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Statocysts of Hydromedusae

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Summary. The statocysts of Leptomedusae are formed as a depression in the velum. They are lined on the inside towards the distal part of the velum by thin epithelium and towards the proximal part by ciliated sensory cells. Lithocytes are present in the centre. The concretion contains calcium sulphate and in some cases, calcium phosphate is also present in addition to some membranous material.

The statocysts of Narcomedusae arise from the exumbrellar nerve ring as free sensory clubs. They have a proximal basal cushion of sensory cells from the centre of which arises a sensory club (*Aegina*) or a sensory papilla carrying a sensory club (*Solmissus*). The sensory club has an axial strand of endodermal cells covered by ciliated sensory cells. Some of the endodermal cells have a concretion. While the statocysts of Leptomedusae are totally ectodermal, those of Narcomedusae are ecto-endodermal in origin.

The sensory cilia of Leptomedusae, especially those present on the sensory cells adjacent to the lithocyte, run close and parallel to the lithocyte membrane. In Narcomedusae the sensory cilia of the basal cushion and sensory papilla are tall and strong. Ciliary rootlets are missing in the sensory cilia of Leptomedusae and in the sensory club of Narcomedusae but they are strongly developed in the cilia of basal cushion and sensory papilla. The cilia have 9+2 filament content. A ring of stereocilia surrounds the kinocilium of the sensory club cells. Mechanism of statocyst function is discussed.

Key words: Statocysts (Hydromedusae) — Concretion — Sensory cilia, stereocilia — Equilibrium.

Introduction

The light microscope account of the statocysts of hydromedusae was given by Hertwig and Hertwig (1878), Linko (1900), Russell (1953) and Bouillon (1956 to 1957). Recently Horridge (1969) studied the ultrastructure of a number of Trachymedusae and a Narcomedusa. Horridge also proposed the evolution of statocysts and stereocilia in medusae. Fränkel (1925) and Bozler (1926) investigated the significance of the statocysts of scyphomedusae in maintaining equilibrium; comparable studies on statocyst function in hydromedusae appear non-existent. Spangenberg (1968) and Spangenberg and Beck (1968) investigated the chemical nature of statocyst concretions in *Aurelia aurita* but again there is no comparable information for hydromedusae. The statocysts of Leptomedusae

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represent a line of statocyst evolution entirely different from that of other medusae but their fine structure has been unknown. Although Horridge's (1969) study includes some information on the narcomedusan *Cunina*, his account is brief and needs to be supplemented by study of other Narcomedusae, especially as the group occupies a key position in the evolutionary series so far as the statocysts are concerned. Thus the present study was directed toward the fine structure of statocysts of both Leptomedusae and Narcomedusae. A histochemical inverstigation of the statocyst concretion was undertaken, which provides a basis for comparison of these structures with their counterparts in the scyphomedusae.

Aequorea aequorea (Order Leptomedusae) is particularly suitable for experimental study because a good deal of information on their musculature and its function in the execution of different movements is already known (Horridge, 1955). Experiments were carried out on *Aequorea* to ascertain how righting ability depends on the statocysts.

Materials and Methods

The fine structure of the statocysts of *Tiaropsis multicirrata*, *Mitrocomella polydiademata*, *Halistaura cellularia*, *Phialidium gregarium*, *Aequorea aequorea*, *Aegina citrea* and *Solmissus marshalli* was studied. The first five belong to Leptomedusae and the last two are Narcomedusae. The material was prepared for electron microscopy using modified Dorey fixative in which 2% sodium chloride was used in place of sucrose (Dorey, 1965).

The fixative consists of a mixture of equal volumes of (a) 4% osmium tetroxide solution in double distilled water and (b) a mixture of potassium chromate 2 gms, calcium chloride. 055 gms, sodium chloride 4 gms, and distilled water to make 100 mls. 0.1N hydrochloric acid was used to bring up the pH to 7.5. Tissue was fixed for one hour at 4°C. After fixation the material was passed through graded alcohols at 4°C to propylene oxide and was embedded in Epon 812 according to the method of Luft (1961). Sections were cut with a diamond knife on Reichert UM-2 ultramicrotome. Sections were stained with uranyl acetate and lead citrate (Veneable and Coggeshall, 1965) and studied with Philips EM-100B. 0.5μ thick sections were stained with Richardson's methylene blue and Azur 2 mixture (Richardson, Jarett and Finke, 1960).

a) Methods Demonstrating Calcium in Statocysts

Small pieces of tissue from the medusae of *Aequorea aequorea*, *Mitrocomella polydiademata*, *Phialidium gregarium*, and *Halistaura cellularia* were removed in sea water and fixed in 90% ethanol 18 hours at room temperature. The material was dehydrated by 10 min steps in 95% and absolute ethanol, then placed in paraplast at 60° for three hrs, embedded and cut into 7μ sections on the Spencer rotary microtome.

i) Von Kossa method for calcium was used as described by Humason (1966) except that the slides in $AgNO_3$ solution were exposed to ultraviolet instead of bright light. The UV reduces silver nitrate faster.

ii) Lillie's (1965) McGee Russell alizarine red procedure for calcium was also used.

b) Technique Involving Statocyst Removal

The righting behaviour of *Aequorea aequorea* was observed in running sea water tank. Then the medusa were relaxed with equal volumes of isotonic $MgCl_2$ solution and the sea water, and the statocysts were removed with a vibrating needle (Wenger, 1967). The animals were strained during the operation by suction holders attached at various points using Prior micromanipulators. Following this, the medusae were left in running sea water to revive. After four hrs righting behaviour was usually observed.

Observations

A. Structure of Statocysts

Leptomedusae

The statocysts of Leptomedusae lie on the bell margin. Their number varies from 8 in *Tiaropsis* to more than 300 in *Aequorea* (approximately 6 cm in diameter). They are formed as a pocket in the velum which remains open on the proximal side in *Tiaropsis* and *Mitrocomella* (Fig. 1) but is closed in *Halistaura*, *Phialidium* and *Aequorea* (Fig. 2). The size of the statocyst varies a great deal. Each statocyst may extend 60 μ (*Aequorea*) to 300 μ (*Halistaura*) around the umbrella margin, 50 μ (*Aequorea*) to 125 μ deep (*Halistaura*) and 40 μ (*Aequorea*) to 120 μ (*Tiaropsis*) wide. Except for these differences in size and number, the statocysts of Leptomedusae show a great deal of similarity in their structure. The statocysts are covered on the outside by a single layered epithelium, lined inwardly on the distal side by a thin epithelium and on the proximal side by sensory cells. In the center they contain lithocytes (Figs. 1 and 2).

