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Fine structure of the cephalic sensory organ in the larva of the nudibranch *Rostanga pulchra* (Mollusca, Opisthobranchia, Nudibranchia)

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Summary. The cephalic sensory organ in the veliger larva of *Rostanga pulchra* is situated dorsally between the rhinophores, emerging as a tuft of cilia. This organ is made up of three types of sensory cells, and based on their morphology have been termed ampullary, parampullary and ciliary tuft cells. The cell bodies of the organ originate in the cerebral commissure, and their dendrites pass to the epidermis as three tracts. Dendrites terminate in the epidermis to form a sectorial field. Axons of these cells run into the mass of neurites in the cerebral commissure but no synapses were observed in this area. Morphological evidence suggests that the cephalic sensory organ may function in chemoreception and mechanoreception related to substrate selection at settlement, feeding, or other behaviors.

A. Introduction

A new sensory structure, the cephalic sensory organ, in the veliger larva of the nudibranch *Phestilla sibogae* was discovered by Bonar (1978a, b) who showed that this organ is composed of flask-shaped sensory cells. He suggested that these cells were involved in chemoreception. More specifically, the cephalic sensory organ was involved in perception of chemical cues emitted by the adult food, which in turn, induce settlement and metamorphosis.

Preliminary observations of the veliger larva of the nudibranch *Rostanga pulchra* indicated that it possessed a cephalic sensory organ, situated between the velar lobes, but differing from that of *Phestilla* in a number of ways. Fine structural observations in this study have shown that the cephalic sensory organ consists of at least three types of receptor cells. This indicates a greater degree of specialization; it is possible that the cephalic sensory organ in *Rostanga pulchra* may function in more than one modality, i.e., chemosensation and mechanosensation.

B. Materials and Methods

Veligers of *Rostanga pulchra* were reared during the summer months at Friday Harbor Laboratories, University of Washington (USA), by a technique previously described (Chia and Koss 1978).

For histology, transmission electron microscopy (TEM), and scanning electron microscopy (SEM) larvae were prepared by an initial 5 min relaxation period in a solution of chloretone and millipore-filtered seawater (1/5 v/v) at 0° C. This was followed by a 1 h fixation in 2.5% glutaraldehyde in 0.2 M phosphate buffer at pH = 7.6. During this time the larval shells were decalcified according to the technique of Bonar and Hadfield (1974). Specimens were then post-fixed for 2 h in 2.0% OsO4 in 1.25% sodium bicarbonate at pH = 7.2 (Wood and Luft 1965). This was followed by dehydration in an ascending series of ethanol (starting with 30%) and embedding in Epon. Larvae for SEM were dehydrated and prepared according to the technique of Chia et al. (1975). One μm thick sections were stained with Richardson's stain (Richardson et al. 1960). Thin sections were stained with uranyl acetate and lead citrate, each for a 15 min period.

C. Results

1. General observations

The advanced veliger of *Rostanga pulchra* (20 days or more after hatching) possesses a cephalic sensory organ that is visible as a tuft of cilia on the surface; it is situated dorsally between the rhinophores toward the rim of the mouth. This structure is not conspicuous because in the majority of instances it is covered by the long velar cilia that surround the mouth (Fig. 1). A more obvious tuft of cilia is situated below the cephalic sensory organ (Fig. 1). However, these cilia do not contribute to the organ, and arise from a group of cells situated entirely within the epidermis (Figs. 2, 7).

The ciliary tuft of the cephalic sensory organ emerges from cell processes that are subepithelial in origin. That is, their cell bodies are found beneath the epidermis, clustered within the dorsal part of the cerebral commissure (Fig. 2). The dendritic processes arise from the mid-region of the cerebral commissure, and curve upwards to follow the contour of the esophagus. They pass through a sinus, spanning approximately 3.5 μm, and terminate in an area of the epidermis just above the mouth. At a fine structural level, processes from these sensory cells ascend to the epithelium in three distinctly separate tracts (Figs. 3, 4). Each tract varies from 2.25 to 5.5 μm in diameter and is comprised of a collection of three to four dendrites. Once in the epidermis, the dendrites terminate in scattered groups forming a sectorial field that covers about 160°. The base (arc) of the field is 10 to 15 μm in width.

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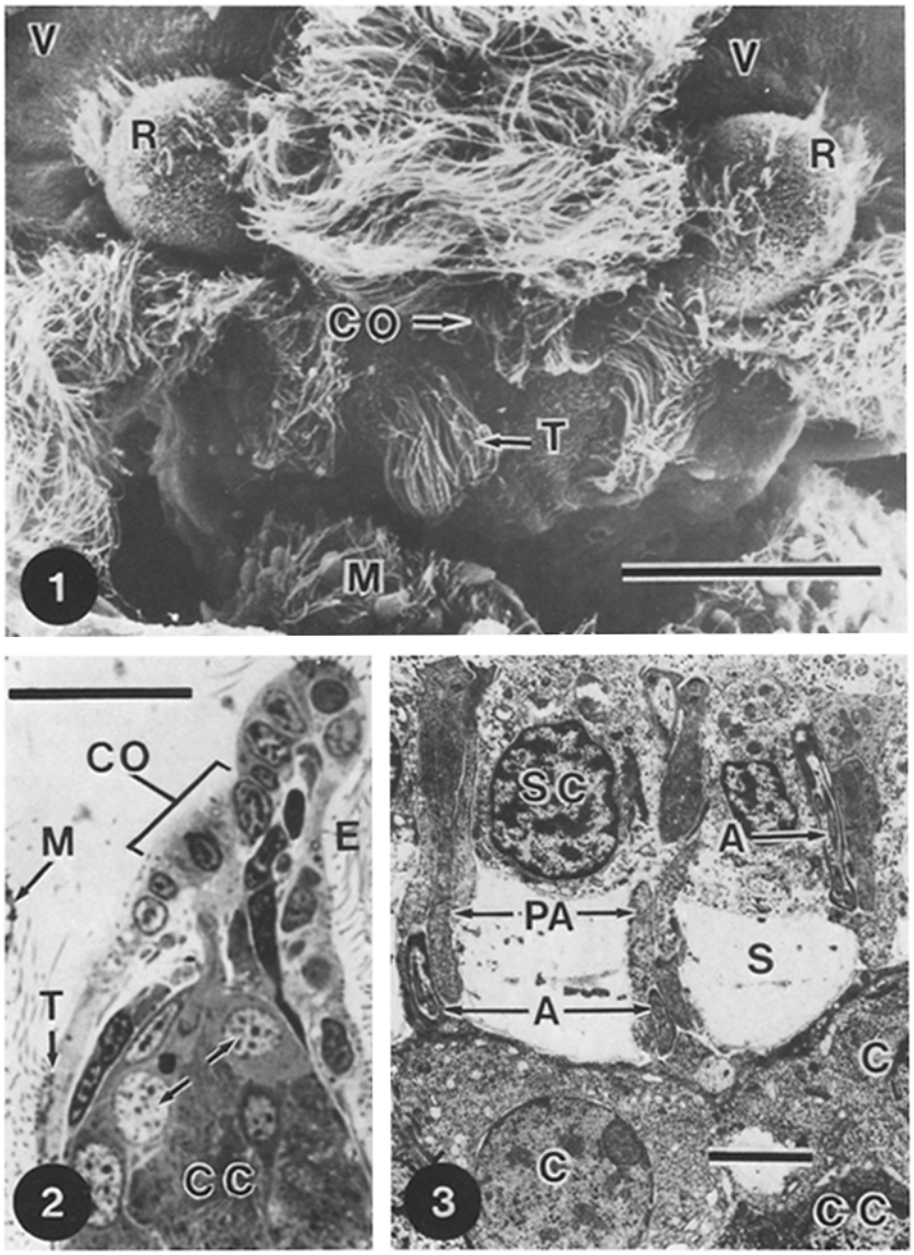

