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Ocelli of Hydromedusae

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Summary. The very simple ocelli of *Leuckartiara octona* are formed of a sheet of mixed ectodermal receptor and pigment cells, whereas in *Bougainvillia* the cell sheet is invaginated to form an ocellar cup. The ocellar cup of *Tiaropsis* is formed of endodermal pigment cells. The receptor cell bodies of *Tiaropsis* lie outside the cup, their distal processes filling the cup. Each receptor cell process bears a single cilium at its distal end except in *Bougainvillia* where the number of cilia may vary from one to three. Lateral microvilli are missing from the ciliary membrane of *Leuckartiara*, poorly developed in *Tiaropsis* and well developed in *Bougainvillia.* The proximal part of the receptor cell forms an axon which enters into the subumbrellar nerve ring in *Tiaropsis* and exumbrellar nerve ring in the other two. The pigment cells lack distal processes in *Tiaropsis,* in *Leuckartiara* they bear microvilli and in *Bougainvillia* they form a strand of 1µ diameter which passes through the ciliary region and then divides into a number of tubules to fill the distal region of the ocellar cup. *Bougainvillia* medusae showed a swimming "off response" to light of 446–625 nm wavelength but no such response was observed when the ocelli are removed. The evolution of ocelli in hydromeduase is discussed.

Key words: Ocelli — Receptor cells — Pigment cells — Off response — Evolution.

Introduction

The ocelli of medusae are of particular interest as they range from very simple to quite complex types of photoreceptor organ. Light microscope accounts of the ocelli of medusae were given by Hertwig and Hertwig (1878), Schewiakoff (1889), Berger (1900) and Linko (1900). There have been no studies of these ocelli using the electron microscope except on those of *Polyorchis penicilatus* (Eakin and Westfall, 1962) and *Sarsia sp.* (G. O. Mackie and R. M. Eakin, personal communication). Ocellar function in hydromedusae has not been analysed in detail although there are various accounts of behaviour (Romanes, 1877; Hyman, 1940; Hisada, 1956; Tamasige and Yamaguchi, 1967), which indicate that medusae possessing the ocelli are photosensitive. Passano, Mackie and Pavans de Cecatty (1967) state that illumination of the ocelli alters the marginal pulse and swimming pacemaker outputs in *Sarsia.* There have been no electrical recording from the ocelli themselves or their nerves except those of *Spirocodon* (M. Yoshida personal communication). Hyman (1940) studied the function of ocelli of *Sarsia sp.* by extirpating the tentacles bearing the ocelli but as she probably also removed the tentacular ganglia, her results are open to more than one interpretation. The present studies of the ocelli of Anthomedusae and Leptomedusae were carried out in an effort to clarify the structure and evolution of photoreceptors in coelenterates. Electrical activity was recorded in *Bougainvillia,* which shows a

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characteristic alteration in the pattern of electrical signals recorded from the margin when the animal is exposed to a sudden decrease in illumination. These recordings demonstrate that the ocelli are functional photoreceptors, responding to a limited range of light.

Material and Methods

a) Electron microscopy

The fine structure of the ocelli of the following hydromedusae was studied: *Leuckartiara octona*, *Bougainvillia principis* and *Tiaropsis multicirrata*. The animals were relaxed in sea water diluted with an equal volume of isotonic magnesium chloride (67.5 gms $Mgcl_26H_2O$ per liter), pieces of tissue 2–3 mm in size were removed from the medusae and transferred to the fixative. In some cases whole medusae were fixed and pieces were dissected out later. The material was fixed for one hour at 4°C in (a) 2% osmium tetroxide buffered with s-Collidine at pH 7.4 (Bennett and Luft, 1959) and (b) a modified Dorey fixative. This is a modification of the original Dorey formula (Dorey, 1965) in which 2% sodium chloride is used in place of sucrose. This modification avoids the rupture of large cytoplasmic vesicles and mitochondrial swelling which occurs in Dorey sucrose but otherwise gives similar results. In the case of (a), fixation was followed by ten seconds wash with distilled water; after fixation in (b), tissue was transferred directly to 35% alcohol. Subsequently the tissue 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 a Reichert UM-2 ultramicrotome. Sections were stained with uranyl acetate and lead citrate (Venable and Coggeshall, 1965). Thick sections were stained with Richardson's methylene blue and Azue 2 mixture (Richardson, Jarett and Finke, 1960). s-Collidine buffered osmium gave satisfactory results with *Bougainvillia*, the modified Dorey mixture with other species.

b) Electrophysiology

The behaviour of medusae of *Bougainvillia* was studied following changes in illumination from a tungsten light source. Electrical events accompanying swimming were used as an indication of the photic response of the animal. The medusae were kept in sea water and were exposed to 6 volts tungsten light from a distance of approximately four inches. Balzers monochromatic filters were used for light of different wavelengths. The energy output was controlled by a rheostat calibrated with a radiometer. Thus the animals were exposed to different wavelengths of light having the same amount of energy output. The animal's sensitivity to different wavelengths was estimated by measuring the response latency. Electrical signals were recorded on a grass polygraph having E.E.G. amplifiers (Josephson, 1965). Plastic suction electrodes were attached to the margin of the jellyfish to register the muscle potentials accompanying contractions.

The term "on response" and "off response" refers to swimming behaviour following switching on and off respectively of the light. Between experiments using different wavelengths the animals were treated under white light as a control. They were exposed for a period of five minutes of white light and five minutes of dark. In some experiments the ocelli of anaesthetised animals were removed with a "vibrating needle" (Wenger, 1967). The animals were then transferred to running sea water to recover before their photo-sensitivity was tested.

Observations

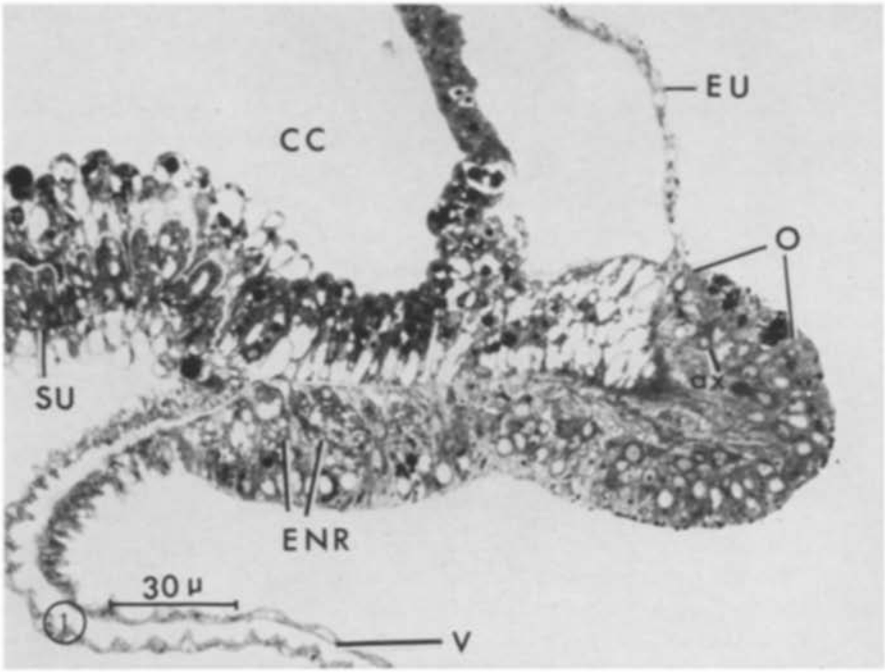
The ocelli of *Leuckartiara* and *Bougainvillia* are of the erect or everted type as compared to the inverted type of ocelli found in *Tiaropsis*. An abaxial crimson-coloured ocellus of 30 μ diameter is present on each tentacular and rudimentary bulb of *Leuckartiara octona* (Fig. 1), whereas in *Bougainvillia* the ocelli are black and lie adaxially on the basal part of each marginal tentacle. *Tiaropsis* ocelli are present on the subumbrella close to the margin, near the statocyst in the adradial position (Fig. 9).