Outer Epithelium. The statocysts of *Tiaropsis*, *Mitrocomella* and *Halistaura* are covered on the outside by vacuolated cells, whereas those of *Phialidium* and *Aequorea* are lined by thin epithelium. The vacuolated cells of *Halistaura* are cuboidal (4–7 μ in length and breadth). In *Tiaropsis* and *Mitrocomella* the smaller vacuolated cells 8–10 μ tall and 6–8 μ broad lie close to the velum, whereas the large cells roughly 20 μ tall and 10 μ wide cover the central part of the statocyst. A large vacuole is present in the center of each cell but it may be missing in the cells lying close to the exumbrellar sensory epithelium of *Tiaropsis*. The vacuole fills almost the whole of the cell soma; thus the cytoplasm is restricted to the cellular periphery. The nucleus in most cases lies towards the free surface. The cytoplasm has a few mitochondria, a Golgi complex, endoplasmic reticulum and small vesicles 150–400 mμ in diameter. Most of the vesicles are empty but some contain electron dense material. In *Tiaropsis* cells lying across the exumbrellar sensory epithelium contain dark pigment granules of 1 μ diameter. The outer and inner thin epithelium have a similar structure; therefore a common description is given for both.

Mesoglea. The mesoglea of the velum is continuous in the region of the statocyst and separates the inner epithelium from the outer. It is formed of amorphous material containing some electron dense material and a few radially oriented fibres roughly 60 Å thick.

The Thin Epithelium. The cell bodies are thin, squamous, flat and roughly 1 μ tall but the height may reach up to 3 μ near the nucleus. The cell body contains a central nucleus, a large number of empty vesicles of 200–300 mμ diameter, mitochondria, Golgi component, endoplasmic reticulum and sometimes a lysosome. Some of these vesicles contain electron dense material.

Sensory Epithelium. A single layer of ciliated sensory cells is present on the proximal side (Figs. 1 and 2). In *Tiaropsis* and *Mitrocomella* the epithelial cells are tall, columnar and fairly uniform in size and shape except the sensory cells lying adjacent to the lithocyte, which may be triangular thus differing in size and shape from the rest of the sensory cells. Such triangular cells are also present adjacent to the lithocytes of *Halistaura*, *Phialidium* and *Aequorea*. A part of the

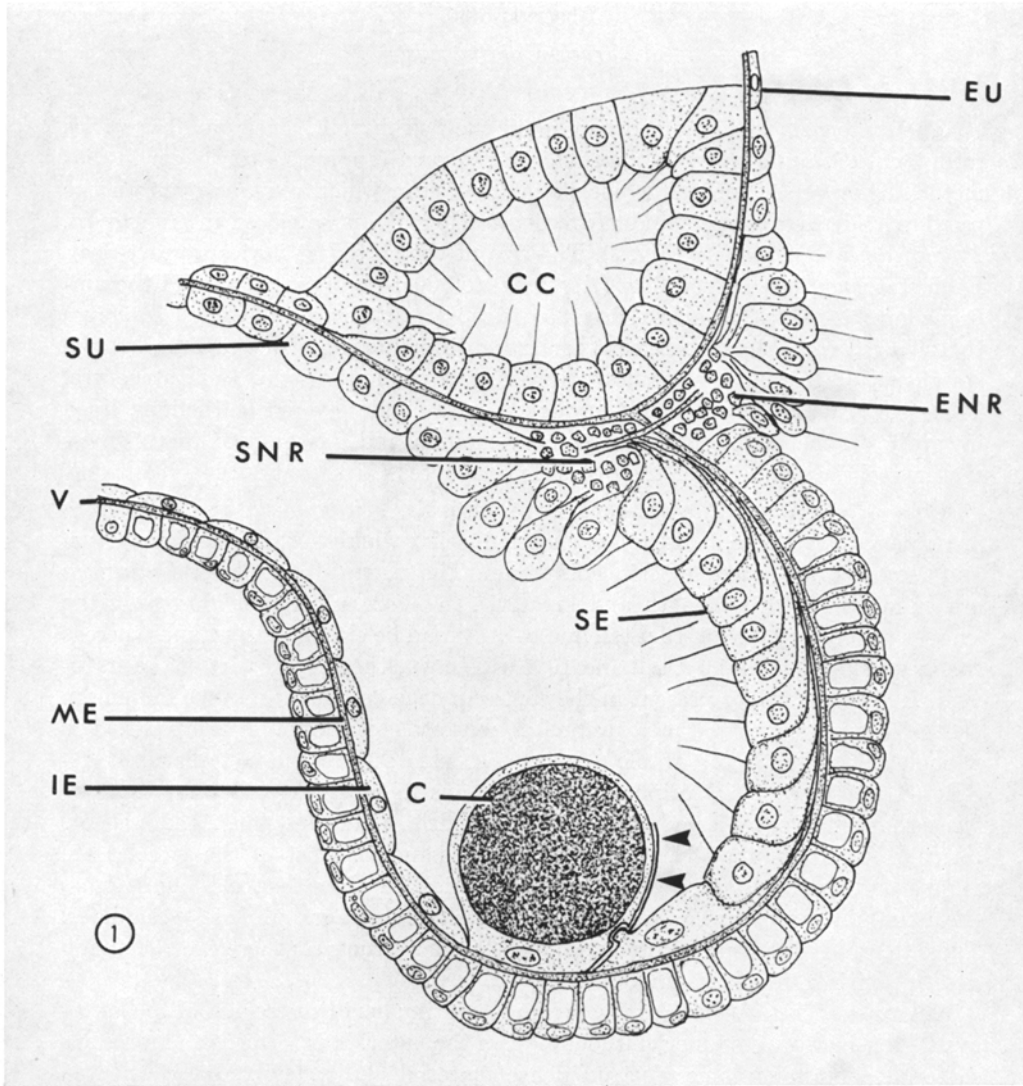


Fig. 1. Diagram showing a radial section of the open type statocyst of Leptomedusae. Note the inner thin epithelium towards the velum, lithocyte, and the sensory cell. *C*, concretion; *CC*, circular canal; *ENR*, exumbrellar nerve ring; *EU*, exumbrellar surface; *IE*, inner thin epithelium; *ME*, mesoglea; *SE*, sensory epithelium; *SNR*, subumbrellar nerve ring; *SU*, subumbrella and *V*, velum. The pointer indicates sensory cilium

above sensory cell extends between the lithocyte and mesoglea (Fig. 3). In *Halistaura*, *Phialidium* and *Aequorea* the shape of the sensory cells varies gradually from the lithocyte to the subumbrellar nerve ring. The cells close to the lithocyte are more broad than tall, whereas the sensory cells farther away from the lithocyte are more tall than broad. Each sensory cell has a distal cilium and the proximal

