Eyes as optical alarm systems in fan worms and ark clams

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SUMMARY

Eye structure and optics were investigated in two sabellid polychaetes (*Sabella melanostigma*, *Dasychone conspersa*) and three arcacean bivalves (*Arca zebra*, *Barbatia cancellaria*, *Anadara notabilis*). The polychaetes have numerous compound eyes arranged in pairs along the branchial tentacles. Each ommatidium is composed of three cells: one receptor cell forming a ciliary receptive segment, and two pigment cells forming an extracellular lens (crystalline cone). The ark clams *Arca* and *Barbatia* possess large numbers of compound eyes arranged along the mantle edge. The ommatidia of these eyes are composed of one or two ciliary receptor cells surrounded by several layers of pigment cells. There are no lenses in the ommatidia of the clam eyes. All three species of ark clam also have many pigment-cup eyes on the mantle edge. The cup eyes lack lenses, and the cavity of the cup is filled with rhabdomeric microvilli from the receptor cells.

The crystalline cones in the sabellid compound eyes are powerful lenses that reduce the field of view of the receptor cells to slightly more than 10°. The lensless ommatidia of *Barbatia* have much larger fields of view (≈ 30°). This difference correlates with a behavioural response to much finer moving stripes in the fan worms. A comparison of compound eyes and cup eyes in *Barbatia* reveals a poor resolution in both, but a much higher sensitivity is estimated for the cup eyes.

The tentacular eyes of fan worms and the mantle eyes of ark clams trigger protective responses: retraction into the tube and shell closure, respectively. The responses are triggered by visual motion and the eyes work as burglar alarms rather than imaging eyes. For this purpose, the compound eyes may seem to occur in affluent numbers: 240 eyes with a total of 12 000 ommatidia in *Sabella* and 300 eyes with a total of 39 000 ommatidia in *Barbatia*. The number of ommatidia that simultaneously monitors any direction in space is, on average, 43 in *Sabella* and 755 in *Barbatia*. The large number of eyes is explained as a visual strategy which provides a robust alarm system designed to reliably detect predators without causing false alarms.

The literature on tentacular eyes of fan worms and mantle eyes of bivalves is reviewed, and the evolutionary origin of these independently-acquired visual organs is discussed. I suggest the possibility that hyperpolarizing photoreceptor cells (shadow detectors) evolved from chemoreceptors that were inhibited by light.

1. INTRODUCTION

Tubiculous polychaetes such as sabellids and serpulids respond to shadows and visual motion cues by swiftly retracting their tentacular crown into the tube (Nicol 1950). The visual sensors for this protective reflex are compound eyes located at various positions on the tentacles (Andrews 1891; Hesse 1899). An analogous visual system is found in many ark clams (*Arca*, *Barbatia*, *Pectunculus*) where the mantle edge bears numerous compound eyes providing the optical input to the shell closure response (Patten 1886; Hesse 1900; Küpfer 1916; Jacob 1926; Nowikoff 1926; Braun 1954). These polychaete and bivalve eyes are the only examples of compound eyes outside the Arthropoda; two cases that are difficult to classify are left out: the aggregated receptor cells of the arrow-worm *Eukrohnia* (Ducret 1978) and the optic cushions of starfish (Eakin & Brandenburger 1979). Within the Arthropoda, compound eyes are elaborate structures (see Nilsson 1989) that have been around at least since the Cambrian, and there are probably not many traces left revealing the reasons why compound eyes originally evolved instead of camera-type eyes. The compound eyes of polychaetes and bivalves have evolved independently and more recently. There are still species where the individual ommatidia are so distant from one another that they form intermediates between compound eyes and groups of individual ocelli (Hesse 1899, 1908). In sabellid and serpulid polychaetes (fan worms) the varying placement of the compound eyes on the branchial tentacles (Andrews

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1891) seems to indicate that compound eyes have evolved independently several times even within these families.

Fan-worm and bivalve lineages can be aptly described as evolutionary eye factories, in the sense that they have developed eyes of many different types, often at unusual positions on the body. In addition to their compound eyes they often possess simple eyes of a pigmented pit or cup design, in various locations on the body. In sabellid polychaetes, such eyes are found in the head, in the pygidial epithelium and laterally in each segment (Ermak & Eakin 1976; Dragesco-Kerneis 1980a), whereas in ark clams, large cup eyes are scattered between the compound eyes on the mantle edge and cephalic or branchial cup eyes exist in some species (Patten 1886; Morton 1987; Janssen 1991). It thus seems that if any recent animals hold the key to why eyes evolve to become compound or simple, these animals must be sabellid polychaetes and ark clams.

