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Fine structure and molting of aesthetasc sense organs on the antennules of the isopod, *Asellus aquaticus* (Crustacea)*

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Summary. In *Asellus aquaticus* certain distal antennular segments bear single sensilla referred to as aesthetascs. These show a proximal stem and a distal bulbous region. Depending on its position, each aesthetasc is innervated by either 50–60 or 70–80 bipolar sensory cells, the perikarya of which are situated within the pedunculus. Within the antennular segment the dendrites develop unbranched cilia ($9\times2+0$ structure). The sensory cells are unusual in that mono- as well as biciliary dendrites are present within a single aesthetasc, the ratio of both types being correlated with the number of sensory cells. Cilia and receptor lymph cavity are enveloped by a set of 3–4 inner and 13–14 outer sheath cells, which terminate at the base of the sensillum, so that the delicate and poreless cuticle of the bulbous region encloses only outer segments within the receptor lymph fluid.

A new molting type in arthropods is described in which the outer sheath cells alone build the new cuticle, whereas the inner sheath cells most probably have a protective function.

A definition of aesthetascs is proposed based on fine-structural criteria. Functionally the sensilla are considered to be chemoreceptors. This assumption is confirmed by experiments with diluted vital dye as well as lanthanum showing that dissolved substances penetrate the poreless cuticle instantaneously.

Key words: Crustacean sensilla – Molting – Cuticle – Aesthetasc – Chemoreception

On the antennules of most crustaceans a distinct class of sensilla is detectable clearly differing from the setae commonly found in crustaceans. They typically show a zonation into a stem-like basal part and a bulbous distal region or they may also be developed as long, annulated, tube-like structures. These sensilla commonly are referred to as "aesthetascs" (cf. Table 1; Ache 1982), a term that lacks a clear definition and that is generally based on external features. Studies on insect sensilla show that a classification according to external features alone is insufficient, whereas fine structural criteria are indicative of the specific function (see review by Altner 1977; Altner and Prillinger 1980). However, only very few fine-structural investigations on sensilla, which are referred to as aesthetascs, exist at the present time (cf. Table 1). Comparing these results, it appears that either different sensilla have been united under this term or that aesthetascs have developed a multitude of variational characteristics. Thus, the question arises, do aesthetascs exist as a specific type and what are the morphological characters that may define these sensilla?

To study this question the fresh-water isopod *Asellus aquaticus*, as a representative of the highest evolved crustacean group, was chosen. This enables a comparison with the aesthetascs of older groups. To obtain information on the functional properties of the cells involved, it is of great interest to investigate additionally the molting process, which has previously not been studied in aesthetascs.

Materials and methods

Asellus aquaticus collected from local ponds were cultured in the laboratory.

Specimens for *scanning electron microscopy* were either fixed in 4% formaldehyde or 4% glutaraldehyde, postfixed in 2% OsO_4, critical-point dried (Technics CPA II), gold coated (Hummer II, Technics) and examined in a Cambridge Stereoscan S4-10. Slight shrinkage of the distal aesthetasc part could not be avoided due to the delicate nature of this region.

For *transmission electron microscopy* a variety of fixatives was tested. Best results were obtained by fixation in 4% glutaraldehyde, buffered in 0.1 M Sorensen phosphate buffer (pH 7.2) for 4 h at 4° C and postfixation in 2% OsO_4 in 0.1 M phosphate buffer for 2 h. The samples were embedded in Durcupan A/M, serially sectioned on a Reichert Ultracut, contrasted by standard methods, and examined with a Siemens Elmiskop 101. A fine electron-dense precipitate typically observed near to the cell membrane of the sheath cells is interpreted as a phosphate and/or osmium complex.

For *light microscopy* animals were fixed in 4% formaldehyde and examined with a Zeiss photomicroscope or with Nomarski interference-contrast optics (Zetopan, Fa. Reichert).

Vital staining was performed with 0.05% methylene blue diluted in filtered pond water or distilled water on isolated heads, on single antennules, as well as on whole living animals. Experiments were carried out at 4–6° C over a time of maximally 20 min.

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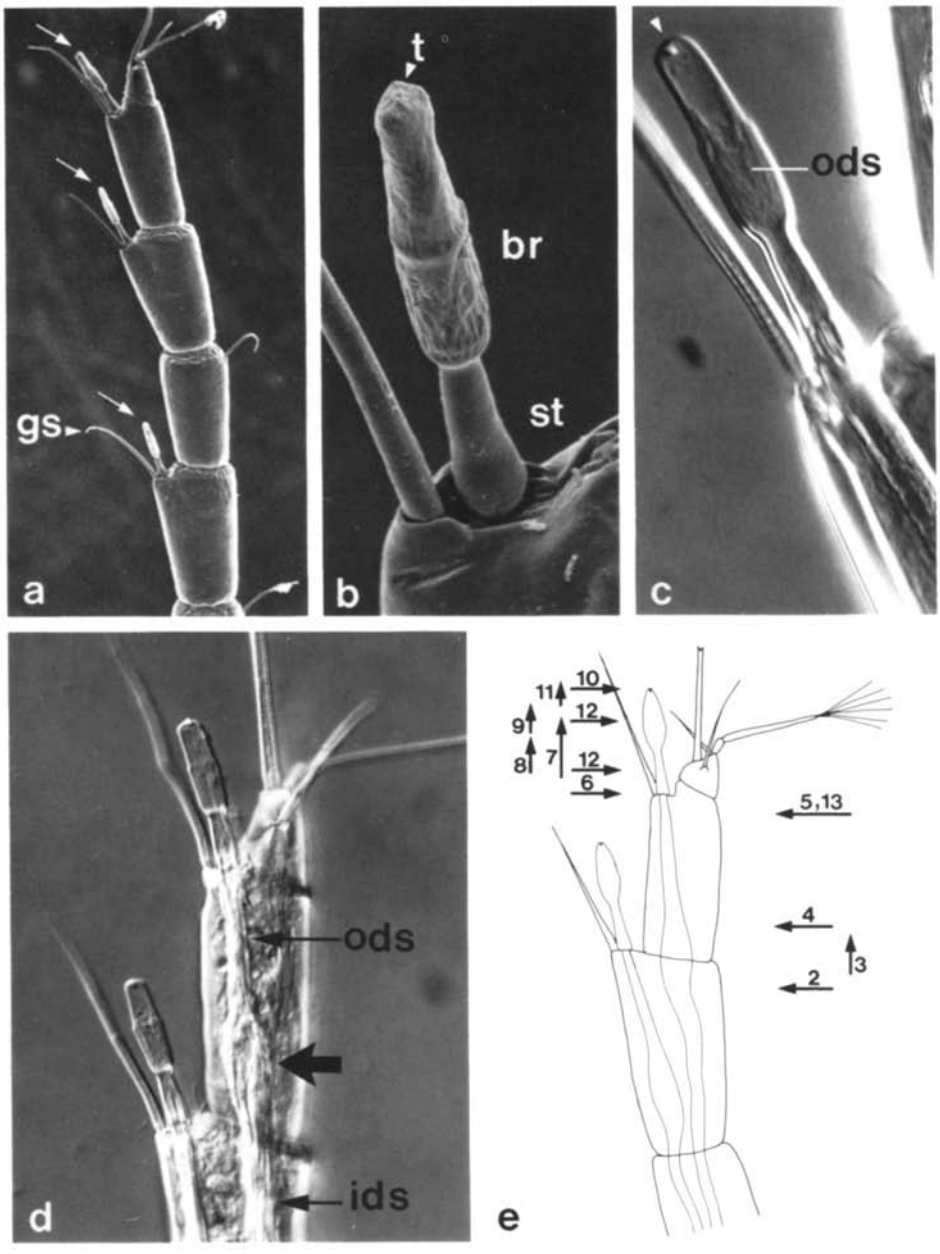

Fig. 1 a–e. Location and shape of aesthetascs of *Asellus*.
a Certain terminal antennular segments carry aesthetascs (*arrow*) singly; *gs* guard seta.
b An aesthetasc is divided into a proximal stem (*st*) and a distal bulbous region (*br*); *t* tip.
c At the tip (*arrowhead*) a central invagination is developed. Accumulation of outer dendritic segments (*ods*) in proximal half of bulbous region is artificial.
d Within the antennule the course of inner (*ids*) and outer (*ods*) dendritic segments is distinguishable. The spindle-shaped distention marks the transitional zone (*arrow*).
e Diagram with figure number indicating plane and position of section in reference to terminal aesthetasc. a ×180; b ×1600; c ×1100; d ×400

Experiments with lanthanum nitrate ($LaNO_3$) were performed on whole living animals, which were placed in filtered pond water (4–8° C) containing 1% $LaNO_3$. After 10 min animals were fixed according to the methods described above. Uncontrasted sections were examined at 40 and 60 kV.