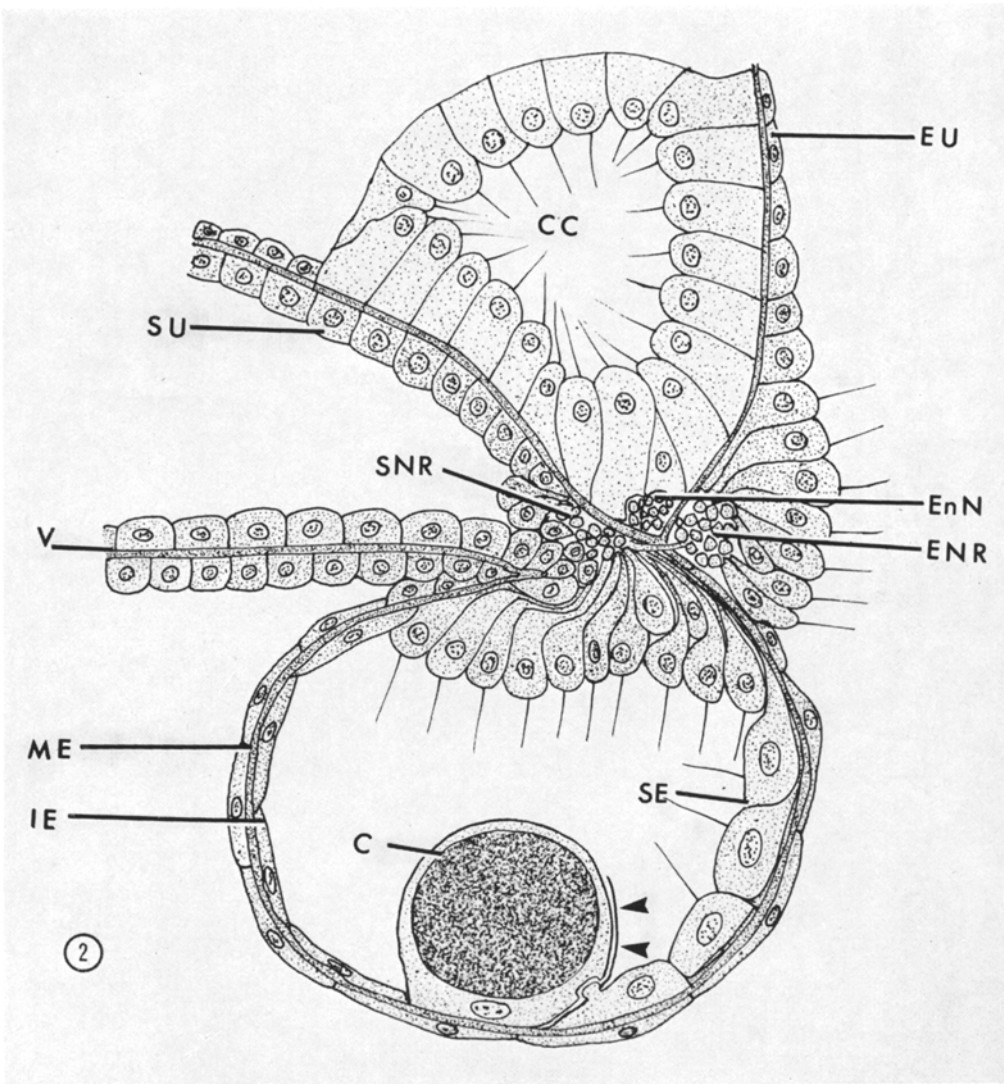
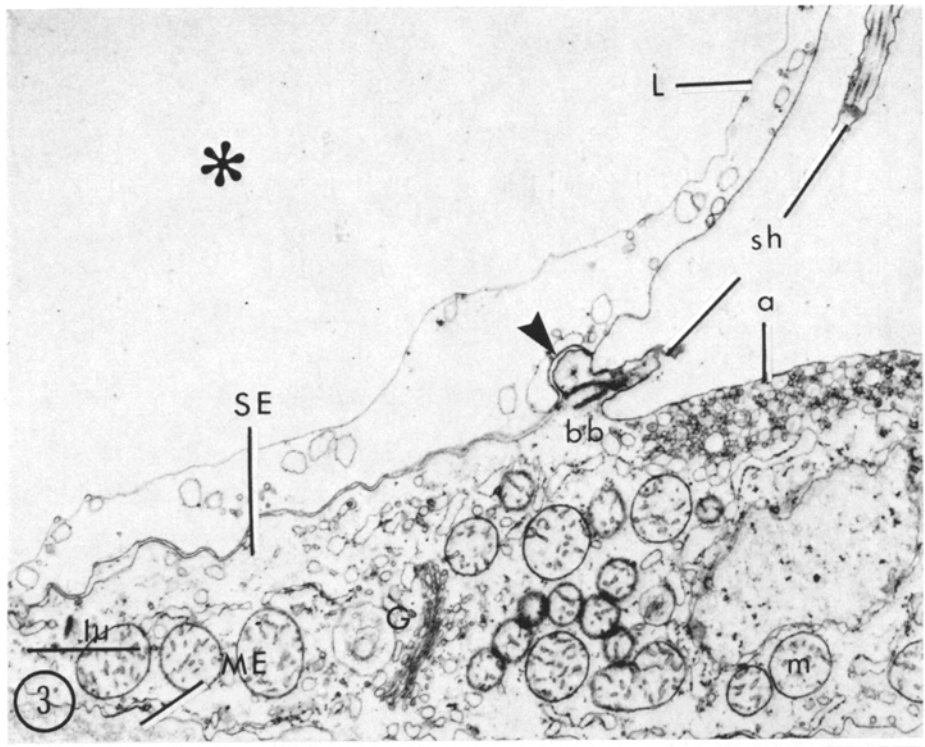


Fig. 2. Diagram showing a radial section of the closed type statocyst of Leptomedusae. Note the velum, inner thin epithelium towards the velum, lithocyte and sensory epithelium. *C*, concretion; *CC*, circular canal; *EnN*, endodermal nervous mass; *ENR*, exumbrellar nerve ring; *EU*, exumbrellar surface; *IE*, inner thin epithelium; *ME*, mesoglea; *SE*, sensory epithelium; *SNR*, subumbrellar nerve ring; *SU*, subumbrella and *V*, velum. The pointer indicates sensory cilium

part forms an axon. The sensory cilia are roughly 10 μ long and have 9 + 2 filament content, a basal body but no rootlets. The sensory cell adjacent to the lithocyte shows a projection of cell membrane near the base of the cilium which fits into a cup-like depression in the membrane of the lithocyte (Figs. 1–3).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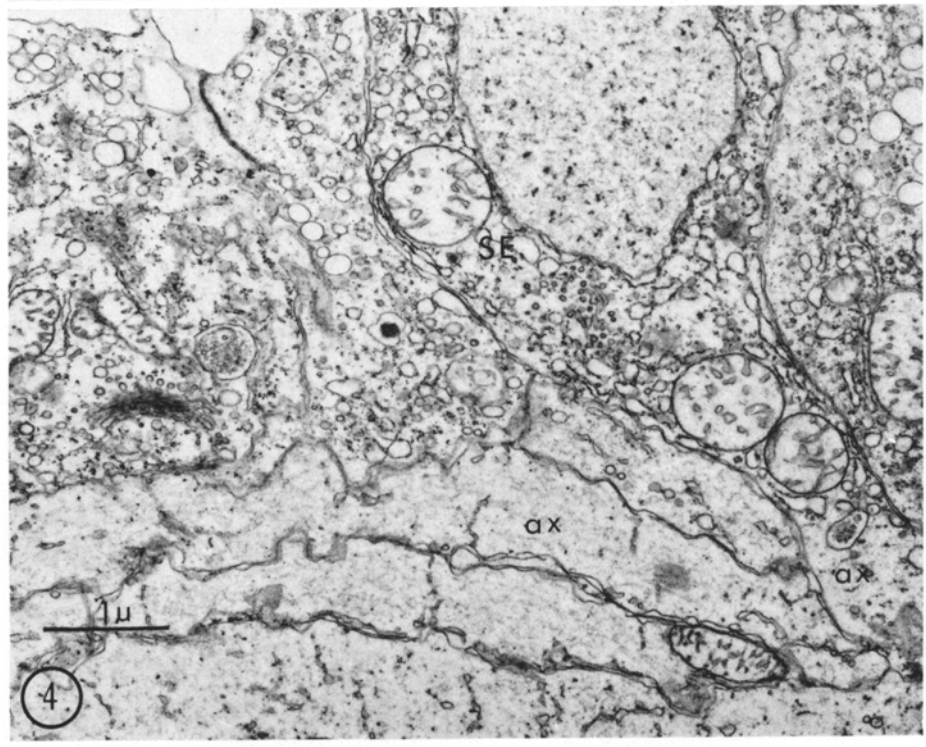
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The large nucleus may be present in the distal, central or proximal region of the cell. The cytoplasm contains a number of mitochondria distributed throughout the cytoplasm, one or two Golgi components, a large number of vesicles and sometimes a multivesicular body. The vesicles can be differentiated into small empty vesicles roughly 50–60 μ diameter which resemble the Golgi vesicles, and vesicles roughly 100–250 mμ in diameter. The latter type can be further divided into two categories, i.e. a) empty vesicles and, b) vesicles containing electron-dense material. The sensory cell adjacent to the lithocyte has an accumulation of all the three types of vesicles in its apical region (Fig. 3). Such an accumulation of vesicles has not been observed in any other type of cell nor from any other region in the cytoplasm of cells of this region.