A related problem is the evolutionary origin of photoreceptor cells. The photopigment, which is membrane-bound, is located either in the membrane of modified cilia or in the membrane of microvilli. This led Eakin (1963) to propose two lines of photoreceptor-cell evolution: a ciliary line in deuterostomes, involving elaborations of the ciliary membrane, and a rhabdomeric line in protostomes, with microvilli protruding from the cell membrane proper. Later investigations have disclosed so many exceptions to this theory that modified or alternative theories had to be erected (Vanfleteren & Coomans 1976; Salvini-Plawen & Mayr 1977; Eakin 1982; Burr 1984). Originally, mollusc and annelid photoreceptors were thought to be rhabdomeric (Eakin 1963), and indeed most of them are. Prominent exceptions, however, are the compound eyes of sabellid polychaetes (Lawrence & Krasne 1965; Kerneis 1966) and ark clams (Levi & Levi 1971).

Most animals, even those with excellent vision, make do with a single pair of eyes, sometimes complemented by medial eyes. But in sabellid

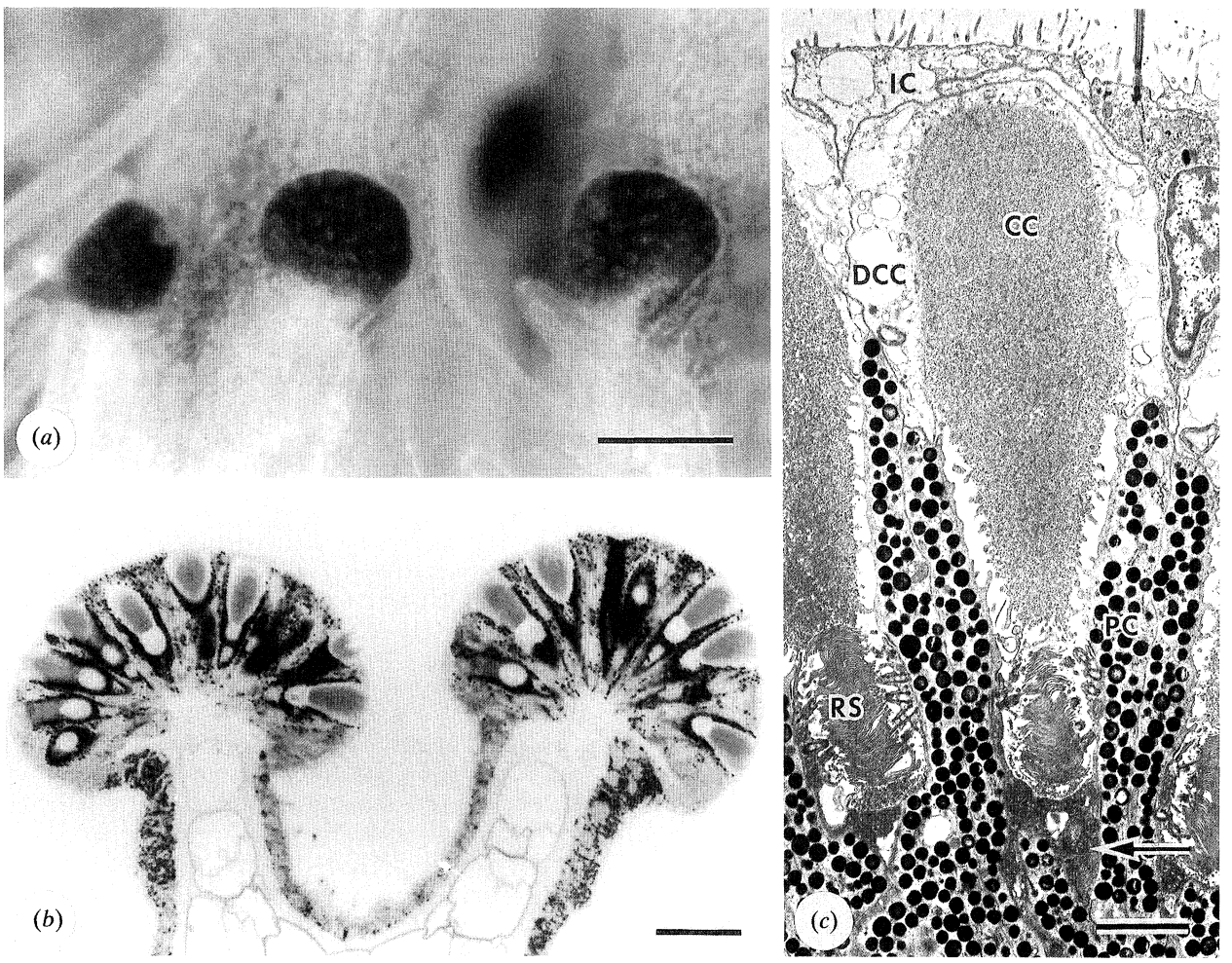

Figure 1. Compound eyes of sabellid polychaetes. (*a*) Part of two radioles of a live *Sabella melanostigma*, showing three compound eyes in focus. (*b*) Semi-thin section through a pair of compound eyes of *Sabella melanostigma*. The eyes sit at the distal end of a pair of ridges on the radiole, giving the false impression of eye stalks in the section. (*c*) Electron micrograph of an ommatidium in the compound eye of *Dasychone conspersa*. Note the density gradient in the crystalline cone, the cilium on one of the interstitial cells and the mitochondria (arrow) below the receptive segment. Abbreviations: CC, crystalline cone; DCC, distal cone cell; IC, interstitial cell; PC, pigment cell; RS, receptive segment of receptor cell. Scale bars: (*a*) 100 μm; (*b*) 25 μm; (*c*) 2 μm.