Molting stages were determined according to Drach and Tschernigovtzeff (1967).

Results

General anatomy

The antennules of *Asellus* consist of four peduncular and a varying number of flagellar segments and are oriented slightly upward in a fronto-lateral position. The total length of the antennules (♀: 1.4 mm; ♂: 2.1 mm) as well as the number of segments (♀: 14; ♂: 19) is correlated with age and sex of the animal.

Aesthetascs are always found singly on certain distal antennular segments with the exception of the small terminal one (Fig. 1a). Total number and distribution of aesthetascs are variable and differ not only according to age and sex but also within the left and right flagellum. Adult females show 3–4, adult males 3–6 aesthetascs distributed usually on the penultimate and antepenultimate segment, followed by an alternation of aesthetasc-free and aesthetasc-bearing segments (Fig. 1a). The development of two or even three aesthetascs on one segment was observed on rare occasion.

The aesthetascs articulate with an indentation of the distal margin of an antennular segment, are directed medioventrally, and are flanked by a simple-pointed guard seta (Fig. 1a, d). Each aesthetasc shows a clear zonation into a basal stem and a distal bulbous region (Fig. 1b, e). The

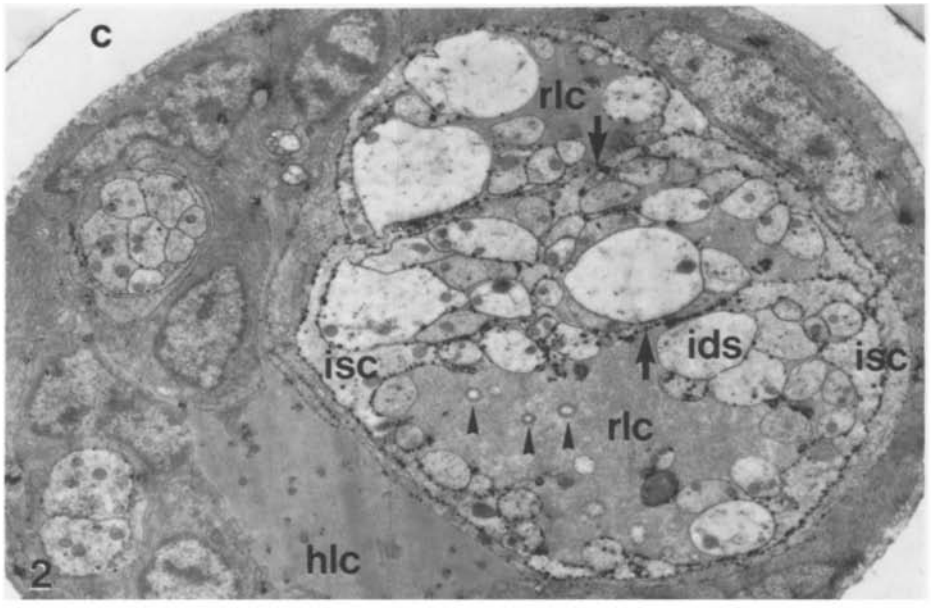

Fig. 2. Basal part of spindle-shaped distention in cross section. Inner dendritic segments (*ids*) are situated in a spacious receptor lymph cavity (*rlc*), which is delimited by the inner sheath cells (*isc*) and subdivided by processes thereof (*arrow*). Only few outer dendritic segments are present (*arrowhead*); *c* cuticle; *hlc* hemolymph cavity. ×9000

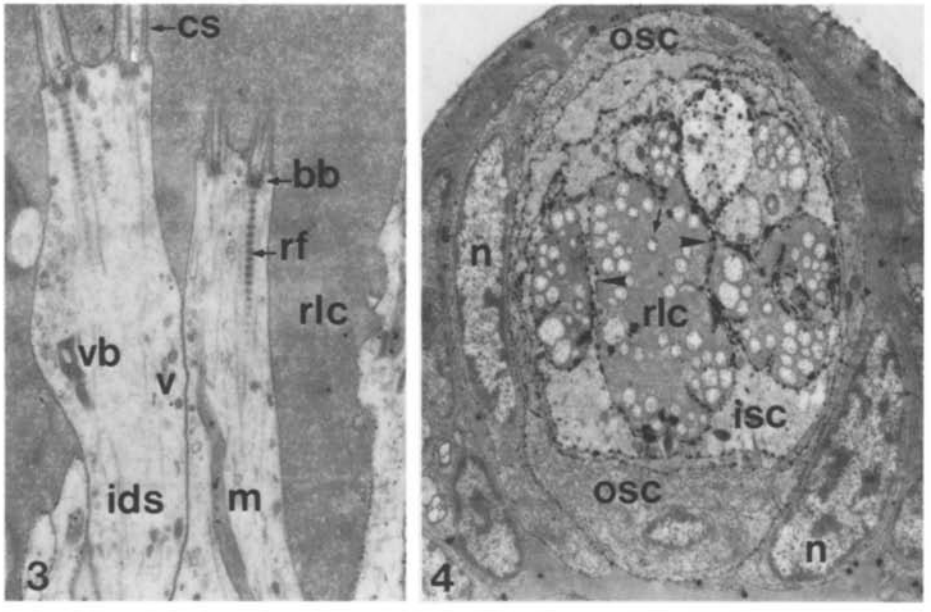

Fig. 3. Terminal part of inner dendritic segments (*ids*) in longitudinal section. Some sensory cells carry two outer segments showing a short rootlet fiber (*rf*). The extension of the receptor lymph cavity (*rlc*) far between the inner segments is uncommon. *bb* basal body; *cs* ciliary shaft; *v* vesicle; *vb* multivesicular body. ×18000

Fig. 4. Distal part of spindle-shaped space in cross section. Receptor lymph cavity (*rlc*) and outer dendritic segments (*arrow*) become subdivided into interconnected compartments or groups by processes (*arrowheads*) of inner sheath cells (*isc*). Here, the first outer sheath cells (*osc*) occur with the nucleus (*n*) situated in the basal region. ×7500

base is surrounded by a small socket, the ridge of which is particularly developed on the ventrally oriented side, leaving only a small cleft between socket and stem (Fig. 1b). The stem (diameter: proximally 6–9, distally 4–5 μm; length 16–22 μm) merges into the bulbous region, which extends over a length of 26–38 μm and has a maximum diameter of 6–10 μm. At the tip there is a central invagination with a depth of ca. 2 μm (Fig. 1c). No pores are visible in any part of the sensillum.