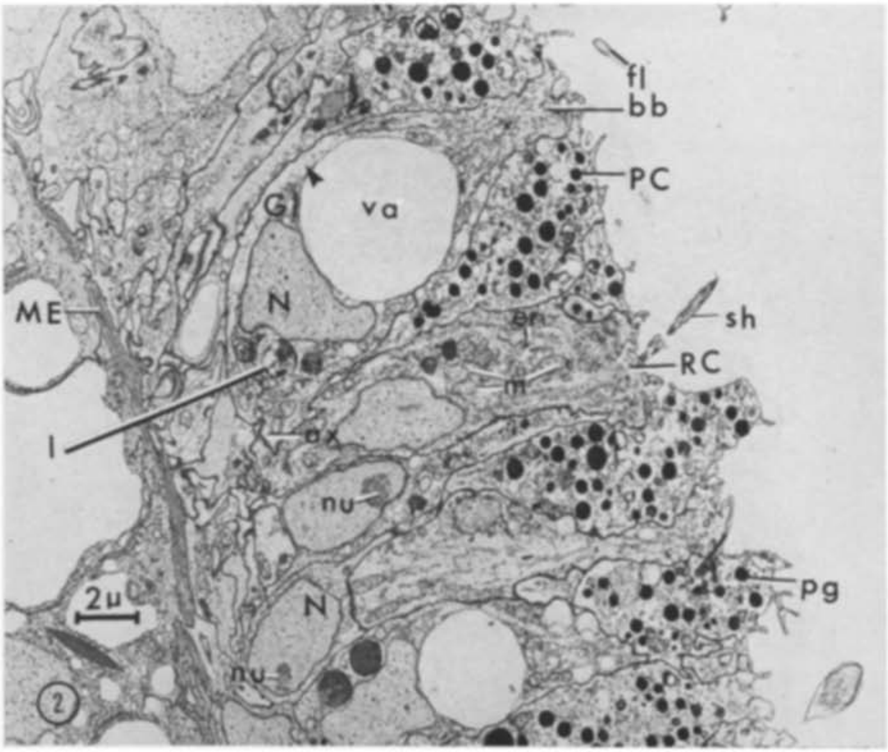
Leukartiara has the most simple type of ocellus, formed of pigment and photoreceptor cells lying side by side in a layer of cells (Fig. 2). A similar layer is curved to form an ocellar cup (45 μ deep and 50 μ wide) in *Bougainvillia* (Fig. 4). In *Tiaropsis* the ocellar cup (30 μ deep, 35 μ maximum width and 25 μ mouth opening) is formed of pigment cells only, these being separated from the photoreceptor cell processes by a layer of mesoglea (Figs. 9 and 10). The photoreceptor cell bodies lie outside the ocellar cup. One peculiar feature of the ocellus of *Tiaropsis* is the presence of a cavity (ocellar cavity Fig. 10) into which the cilia project. At high magnification it appears to contain a fine fibrous material. There is no evidence concerning the cavity's properties in the living organ. It lacks the regular arrangement of fibrils of mesoglea and appears to be less dense.

a) Photoreceptor Cells

The photoreceptor cells are bipolar having a cell body with a distal receptor process and the proximal part forming an axon roughly 1 μ diameter which enters into the exumbrellar nerve in *Leuckartiara octona* and *Bougainvillia principis*, whereas in *Tiaropsis multicirrata* it enters into the subumbrellar nerve ring. The receptor cell bodies vary in size and shape. These are spindle shaped (roughly 10–12 μ diameter) in *Leuckartiara*, variable in *Bougainvillia* (8–10 μ tall and 5–6 μ in thickness) and oval in *Tiaropsis* (12–15 μ in diameter). The cell body contains a central spherical nucleus in *Bougainvillia* and *Tiaropsis* but in *Leuckartiara* due to the frequent presence of a supranuclear vacuole (4–6 μ in diameter) it may be cylindrical or cone-shaped (Fig. 2). A supranuclear vacuole is unique to *Leuckartiara* and has not been observed in the photoreceptor cells of other medusae. The cytoplasm has a number of Golgi elements, mitochondria, microtubules (200–400 Å in diameter), endoplasmic reticulum and a large number of vesicles (400–3000 Å in diameter).

The distal region of the receptor cell of *Leuckartiara* is similar to the photoreceptor process in the ocelli of other hydromedusae. The process on coming to the surface enlarges. From the distal end of each cell process arises a sensory cilium and a few microvilli (2 μ long and 0.5 μ in diameter; Figs. 2 and 3). The cilium has 9 + 2 filament content, a basal body but no rootlets. The receptor cell process of Bougainvillia is 8–11 μ tall and less than a micron in diameter (Figs. 4 and 5). It passes through the pigment cells and enlarges on entering the ocellar cup. Distally each sensory process bears one, two or three cilia (Fig. 6). Each cilium has a 9 + 2 filament content, a basal body and a striated rootlet. The ciliary membrane gives off lateral microvilli 200–300 mμ in thickness (Fig. 7). These remain in small groups close to the basal region of the ocellar cup (Fig. 5), and the groups are separated by the pigment cell strand. In *Tiaropsis* the receptor processes vary from 20–70 μ in length and are one micron in cross-section (Fig. 10). About 400–500 such processes enter the ocellar cup. The number was estimated from the area of the opening and the area of the cross-section of the receptor process making allowance for the presence of some cell bodies. They contain a