Fig. 1. SEM of a competent veliger showing rhinophores (*R*), velum (*V*), and mantle (*M*). Note that cephalic sensory field (*CO*) is covered by velar cilia, and positioned above a visible tuft of cilia (*T*). Scale: 40 μm.

Fig. 2. Sagittal section (1 μm thickness) showing cephalic sensory field (*CO*) in relation to esophagus (*E*), mantle (*M*), and ciliary tuft (*T*) that arises from intraepithelial cells. Note cells (*arrows*) that contribute to cephalic sensory organ are situated in cerebral commissure (*CC*). Scale: 5 μm

Fig. 3. Oblique section of cephalic sensory organ showing three dendritic tracts passing from cerebral commissure (*CC*) through a sinus (S) to epidermis. Tracts contain ampullary (*A*) and parampullary (*PA*) receptors that terminate among supporting cells (*SC*) in epidermis. Cell bodies of ciliary tuft cells (*C*) are visible in cerebral commissure (*CC*). Scale: 2.5 μm

The epidermal cells of the cephalic sensory field are thickened in comparison to the thin squamous cells situated away from the field (Figs. 2, 7). These thickened epidermal cells (supporting cells) are interspersed among receptor-cell groupings (Fig. 6). All cells of the cephalic sensory field are interconnected by septate junctions. Supporting cells contain elliptical nuclei, mitochondria, endoplasmic reticulum and electron dense granules of approximately 0.5 μm in diameter. Microvilli and occasionally a cilium arise from the apical surface of these cells.

At the fine structural level, it can be recognized that at least three morphologically different types of receptor cells make up the cephalic sensory organ (Figs. 3, 4, 5, 6). These are: 1. ampullary cells that possess a deep ciliated lumen; 2. ciliary tuft cells with a finely granular cytoplasm, and at least 20 cilia arising from the apical surface; 3. parampullary cells that give rise to one or two cilia and numerous microvilli on the receptive surface.

2. Sensory cells

Ampullary cell. Each of the four ampullary or flask-shaped receptor cells contains a deep lumen that is similar in form to that of the cell (Fig. 7). The lumen extends almost to the base of the cell where it expands to a maximum of 5 μm. Apically, it constricts into a long narrow channel or neck measuring 0.75 μm in diameter. This passage eventually opens to the exterior through a tiny pore at the epidermal surface (Fig. 6). Constrictions of both lumen and sensory cell occur near the region where the cell leaves the cerebral commissure to join a dendritic tract. The ampullary receptor cell that joins a given tract of dendrites also terminates in that particular grouping at the level of the epidermis (Fig. 6). Each of the three tracts contains at least one ampullary cell, although the right bundle contains two of these receptors (Figs. 4, 6).