Internal anatomy

Each aesthetasc is innervated by a high and varying number of bipolar sensory cells. The terminal aesthetasc possesses 70–80, the others only 50–60 sensory cells. Their perikarya as well as those of other sensilla are situated up to 1500 μm further proximally in the third and second peduncular segment within a common antennal nerve. The antennal nerve runs freely within a spacious hemolymph cavity and is bound by a layer of thin glial cells, which send processes between cell bodies and fibers. The cell bodies (diameter 5–7 μm; length 10–15 μm) are oriented longitudinally. In addition to the normal set of organelles they contain irregularly shaped, lamellated lysosome-like bodies of extremely high density showing in part a cristalline substructure. Proximally the axons run into the deutocerebrum, distally the dendrites take their course up into the flagellum, displaying a slightly varying diameter (0.1–0.7 μm).

The dendrites separate from the antennal nerve approximately three segments proximal from the aesthetasc they innervate. From this point the dendritic bundle (diameter 2–4 μm) is completely enveloped by three (seldom four) cells, which are interdigitated and separate the dendrites from hypodermal cells and hemolymph. These cells, which occasionally send short processes between the dendrites, extend up into the basal part of the stem, thus covering a span of up to 200–260 μm. These inner sheath cells envelop not only outer but inner dendritic segments as well.

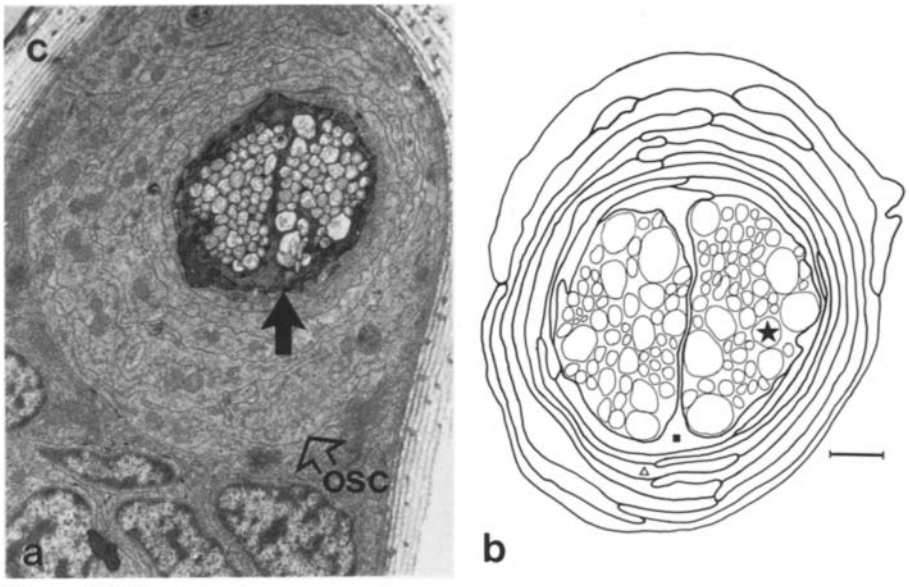

Fig. 5a, b. Outer dendritic segments and sheath cells in distal part of antennular segment.
a 13–14 interdigitated outer sheath cells (*osc*) envelop 3–4 inner sheath cells (*arrow*), which in this case divide 122 outer dendritic segments in two groups; *c* cuticle.
b Camera-lucida drawing indicating position of outer (△) and inner (■) sheath cells as well as outer segments (*); scale 1 μm. a ×6000; b ×7000

Distally, they become enclosed by a second set of enveloping cells. The inner sheath cells are characterized in their basal region by a most extensive granular endoplasmatic reticulum (GER), vesicles and a high number of Golgi complexes adjacent to spherical dense bodies. Approximately 30–60 μm further distally a distinct change in their structure takes place. The cells taper and nucleus, GER and Golgi complexes are no longer present. They display an electron-lucid cytoplasm containing relatively few organelles such as light-cored vesicles, microtubules, a few small mitochondria and single multivesicular bodies.

In light micrographs it is recognizable that within the proximal part of an aesthetasc-bearing segment, the chord of inner dendritic segments merges into a spindle-shaped space (longitudinal extension 36–50 μm, maximum diameter 12–16 μm) (Fig. 1d, e). Here, all dendrites are contained in the distended part of a large receptor lymph cavity delimited by the inner sheath cells. From this region on, the latter are enveloped by a second set of cells termed outer sheath cells (Figs. 2, 4, 14).

Dendrites. Within the basal part of the spindle-shaped space the first dendrites develop cilia. Further distally the remaining dendrites continuously develop cilia until only outer dendritic segments are present in the distal part of this compartment (Fig. 4). Thus, the cilia do not originate in the same plane but over a distance of approximately 30–45 μm. The dendrites of a single aesthetasc may develop either one or two cilia, the ratio of both types differing within the aesthetascs of a single antennule. Thus, 50–60% of the sensory cells in the terminal aesthetasc are monociliary, whereas these constitute only 7–10% in the more proximal aesthetascs. Therefore, all aesthetascs contain approximately the same number of outer dendritic segments (ca. 104–120) despite differing numbers of sensory cells.

Except for the different number of cilia no structural difference between the two types of sensory cells is detectable. Within its terminal part the inner dendritic segment is slightly reduced in diameter (0.4–0.8 μm). In the case of dendrites carrying two cilia, both basal bodies (ca. 0.16 × 0.16 μm) are situated in the same plane (Fig. 3) and connected to the dendritic membrane via transitional fibers. From each basal body a single rootlet extends up to 14 μm proximally (length usually 4–8 μm) and displays a weak banding (spacing approximately 60 nm) and a small diameter (60–120 nm). Branching of outer segments does not occur in *Asellus*.

From the distal end of the spindle-shaped space onward, only outer dendritic segments, usually containing 10–20 microtubules, ascend within the receptor lymph fluid into the aesthetasc (Figs. 4, 5a, 6). Only 4–6% of the cilia display a small diameter (0.08–0.16 μm) and contain less than five microtubules. It is assumed that these cilia represent those 3–4% of outer dendritic segments that terminate below the bulbous region.

Sheath cells and receptor lymph cavity. In contrast to other crustacean sensilla the receptor lymph cavity extends proximally far between the inner dendritic segments (Figs. 2, 3) and is delimited by the inner sheath cells. Here, these display only few organelles such as microtubules, vesicles and a few mitochondria within an electron-lucid cytoplasm. The inner sheath cells develop processes that divide both receptor lymph cavity and dendrites over some distance into interconnected compartments or groups (Figs. 2, 4, 5).

Distal to the basal part of the spindle-shaped space, the inner sheath cells become enveloped by 13–14 outer sheath cells organized as thin flattened lamellae (thickness 0.1–0.4 μm) in an alternating semicircular arrangement. Each cell spans an arc of approximately 220°, resulting in mutual overlapping (Fig. 5a, b). The innermost cells are situated most proximally with more cells being added further distally until the total number of 13–14 outer sheath cells is completed (Fig. 14). Their oblong nuclei (diameter 1–2 μm, length 7–15 μm) are situated in the basal and slightly distended part of the cell. This region is also characterized by GER, Golgi complexes, mitochondria, microtubules, vesicles and vesicular bodies, while in the intermolt state the apical part of the cell mainly contains a high number of vesicles and microtubules in addition to a few mitochondria. The processes of the inner sheath cells are less developed in the distal part of an aesthetasc-bearing

