal structure of the receptor hair.

The length of the crustacean aesthetascs varies between 100 and 2000 μm. The number varies from one pair to 1500 in some deep sea crustaceans (Barber 1960). The highest number of aesthetascs observed in *Saduria* is 36–38 pairs in both antennules.

In species (*Cryptoniscina*-species, *Porcellio scaber* and *Idotea baltica*) from the order Isopoda which have been studied the aesthetascs are long, cylindrical structures having approximately the same diameter both distally and proximally (Nielsen & Strömberg 1973, Risler 1977 and Guse 1983). The importance of the terminal pore in aesthetasc function is sometimes discussed, but there is no clear evidence if the terminal pore exists in the aesthetascs of Isopoda-species. Among the *Cryptoniscina*-species the aesthetasc hairs terminate in a rounded tip or terminal knob (Nielsen & Strömberg 1973). A general idea is that before a molecule can be sensed, it must come into contact with the dendrites in the lumen of the aesthetascs. There are two ways in which this situation may come about: the substance can either penetrate through the aesthetasc wall, or enter via the presumed terminal pore. In the dye penetration experiments either the dye was entering through the presumed terminal pore, or the apex of the hair was more permeable to the dye than other parts of the hair. It is also possible that the detected molecule does not penetrate into the lumen of the receptor at all, but causes a release of a transmitter substance from the epitel which has an effect on the dendrites themselves.

The inner structure of the aesthetasc shows a lengthwise striated loose structure of the distal wall of the aesthetasc. This might give some toughness or protect the hair against violent stretching or bending. The wall is covered with 0.2 μm ledges, which increase the surface area of the aesthetasc, but whose exact function is unknown. Same kind of cuticular projections have also been perceived on the walls of *Idotea baltica* aesthetascs (Guse 1983).

The antennular chemoreceptor hairs are often somewhat larger in the male than in the female crustacean (Barber 1960). This has been observed, for example, among the orders Copepoda and Amphipoda. This difference in size is most likely not a sign of the differences in functional efficiency, but merely a form of sexual dimorphism. Male *Saduria* also have some aesthetascs which are larger than in female individuals.

Both fresh- and salt water crustaceans have been observed to bear an epiphytic growth on their antennular chemoreceptors. Shelton (1974) has observed a filamentous bluegreen alga growing on the antennules of *Crangon crangon*. He postulates that the reason for the concentrated growth on the antennules is the transport of nutrients from the mouthparts onto the antennular surface. When burrowed in sediment, the animal continues to keep its antennules above the surface of the sediment. The need for light is also satisfied in this way. No particular impairment of the normal functioning of the receptors due to the algae has been observed.

The antennules of *Crangon crangon* are even contaminated by filamentous bacteria (Shelton et al. 1975). The easily broken tips of the aesthetascs obviously offer a good growth medium for bacteria. Snow (1974) observed that about 70% of the aesthetascs of *Pagurus alaskensis* were broken at the tip and contaminated by fungal hyphae.

4.2. Function of the chemoreceptors

The chemoreceptors of crustaceans can be divided into two groups according to their function. The distance chemoreceptors are situated mainly on the antennae, either in the distal segment of the antennules, as is the case among the Isopoda; or in the outer ramus of the two segments of the antennule, as is the case in Decapod crustaceans. The contact chemoreceptors are situated on the mouthparts or on the first pair of walking legs. The sensitivity of these receptors has been observed to be markedly lower than that of antennular receptors (Shepheard 1974). The importance of antennular receptors in Decapods in feeding and in searching for food has been demonstrated in several studies (Holmes & Homuth 1910, Hodgson 1958 and McLeese 1973). Following ablation of the antennules, there is an appreciable lengthening of the time period needed to locate the food source, while

some species find it totally impossible to locate the bait.

In *Saduria* the ablation of antennules causes a definite inability to locate the bait over long distances. Some individuals are still able to locate the bait if they happen to come in contact with it during their rheotactic movement, which is activated by an alert reaction triggered by sensing the presence of food.

When the animals were ablated only unilaterally, a special disorientation was observed: the animals passed the bait mostly from the side with the intact antennule. It has been stated that the explanation for this phenomenon is the disturbance of normal tropotactic behaviour. In a normal situation *Saduria* is able to orientate towards the food source on the basis of information received by the bilateral chemoreceptors. The stimulus coming to the antennular pair is of unequal strength, and the animal tends to turn towards the stronger stimulus. When one antennule is missing, a supernormal stimulus reaches the remaining antennule and the animal turns disproportionately violently to the side of the untouched antennule. In the lobster unilateral ablation does not influence the entire feeding behaviour, but its effect is clearly seen in the animal's failing to follow odour trails of sharply curved form.

Devine & Atema (1979) have noted that unilateral ablation of the lateral antennules is corrected through the function of the receptors in the walking legs. If the walking leg receptors have been blocked, the lobster has a tendency to turn towards the side of the intact antennule. This kind of mechanism of partial overlap of antennules and walking leg receptors may help the animal in a situation where it has lost one of its appendages.

Constant exposure of the receptors soon leads to the adaptation of receptors and problems in orientation. Most decapod crustaceans periodically flick their antennules, which is assumed to retard adaptation in the antennular receptors. By means of electrophysiological experiments, Price & Ache (1977) have shown that this flicking decreases membrane resistance via compression of the receptor dendrites. Another possible explanation for this antennular movement is the function of circulating water over the surface of the antennule and receptors. Such flicking behaviour has not yet been observed in *Saduria*, but it is possible that the combing of the antennules with the walking legs might serve the same function.

In *Idotea baltica*, which possesses aesthetascs of a similar type to those of *Saduria entomon*, observations have been made of their function during the moulting stages (Guse 1983). During the early stages of moulting, in apolysis the dendritic branches in the aesthetasc lumen are exposed to the exuvial fluid.

Dendrites are gradually dissolved and during this period the aesthetasc hairs cease to function due to the fact that no contact exists between the receptor and the central nervous system. Compensating for the missing receptors following the loss of appendages can be either functional, or structural due to the good regeneration ability of crustaceans. Maynard & Dingle (1963) ablated segments of *Panulirus argus* antennules and then followed the regeneration process. After regeneration the antennules seemed to work both mechanically and chemically in quite a normal manner. There was only some disturbance to the flicking response, a fact which might indicate that all the nerves had not been completely regenerated. Within 3 months antennules of *Saduria entomon* have regrown to one-third of their original length, but possess no aesthetasc hairs. Presumably after a few moulting cycles the antennules will regenerate totally and will be accompanied by the receptor structures.

Functional compensation of the missing antennular receptors has been observed to occur through a lowering of the threshold value of dactylopodite receptors (Hazlett 1971). The increased sensitivity effectively compensates the role of the missing antennules. No phenomenon of this kind was observed in *Saduria*. Ablated animals were tested again after 4 weeks and they did not perform any better in feeding tests. It is not completely clear what kind of cellular mechanisms underlie this phenomenon, but most likely the latter is connected with central nervous system mechanisms and the summative effect of the afferent neuronal information there.

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