The basal parts of the sensory cells run as axons into the subumbrellar nerve ring (Fig. 4). The axons contain neurotubules of 300 Å diameter, elongated mitochondria and small vesicles of 150 mμ diameter some with and others without an electron-dense material. A large axon roughly 30 μ long and 15 μ diameter has been observed in the subumbrellar nerve ring of *Tiaropsis*. An asymmetrical synapse has been seen in subumbrellar nerve ring of *Tiaropsis*. Nervous pathways between the subumbrellar and exumbrellar nerve rings have been observed in *Tiaropsis*, *Mitrocomella* and *Aequorea*.

Lithocytes. The lithocyte number varies from a single lithocyte per statocyst in *Phialidium* to numerous in *Halistaura*. Each lithocyte cell body is approximately 20 μ in diameter having a large vacuole which occupies most of the cell leaving a small peripheral shell of cytoplasm. Each vacuole contains a large concretion in its lumen. The nucleus may lie in the proximal or the distal region of the cell. The cytoplasm contains mitochondria, small vesicles and some endoplasmic reticulum.

Narcomedusae

The statocysts of Narcomedusae lie on the exumbrellar surface just above the exumbrellar nerve ring (Figs. 5 and 9). *Aegina* has four to eight statocysts between each pair of tentacles and the total may reach more than thirty in the adult. *Solmissus* specimen roughly of 3 cm diameter has eighty statocysts. Each statocyst has a basal cushion of tall epithelial cells and in the center of it arises a freely hanging body, i.e., a sensory club (*Aegina*) or a sensory papilla carrying a sensory club (*Solmissus*).

Basal Cushion. It is much less developed in *Solmissus* than in *Aegina*. The cells of the basal cushion vary in size. They are roughly 8–40 μ tall and 6–8 μ in cross-section. The cells show gap junctions (Fig. 7). Each cell has a distal cilium

Fig. 3. A radial section of the statocyst of *Halistaura cellularia*. *a*, an accumulation of vesicles both with and without electron dense material; *bb*, basal body; *G*, Golgi complex; *L*, lithocyte; *m*, mitochondrion; *ME*, mesoglea; *SE*, sensory cell; *sh*, sensory cilium and the pointer indicates a peg-like portion of the sensory cell which fits into a depression in the lithocyte. *indicates the location of a missing concretion

Fig. 4. Axons from the sensory cells of the statocyst of *Tiaropsis multicirrata*. *ax*, axon and *SE*, sensory cell

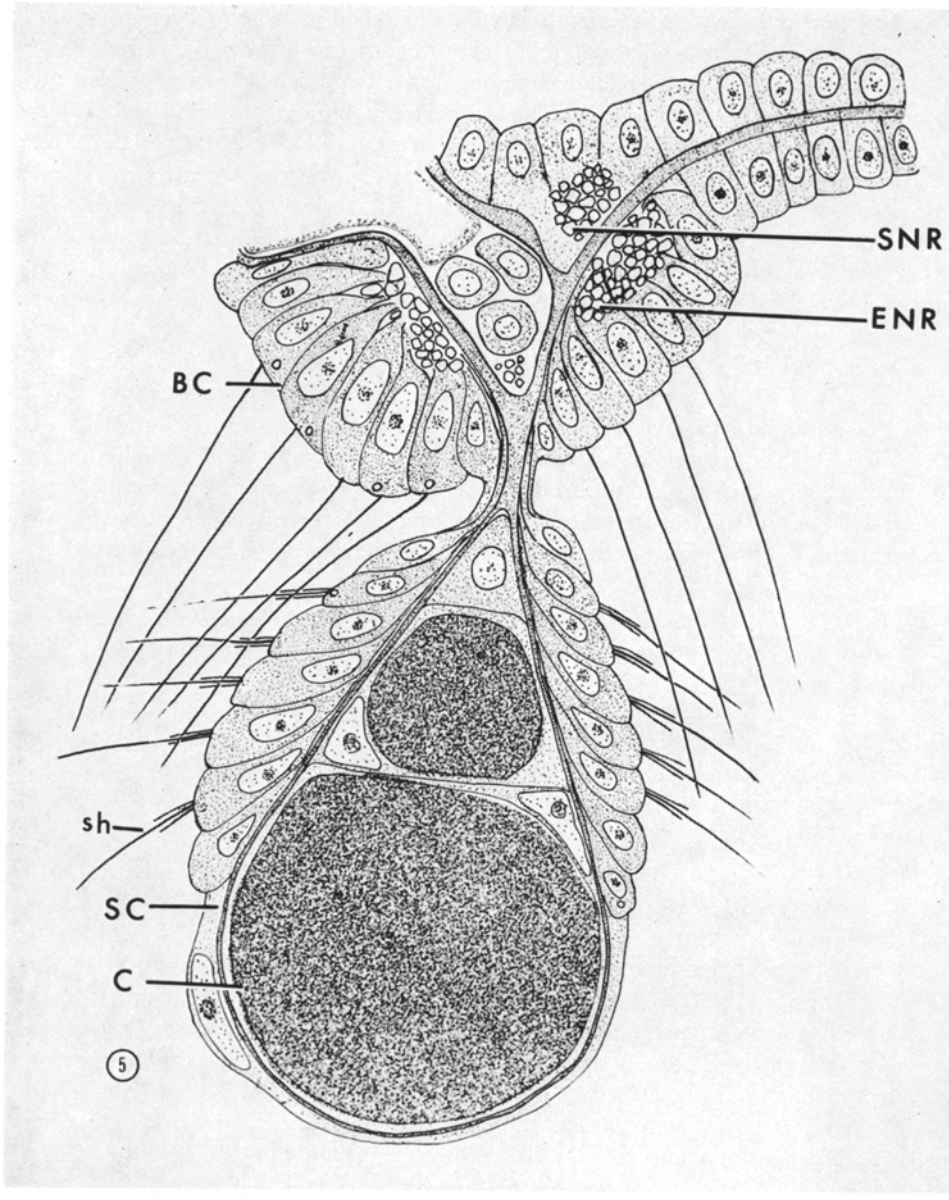


Fig. 5. Diagram showing the radial section of the statocyst of *Aegina citrea*. *BC*, basal cushion; *C*, concretion; *ENR*, exumbrellar nerve; *SC*, sensory club; *sh*, sensory cilium and *SNR*, subumbrellar nerve ring