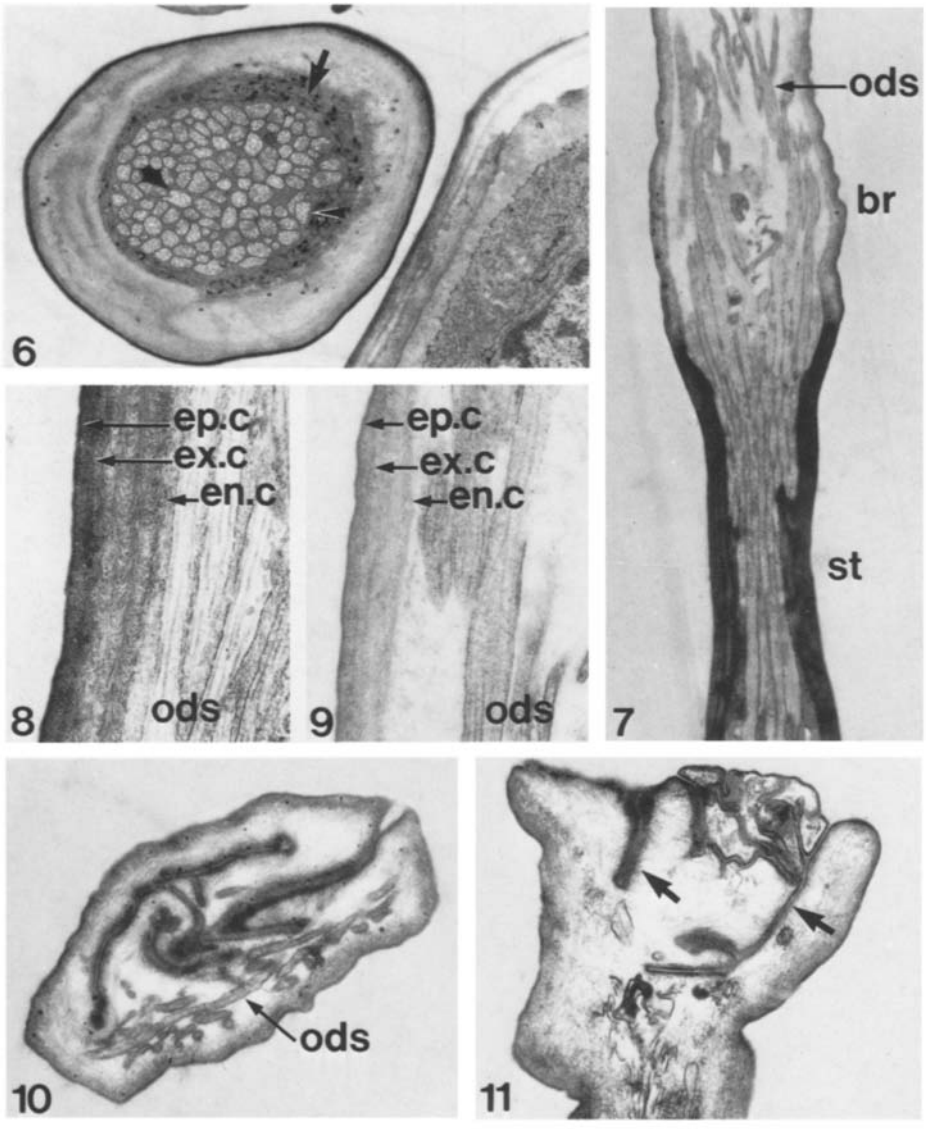

Fig. 6. Cross section of socket region. The interdigitated inner sheath cells (*arrow*) extend into the basal part of the stem where they terminate; *arrowhead* outer dendritic segments. ×9000

Fig. 7. Longitudinal section showing transition of electron-dense cuticle of the stem (*st*) into the delicate and light form of the bulbous region (*br*). Outer segments (*ods*) continue in a loose spiral course to the tip. ×6300

Fig. 8. Basal part of bulbous region in longitudinal section. The endocuticle (*en.c*) consists of 3–4 layers of parabolic-oriented microfibrils; no substructures are detectable within the dense and granular exocuticle (*ex.c*); *ep.c* epicuticle; *ods* outer dendritic segments. ×21000

Fig. 9. Middle part of bulbous region in longitudinal section. The poreless cuticle is thin, tenuous and light; *en.c* endocuticle; *ep.c* epicuticle; *ex.c* exocuticle; *ods* outer dendritic segments. ×21000

Fig. 10. Subterminal cross section of tip. Approximately 20% of outer segments (*ods*) extend into the immediate tip region. ×20000

Fig. 11. Paramedian longitudinal section of tip. At the poreless tip a folded invagination of high electron density (*arrow*) ontogenetically representing a molting pore is developed. ×20500

segment and usually divide the receptor lymph cavity into two compartments. They are reduced to small finger-like extensions proximal to the socket. In their terminal region the outer sheath cells are tightly linked by digitiform extensions and are connected to the adjacent one by zonulae adhaerentes (Fig. 14). No junctions were observed between the two sets of sheath cells. Corresponding to the graded vertical distribution of the outer sheath cells, each cell terminates on a different level with the outermost cells extending to the socket, whereas the more central ones end more proximally (Fig. 14). Thus, in addition to structural, numerical and positional characteristics a difference in longitudinal extension is also present (inner sheath cells: 200–260 µm; outer sheath cells: ca. 60 µm).

External anatomy

Stem. Within the socket region the cuticle is 0.8–1.3 µm thick (Fig. 6) and displays – as in the entire aesthetasc – three distinct layers, in the following termed endo-, exo- and epicuticle. The cuticle of the stem region generally shows a high electron density (thickness 0.3–0.4 µm) (Fig. 7). It consists of an endocuticle composed of 3–4 layers of microfibrils, a granular exocuticle without distinct substructures and an epicuticle in which two dark bands border a lighter central lamina (Fig. 8). The epicuticle (thickness 10–12 nm) is homogeneously developed along the entire sensillum.

Within the stem only inner sheath cells, outer dendritic segments and receptor lymph fluid are present (Fig. 7). The inner sheath cells closely adjoin the cuticle, terminate 5–6 µm distal to the socket and are connected to one another in their apical part by zonulae adhaerentes. In this region they are very tightly interdigitated by thin lamellated extensions (Fig. 6) and contain only microtubules and a high number of electron-dense vesicles. Due to the tight packing of the cilia (diameter 0.2–0.3 µm) the receptor lymph cavity becomes restricted to small fissures (Figs. 6, 7).

Bulbous region. The transitional zone from stem to bulbous region is very short and marked by a sudden increase in diameter from 4–5 to 6–10 µm (Figs. 1b, c; 7). Within 1–2.5 µm in longitudinal extension the electron density changes, and the cuticle merges into a light and delicate one (Fig. 7). The endocuticle (thickness 0.2–0.3 µm) be-