polychaetes and ark clams the number of eyes is astounding: *Sabella* may have over 200 eyes, each consisting of some 60 ommatidia, and the ark clam *Barbatia* may have 300 compound eyes, each composed of more than 100 ommatidia, and in addition some 2000 pigmented cup eyes with numerous photoreceptor cells in each. Such massive expenditures on eyes must imply that vision is extremely important to these animals. Surprisingly, very little is known about the visual performance of any of these eyes.

In the present paper, I describe the structure and optics of eyes in two species of sabellid polychaete and three species of ark clam. This new information together with a review of previous work provides the framework for approaching two fundamental evolutionary questions in vision: (i) why are some eyes compound and others simple?; and (ii) why are some photoreceptor cells ciliary and others rhabdomeric?

2. MATERIALS AND METHODS

Two species of sabellid polychaete and three species of ark clams were collected in the waters around Carrie Bow Cay on the barrier reef of Belize, Central America. The polychaetes were *Sabella melanostigma* (Schmarda), and a smaller species, with some uncertainty determined as *Dasychone conspersa* (Ehler). The clam species were the Turkey wing, *Arca zebra* (Swainson), the Red-brown ark, *Barbatia cancellaria* (Lamarck) and the Eared ark, *Anadara notabilis* (Röding). All work on live animals was carried out at Carrie Bow Cay research station.

For histology, the eyes were cut off into sea water with 2.5% glutaraldehyde and left refrigerated for at least 2 h. They were then rinsed in cacodylate buffer, stained in 1% OsO_4 for 1 h, dehydrated in an alcohol series and embedded in Epon resin. Semi-thin sections for light microscopy were cut with a glass knife and stained with Methylene Blue and Azure Blue. For electron microscopy, sections were cut with a diamond knife and stained with lead citrate and uranyl acetate.

The refractive index of the optical components of the eyes was measured with a Zeiss interference microscope (Jamin-Lebedeff), after the eyes had been disrupted with fine needles in a drop of sea water. The same type of preparation was also used to measure the focal distance of the lenses (crystalline cones) in the sabellid eyes.