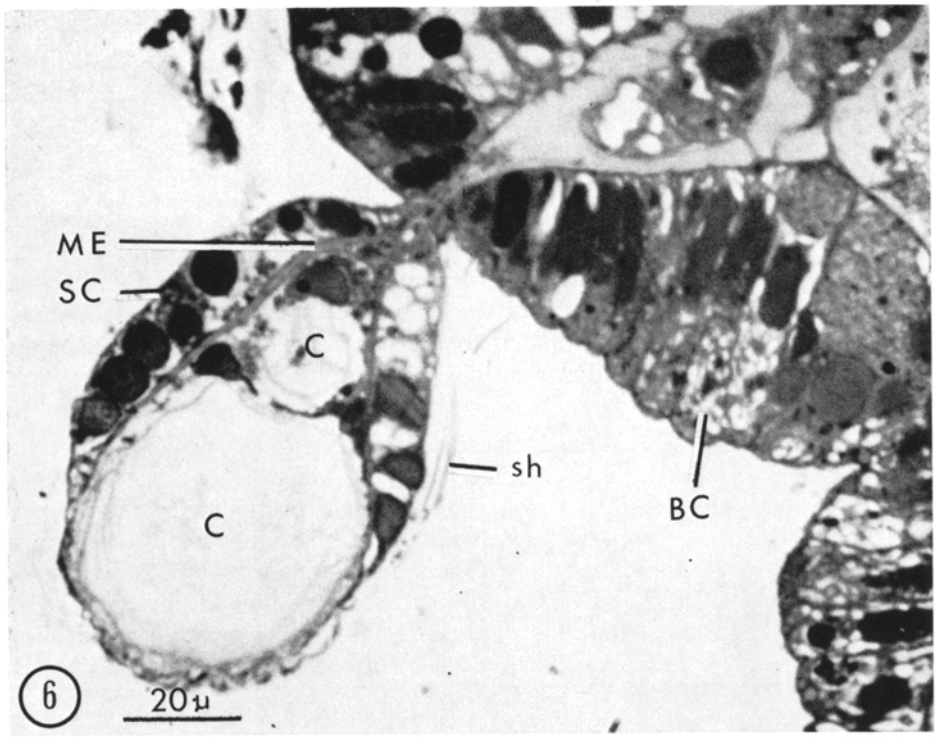
and the proximal part forms an axon which enters into the exumbrellar nerve ring. The cilia are very long, arise in the center of a cup-shaped depression and the basal part of each cilium is covered by an amorphous extracellular material (Fig. 7). The cilium has $9+2$ filaments, a basal body and a very strong striated

rootlet. Observations on living specimens show that the cilia are non-motile. The sensory club of *Aegina* and the sensory papilla of *Solmissus* is surrounded on all sides by these non-motile cilia (Figs. 6 and 9). In addition to a cilium each sensory cell has a number of microvilli projecting from the cell surface. Each cell has a large nucleus, a number of mitochondria, Golgi apparatus, endoplasmic reticulum and a number of empty vesicles roughly 200–300 mμ in diameter.

Sensory Papilla. The sensory papilla of *Solmissus* is a cone-shaped structure roughly 95 μ tall and 85 μ in diameter at its broadest end. It arises at the center of the basal cushion and is attached to the umbrellar margin with an axial strand of mesoglea surrounded by axons of the sensory cells of papilla and the club. The mesogleal strand opens into the circular canal. The sensory papilla hangs with its broadest end facing downwards. From its center arises the sensory club (Figs. 9 and 10).

The sensory papilla is formed of epithelial sensory cells which are similar to the cells of the basal cushion. These cells bear kinocilia at their distal end and the proximal part forms an axon which enters into the exumbrellar nerve ring. The cells on their distal end bear microvilli in addition to kinocilia. Generally each cell has a single cilium but more than one cilium may be found on the cells of the sensory papilla. The cilia are long, straight, non-motile and may even extend beyond the tip of the sensory club. Each cilium arises in a cup-shaped depression, the proximal part (roughly 2–3 μ) of each cilium is covered by an amorphous material. It has $9+2$ filaments, a basal body and very strongly developed rootlets. The cell body is roughly 20–30 μ long and 5–6 μ broad with some of the largest cells lying near the distal end of the sensory papilla. Each cell has a large nucleus with one or two nucleoli. The cytoplasm contains a number of mitochondria, a Golgi complex, a large number of empty vesicles roughly 100–200 mμ in diameter.

Sensory Club. Aegina has an elongated sensory club of 80–90 μ tall and 45–50 μ in cross-section (Fig. 6) whereas in *Solmissus* it is pear-shaped of 40–50 μ in diameter (Fig. 10). It has an axial strand of two (*Solmissus*) or three to five (*Aegina*) endodermal cells surrounded by a core of ectodermal ciliated sensory cells. The two cell types are separated by 100–500 mμ thick layer of mesoglea. The endodermal cells vary in size and shape. The largest cell is present at the distal end, whereas the smallest lies towards the proximal end. The two or three distal cells of *Aegina* and a single distal cell of *Solmissus* contain a concretion which fills almost the whole of the cell body. Thus the cytoplasm is restricted to the cellular periphery. Most of the concretion material is lost during the process of fixation and staining. The concretion shows some indication of membranous or fibrous structure. The concretion cell nucleus is triangular (*Aegina*) or bean-shaped (*Solmissus*). The cytoplasm contains a few mitochondria, a Golgi complex and a number of small vesicles. The cells covering the sensory club vary in size and shape, they are tall in the proximal part of the club but become flat in the distal region. Each cell has a large nucleus, a number of mitochondria, Golgi complex, rough endoplasmic reticulum, small vesicles of about 150 μ in diameter without any electron dense material and in some cases a multivesicular body is present. The proximal cells bear on their distal end a kinocilium surrounded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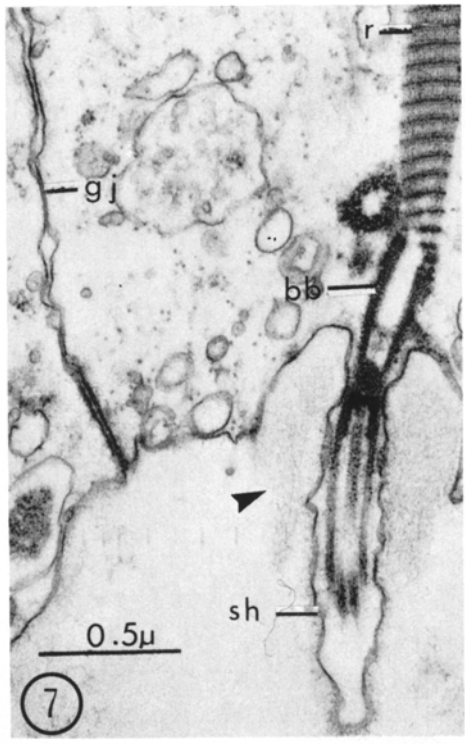
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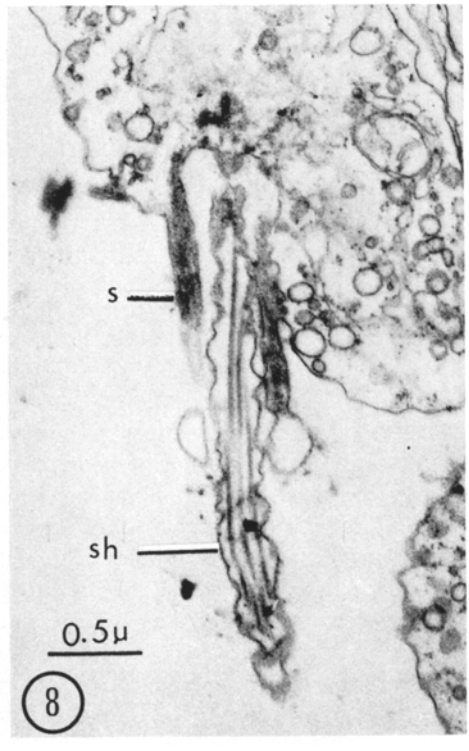
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by a ring of stereocilia (Figs. 8 and 11). Each kinocilium has $9+2$ filament content, a basal body, but no rootlets. The basal part of the sensory cells forms an axon which, like the axons of the basal cushion and the sensory papilla cell axons, enters into the exumbrellar nerve ring.