Figs. 1 and 2

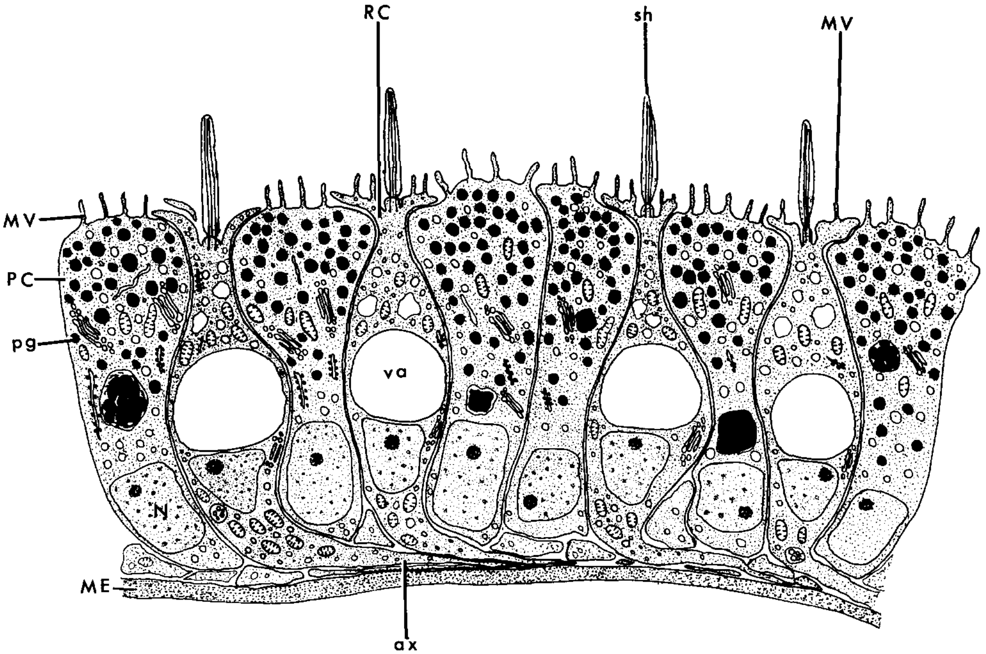


Fig. 3. Diagram of the simple form of ocellus of *Leuckartiara octona*. *ax* axon; *ME* mesoglea; *MV* microvilli; *N* nucleus; *PC* pigment cell; *RC* receptor cell; *sh* sensory cilium; *va* large vacuole

number of microtubules (roughly 300 Å thickness), small vesicles (1500 Å–3000 Å diameter) and mitochondria (Figs. 11 and 12). Each process has a cilium at its distal end arising in 1 μ deep pit (Fig. 12). The cilium has a basal body and striated rootlets. The ciliary membrane gives off lateral microvilli (600 Å thick). Small vesicles of 1500–3000 Å diameter are also present in the ciliary shaft but in some cases they are 6000 Å in diameter. The cilia has 9 + 2 filaments.

b) Pigment Cells

The pigment cells of *Leuckartiara* and *Bougainvillia* are ectodermal in origin but those of *Tiaropsis* are endodermal in origin. *Leuckartiara* pigment cells are approximately 20 μ long and have 8 μ maximum width. At their distal end they

Fig. 1. Light photomicrograph of a radial section through the umbrellar margin of *Leuckartiara* showing the ocellus in relation to other marginal structures. *ax* axon; *CC* circular canal; *ENR* exumbrellar nerve ring; *EU* exumbrellar epithelium; *O* ocellus; *SU* subumbrellar region; *V* velum

Fig. 2. Electron micrograph of a radial section of the ocellus of *Leuckartiara* showing the receptor and pigmented cells. *ax* axon; *bb* basal body; *er* endoplasmic reticulum; *fl* ciliary filaments; *G* Golgi complex; *l* lysosome; *m* mitochondria; *ME* mesoglea; *N* nucleus; *nu* nucleolus; *PC* pigment cell; *pg* pigment granule; *RC* receptor cell; *sh* sensory hair; *va* large vacuole. The pointer indicates the microtubules

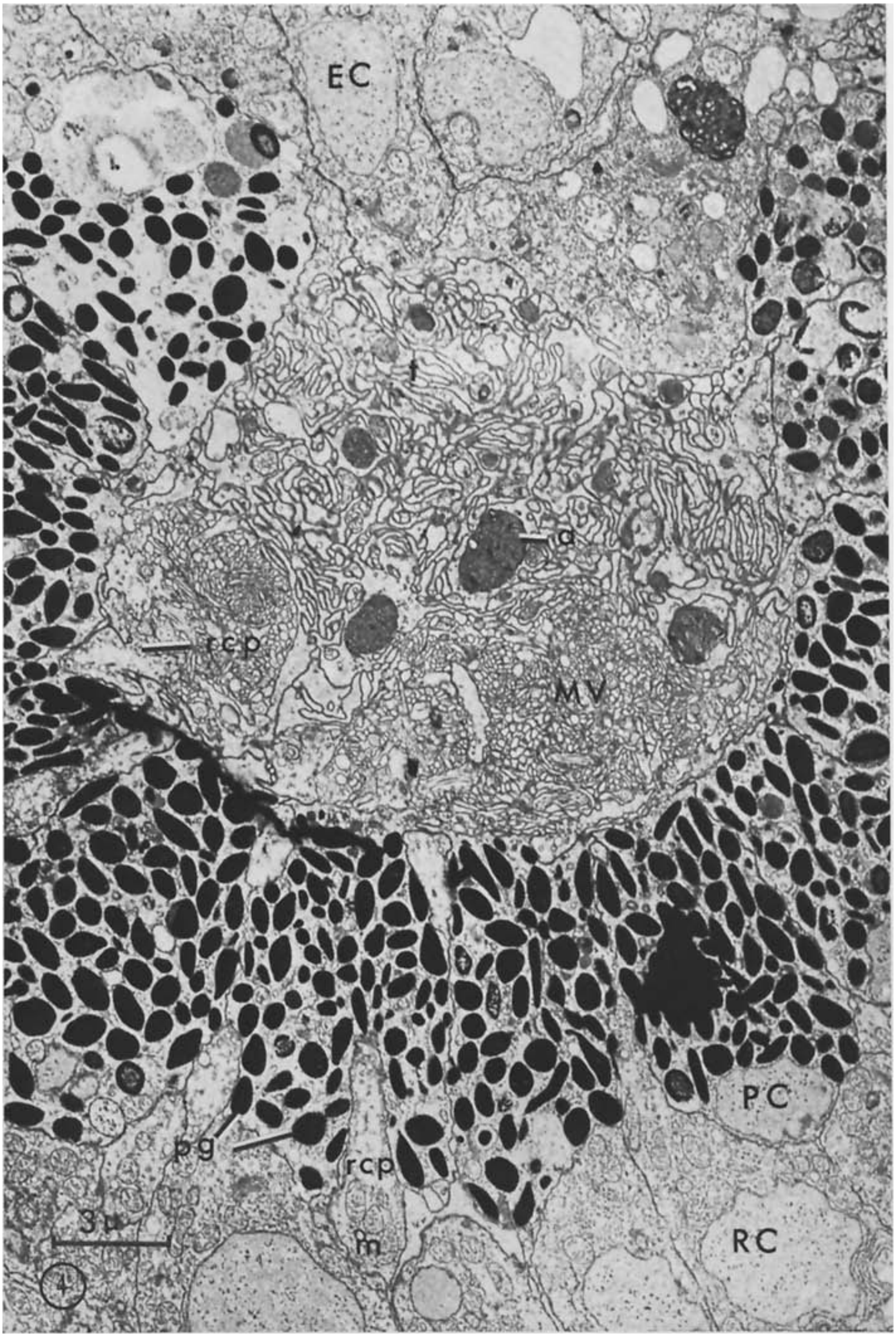


Fig. 4. Electron micrograph of a radial section of the ocellus of *Bougainvillia principis* showing the general structure. *a* a group of vesicles enclosed in a membrane; *EC* epithelial cell; *m* mitochondrion; *MV* microvilli from the ciliary membrane *PC* pigment cell; *pg* pigment granules; *RC* receptor cell; *rcp* receptor cell processes; *t* tubules from the pigment cell strand