The lumen of ampullary sensory cells is tightly packed

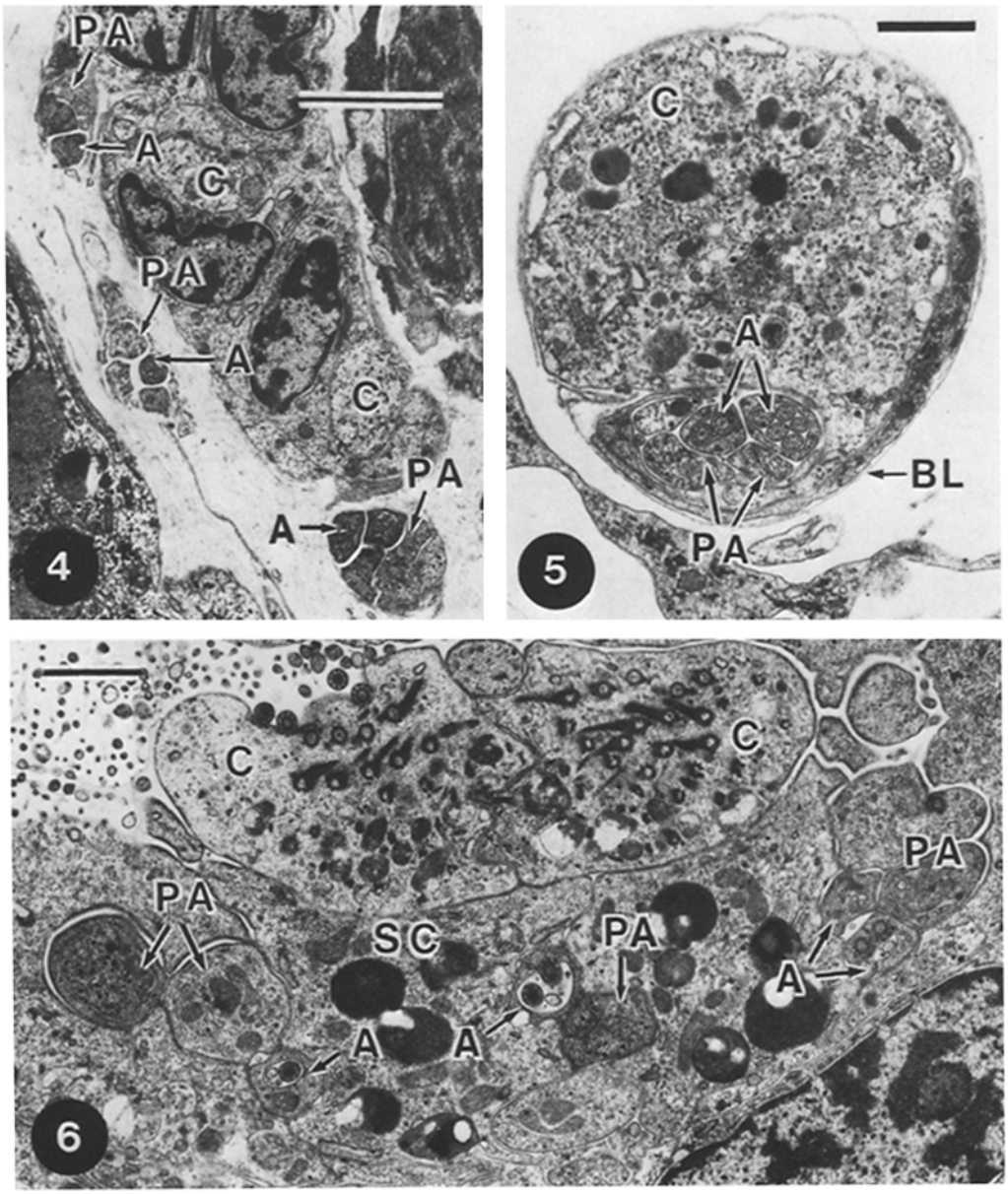

Fig. 4. Section through three bundles of dendrites containing ampullary (*A*) and parampullary (*PA*) sensory cells. Note that ciliary tuft cell processes (C) have not yet connected to their respective bundles. Scale: 2.5 μm

Fig. 5. Dendritic bundle showing ampullary cells (*A*), ciliary tuft cell (*C*), and parampullary cells (*PA*) enclosed by basal lamina (*BL*). Scale: 1 μm

Fig. 6. Cephalic sensory field, at level of epidermis, revealing its sectorial shape. Ciliary tuft cells (*C*) occupy apex and groupings of ampullary (*A*) and parampullary (*PA*) cells form arc (base) of field. These groupings terminate among supporting cells (SC). Scale: 1 μm

with cilia. All of the cilia originate from the cell surface inside the lumen; they appear to be oriented in opposing directions. Cilia that are situated toward the floor point upward, whereas those situated toward the neck point downward. The expanded region of the cell contains 50 to 60. In cross-section they appear to be arranged in rows of not more than eight cilia (Fig. 8). The neck regions of these cells, in contrast, contain only one or two cilia (Figs. 4, 5, 6). No cilia were observed to pass through the narrow neck to extend beyond the epidermal surface. The cilia occupying this channel are in close apposition and display a convoluted interfolding of opposing membranes. No rootlets were observed associated with cilia, although there are basal feet.

An elliptical nucleus occupies the basal region of ampullary cells. As many as three Golgi bodies are situated between the bottom of the lumen and the nucleus. Mitochondria are scattered around nuclear areas and upwards into the thin walls forming the flask. Cisternae of rough endoplasmic reticulum are occasionally found in the regions of the cell adjacent to the lumenal surface. A few electron dense granules measuring from 0.3 μm in diameter are