B. Composition of Statolith (Concretion)

The concretions in the Leptomedusae *Mitrocomella polydiademata*, *Halistaura cellularia*, *Phialidium gregarium* and *Aequorea aequorea* are spherical and roughly the same size. They give a positive test for calcium i.e. an orange-red coloration with McGee Russell's alizarin red in all four medusae mentioned above, and also show birefringence under polarized light, which suggests the presence of calcium salt. According to Lillie (1965) the alizarin red test probably indicates calcium sulphate. *Mitrocomella*, *Phialidium* and *Aequorea* statoliths became black when treated with silver nitrate solution according to the Von Kossa method for calcium, but no such reaction was observed on the concretions of *Halistaura*. This test is specific for phosphates and amorphous carbonates, and since the soluble phosphates and carbonates are washed out, calcium phosphate and carbonate are presumably the only remaining materials which could react with silver nitrate (Lillie, 1965). The possibility of calcium carbonate is ruled out because the concretions appear crystalline under the microscope. Presence of calcium is further confirmed as no reaction was observed in sections treated with 0.25% nitric acid prior to immersion in silver nitrate solution. In addition to the inorganic material the statoliths of Leptomedusae contain fibrous material arranged in concentric rings as seen under the electron microscope.

C. Righting Behaviour of Aequorea aequorea

The medusae of *Aequorea aequorea* in their horizontal position showed symmetrical contractions of the bell margin all around the umbrellar margin. When the medusae were tilted out of the horizontal position the bell continued to pulsate at the upper end but the pulsations almost stopped on the lower end. The velum on the upper end generally formed a right angle with the vertical axis through the animal, whereas, on the lower side the angle varied roughly from 120° to 150°. After removal of the statocysts the bell in the tilted position showed normal beating and there was no difference in the contractions of the bell margin between the upper and the lower end of mudusae. The velum formed almost a right angle with the vertical axis both on the upper end and the lower sides. The righting

Fig. 6. Radial section of the sensory club of *Aegina citrea*. *BC*, basal cushion; *C*, concretion; *ME*, mesoglea; *SC*, sensory club and *sh*, sensory cilium

Fig. 7. Basal cushion cell of *Aegina* showing the kinocilium surrounded by an amorphous material and has a very strongly developed rootlet. *bb*, basal body; *gj*, gap junction; *r*, rootlet; *sh*, sensory cilium and the pointer indicates the amorphous material present around the basal part of the kinocilium

Fig. 8. Sensory cell from the sensory club of *Aegina*. *sh*, sensory cilium (Kinocilium) and *s*, stereocilium

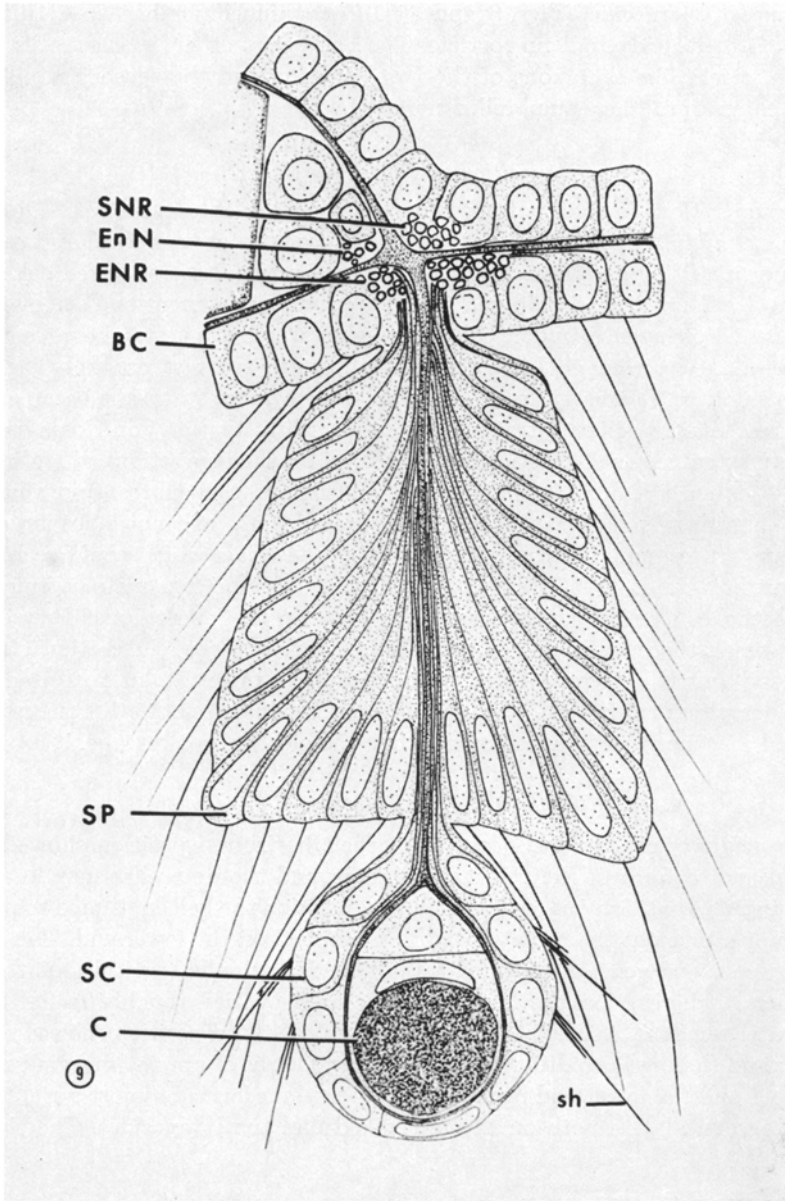
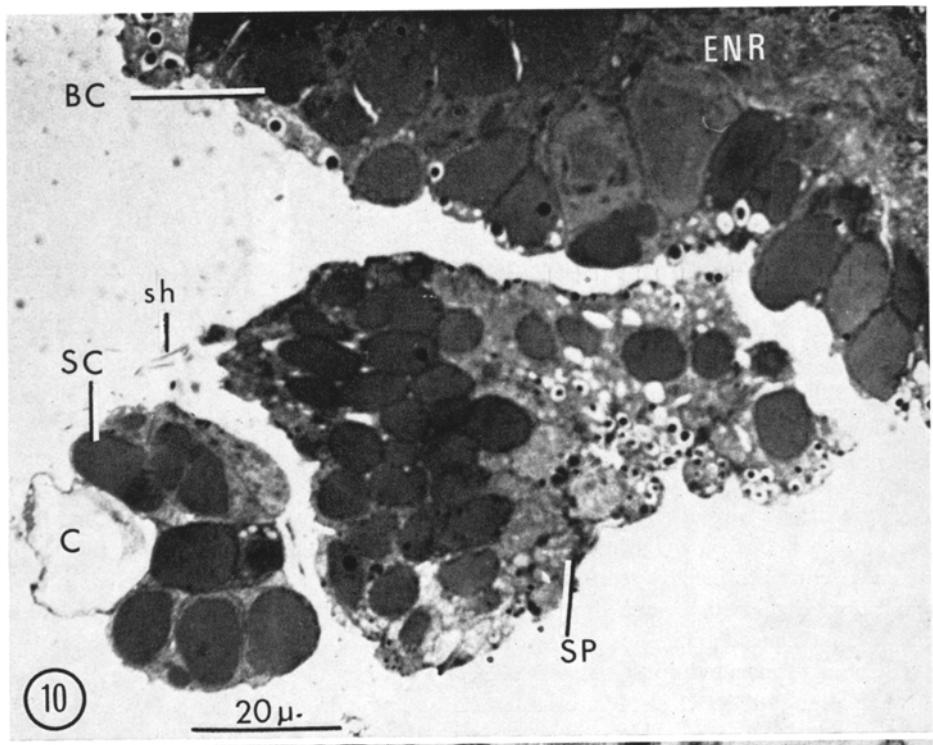