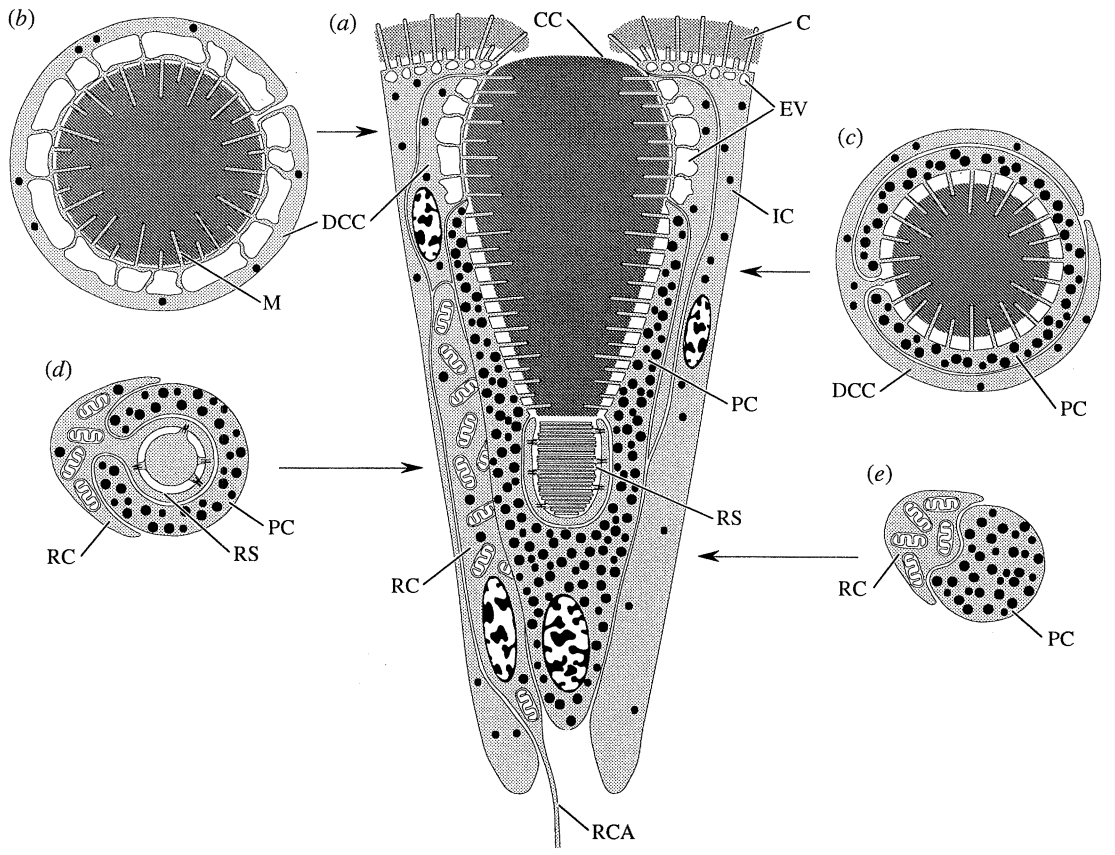

Figure 2. Semischematic diagram of an ommatidium of *Sabella melanostigma*. The level of the cross-sections (*b–e*) are indicated by arrows. Cell nuclei, mitochondria and pigment granules are schematically illustrated. The ommatidium of *Dasychone conspersa* differs from the diagram by: (i) having a more elongated crystalline cone which is covered distally by the distal cone cell and interstitial cells; (ii) having the main mass of receptor cell mitochondria just proximal to the receptive segment; and (iii) having a more distal placement of the pigment cell nucleus. Abbreviations: C, cuticle; CC, crystalline cone; EV, empty vesicles; DCC, distal cone cell; IC, interstitial cell; M, microvilli; PC, pigment cell; RC, receptor cell with its ciliary receptive-segment (RS) and axon (RCA).

Preliminary behavioural studies were made on animals placed in a fish tank exposed to sunlight. Visual stimuli were presented outside the glass wall of the fish tank. The responses of the animals to the movement of single black stripes of different widths were tested and recorded on video. The stripes, made of black card, were vertical (the length subtending about 30° of visual angle) and moved back and forth in the horizontal plane. The background was stationary and white, ensuring that the moving