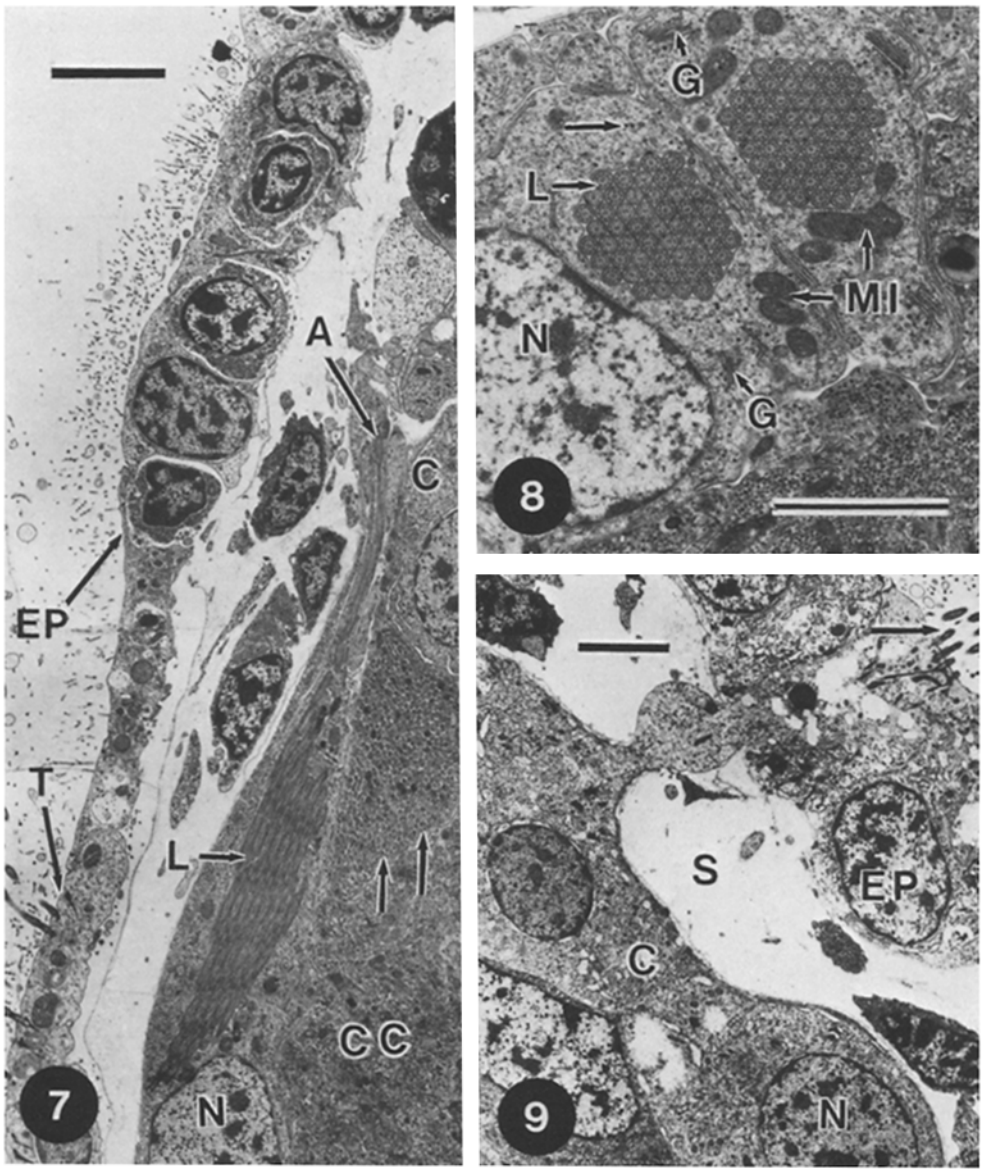

Fig. 7. Sagittal section showing ampullary cell (*A*) with nucleus (*N*) and deeply invaginated, ciliated lumen (*L*). Within cerebral commissure (*CC*) tracts of neurites (*arrows*) and a ciliated cell body (*C*) are shown. Also note thickened epidermis (*EP*) indicating position of cephalic sensory field in relation to intraepithelial ciliated cell (*T*) and cerebral commissure. Scale: 2.5 μm

Fig. 8. Cross section of ampullary receptors showing dense packing of cilia within lumen (*L*). Nucleus (*N*), Golgi bodies (G), mitochondria (MI), and small vesicles (arrows). Scale: 2.5 μm

Fig. 9. Ciliary tuft sensory cell (*C*) spanning sinus (*S*) between epidermis (*EP*) and cerebral commissure. Apical cilia (*arrow*) and nucleus (*N*) of other ciliary tuft cell are also shown. Scale: 2.5 μm

found distributed around the nucleus. Smaller electron dense vesicles of approximately 0.07 μm in diameter are generally distributed throughout the cell but tend to be concentrated toward the basal regions. Axons of these cells possess microtubules, occasional mitochondria and small electron dense vesicles. Axons pass into the mass of neurites composing the cerebral commissure, although they were not observed to synapse with these neurites. Synapses of any form, including those involving axons of the other two types of receptor cells, were not observed. It is possible that axons may bifurcate and send separate processes to each cerebral ganglion. Moreover, a cell body could give rise to more than one axon, whose eventual destination would be the cerebral ganglia. Obvious synapses become apparent in the ganglia. It should be noted that the axons of these sensory cells could not be traced to their fullest extent owing to the intricate network of fibers composing the cerebral commissure. The general morphology of ampullary cells of *Rostanga pulchra* veligers resembles the flask-shaped cells described in *Phestilla sibogae* (Bonar 1978a).

Ciliary tuft cell. The two ciliary tuft receptors have perikarya that contain densely staining spherical nuclei (Figs. 3,

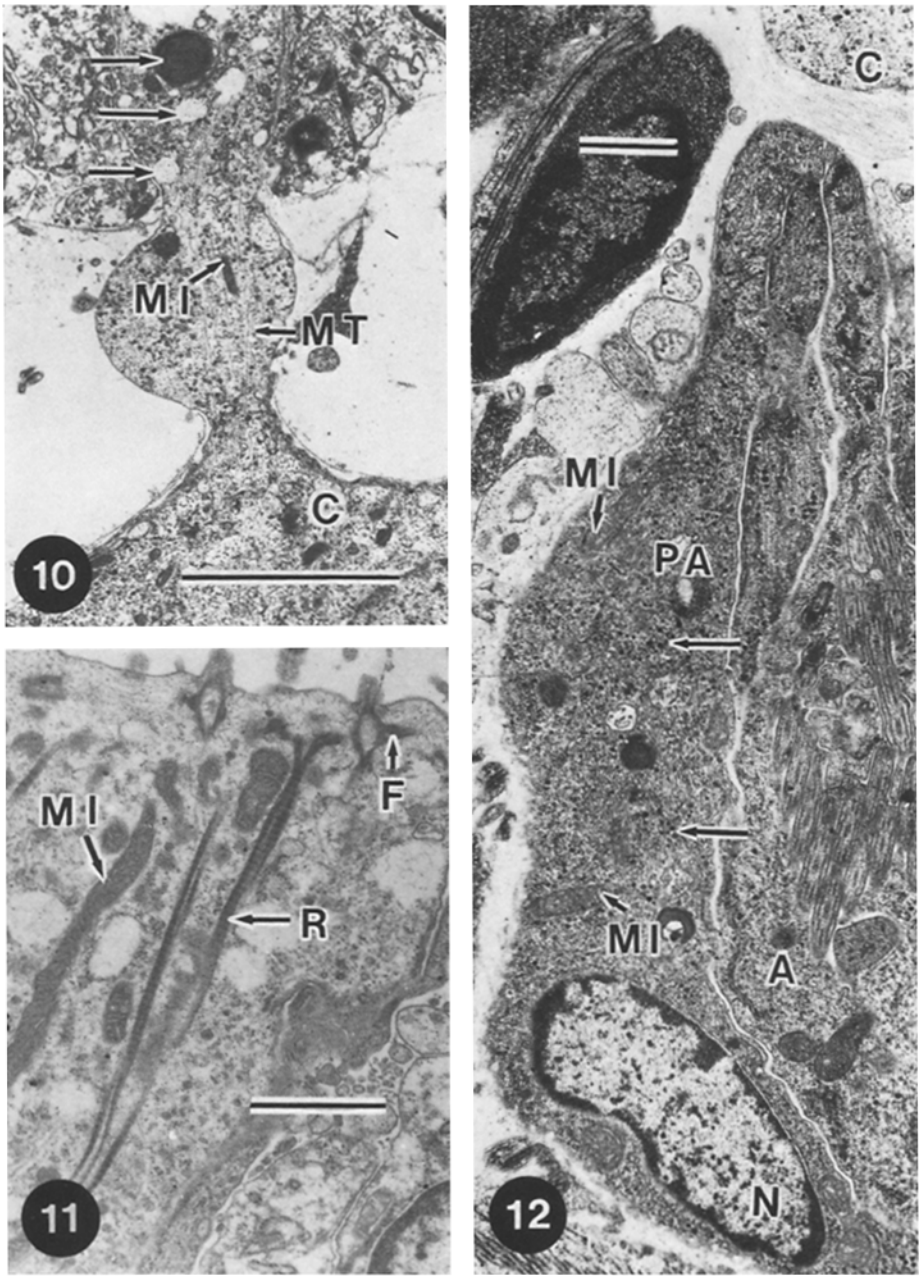

Fig. 10. Higher magnification of ciliary tuft cell dendrite (*C*) showing microtubules (*MT*), mitochondria (*MI*), electron translucent and dense granules (arrows) contained within finely granular cytoplasm. Scale: 2.5 μm