Fig. 9. Diagram showing a radial section of the statocyst of *Solmissus marshalli*. *BC*, basal cushion; *C*, concretion; *EnN*, endodermal nerve mass; *ENR*; exumbrellar nerve ring; *SC*, sensory club; *sh*, sensory cilium; *SNR*, subumbrellar nerve ring and *SP*, sensory papilla

Fig. 10. Tangential section of a statocyst of *Solmissus* showing three parts of the statocyst. *BC*, bassal cushion; *C*, concretion; *ENR*, exumbrellar nerve ring; *SC*, sensory club; *sh*, sensory cilium (kinocilium); *SP*, sensory papilla

Fig. 11. Sensory cell from the sensory club of *Solmissus* showing a kinocilium and stereocilium. *bb*, basal body; *s*, stereocilium and *sh*, sensory cilium (kinocilium)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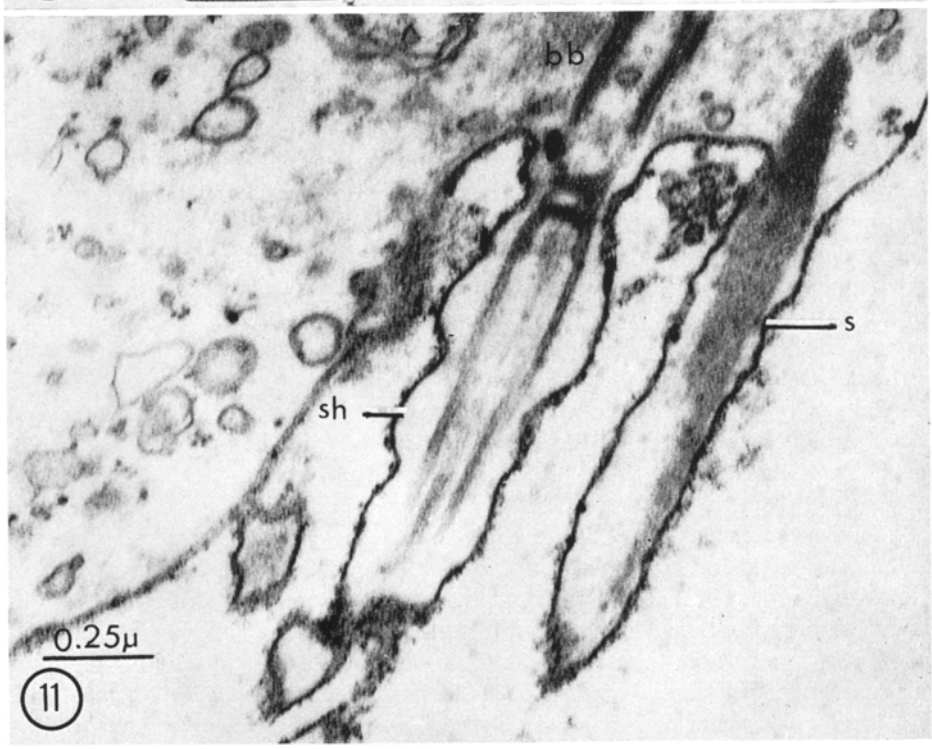
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behaviour of *Aequorea* can be distinguished from the feeding response as it lacks the tentacular contraction component and there is no visible change in the position of the manubrium. Furthermore, there appears to be no contraction of the subumbrellar radial muscles, as occurs during feeding.

Discussion

A. Types of Sensory Cells

We can distinguish three morphological categories of sensory cells associated with statocysts in hydromedusae examined and these may be designated as types A, B and C. All three possess a basal nerve process and must therefore be regarded as receptors, although it does not follow that they all respond to the same type of stimuli. Type A, characteristic of Leptomedusae, bears a single kinocilium of moderate length. The cilium has no rootlet system in the cytoplasm. No stereocilia are present adjacent to the kinocilium. Some of these cells lie adjacent to lithocyte membrane, and it appears that in such cases the cells are directly involved in registering position changes, as the kinocilium would tend to be deflected by lithocyte movement. The cells adjacent to the lithocyte are also characterized by concentration of three types of vesicles in their distal part. As these vesicles are limited to the distal part of the sensory cells they may be acting as chemical mediator in transduction of the nerve impulse. Chemical triggering of nerve impulses has also been suggested for cochlea of mammals by Webster (1966). It is of interest to note that closely similar cells occur next to those type A cells which lie beside the lithocyte, and they appear to form a pure sensory epithelium lining the pocket of the statocyst over a considerable area. It is clear that they cannot all be implicated in equilibrium perception. They differ from the cells adjacent to the lithocyte only in that they lack the concentration of vesicles near the free pole. Possibly we are dealing here with receptors sensitive to water movements, functioning analogously to the ampullary receptors in the mammalian inner ear or to the receptors of the cristae in the statocysts of the *Octopus* (Young, 1960) in the movement perception. Alternatively they might be concerned with perception of water borne vibrations. As the cilia are coupled with the sea water in the open type of statocysts and with the statocyst fluid in the closed type of statocyst, vibrations in the sea water might be registered through these cilia. There is, however, no experimental evidence for either of these possible functions.