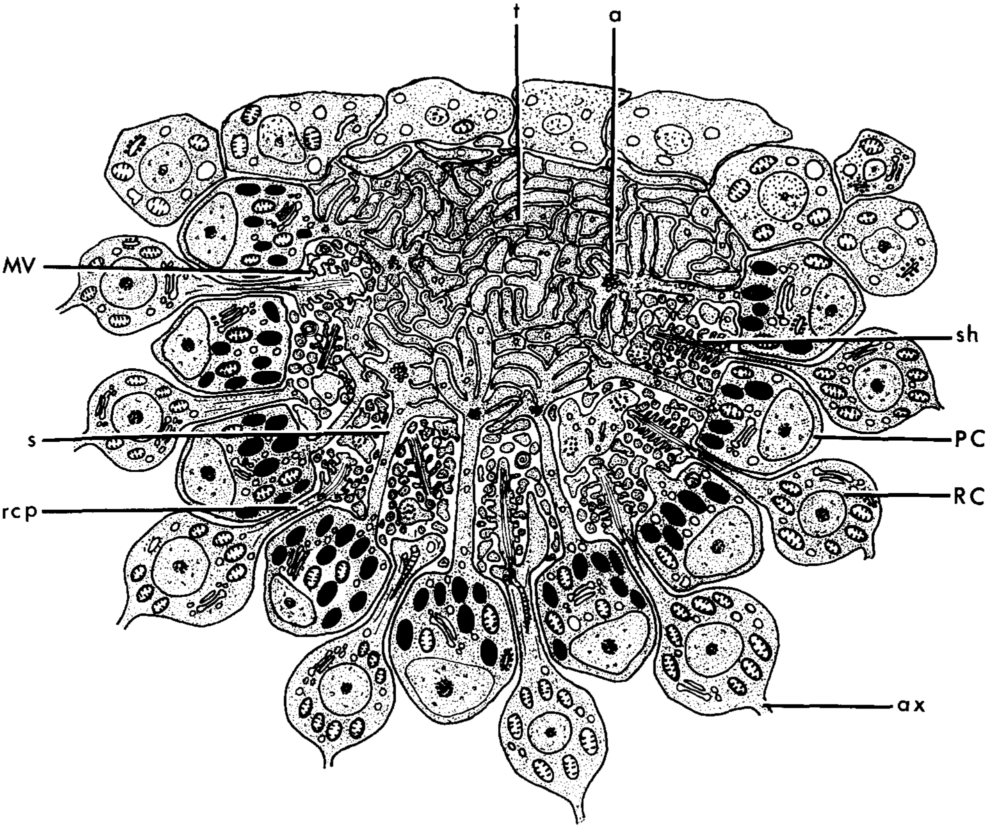
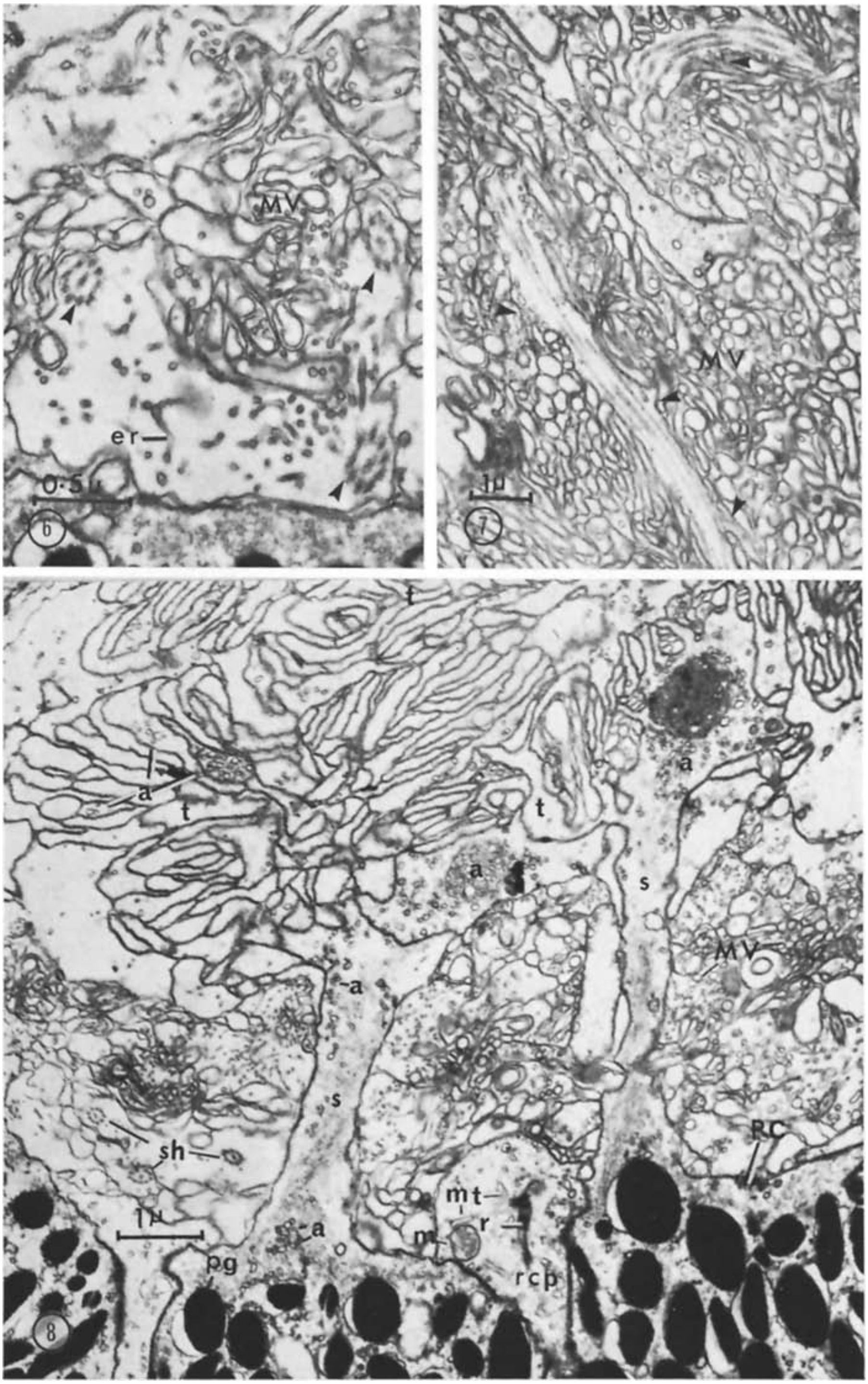