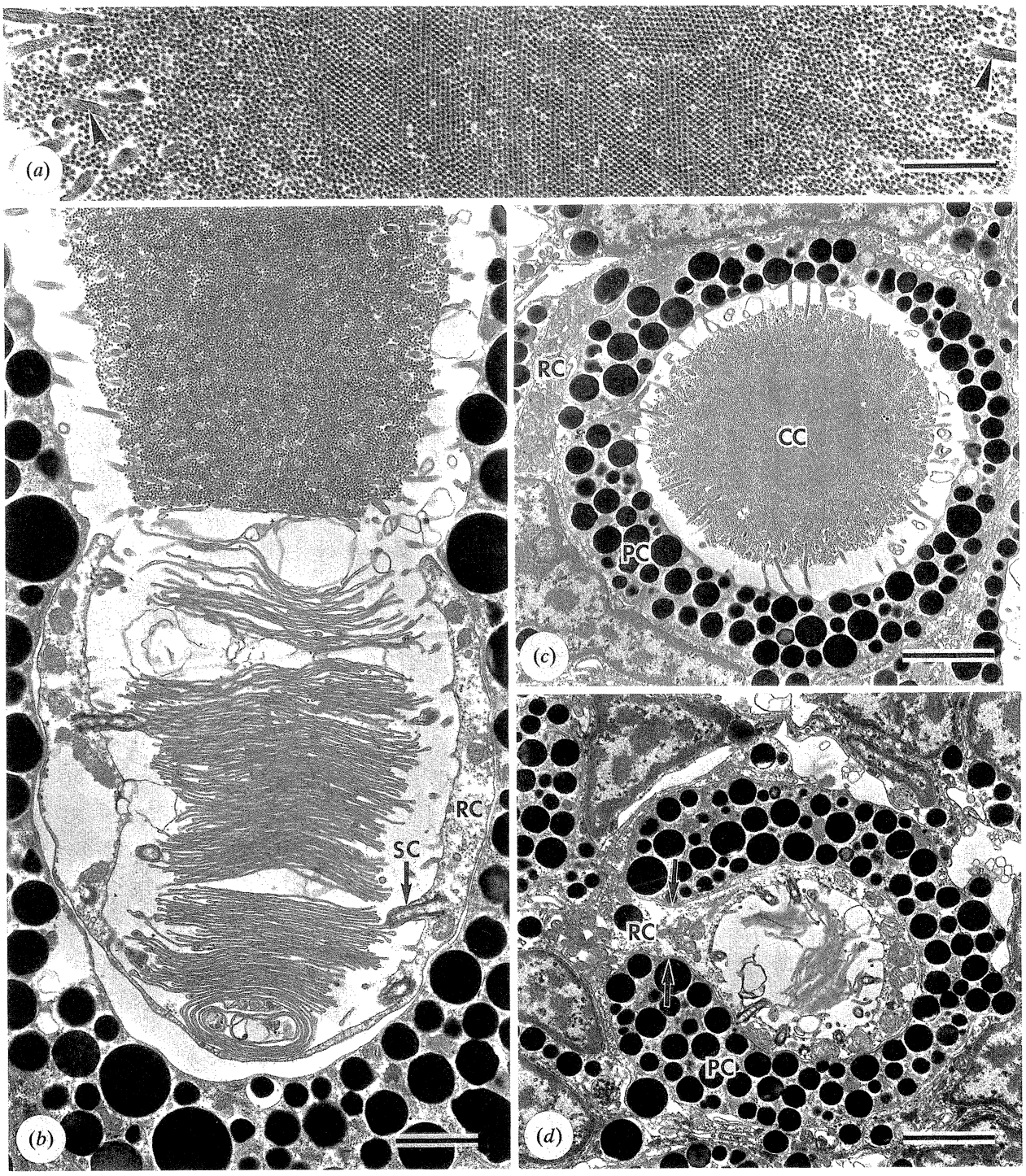

Figure 3. Electron micrographs of the compound eye of *Sabella melanostigma*. (*a*) High magnification micrograph across the crystalline cone, showing the density gradient and the crystalline packing of granules in the central core. Microvilli (arrowheads) invade the periphery of the cone. (*b*) Longitudinal section through the receptive segment of the receptor cell and the proximal tip of the crystalline cone. The receptor cell forms a cytoplasmic cup around the stack of flattened ciliary membrane-sacs. (*c*) Cross-section through the proximal part of the crystalline cone enveloped by the pigment cell. (*d*) Cross-section through the receptive segment of the receptor cell showing the connection (between arrows) to the cell body. Abbreviations: CC, crystalline cone; PC, pigment cell; RC, receptor cell; SC, sensory cilium. Scale bars: (*a*) 0.5 μm; (*b*) 1 μm; (*c*,*d*) 2 μm.

stripe caused no modulation of the average luminance on the animal. After a stripe had been introduced in the visual field, it was left stationary until the animals resumed feeding behaviour.

3. RESULTS

(*a*) *Compound eyes of sabellids*

The compound eyes of *Sabella melanostigma* are clearly visible as pairs of black dots along the branchial tentacles (radioles). In large specimens there may be a pair of eyes at five regularly-spaced positions along each radiole. This makes a total of some 240 compound eyes on the tentacular crown of a single individual. Each eye is 50–100 μm in diameter and contains 40–60 irregularly-packed ommatidia. Although the ommatidia are clearly visible in live animals (figure 1*a*), there is no pseudopupil phenomenon as in most arthropod compound eyes (see Stavenga 1979). The compound eyes of *Dasychone conspersa* occur in pairs as in *Sabella*, but more irregularly and only at 2–3 levels on each radiole and only with 10–20 ommatidia in each eye.