Fig. 11. Terminal of ciliary tuft sensory cell showing mitochondria (MI), ciliary rootlet (*R*) and basal foot (*F*). Scale: 1 μm

Fig. 12. Parampullary sensory cell (*PA*) showing nucleus (*N*), mitochondria (*MI*), and small vesicles (*arrows*). Note densely staining cytoplasm of ampullary (*A*) and parampullary receptors in comparison to ciliary tuft sensory cells (*C*). Scale: 1 μm

9). A relatively large amount of rough endoplasmic reticulum is scattered around each nucleus (Figs. 3, 7). This area is also occupied by Golgi bodies and mitochondria. Axons arise from the basal region of the cell bodies and pass into the mass of neurites in the cerebral commissure. They contain microtubules and small electron dense vesicles measuring about 0.05 μm in diameter. Many of these vesicles, together with several larger electron dense granules averaging 0.4 μm in diameter, are found throughout the cell. The cytoplasm, especially in the dendritic parts of these cells, stains less densely than other sensory cell types (Figs. 4, 5).

The dendrites of ciliary tuft cells traverse the sinus between the epidermis and the cerebral commissure in separate bundles. They occupy the innermost region of their respective dendritic tract (Fig. 5). These dendrites measure approximately 4.2 μm in diameter in comparison to an average diameter of 1.1 μm for other receptor dendrites. The two ciliary tuft cells eventually terminate adjacent to each other in the epidermis. They constitute the apex of the cephalic sensory field (Fig. 6). Twenty or more cilia arise from the surface of each dendritic terminal, and the cilia from both endings contribute to the tuft in the intravelar area. Individual cilia possess a 9+2 tubule arrangement. A basal foot and ciliary rootlet arise from the basal body (Fig. 11). Ciliary rootlets span the thickness of the epithelium, and mitochondria are commonly found among these structures (Figs. 9, 11). Electron translucent vacuoles measuring from 0.25 to 0.55 μm in diameter, are restricted to the epidermal segment of the dendritic ending (Figs. 9, 10). Each terminal also possesses parallel arrays of microtubules and the aforementioned electron dense vesicles (Fig. 10).

Parampullary cell. These cells resemble the ampullary cells in general morphology. However, they lack a ciliated lumen

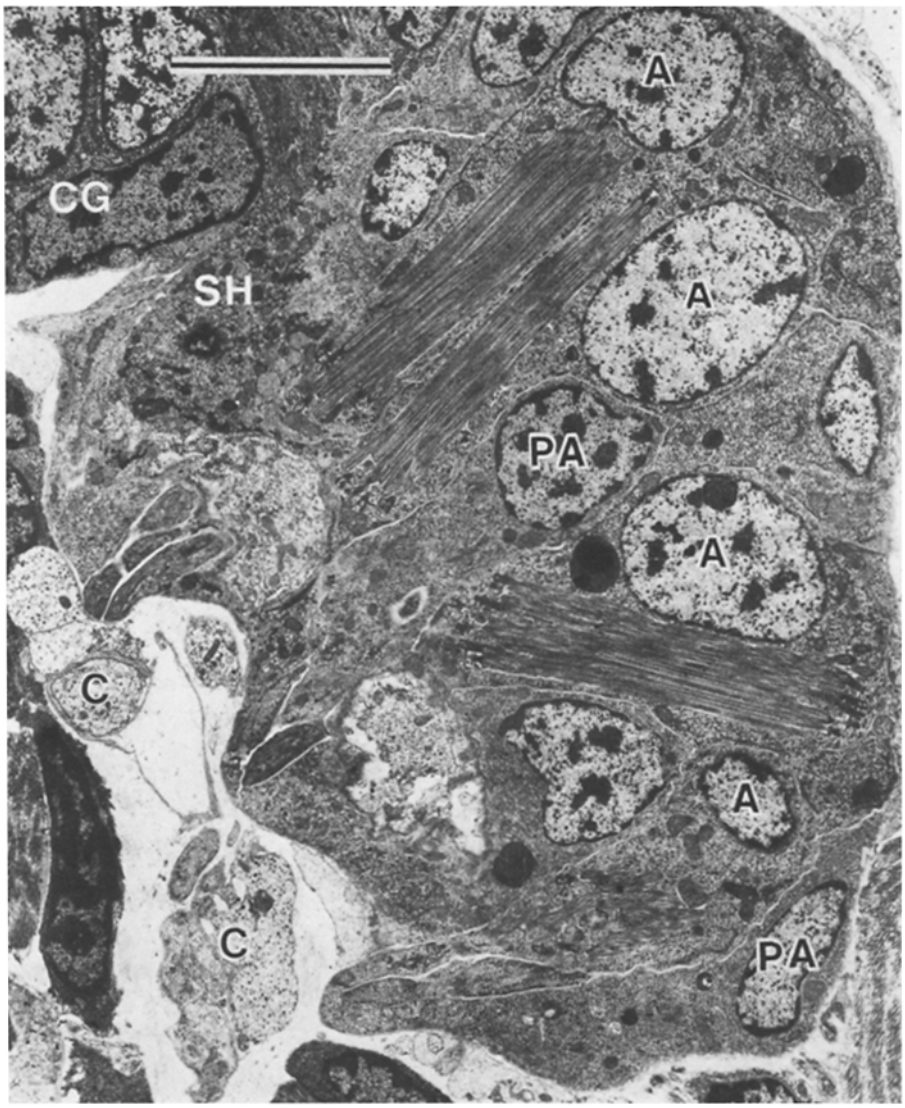

Fig. 13. Section through cerebral commissure showing ciliary tuft cell dendrites (*C*) and cell bodies of ampullary (*A*) and parampullary (*PA*) receptors. Also note sheath cell (*SH*) and right cerebral ganglion (*CG*). Scale: 5 μm

and are characterized by the presence of small electron opaque vesicles averaging 0.07 μm in diameter (Figs. 3, 12). The nucleus occupies the very base of the cell, and several Golgi bodies occur in perinuclear regions. A small quantity of rough endoplasmic reticulum is interspersed among mitochondria, multivesicular bodies and a few large electron dense granules. These structures are situated in the area surrounding the nucleus but tend to be concentrated toward the dendrite. A basally derived axon passes into the cerebral commissure and contains microtubules as well as small vesicles.