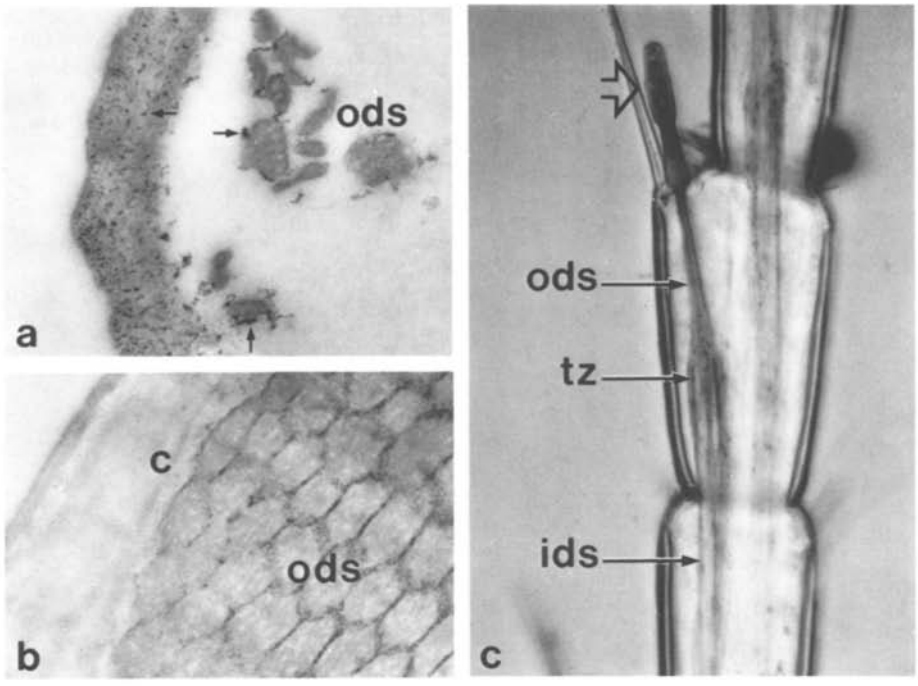

Fig. 12a, b. Lanthanum-treated animal. *c* Vital stained aesthetasc. **a** Lanthanum (*arrow*) is detectable not only within the cuticle of the bulbous region but also adhering to outer segments (*ods*) as an electron-dense precipitate, showing that the poreless cuticle is permeable for dissolved substances. **b** Stem of same aesthetasc as control. Lanthanum is present within the receptor lymph fluid between outer segments (*ods*); no precipitate within the cuticle (*c*). **c** The dye (0.05% methylene blue) instantaneously penetrates the cuticle of the bulbous region (*arrow*) proceeding via stem, outer segments (*ods*), transitional zone (*tz*) to inner segments (*ids*). a, b uncontrasted section ×38000; c ×400

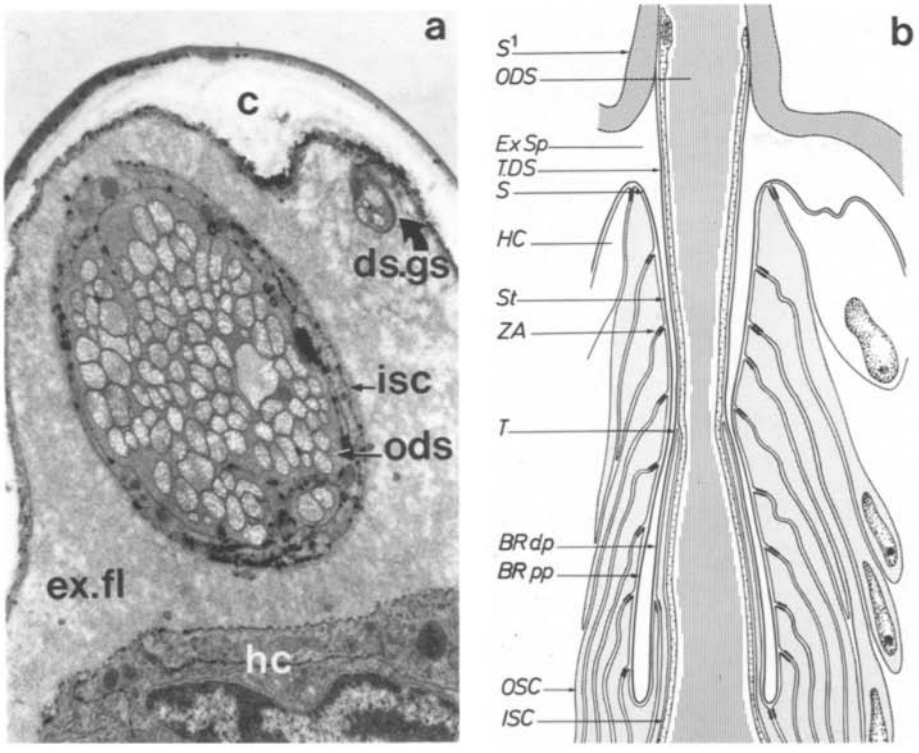

Fig. 13a, b. Aesthetasc in premolt state. **a** Cross section proximal to socket (stage D1). Outer dendritic segments (*ods*) are protected against the exuvial fluid (*ex.fl*) by inner sheath cells (*isc*) alone, not by a dendritic sheath, as, for example, the guard seta (*ds.gs*); *c* cuticle; *hc* hypodermal cell. **b** Diagram of late molting stage (D2–D3); external part of old aesthetasc omitted. Outer dendritic segments (*ODS*) become protected by inner sheath cells (*ISC*) and in a late molting stage by a temporary dendritic sheath (*T.DS*), which is shed during molting. New aesthetasc lies folded back in an invagination of outer sheath cells (*OSC*), which build the new cuticle (*bold line*). *BRdp* bulbous region, distal part; *BRpp* bulbous region, proximal part; *ExSp* exuvial space; *HC* hypodermal cell; *S* socket, new aesthetasc; S^1 socket, old aesthetasc; *St* stem; *T* tip; *ZA* zonula adhaerens. a ×11500

comes electron lucid and displays 3–4 layers of microfibrils arranged in a parabolic pattern (Fig. 8). The exocuticle (thickness 70–110 nm) has a slightly higher density and shows a granular substructure (Fig. 8). Distal to the transition zone the cuticle is thinner (0.25–0.32 μm) and even more electron lucid (Figs. 7, 9). This is particularly due to changes within the endocuticle, which tapers to 0.13–0.2 μm and becomes indistinct in appearance because the stratified and regular arrangement of the parabolic fibers merges into an irregular and loose orientation. The exocuticle remains mostly unchanged except for a slight decrease in density and a more irregular inner surface.

Within the bulbous region the outer dendritic segments continue up to the tip taking a slightly spiral course within the spacious receptor lymph cavity (Fig. 7). In the proximal region the majority of outer segments (diameter 0.18–0.32 μm) contains, with the exception of few small cilia, a high number of microtubules (10–20). Distal to the

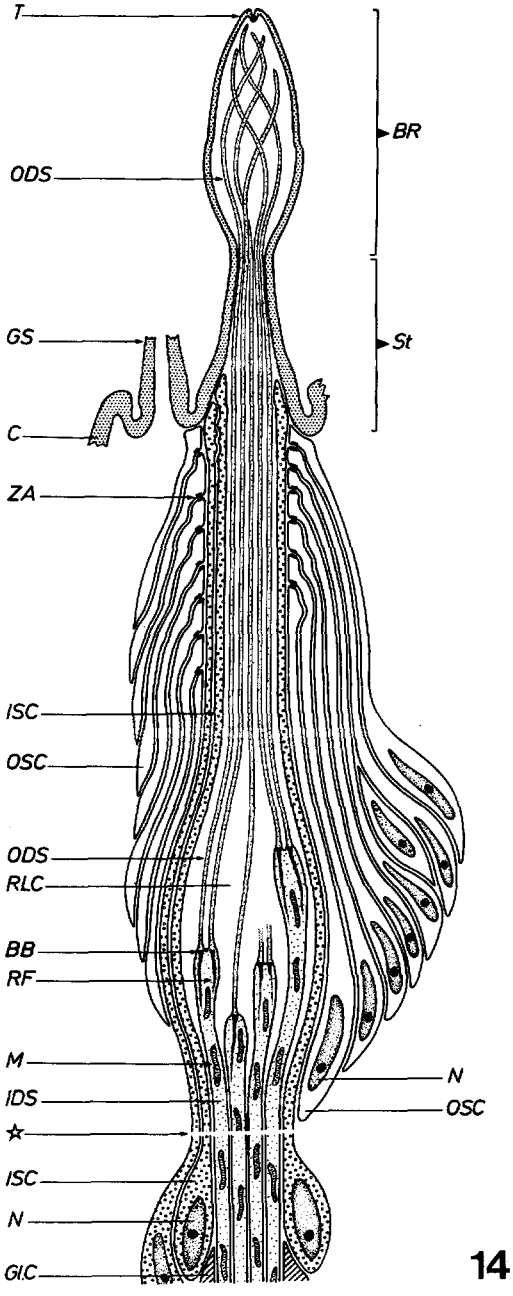

Fig. 14. Diagram of aesthetasc of *Asellus*. Proportions not to scale; only 4 of up to 80 dendrites and 8 of up to 14 outer sheath cells (*OSC*) shown; processes of inner-sheath cells (*ISC*) omitted. Note that mono- as well as biciliary dendrites are developed (see text). *BB* basal body; *RB* bulbous region; *C* cuticle; *Gl.C* glial cell; *GS* guard seta; *IDS* inner dendritic segment; *M* mitochondrium; *N* nucleus; *ODS* outer dendritic segment; *RF* rootlet fiber; *RLC* receptor lymph cavity; *St* stem; *T* tip; *ZA* zonula adhaerens; *star* represents omission of approximately one antennular segment

middle of the bulbous part the outer segments begin to terminate so that close to the tip only approximately 60–70% of the cilia are detectable.