The ommatidial construction in the two sabellid species is so similar that the description of it can be made general. Each ommatidium is a tapering pigmented tube, in the bottom of which is the receptive segment of a single photoreceptor cell (figure 1*b,c*). Distal to this segment, the pigmented tube is filled by an extracellular lens which may be called a crystalline cone in analogy with the similarly shaped structure of arthropod compound eyes. The distal part of the crystalline cone is encircled and produced by a weakly pigmented cell, the distal cone cell, which contains large empty vesicles surrounding the crystalline cone (figure 2*a,b*). The proximal part of the crystalline cone is formed by a pigment cell which also folds around the receptive segment of the photoreceptor cell. The crystalline cone is an aggregation of extracellularly secreted minute (30 nm) granules, possibly glycogen (Kerneis 1968, 1973). In the centre of the crystalline cone, these granules are densely packed in a crystalline pattern whereas in the periphery they are more loosely and irregularly packed (figure 3*a*). The crystalline cone is suspended in a regular array of microvilli projecting from the distal cone cell and the pigment cell. These microvilli extend into the periphery of the cone but never into its centre (figures 2*a–c*, 3*a–c*). In *Sabella melanostigma* the distal face of the crystalline cone is contiguous with the cuticle but in *Dasychone conspersa* both the distal cone cell and interstitial cells lie between the cone and the cuticle (figures 1*c*, 2).

Below the crystalline cone, the receptor cell forms a cup-shaped cavity with its opening towards the crystalline cone (figure 2). The wall of the cup is a thin cytoplasmic layer from which numerous short cilia project into the cavity (figure 3*b,d*). The membrane of each cilium is expanded to a large flattened sac. In *Sabella*, a total of 100–150 cilia together produce a membrane stack of the same number of flattened sacs. The receptor cells of *Dasychone* are much smaller and carry fewer than 80 cilia and membrane sacs. In both species, the cilia lack the central pair of microtubules ($9 \times 2 + 0$ structure), and the basal bodies have no rootlets.

The receptor cell has its nucleus outside the pigment tube and a thin process joins it to the receptive segment under the crystalline cone (figure 3*d*). Proximally, a thin axon emerges from the eye and enters the branchial nerve (see Santer & Laverack 1971). The main mass of receptor-cell mitochondria are found in different places in the two species: in *Sabella* they occupy the space around and below the nucleus (figure 2), in the main cell body, whereas in *Dasychone* they lie proximally in the receptive segment of the cell (figure 1*c*). In both species, mitochondria are also present in the narrow cytoplasmic space around the stack of ciliary membrane.

The ommatidium is thus composed of three cells, the distal cone cell, the pigment cell and the receptor cell (figure 2). An undetermined number of interstitial pigment cells lie between the ommatidia. Distally these cells carry microvilli projecting into the thin cuticle. Some of the interstitial cells also bear long unmodified cilia anchored by striated rootlets (figure 1*c*).

For optical investigations of the crystalline cones, eyes were torn apart with fine needles on an object slide. Occasionally this produced preparations that could be used for measurements of refractive index and focal distance. However, attempts to measure the refractive index of the crystalline cones were mostly

Table 1. *Some parameters of optical significance*

	Sabella melanostigma (compound eye)	*Dasychone conspersa* (compound eye)	*Barbatia cancellaria* (compound eye)	*Barbatia cancellaria* (cup eye)[a]	*Anadara notabilis* (cup eye)[a]
Diameter of distal aperture	12–14 μm	5–6 μm	14–19 μm	14 μm	17 μm
Aperture to receptor distance	15–18 μm	10–13 μm	26–32 μm	40 μm	60 μm
Receptor diameter	2.5–3.0 μm	1.2–1.5 μm	2.0–2.2 μm	⩾ 7 μm	⩾ 6 μm
Receptor depth	5–7 μm	2.7–3.3 μm	3–4 μm	≈ 35 μm	≈ 18 μm
Divergence of neighbouring visual axes	22°–30°	18°–21°	0°–40°	≈ 18°	≈ 7°

[a] Typical values from reasonably large eyes.