Fig. 5. Diagram of the ocellus of *Bougainvillia* showing the general structure. *a* small vesicles; *ax* axon from the receptor cell; *MV* microvilli from the ciliary membrane; *PC* pigment cell; *RC* receptor cell; *rcp* receptor cell processes; *s* pigment cell strand (stem); *sh* sensory cilium and *t* tubules from the pigment cell

bear microvilli of 100 mμ thickness and 1 μ long. The pigment bodies are round (0.5–1 μ diameter) and each one is enclosed in a membrane (Fig. 2). They occur mostly in the distal part of the pigment cell. In some cases several small pigment bodies may be enclosed by a common membrane or fused to form a single large pigment body of 2 μ diameter, The cytoplasm in addition to pigment bodies also contains mitochondria, Golgi elements and vesicles. Mitochondria are fewer in number than in the receptor cell. In some cases the Golgi complex and the vesicles look so electron dense that it appears as if the Golgi might be involved in pigment synthesis.

Bougainvillia pigment cells are almost cuboidal (5–8 μ broad and 7–9 μ tall). The cell body contains numerous oval pigment bodies of 0.7 μ diameter enclosed in a membrane, small vesicles of 1000 Å diameter and Golgi elements. From the distal region of the pigment cell arises a stem or strand of approximately 1 μ diameter which passes through the ciliary region already mentioned and gives



Figs. 6—8

rise to tubular processes (Fig. 8). These processes are larger than those of photoreceptor cells (300–400 mμ in thickness) and differ in vesicular content. The processes fill the distal region of the ocellar cup (Figs. 5 and 8). They are irregular and show no consistent orientation. Small vesicles of 1 000 Å diameter are present in the basal part of the stem, the stem proper, and in the tubular processes. Sometimes an accumulation of these vesicles which may be enclosed in a membrane has been observed, in the distal part of the stem.

In *Tiaropsis* the pigment cells form an outer border of the ocellar cup. These cells are approximately 20 μ long and 5 μ broad and full of spherical pigment granules of 1 μ diameter enclosed in a membrane. These cells like other endodermal cells in this region often contain vacuoles presumed to be food vacuoles.

c) Photosensitivity in Bougainvillia principis

The medusae of *Bougainvillia* showed an "off response" but no "on response" (Fig. 13A and B). During the experiments with the monochromatic light the sensitivity was recorded for light of 446–625 nm wavelengths but no "off response" was noticed for 405 nm or 655 nm wavelengths. The latency period for "off response" was shorter for blue-green light than yellow-orange (Fig. 14). The animal lost the "off response" when the ocelli were removed (Fig. 13C) though "marginal pulses" (Passano, 1965) were occasionally recorded, and the animals were still capable of spontaneous swimming, indicating that the nervous system was still functioning normally in other respects.

Discussion

a) Ocellar Morphology

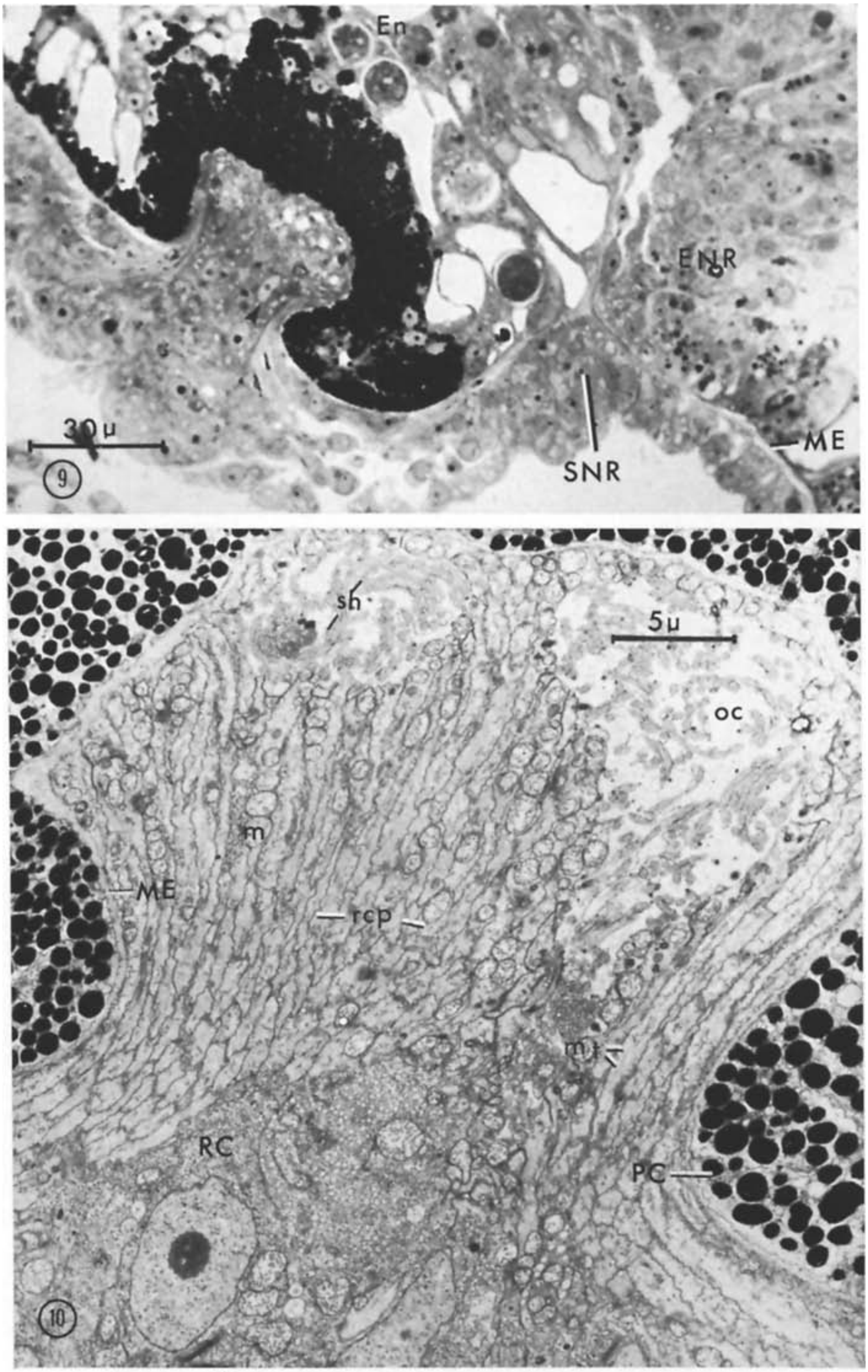
The photoreceptor cells of hydromedusae described in this paper are of the ciliary type. They have a usual $9+2$ filament structure. The presence of the two central fibres in cilia have also been reported in a number of other coelenterates (Eakin and Westfall, 1962; Lentz and Barrnett, 1965; Jha and Mackie, 1967 and Horridge, 1969). This supports Eakin's (1972) view that in the evolution of sensory cilia the central fibres are lost somewhere above the coelenterate line.