Tip. At the tip there is a centrally situated terminal invagination (Fig. 1c), which represents a molting pore (see below). Here, the cuticle is intensely folded. The folds are so tight that the external medium is, if not excluded completely, restricted to minute interspaces (Figs. 10, 11). The cuticle of the tip region measures 0.16–0.23 µm and is very electron lucent. The endocuticle is more filamentous and appears as a light and very loose meshwork of approximately 80–90 nm thickness. In the most distal part this layer is often no longer detectable. Thus, receptor lymph fluid and outer dendritic segments are separated from the outside by an extremely thin cuticle (50–90 nm), which consists of a light and granular exocuticle (thickness 40–80 nm) and the epicuticle (Figs. 10, 11).

The invaginated cuticle differs clearly from the more distal one in that the exocuticle is more homogeneous and of higher density. The endocuticle is occasionally lacking in the proximal part. The bottom of the invagination is sealed off from the inside by a substance of homogeneous and high electron density. A contact between this material and the cilia could not be observed. Within the immediate tip region, i.e., the terminal 2–3 µm, 20% of outer segments were observed (Fig. 10). They contain, with rare exceptions, only a few microtubules ($\leqq 4$). Pores or pore-like structures are not developed either in the tip or in any other region of the aesthetasc.

Vital staining

Methylene blue. Whole animals or isolated antennules were placed into a 0.05% solution of methylene blue. The dye penetrates instantaneously into the bulbous part of the aesthetasc (Fig. 12c). Subsequently the dye progresses via the stem into the antennular segment where it can be traced over two segments maximally. The dye is present as a distinct blue strand corresponding to the spatial extension of the receptor lymph cavity, also reaching more proximally. Especially the bulbous part, the stem, as well as the spindle-shaped space become intensively stained. No other structures on the body or appendages of *Asellus* were stained concurrently.

Lanthanum nitrate. In lanthanum-treated specimens the tracer penetrates the poreless cuticle and is detectable as a fine granular precipitate of very high electron density (Fig. 12a). In the bulbous region lanthanum is present within each of the cuticular layers as regularly dispersed granules, which in part form clusters (Fig. 12a). Lanthanum is attached to the dendritic membrane of the outer segments in the same manner but is not present within the cilia. In the stem region the cuticle is completely free of lanthanum, whereas it is present tightly packed between the outer segments within the receptor lymph fluid (Fig. 12b).

Molting

In an early premolt stage (D0) the exuvial space expands between hypodermal cells and cuticle and in the course of time extends proximally between inner and outer sheath cells. The result is that the outer dendritic segments of the aesthetasc run within the exuvial space. They are separated from the exuvial fluid by the inner sheath cells (Fig. 13a) instead of a dendritic sheath as is the case within the setae commonly found in crustaceans. Even though the exuvial fluid extends into the socket region, no contact between receptor lymph and exuvial fluid is detectable because of the tight connection between inner sheath cells and cuticle (Fig. 13b).

In the further course of premolt (stage D1) the exuvial space expands proximally to the distal region of the spindle-shaped space. The exuvial fissure extends between the two (sometimes three) innermost outer sheath cells, on the one side, and the remaining outer sheath cells, on the other side. Thus, a cylindrical invagination is present, the inner wall of which consists of the inner and the two (or three) outer sheath cells. Its outer wall is formed by outer sheath cells alone (Fig. 13). The cuticle of the new aesthetasc is produced exclusively by the outer sheath cells. Because of their graded arrangement in the longitudinal axis, each cell secretes a belt-like area of the new sensillum. According to its position, the socket is developed by the outermost and most distal sheath cells. The cuticle of the stem and the basal half of the bulbous region is produced by the more central and proximal cells. The distal half of the bulbous region and the tip are invaginated into the proximal half, thus pointing to the exterior; its cuticle is formed by the two (or three) innermost outer sheath cells. Accordingly, the tip of the new aesthetasc does not reach the socket of the old one but is situated far more proximally (Fig. 13b).

In the premolt state the outer sheath cells display a pronounced GER, a considerably higher number of Golgi complexes, numerous vesicles and multivesicular bodies. The surface adjacent to the exuvial space becomes enlarged by numerous protrusions, which show the first cuticulin patches; these later fuse into an electron-dense outer cuticle layer (stage D3).

Only in a late molting stage (D2–D3) is a thin layer of high electron density attached to the hitherto free outer surface of the inner sheath cells (Fig. 13b). The origin of this layer, which is in continuation with the dense outer cuticle layer of the new sensillum, could not be established. The inner sheath cells at least show no organelles indicative of higher cellular activity. This layer does not represent a dendritic sheath in the common sense and due to its transitory nature is termed "temporary dendritic sheath". It must be emphasized that this sheath is not present in molted animals – it is shed during the molt as part of the exuviae.

Discussion

A. Morphological characteristics of aesthetascs

Our knowledge of those sensilla referred to as aesthetascs is rather limited because only few fine-structural examinations exist at the present time. Table 1 summarizes the relevant data from these studies and shows that in some aesthetascs certain structures are obviously correlated, while in others they are not. Thus, in the following account, it will be examined whether and to what extent heterogeneous sensilla have been united under this term and by what morphological criteria aesthetascs may be defined.

In an initial comparison two groups may be distinguished. One is a smaller group represented by the phyllopod *Leptestheria*, the podocopid ostracod *Notodromas*, and the isopod *Porcellio* (cf. Table 1). These can be characterized by the following features: 1) low number of sensory cells, 2) monociliary dendrites, 3) dendritic sheath, 4) unbranched cilia (exception: *Leptestheria*). The remaining sensilla can be characterized by different features upon which the following discussion will center.

Sensory cells. The aesthetascs of decapods are the most strongly innervated sensilla in crustaceans counting between 100 and 500 sensory cells each (ref., see Table 1). Myodocopid ostracods (*Conchoecia, Skogsbergia, Cylindroleberis*), mysids and the isopod *Asellus* also have high numbers, ranging between 25 to 80 cells each (ref., see Table 1). For the first time it has been observed in this study that within the same species individual aesthetascs are innervated by different numbers of sensory cells. Nonetheless, the number of outer dendritic segments is nearly the same in all aesthetascs examined due to the higher portion of monociliary dendrites in the terminal aesthetasc.

Additionally, the aesthetascs of *Asellus* represent the first arthropod sensillum containing monociliary as well as biciliary sensory cells. In decapods and mysids at least two outer segments per sensory cell are developed, whereas myodocopid ostracods develop multiciliary dendrites (ref., see Table 1). It is tempting to see an evolutionary trend in the numerical decrease of outer dendritic segments from ostracods (as an old group) over decapods and mysids to the isopod *Asellus*, as a representative of the most highly evolved crustacean group. Branching of outer dendritic segments as regularly observed in other species does not occur in *Asellus*.