Dendrites of this cell type join into each of the three tracts of sensory cells (Fig. 3). Two to four of these processes can be distinguished in each tract and average 1.2 μm in diameter (Figs. 4, 5). The dendrites are characterized by possessing a few mitochondria, microtubules and the small electron dense vesicles mentioned above. They terminate in the epidermis among the groupings of other receptor cells (Fig. 6). Only one of these terminals is found in conjuction with the ciliated receptor endings, whereas the remaining eight or nine are associated with ampullary receptor assemblages (Fig. 6). Together with the ampullary sensory cells they represent the broad arc of the sector of the cephalic sensory field. Microvilli and one or two cilia arise from the apical surface of each cell. In the majority of instances the cilia appear to be bent into a position that is parallel to the epidermal surface.

3. Cerebral commissure

The mid-region of the cerebral commissure consists of neurites that appear to be partitioned into several separate tracts. Each tract runs parallel to the other (Fig. 7). Sensory cell bodies are clumped together above these neurites, in the medial and peripheral area of the commissure (Figs. 7, 13). The perikarya of ampullary and parampullary sensory cells are found along the outer dorsal margin, whereas ciliary tuft cells are situated on the opposite, inner dorsal side of the cerebral commissure (Figs. 7, 13). The cell bodies of ampullary cells occur in two groups of two cells with the parampullary cells distributed around them (Fig. 13). All receptor cell perikarya appear to be segregated from the neurites by long thin processes. The bundles of neurites are also separated from each other by these processes (Fig. 7), which originate from sheath cells that have been described elsewhere (Chia and Koss 1982, 1983). Sheath

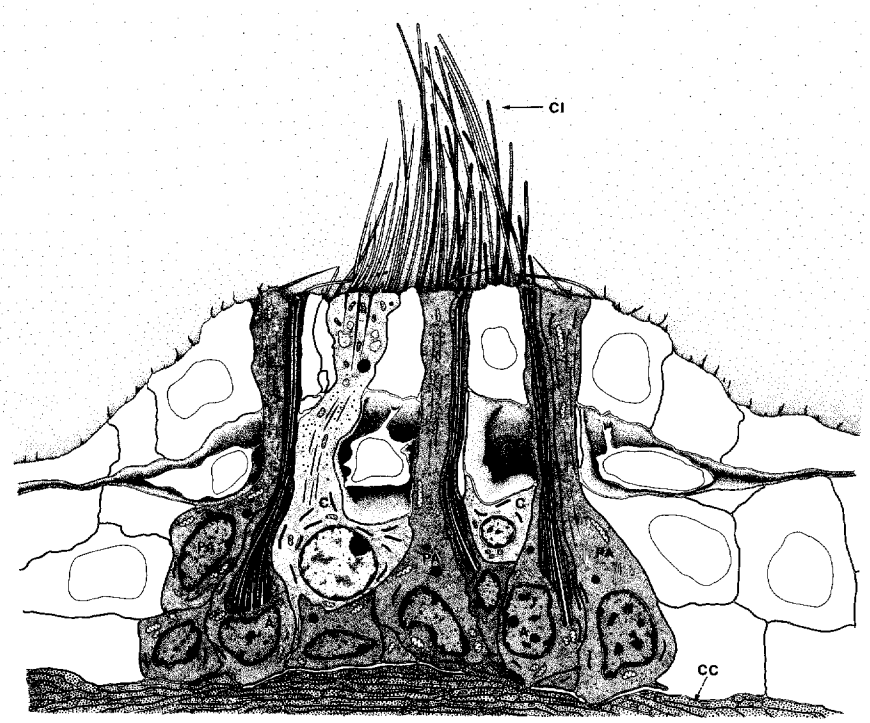

Fig. 14. Schematic drawing of cephalic sensory organ, in ventral view, illustrating relationships of ciliary tuft (*C*), ampullary (*A*), and parampullary (*PA*) sensory cells in cerebral commissure (*CC*). Sensory cell processes pass through a sinus (*S*) into epidermis as three bundles. Tuft of cilia (*CI*) at epidermal surface is also shown

cells are similar, if not identical, to the supporting cells described in the abdominal ganglia of *Aplysia* veligers (Schacher et al. 1979). The relationships and features of the cephalic sensory organ are summarized in Fig. 14.

Discussion

The morphology of superficial sensory receptor cells of adult gastropods has been extensively studied (Crisp 1971; Emery and Audesirk 1978; Kataoka 1976; Matera and Davis 1982; Philips 1979; Storch and Welsch 1969; Wright 1974a, b; Zylstra 1972). These cells are thought to have mechanosensory or chemosensory functions, although to date there are no morphological criteria that separate each into a modality (Crisp 1971). Therefore, most of these structural studies have concentrated on specific areas of the head, which are known to subserve a particular function from behavioral or electrophysiological evidence (refer to Emery and Audesirk 1978; Matera and Davis 1982; Wright 1974a, b). The situation is more complicated when relating structure to function in veliger larvae as the animals are too small for behavioral and electrophysiological studies.

The sensory cells described here closely resemble those described for adult gastropods in that cilia arise from the apical surface, and an axon leads from the basal region of each cell type (Emery and Audesirk 1978; Matera and Davis 1982; Wright 1974a, b). Furthermore, these cells are collectively organized into a delineated structure that is embedded in and contributes to ganglionic tissue. The organ is exposed to the external environment by being positioned in the anterior region of the head, between the velar lobes, and would therefore be continuously bathed in water currents created by the velum.

The profile of the cephalic sensory organ in a *Rostanga* veliger is similar to that reported for *Phestilla sibogae* (Bonar 1978a). The receptors originate from the cerebral commissure and terminate in the epidermis. The ampullary sensory cells also resemble the flask-shaped cells in *Phestilla*. However, the organ in *Rostanga pulchra* contains three types of cells that are arranged in a specific manner. It is reasonable to suggest that this organization reflects a higher degree of specialization. For example, at least 14 cells comprised of three different types of receptors contribute to the cephalic sensory organ in *Rostanga pulchra*. This is compared to five or six cells of a single type in *Phestilla sibogae* (Bonar 1978a). In the former species, dendrites from the different sensory cells form tracts that end, at the level of the epidermis, in a sectorial field. The apex of the field is represented by ciliary tuft receptors and the arc (base) by three clusters of ampullary and parampullary receptor cells. Further, the ampullary sensory cells in *Rostanga pulchra* differ in that they are exposed to the exterior through a small pore rather than a larger opening. In *Phestilla*, cilia project beyond the level of the epidermis through this opening, whereas in *Rostanga* they do not.