Bougainvillia is unusual among the hydromedusae studied in having many cilia per photoreceptor cell. Many cilia have been reported in the photoreceptor cells of *Pleurobrachia pileus* (Horridge, 1964), *Branchiomma vesiculosum* (Kranse

Fig. 6. Electron micrograph of the ocellus of *Bougainvillia* showing a receptor process having a number of cilia. *er* endoplasmic reticulum; *MV* microvilli from the ciliary membrane and the pointer indicate three cilia cut in transverse section present in a single receptor process

Fig. 7. Electron micrograph of the ocellus of *Bougainvillia* showing the sensory cilia. Note the formation of microtubules from the ciliary membrane. *MV* microvilli of the ciliary membrane. The pointer indicates the origin of microvilli from the ciliary membrane

Fig. 8. Electron micrograph of a radial section of an ocellus of *Bougainvillia* showing the pigment cell strand, a group of microtubules from the ciliary membrane. *a* group of small vesicles; *m* mitochondrion; *mt* microtubules inside the receptor cell processes; *MV* microvilli from the ciliary membrane; *PC* pigment cell; *pg* pigment granule; *rcp* receptor cell process; *r* rootlets; *s* strand; *sh* sensory cilia; *t* tubules from the pigment cell strand



Figs. 9 and 10

and Lawerance, 1966), *Cardium edule* (Barber and Wright, 1969) and in the distal retina of *Pecten maximus* (Barber, Evans and Land, 1967). The cilium of *Bougainvillia* differs from others mentioned above in having central fibres, a proximal centriole and striated rootlets. The presence of many cilia could increase the photoreceptor area by forming more microvilli.

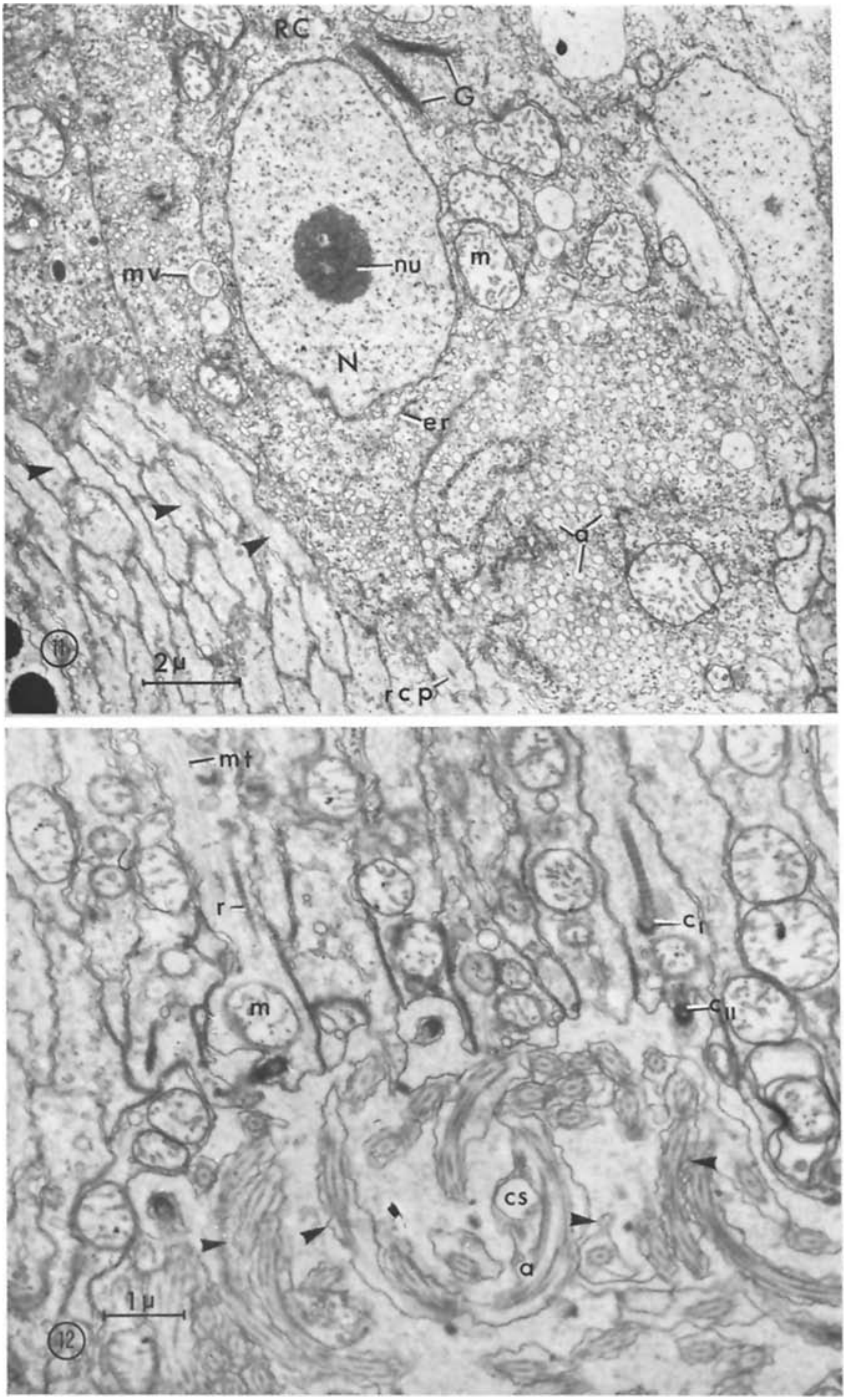
In simple cup-shaped ocellus as those of coelenterates the pigment cells are usually considered to function as a barrier, allowing light to enter from only one direction, this has not been proved. The pigment cells also provide mechanical support to the receptor cells due to their close proximity. If so the support would be increased in *Polyorchis* (Eakin and Westfall, 1962) and *Sarsia* (personal communication from G. O. Mackie and R. M. Eakin) where the microvilli from the ciliary membrane intermingle with the microvilli from the pigment cells. However, in *Bougainvillia* the pigment cells have undergone further specialization, namely the strand passing through the sensory region and forming a mass of tubules which fill the distal region of the ocellus. This mass was referred as "Glaskörper" in the hydromedusae *Hippocrene superficiliaris*, *Staurostoma artica* and *Sarsia mirabilis* (Linko, 1900). The formation of a similar structure from the pigment cell strand has been described in the polychaetes *Nereis vexilosa*, *Neanthis succinea* and *Nereis limnicola* (Eakin and Westfall, 1964). This structure was called a "primitive lens" by Eakin and Westfall (1964) and a "vitreous body" by Hermans and Cloney (1966). The so-called primitive lens in *Nereis* has a spherical structure but in *Bougainvillia* it has no definite shape. Linko (1900) suggested that the "Glaskörper" in hydromedusae protects the delicate appendages of the receptor cells. Eakin and Westfall (1964) implied that the "primitive lens" in polychaetes gathers light. The exact function of this primitive structure in *Bougainvillia* remains unknown. Further study of the refractive index of the tubular material might help to explain its role in photoreception. The pigment cell strand probably serves for the flow of vesicles and metabolites from the cell body to the tubules for the synthesis of tubular material (Eakin and Westfall, 1964).