Cells of type B are found on the distal part of the sensory club in *Aegina* and *Solmissus*. They bear a single kinocilium, which is surrounded by a ring of stereocilia. The kinocilium lack the basal rootlets. Similar cells were described by Horridge (1969) in *Cunina* (O. Narcomedusae), *Rhopalonema* and *Geryonia* (O. Trachymedusae). In the latter, they are the only sensory processes present in the statocyst and the statocysts are of the enclosed type. Their presence in this situation can be confidently interpreted as evidence of their involvement in equilibrium perception. Presumably the pressure of the statocyst against the wall of its vesicle results in the movement of the kinocilium and the production of an impulse in the cell or its basal process. The role of the stereocilia is conjectural. Hawkins (1965) considers that the stereocilia serve as microlevers to transmit

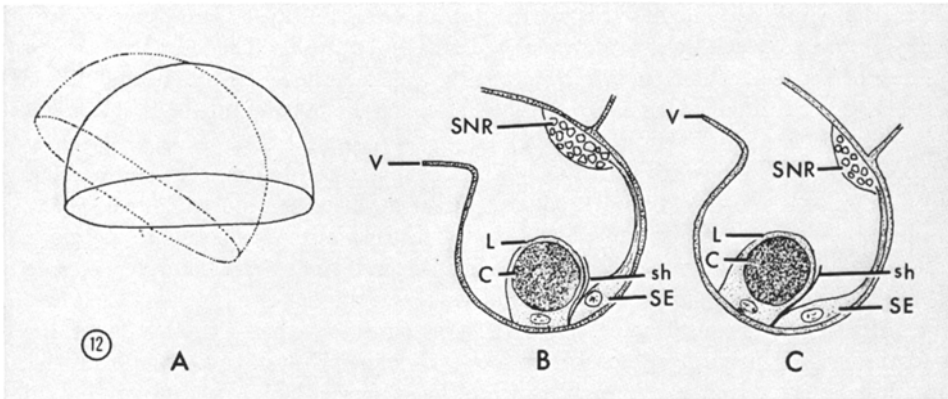

Fig. 12. Diagram to explain possible mechanism of statocyst function in Leptomedusae. A: solid and dotted lines showing the medusa in a horizontal and tilted position respectively. B: is the view of a statocyst chamber in the horizontal position and C: in the tilted position. Note the position of the lithocyte membrane, concretion and the sensory cilium. Diagrams B and C are based on the inference drawn from the ultrastructure study. *C*, concretion; *L*, lithocyte; *SE*, sensory cell; *sh*, sensory cilium; *SNR*, subumbrellar nerve and *V*, velum

vibratory energy from the tectorial membrane to the cuticular plate in the cochlea of vertebrates. There is a possibility that by enclosing the base of the kinocilium they dampen its sensitivity to vibrations and high frequency movements, restricting to large amplitude deflections or ones of long duration. The close resemblance of these cells as described by Horridge (1969) in the enclosed statocyst of Trachymedusae to the sensory cells of the sensory club of Narcomedusae suggests that in the latter case, the cells in question are also concerned with equilibrium perception. As there is no surrounding vesicle, it must be assumed that the effective stimulus involves contact of the kinocilium of the type B cells with the body wall of the medusa, or possibly with the bristle-like processes of the type C cells of the basal cushion (or both) under different orientations.

Type C cells occur only in the basal cushion (*Aegina*) or basal cushion and sensory papilla (*Solmissus*). Their processes are extremely long (50–60 μ) and appear stiff. They are non-motile. They have a well-developed rootlet system running down into the cytoplasm. No stereocilia are present. As already noted, the presence of nerve processes running into the exumbrellar nerve ring clearly identifies these cells as receptors, but whether or not they are equilibrium receptors is not clear. Possibily the inter-action of their long, stiff hairs with the shorter hairs of the distal part of the sensory club results in the generation of impulses in the B cells under certain conditions and in the C cells or in both together under other conditions, providing a more comprehensive range of sensitivities than could be achieved with one sort alone.

B. Possible Mechanism of Statocyst Function

The distribution of the sensory cells in the statocyst of Leptomedusae and the apical modification of those lying adjacent to the lithocyte membrane suggest the possible mechanism of statocyst function. When the medusa is tilted as shown in

Fig. 12 the lithocyte membrane in the statocysts on the bell bends towards the adjacent sensory cell due to the weight of the concretion and presses the sensory cilium of this cell which in turn deforms the cell membrane. Hillman and Lewis (1971) showed the displacement of cilia with a change in orientation in the vertebrate inner ear equilibrium receptors of sacculus and utriculus. An electrical depolarization has been recorded as a result of distortion in the cell membrane of lobster giant axons (Goldman, 1965) and insect mechanoreceptors (Thürm, 1965). Similarly a nerve impulse may be produced in the sensory cells of the statocyst and carried to the subumbrellar nerve ring through their axons. In *Aequorea* in the tilted position the upper end continues rythmically beating, whereas the lower end almost stops pulsating. Horridge (1955) considers that stimulation of the radial muscles during feeding inhibits spontaneous rhythm of the beat. From this it can be inferred that nerve impulses from the subumbrellar nerve ring are passed on to the radial muscles through efferent nerve fibers. This response leads to restoration of equilibrium by throwing water from the upper end towards the lower end and moving the lower end back into its horizontal position. The righting behaviour of scyphomedusae differs completely from that of hydromedusae. Fränkell (1925) and Bozler (1926) observed that when a scyphomedusan is tilted out of its horizontal position the upper end showed weaker muscular movements whereas the lower end showed strong muscular movement, and it is the muscular movements of the lower end which helps the medusa to regain its equilibrium. The significance of statocysts in maintaining equilibrium is further shown as medusae lost righting ability when the statocysts were removed. Similar results were recorded by Fränkel (1925) and Bozler (1926). As the statocysts are uniformly distributed, the medusa can right itself when tilted in any direction. It has already been suggested that the sensory cells, except those lying adjacent to the lithocyte, in the statocysts of Leptomedusae are possibly involved in the vibration or water movement perception. If so, it would appear that movement perception and the static sense evolved together in the same organ. A. parallel evolution in the ampulla and vestibule of vertebrates, and the crista and macula of the *Octopus* resulted in the combination of static sense and movement sense in the one organ.

The statocysts of Narcomedusae are freely suspended from the umbrellar margin in the water, which suggests that when the animal tilts, the sensory organ swings and the sensory cilia of the sensory club come in contact with the body wall or possibly with the bristle-like processes of the type C cells of the basal cushion (or both) under different conditions and a nerve impulse is generated. As the cilia are mechanically coupled with water this organ according to Horridge (1969) also works as a vibration receptor .In closed type statocysts (e.g. *Limnocnida tanganyicae*) Bouillon (1956–57) infers on the structural grounds that the sense organ worked like a clapper in a bell. A similar explanation could be applied to closed statocysts of other Limnomedusae and Trachymedusae.

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