The morphology of superficial mechanoreceptors in gastropods is relatively unknown, although in nudibranchs electrophysiological studies confirm their existence (Alkon et al. 1978; Audesirk and Audesirk 1980a, b). The majority of studies on superficial receptors have associated them with a chemoreceptive modality. The morphology of the cells comprising the cephalic sensory organ in *Rostanga pulchra* indicates that they display certain consistencies with those cells of known structure and function in adult gastropods, except for the ampullary receptors, that remain an enigma. It is a unique cell type that has not been described in adult

gastropods, but is common among cephalopod molluscs. In cephalopods, flask-shaped cells have been implicated in chemoreception (Altner and Prillinger 1980). However, in *Rostanga pulchra* the sensory surface is not in direct contact with the environment and may well function as a mechanoreceptor, or more specifically as a vibration or pressure receptor. This has been suggested for a similar receptor in *Octopus* (Emery 1976; Altner and Prillinger 1980).

Ciliary tuft and parampullary cells are similar to those described in adult opisthobranchs (Emery and Audesirk 1978) and pulmonates (Wright 1974a, b). Extrapolating from the situation in adult gastropods, it is reasonable to suggest that these two cell types may function in chemoreception. By analogy with the vertebrates, tuft cells could be distance chemoreceptors because they possess a large number of cilia, whereas parampullary cells could be contact chemoreceptors because they possess only a few cilia (Laverack 1974; Emery and Audesirk 1978). The cephalic sensory organ is therefore suited to perception of a chemical emitted by the adult prey that induces settlement and metamorphosis. In *Rostanga pulchra,* competent veligers metamorphose in response to the presence of the adult food species, a sponge, *Ophlitaspongia pennata* (Chia and Koss 1978). The high degree of morphological specialization displayed by the larva of *Rostanga pulchra,* which includes a cephalic sensory organ as well as rhinophores (Chia and Koss 1982), suggests that the nervous system is finely tuned for locating this substrate at settlement. This is not unusual considering the patchy distribution of the sponge and the lengthy obligatory planktonic period. Conceivably, distance chemoreceptors such as those in the rhinophores could initially sense the potential settling site (Chia and Koss 1982). Receptors such as those situated in the cephalic sensory field, with similar capabilities to those above, could further discriminate between appropriate chemical cues and maintain a constant orientation toward the appropriate substrate. After settlement, and when the larvae are crawling, the contact chemoreceptors would take effect and in turn initiate metamorphosis. It is of significance that the cephalic sensory organ is connected to the cerebral ganglia because these ganglia control the activity of the velum, that in turn controls swimming (Mackie et al. 1976). Initially a larva would be oriented toward the substrate. Stoppage of the velar cilia would deposit the larva on the sponge, effecting settlement and possibly initiating crawling. In the crawling larva, the cephalic sensory organ would be in close proximity to the substrate, and it is possible that contact or high threshold chemoreceptor cells could be stimulated to initiate irreversible metamorphosis. Again it is important that these cells contribute to the cerebral ganglia, because the initial phase of metamorphosis involves loss of the ciliated velar cells and reabsorption of the velum (Chia and Koss 1978).

Development of the cephalic sensory organ does not appear to be a critical morphological event that determines larval competency in *Rostanga pulchra.* In this species, competency is established by the sequential differentiation of the eye, propodium and finally the rhinophores (Chia and Koss 1978). The degree of differentiation of the cephalic sensory organ in precompetent veligers (those without rhinophores) is identical to that of competent veligers. Larvae that are precompetent will not metamorphose, therefore indicating that the cephalic sensory organ may not be a structure only devoted to settlement and metamorphosis. It may be involved in other functions such as: 1. monitoring the position of the larva when in an inverted position; 2. control of the quality of water in the mantle cavity; 3. co-ordinating retraction or protraction of the velum and cephalopedal mass into and out of the shell; 4. involved in feeding by sorting and selecting food items.

Early stage veligers occasionally invert and spin around, with the velum applied to a surface, much in the manner of a "spinning top". The cephalic sensory organ would be in a position where it could perceive the immediate presence of that surface, an object on that surface, or the texture of the surface. A similar set of temporal conditions may be required, and monitored by the cephalic sensory organ, at the time of settlement when crawling is effected. This would involve touch or tactile perception.

Retraction of the mantle, a phenomenon described for many opisthobranch larvae, results in a large cavity remaining within the larval shell. The appearance of the larval heart is coincidental with mantle retraction in veligers of *Rostanga pulchra* (Chia and Koss 1978). The larval heart could be involved in circulating seawater in and out of the mantle cavity (refer to Switzer-Dunlap 1978). It is possible that the cephalic sensory organ, owing to its position at the entrace to the mantly cavity, chemically monitors the quality of seawater in the mantle cavity and co-ordinates the activity of the larval heart. That is, to increase or decrease the flow of water in and out of the mantle cavity.

Because the cephalic sensory organ is situated at the level of the shell aperture, it could also regulate or integrate withdrawal of the velum into the shell, and conversely the extent of extrusion of this structure. This would involve mechanical stimulation of the receptors of the organ upon retraction into the shell. Again it is significant that the cells of the organ are in contact with the cerebral ganglia. Withdrawal of the velum involves ciliary arrest and the appropriate folding of the velar lobes to accommodate them in the shell. When the cephalopedal mass is everted beyond the organ this would indicate to the larva that protrusion had been accomplished. Events such as these would involve receptors of the cephalic sensory organ.

The position of the cephalic sensory organ, between the velar lobes, suggests it may be involved in feeding. Water currents created by the velum could bring potential food items in contact with the organ. This structure may initially select the quality of a particular food item that is to be passed to the mouth for further discrimination. Food could be accepted or rejected on the basis of taste, size, weight, etc., that would involve chemoreception or mechanoreception or both. Any of the above capabilities, including those associated with settlement and metamorphosis, would involve the ability to respond to tactile and/or chemical stimuli. Moreover, such perception could conceivably include any one, or all of the sensory cell types described in the cephalic sensory organ. Therefore, in *Rostanga pulchra,* this structure may be multimodal in function.