b) The Effect of Light on the Behaviour of Medusae

The "off response" of *Bougainvillia* which was lost with the removal of the ocelli without removing the tentacular bulbs clearly demonstrates that the ocelli are photosensory. "Off responses" have also been described in *Spirocodon saltatrix* (Hisada, 1956) and the distal retina of *Pecten maximus* (Land, 1966) and of the *Cardium edule* (Barber and Land, 1967). Photoreceptor cells of *Bougainvillia*, *Pecten* and *Cardium* resemble one another being of ciliary origin and also having

Fig. 9. Photomicrograph of a radial section through the ocellus of *Tiaropsis multicirrata*. *En* endoderm; *ENR* exumbrellar nerve ring; *ME* mesoglea; *SNR* subumbrellar nerve ring, and the pointer indicates a receptor cell lying inside the ocellar cup

Fig. 10. Electron micrograph showing a radial section of the ocellar cup of *Tiaropsis*. The cup is lined on the outside by endodermal pigment cells. On the inside (ectoderm) it is filled by the receptor cell processes. Note the mesoglea separating the ectodermal from the endodermal mass. *m* mitochondrion; *ME* mesoglea; *mt* microtubules; *oc* ocellar cavity; *PC* pigment cell; *RC* receptor cell; *rcp* receptor cell process; *sh* sensory cilia



Figs. 11 and 12

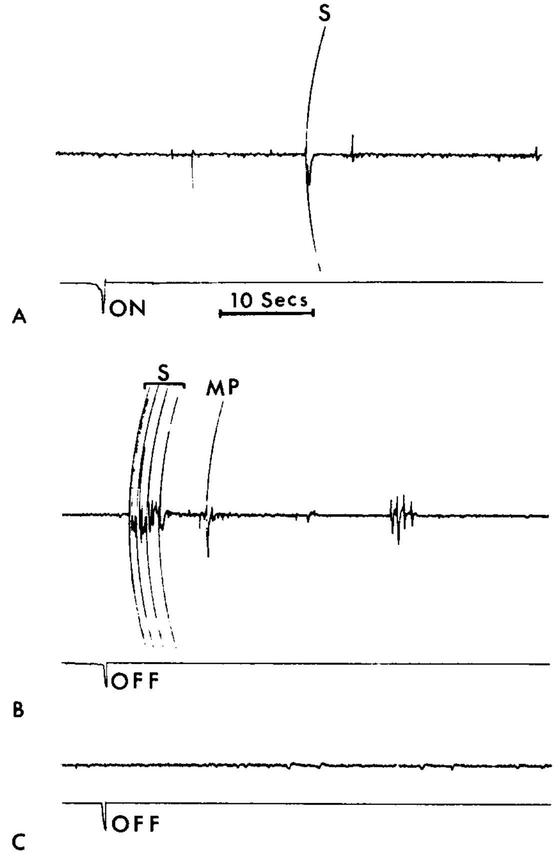


Fig. 13A—C. *Bougainvillia* light response. A shows of an "on response". A single swimming pulse was recorded 30 seconds after the light was switched on, but this is regarded as a spontaneous event not due to photostimulation. In B, a burst of swimming pulses (*S*) follows turning off the light ("off response"). A marginal pulse (*MP*) is also shown. Other events are movement artefacts. C no "off response" was observed when the ocelli are removed

many cilia per photoreceptor cell. Barber and Land (1967) suggested a functional significance between the multiciliary condition of these receptors and the generation of "off response".

The "off response" is considered to be a protective device used by the animal to escape from the predator but this does not seem to be the only function in *Bougainvillia*. A greater sensitivity of *Bougainvillia* to blue-green light

Fig. 11. Electron micrograph of the ocellus of *Tiaropsis* showing photo-receptor cells and distal processes. *a* small vesciles; *er* endoplasmic reticulum; *G* Golgi complex; *m* mitochondrion; *mv* multivesicular body; *N* nucleus; *nu* nucleolus; *RC* receptor cells; *rcp* receptor cell process. The pointer indicates the microtubules inside the receptor process

Fig. 12. Electron micrograph of the ocellus of *Tiaropsis* showing receptor cell processes with cilia and the rootlets. Note the ciliary membrane form microvilli. *a* small vesicles in ciliary shaft; c_1 proximal centriole and c_{11} distal centriole; *cs* intermediate-sized vesicle; *m* mitochondrion; *mt* microtubules; *r* rootlets; the pointer indicates possible presence of microvilli

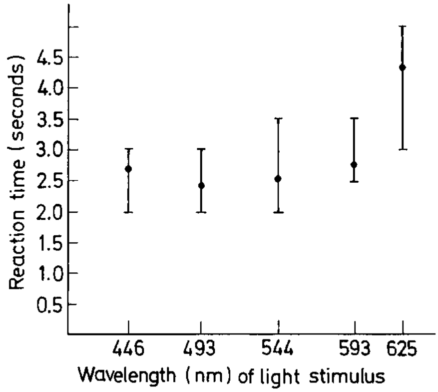


Fig. 14. Latency period for "off response" vs. wavelength shown by *Bougainvillia*. The vertical lines represent the latency period and the circles indicate the mean latency period

(446–593 nm) than to yellow-orange (625 nm) light, although the amount of energy reaching the animals was the same for all wavelengths, indicates a true difference in photosensitivity. Thus it can be implied that the sensitivity may be related to the vertical distribution of the animals. A blue-green light has a higher penetration than a yellow-orange, this suggests that *Bougainvillia* are adapted to life in fairly deep waters. While the vertical distribution of *Bougainvillia principis* is not known, related species occur in depths several hundred meters below the point to which red light can penetrate.

c) Evolution of Photoreceptors in Coelenterates

Several coelenterates e.g. *Hydra*, *Gonionemus* (Hyman, 1940), *Mitrocomella* (Romanes, 1877) are sensitive to light but none of them bear distinct ocelli. Lentz and Barrnett (1965) observed the ciliated sensory cells in the outer epithelium of *Hydra* and later on Lentz (1966) suggested that they are probably photosensory. The same thing might apply to *Gonionemus* and *Mitrocomella*. However, Mackie and Passano (1968) suggested that photosensitivity of *Mitrocomella* might be due to non-nervous elements. The ciliated photosensory cells can act better if they are grouped together in association with some non-ciliated pigmented cells in the form of an organ. Such a concentration of sensory elements shows two lines of ocellar evolution in coelenterates i.e., (a) toward an "everted type" where the pigment and receptor cells lie side by side e.g. *Leuckartiara*, *Polyorchis*, *Sarsia* and *Bougainvillia* and (b) an "inverted type" where the pigment cells form a cup-shaped structure through the mounth of which receptor processes enter to form an enclosed mass, e.g. *Tiaropsis* and *Aurelia*.