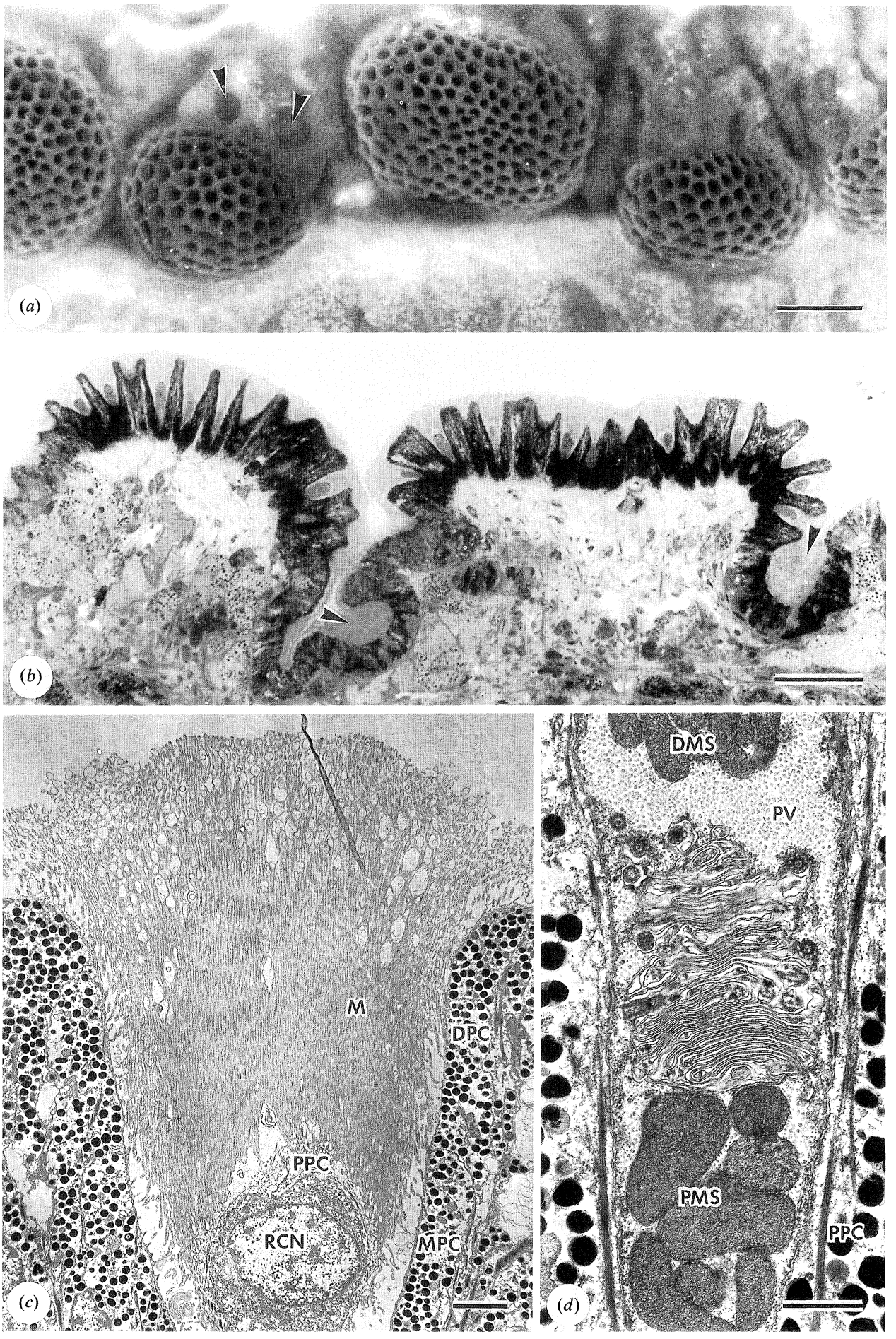

Figure 4. For description see opposite.

unsuccessful because the cones proved difficult to isolate from the surrounding cells (probably because of the microvilli projecting into the cone). Only a few reasonable preparations were obtained from *Sabella melanostigma* but none succeeded in *Dasychone*. Refractive index measurements were taken along the midline of cones lying on their side, thus giving average values across the cones (for method see Nilsson & Odselius 1981). The variation in the resulting values was considerable, covering a range from 1.38 to 1.46. From the ultrastructure of the crystalline cone it is reasonable to suppose that it contains a gradient of refractive index, both radially and longitudinally. Unfortunately the quality of the preparations was not good enough to allow an analysis (see Nilsson *et al.* 1983) of these gradients.