Sheath cells. In most studies little attention has been paid to structure, number and extension of sheath cells. Generally, two groups of aesthetascs seem to exist in relation to the extension of sheath cells. In the first group the transitional zone between the inner and the outer dendritic segment is located within the sensillum (myodocopid ostracods, Heimann 1979, unpublished results; *Pagurus*, Ghiradella et al. 1968a; *Neomysis*, Guse 1979). Here, all sheath cells terminate at the level of the basal bodies. In the second group the basal bodies are situated within the antennular segment. The sheath cells envelop not only the inner but also part of the outer dendritic segments. They terminate at the base of the sensillum or within its basal part (see Fig. 14). In the asymmetrical aesthetasc of the terrestrial crab *Coenobita* they may continue into the sensillum but are restricted to the side of the thick cuticle (Ghiradella et al. 1968b, c).

Myodocopid ostracods and the mysid *Neomysis* contain a single set of sheath cells arranged more or less in a mesaxon-like manner. The number of sheath cells is – in comparison – very low in ostracods (1–4), which might be explained by the reductional trend characteristic for this group. In *Neomysis* up to 8 cells are reported to take part in building the new aesthetasc (Guse 1979).

In the remaining aesthetascs, i.e., of all decapods as well as the mysid *Antromysis* and the isopod *Asellus*, two sets of sheath cells are distinguishable: an inner set adjoining the dendrites and receptor lymph cavity, which all become enveloped by an outer sheath cell set separating the complex from the hemolymph fluid, epidermal cells and cuticle. For decapods no numbers or exact dimensions of sheath cells are known. According to the published figures (Ghiradella et al. 1968a, b, c; Laverack and Ardill 1965; Snow 1973), a high number of cells is present in the aesthetascs of all decapods examined. Studies on *Astacus* (Heimann, unpublished) show that in this decapod 4–6 inner and up to 20 outer sheath cells are present.

In the mysid *Antromysis* (Juberthie-Jupeau and Crouau 1977; Crouau 1978) two inner and two outer sheath cells

Table 1. Comparison of morphological criteria of sensilla referred to as aesthetascs

Genus Author[10]	Position	Dimension in µm	No. of sensilla	No. of sensory cells	Cilia er sensory cell	Position of basal body	Branched cilia	Dendritic sheath	Thickness of cuticle	Sheath cells
Phyllopoda										
Leptestheria Rieder 1980	A 1	25 × 5	600	4–10	1	in ant.	+	+	0.1	5 sheath c.
Ostracoda										
Notodromas Andersson 1975	A 2	70 × 4–6	1	14[1]	1	in ant.	–	+[2]	0.06[3]	5 + hypodermal layer
Conchoecia Heimann 1979	A 1	70–320 × 7–10[8]	2–4	40–60	≤25	in aesth.	+	–	0.06–0.2	3–4 hypodermal c.
Skogsbergia ♂ Heimann unpubl.	A 1	400–450 × 10	2	45	8–12	in aesth.	+	–	0.1–0.3	1–3 sheath c.
Cylindroleberis ♂ Heimann unpubl.	A 1	240–280 × 7–8	1	30–36	10–12	in aesth.	+	–	0.1–0.2	1–2 sheath c.
Decapoda										
Paragrapsus[4] Snow 1973	A 1	600 × 11–12	160–170	130	2	in ant.	+	–	1.3	hypodermal + peripheral glia sheath
Pagurus Ghiradella 1968a	A 1	1000 × 14–15	•	300–500▲	2	in aesth.	+	–	0.4	schwann + hypodermal c.
Coenobita Ghiradella 1968c	A 1	90–100 × 20–22	•	100▲	2	in ant.	+	–	0.35	2 cellular sheaths
Cancer Ghiradella 1968b	A 1	1700 × 14	•	100▲	2	in aesth.	+	–	1.1	•
Panulirus Ghiradella 1968b	A 1	1000 × 14	•	350▲	2	in aesth.	+	–	1.0	•
Mysidacea										
Neomysis Guse 1979	A 1	120–160 × 7–9	23–25	25–40	2	in aesth.	+	–	0.1–0.2	up to 8 sheath c.
Antromysis Crouau 1978[5]	A 1	90 × 5	14–21	30	2	in ant.	+	–	0.08–0.17	2 + 2 sheath c. + 6 hypodermal c.[6]
Isopoda										
Asellus Heimann 1984	A 1	40–60 × 6–9	≤6[7]	50–80[9]	2 + 1	in ant.	–	–	0.16–0.3	3–4 inner + 14 outer sheath c.
Porcellio Risler 1977	A 1	18–20 × 4	15–21	2	1	in ant.	[+]	+	0.16*	1 inner + 3–4 outer sheath c.

•: Data not available; ▲: Data estimated; *: According to figure; [ ]: Data unsupported; (1): In 5 groups; (2): 5 dendritic sheaths; (3): In furrows; (4): Diagram probably based on specimen in premolt stage; (5): Juberthie-Jupeau and Crouau 1977[4]; (6): 11 hypodermal cells according to Fig. 1 in (5); (7): According to age and sex; (8): According to sex; (9): According to position on A 1; (10): Only first author cited

enveloped by six so-called hypodermal cells are present. The diagram in Juberthie-Jupeau and Crouau (Fig. 1; 1977) shows 11 hypodermal cells and is obviously based on an animal in premolt stage (? D2–3), indicating that the hypodermal cells take part in forming the cuticle of the new aesthetasc. Thus, the hypodermal cells are to be interpreted as sheath cells as well, resulting in 10–15 sheath cells in *Antromysis*.

In those aesthetascs having two sets of sheath cells the general situation is comparable to the situation described for *Asellus*: the outer sheath cells are oriented in semicircular concentric layers overlapping one another. They usually terminate immediately below the base of the sensillum. The inner sheath cells continue into the basal part of the aesthetasc. They develop processes extending between dendrites and into the receptor lymph cavity. Especially in decapods and in *Antromysis*, these processes separate the inner dendritic segments into groups or into single isolated dendrites, whereas the outer segments are usually not divided or only partially. In contrast, the inner segments of *Asellus* occur as a homogeneous bundle, while outer segments and receptor lymph cavity become densely subdivided by processes of the inner sheath cells. A functional interpretation of the presence of two different sets of sheath cells is given below. The assumption of Haupt and Coineau (1978) that the number of sheath cells and size of the sensillum is positively correlated cannot be confirmed by this study and is invalid for other aesthetascs described so far.

Receptor lymph cavity. As in other arthropod sensilla the outer dendritic segments of aesthetascs continue within a fluid-filled extracellular space, the receptor lymph cavity.

This cavity is delimited within the antennular segment by the inner sheath cells and within the sensillum by the cuticle. Synonyms used are "cavité lymphatique" (Crouau 1978), "cavité hémolymphatique" (Juberthie-Jupeau and Crouau 1977), "extracellular space" (Snow 1973), "vacuole" (Ghiradella et al. 1968a, b, c) and "Liquorraum" (Guse 1979). The term "cavité hémolymphatique" is deceptive because no connection between receptor lymph cavity and hemolymph sinus exists.

The extension of this cavity reaches distally into the tip, proximally it is delimited by the terminal part of the inner dendritic segments, which typically are interconnected by junctional structures. The aesthetascs of *Asellus* represent an exception in this respect in that the receptor lymph fluid extends far between the inner segments proximally. Several criteria give rise to the assumption that at least in *Asellus* the receptor lymph fluid is produced by the inner sheath cells: 1) In addition to the sensory cells, the inner sheath cells are the only cells having contact with the receptor lymph fluid. 2) The contact area is enlarged by numerous protrusions extending into the receptor lymph cavity. 3) The cytological features of the inner sheath cells are indicative of a high secretory activity. There are indications that similar cellular activities may be expected in the inner (Crouau 1978) and outer (Ghiradella et al. 1968c) sheath cells of other aesthetascs as well.