The "erect or everted type" of ocelli are arranged in an ascending order of complexity as shown in Gig. 15A–E. The ocellus of *Leuckartiara octona* and the simple ocellus of *Aurelia aurita* (Schewiakoff, 1889) present examples of primitive distinct ocellus (Fig. 15B). This is a simple layer formed of a group of ciliated sensory cells in association with pigment cells. The sensory cells of *Leuckartiara* bear microvilli in addition to the cilia on their general surface. The above mentioned layer is modified to form a cup-shaped structure to receive light only from a

Fig. 15A—E

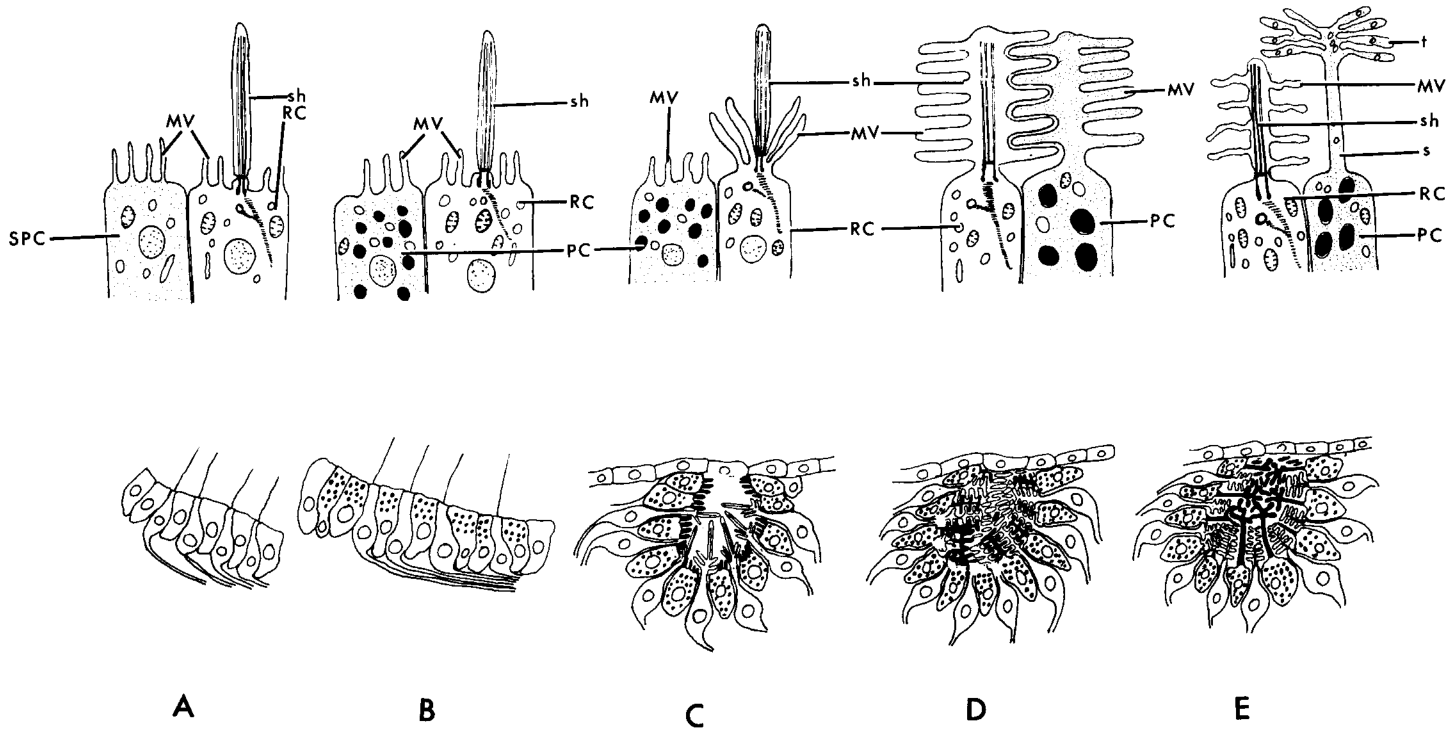


Fig. 15A—E. Stages in the evolution of the everted type of ocellus from simple ciliated sensory cells and supporting cells. The bottom row shows the general ocellar structure and the top row show detailed structure of the photoreceptor and pigment cells. A: A hypothetical indistinct ocellus. B: Diagram of a primitive distinct ocellus (association of pigment and receptor cells) as in *Leuckartiara*. C: Formation of a cup-shaped ocellus, and a shift in the formation of microvilli from the general surface to the base of the cilium of the receptor cell as in *Asterias*. D: Interdigitation of the villous processes of the receptor and pigment cells as in *Polyorchis*. E: Spatial differentiation of the villous processes of receptor and pigment cells as in *Bougainvillia*. *MV* microvilli; *PC* pigment cell; *RC* receptor cell; *sh* sensory cilium; *SPC* supporting cells and *t* tubules. Diagrams C and D are based on Eakin and Westfall (1963) particular direction and we see a shift in the origin of the microvilli from the surface of the receptor cell to the base of the cilium to fill the ocellar cup (Fig. 15C). as there is no known coelenterate having an ocellus in this intermediate category I take examples from echinoderms e.g. *Asterias rubens* (Vaupel von Harnack cited from Florey, 1967), *Henricia leviscula*, *Leptasterias pusilla* and *Patiria minata* (Eakin and Westfall, 1963). Fig. 15D shows that the villous processes of the receptor cells are formed from the plasma membrane covering the cilium and intermingle with similar processes from the pigment cells e.g. *Polyorchis* (Eakin and Westfall, 1962) and *Sarsia* (personal communication, G. O. Mackie and R. M. Eakin). Next stage in evolution is presented by *Bougainvillia* which shows spatial differentiation of villous processes of the pigment and receptor cells (Fig. 15E). The villous processes of the pigment cells form a structure similar to the primitive lens of polychaetes the significance of which has already been discussed. The ocelli of cubomedusa *Charybdea xaymacana* are very highly evolved in having a distinct cornea, vitreous body, lens and the retina (Berger, 1900). The eye of *Charybdea* resembles in many respects the vertebrate eye although the latter is of inverted type. An ultrastructural study of *Charybdea* ocellus might show more similarities between the two.

The "inverted type" of ocellus has been studied in *Aurelia aurita* (Schewiakoff, 1889) and *Tiaropsis diademata* (Linko, 1900). According to Linko the receptor cells are present in the ocellar cup of *Tiaropsis* and they send their axons into the subumbrellar nerve ring. The present study of the ocelli of *Tiaropsis multicirrata* (Singla, 1969) shows that most of the receptor cells are outside the ocellar cup and their axons enter the subumbrellar nerve ring. The ocellus of *Tiaropsis* resembles the vertebrate eye in having ciliary photoreceptors and being of inverted type.

An unexplained feature of the ocellus of *Tiaropsis* is the fact that the opening of the ocellus points downwards, and hence with the animal in its normal orientation, would not receive light from above, except what penetrated the pigment barrier.

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