It should be noted that the cephalic sensory organ may be of some phylogenetic importance in the Spiralia. Bonar (1978b) has suggested that this organ may arise from cells comprising the original apical plate of the trochophore. If this is the case, the cephalic sensory organ may be homologous to structures of the same origin in the Mollusca and possibly other Spiralian phyla. The organ does resemble what appear to be apical plate derivatives of certain larval

Spiralians. For example, the apical organs in polyclad turbellarians possess morphologically similar sensory cells that are clustered together on top of the brain (refer to Lacalli 1983; Ruppert 1978). Unfortunately, no detailed fine structural study of the apical plate, and its derivatives, is available for any molluscan trochophore, which would allow a comparison to the cephalic sensory organ. Therefore, until such studies are conducted, it is not possible to apply the homology theorem (Rieger and Tyler 1979) to determine which (if any) ultrastructural characters of the cephalic sensory organ could be useful in establishing phylogenetic relationships.

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References

Alkon DL, Akaike T, Harrigan J (1978) Interaction of chemosensory, visual, and statocyst pathways in *Hermissenda crassicornis*. J Gen Physiol 71:177–194

Altner H, Prillinger L (1980) Ultrastructure of invertebrate chemoreceptors, thermoreceptors and hygroreceptors, and its functional significance. Intern Rev Cytol 67:69–140

Audesirk G, Audesirk T (1980a) Complex mechanoreceptors in *Tritonia diomedea*. I. Responsiveness to mechanical and chemical stimuli. J Comp Physiol 141:101–109

Audesirk G, Audesirk T (1980b) Complex mechanoreceptors in *Tritonia diomedea*. II. Neuronal correlates of a change in behavioral responsiveness. J Comp Physiol 141:111–122

Bonar DB (1978a) Ultrastructure of a cephalic sensory organ in larvae of the gastropod *Phestilla sibogae* (Aoelidacea, Nudibranchia). Tissue Cell 10:153–165

Bonar DB (1978b) Morphogenesis at metamorphosis in opisthobranch molluscs. In: Chia FS, Rice MF (eds) Settlement and metamorphosis of marine invertebrate larvae. Elsevier/North Holland, New York, pp 177–196

Bonar DB, Hadfield MG (1974) Metamorphosis of the marine gastropod *Phestilla sibogae* Bergh (Nudibranchia: Aoelidacea). I. Light and electron microscope analysis of larval and metamorphic stages. J Exp Mar Biol Ecol 16:227–255

Chia FS, Koss R (1978) Development and metamorphosis of the planktotrophic larvae of *Rostanga pulchra* (Mollusca: Nudibranchia). Mar Biol 46:109–119

Chia FS, Koss R (1982) Fine structure of the larval rhinophores of the nudibranch, *Rostanga pulchra*, with emphasis on the sensory receptor cells. Cell Tissue Res 225:235–248

Chia FS, Koss R (1983) Fine structure of the larval eyes of *Rostanga pulchra* (Mollusca, Opisthobranchia, Nudibranchia). Zoomorphology 102:1–10

Chia FS, Atwood DG, Crawford BJ (1975) Comparative morphology of echinoderm sperm and possible phylogenetic implications. Am Zool 15:553–565

Crisp M (1971) Structure and abundance of unspecialized external epithelium of *Nassarius reticulatus* (Gastropoda, Prosobranchia). J Mar Biol Assoc UK 51:865–890

Emery DG (1976) Observations on the olfactory organ of adult and juvenile *Octopus joubini*. Tissue Cell 8:33–46

Emery DG, Audesirk TE (1978) Sensory cells in *Aplysia*. J Neurobiol 9:173–179

Kataoka S (1976) Fine structure of the epidermis of the optic tentacle in a slug, *Limax flavus*. Tissue Cell 8:47–60

Lacalli TC (1983) The brain and central nervous system of Muller's larva. Can J Zool 61:39–51

Laverak MS (1974) The structure and function of chemoreceptor cells. In: Grant PT, Mackie AM (eds) Chemoreception in marine organisms. Academic Press, New York, pp 1–48

Mackie GO, Singla CL, Thiriot-Quievreux C (1976) Nervous control of ciliary activity in gastropod larvae. Biol Bull 151:182–199

Matera EM, Davis WJ (1982) Paddle cilia (discocilia) in chemosensitive structures of the gastropod mollusk *Pleurobranchia california*. Cell Tissue Res 222:25–40

Phillips CFA (1979) Ultrastructure of sensory cells on the mantle tentacles of the gastropod *Notoacmea scutum*. Tissue Cell 11:623–632

Richardson KC, Jarrett L, Finke EH (1960) Embedding in epoxy resins for ultrathin sectioning in electron microscopy. Stain Technol 35:313–323

Rieger R, Tyler S (1979) The homology theorem in ultrastructural research. Amer Zool 19:655–664

Ruppert EE (1978) A review of metamorphosis of turbellarian larvae. In: Chia FS, Rice MF (eds) Settlement and metamorphosis of marine invertebrate larvae. Elsevier/North Holland, New York, pp 65–81

Schacher S, Kandel ER, Woolley R (1979) Development of neurons in the abdominal ganglion of *Aplysia californica*. II. Non-neural support cells. Develop Biol 71:176–190

Storch V, Welsch V (1969) Über Bau und Function der Nudibranchier-Rhinopheron. Z Zellforsch 97:528–536

Switzer-Dunlap M (1978) Larval biology and metamorphosis of aplysiid gastropods. In: Chia FS, Rice ME (eds) Settlement and metamorphosis of marine invertebrate larvae. Elsevier/North Holland, New York, pp 197–206

Wood RL, Luft JH (1965) The influence of buffer systems on fixation with osmium tetroxide. J Ultrastruct Res 12:2245

Wright BR (1974a) Sensory structure of the tentacles of the slug *Arion ater* (Pulmonata, Mollusca) 1. Ultrastructure of the distal epithelium, receptor cells and tentacular ganglion. Cell Tissue Res 151:229–244

Wright BR (1974b) Sensory structure of the tentacles of the slug *Arion ater* (Pulmonata, Mollusca) 2. Ultrastructure of the free nerve endings in the distal epithelium. Cell Tissue Res 151:245–257

Zylstra U (1972) Distribution and ultrastructure of epidermal sensory cells in the fresh water snails *Lymnaea stagnalis* and *Biomphalaria pfeifferi*. Neth J Zool 22:283–298

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