Cuticle. In all aesthetascs examined to date the cuticular wall shows, at least in its fine structure, two distinct regions: a basal region with which the aesthetasc is joined to the antennule and a more distally situated main region terminating in a more or less distinct tip (ref., see Table 1).

The basal region of an aesthetasc is characterized by a lamellar cuticle of high electron density, which is always strongly developed (Crouau 1978; Ghiradella et al. 1968a, b, c; Guse 1979; Heimann 1979, this study; Snow 1973). Within a short transitional zone that is often characterized by a sudden increase in diameter (Crouau 1978; Guse 1979; Heimann 1979, this study) the cuticle merges into the thin, light and tenuous one of the distal region. Annulation of aesthetascs as typically found in decapods and some ostracods does not occur in *Asellus*. The development of such annules is apparently correlated with the length of the sensillum and with the habitat of the animal. Functionally, they are interpreted as reinforcing structures (Heimann, unpublished results).

Summing up the existing data it can be stated that it is not possible to classify aesthetascs according to cuticular features such as dimension, thickness of cuticle, presence of annulation, and an apical pore alone as proposed by Wasserthal and Seibt (1976). Additionally, an apical pore in the sense of an opening to the external medium as discussed by these authors is never observed in crustaceans. Instead of the deceptive expression "apical" or "terminal" pore the term "molting pore" seems to be more appropriate because this structure ontogenetically represents the point of rupture between old and new sensillum during molting. This molting pore becomes closed by a material of high electron density (Andersson 1975; Crouau 1978; Heimann 1979, unpublished results and this study; Rieder 1978; Rieder and Spaniol 1980; Risler 1977), which is partly present as a molting plug. The nature of this material is unknown; no information of a possible permeability exists.

B. Molting

At present no investigations of aesthetascs during molting exist and only a few fine structural studies deal with this aspect in other crustacean sensilla (Guse 1980a, b; Rieder and Spaniol 1980). From these papers and a number of light-microscopical studies (cf. Dexter 1981; Reaka 1975) it is known that the new seta is formed within a cylindrical invagination of its sheath cells. In comparison to the situation in insects ("molting type I" of Altner and Thies 1972), the dendrites become protected against the exuvial fluid by a dendritic sheath (Guse 1980a; Rieder and Spaniol 1980). Guse (1980b) observed an additional type in which the outer dendritic segments – in part lacking a dendritic sheath – are assumed to be protected by a surface coat. A similar situation may also be present in an arachnid (Haupt 1982).

This "invagination" type is in principle also valid for the aesthetascs of *Asellus* (Fig. 13b). Moreover, it is highly probable that all aesthetascs follow this scheme since the diagrams presented by Snow (Decapoda; 1973, Fig. 2) and Juberthie-Jupeau and Crouau (Mysidacea; 1977, Fig. 1) are obviously based on sections of animals in the premolt stage, both indicating identical processes. All examinations indicate that this type seems to be characteristic for crustaceans in general.

Within the aesthetascs of *Asellus* a special modification, as yet not observed in arthropods is realized. This modification most likely is present in other aesthetascs as well. It depends on the presence of two sets of sheath cells that have different functions: The outer sheath cells alone build the cuticle of the new aesthetasc (Fig. 13b). The inner sheath cells apparently protect the outer dendritic segments against the exuvial fluid during a mid- to early molting stage (approximately stage D0 to D2) and bridge the space between old and new sensillum (Fig. 13a). They take no part in secreting the cuticle of the new sensillum but probably produce the temporary dendritic sheath present in only a limited phase of the molt (approximately from stage D2 up to the molt). According to their fine structure during premolt, the old aesthetasc of *Asellus* appears to be in a functional state just before the shedding of the old cuticle.

C. General characteristics of aesthetascs

Despite our fragmentary knowledge, aesthetascs may be classified as an anatomical distinct class of sensilla within crustaceans. An aesthetasc can be characterized in a broad sense by the following anatomical criteria: (1) a thin, tenuous and poreless cuticle in its distal region; (2) no dendritic sheath; (3) distal position on the first antennae (on the outer ramus in bifurcated antennules); (4) innervation by a high number of sensory cells (≥ 25); (5) two or more outer dendritic segments per sensory cell; (6) branched outer dendritic segments; (7) high number of sheath cells in aesthetascs having basal bodies of sensory cells located within antennular segment, low number of sheath cells where basal bodies are located within the sensillum; (8) no supporting fibers in sheath cells.

If these criteria are applied, certain sensilla commonly referred to as aesthetascs (Andersson 1975; Rieder and Spaniol 1980; Risler 1977) must be excluded due to distinct structural differences, i.e., low number of sensory cells, monociliary dendrites, dendritic sheath and unbranched cilia (exception: *Leptestheria*). Especially a comparison be-

tween the aquatic isopod *Asellus* and the terrestrial isopod *Porcellio* (Risler 1977), and between the ostracods *Conchoecia* (Heimann 1979) and *Notodromas* (Andersson 1975) shows considerable differences. The phyllopod *Leptestheria* (Rieder and Spaniol 1980) incorporates some controversial characters. As long as no intermediary forms are found, these three examples do not represent aesthetascs according to their morphological characters.

D. Functional considerations

For a number of insect sensilla not only the fine structure is known but the appropriate function also established by electrophysiological methods (cf. review by Altner and Prillinger 1980). Within crustaceans only two examinations have combined anatomical with physiological data (apical cone complex of an isopod; Seelinger 1977, 1983; pereiopod setae in a crayfish; Altner et al. 1983). Despite the lack of such studies, all fine structural, behavioral and electrophysiological examinations strongly support the assumption that aesthetascs represent chemoreceptors.

Structural criteria indicative of such a function are the specialized cuticle and the high number of sensory cells (up to 500 in decapods), each carrying two or more branched outer segments. This combination leads to extremely high numbers of ciliary branches per sensillum (up to 23500; Heimann 1979), presumably enlarging the number of receptor sites considerably. Pores and pore-channels serving in chemoreceptive insect sensilla as stimulus-conducting structures are not present in crustaceans. Instead aesthetascs display a specialized cuticle, which is permeable to dissolved substances, as proven by the tracer experiments. Since a comparable cuticle is also present in other aesthetascs, a similar permeability can most likely be assumed for these as well.

Behavioral observations on *Asellus* provide no evidence of a specific function. On the other hand, ablation experiments on decapods all implicate that aesthetascs function as sensitive chemoreceptors, which elicit searching behavior (Atema 1977; Devine and Atema 1982; Gleeson 1982; McLeese 1974; Reeder and Ache 1982; Wasserthal and Seibt 1976). Electrophysiological data on antennular receptors are available only from decapods. From a variety of substances tested, amino acids of low molecular weight seem to represent the most effective stimuli, with thresholds as low as 10^{-12} mol (Ache 1982; Ache et al. 1976; Fuzessery 1978; Fuzessery et al. 1978; Shepheard 1974; Thompson and Ache 1980). It should be noted that all recordings were made of anatomically undefined receptors, all of which most probably belong to aesthetascs.

According to present knowledge, aesthetascs represent a morphologically distinct type of sensillum characterized by certain criteria as discussed in this study. Functionally, they can be defined as chemoreceptors of generally extremely high sensitivity, which serve in food, sex and host recognition and elicit complex search behavior (cf. review by Ache 1982). The apparently ubiquitous presence of aesthetascs in crustaceans indicates that they represent an old type of sensillum of high selective importance.

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