The preparations often contained lumps of pigment cells penetrated by a few crystalline cones that were standing up such that their imaging properties could be studied. With the condenser of the microscope removed, it was possible to measure the position of images of the microscope's field diaphragm, produced behind single cones. Using a water immersion objective (×25), the plane of best image was located 3–6 μm behind the proximal tip of the crystalline cone in eight preparations of *Sabella melanostigma*. Similar but more uncertain values were obtained for *Dasychone conspersa*. The conclusion must thus be that the crystalline cone is capable of producing a focus somewhere within the proximal part of the receptive segment (see table 1 for dimensions of eye components).

Given a refractive index, n_1, of about 1.42 of the crystalline cone, its distal radius of curvature, r (about 7 μm in *S. melanostigma*) would produce an image at a distance:

$$f = n_1 r/(n_1 - n_0)$$

from the surface, where n_0 is the refractive index outside the cone, here taken to be 1.34 (Born & Wolf 1965). Performing this calculation yields a focal length of 124 μm which would place the image far below the eye. This can be taken as proof that a refractive index gradient within the crystalline cone is responsible for the main dioptric power in the ommatidium.

Very simple behavioural experiments were performed on eight individuals of *Sabella melanostigma* kept in an outdoor glass tank exposed to the midday sun. Single black stripes of different widths, presented against a white background, were moved back and forth to trigger the withdrawal response. For each stripe width, the experiment was repeated four times. The movement of the stripe caused no change in general luminance. The results were surprising: a stripe subtending only 1.5° in visual space was enough to repeatedly cause the animals to withdraw. Even a stripe subtending 0.75° occasionally caused a response.

(*b*) *Compound eyes of ark clams*

The two species of ark clam, *Arca zebra* and *Barbatia cancellaria*, have numerous compound eyes along the mantle edge. In bivalves, the mantle edge is divided into three folds, the outer of which carries the eyes in Arcacea (in other bivalves, eyes are found on the middle fold instead: Waller 1980). This means that the eyes of ark clams have to look out through the periostracum, which is secreted in the groove between the outer and middle fold and covers the shell. But since the periostracum is thin and perfectly clear, this situation should not affect vision. In *Barbatia cancellaria* the two halves of the mantle together carry about 300 compound eyes in a single row on the outer fold. In the anterior and posterior parts of the mantle edge, the eyes are so close that they touch each other (figure 4*a*). The compound eyes sit on short stalks and vary considerably in size. The larger eyes contain about 160 ommatidia, whereas the smaller ones may have less than 100 ommatidia. The eye diameter varies accordingly between 180 μm and 300 μm. The closely packed ommatidia look like hollow tubes without any lenses or other refracting structures. This gives the whole eye the appearance of a sponge rather than an eye (figure 4*a*). Some of the larger eyes are conspicuously concave in the centre, resulting in ommatidial axes crossing over each other. Another peculiarity is that neighbouring eyes often have ommatidia that look straight into each other.

The compound eyes of *Arca zebra* are fewer (90–100) and smaller (40 ommatidia) but otherwise similar to those of *Barbatia cancellaria*. Since I did not find any structural differences between the ommatidia of the two species, the description below is given for *Barbatia* which was examined more carefully.

Each ommatidium of *Barbatia cancellaria* is a funnel-shaped pigment tube with a photoreceptor cell in the bottom (figures 4*b*, 5). There are no lenses or other focusing structures. The pigment funnel consists of three types of pigment cell. In the bottom of the funnel two proximal pigment cells surround the receptor cell. More distally, these two cells form an unpigmented thin cover around the receptor cell, and their distal-most parts produce extremely long and straight microvilli which fill the pigment funnel above the receptor cell (figure 4*c*). The microvilli, which are

Figure 4. The compound eyes of *Barbatia cancellaria*. (*a*) The mantle edge with its row of closely spaced compound eyes. Note also the numerous cup eyes (arrowheads). (*b*) Semi-thin section through two compound eyes. The larger eyes typically have a slightly concave centre. Pigment-cup eyes (arrowheads) are located between the compound eyes. (*c*) Electron micrograph of the distal part of an ommatidium, showing the pigment funnel filled with extremely long microvilli. (*d*) The central part of the receptor cell with the membrane-stack of flattened cilia. Abbreviations: DPC, distal pigment cell; MPC, medial pigment cell; PPC, proximal pigment cell; RCN, receptor cell nucleus; M, microvilli; PV, 'photic' vesicles; DMS, distal mitochondrial segment; PMS, proximal mitochondrial segment. Scale bars: (*a*) 100 μm; (*b*) 50 μm; (*c*) 2 μm; (*d*) 1 μm.

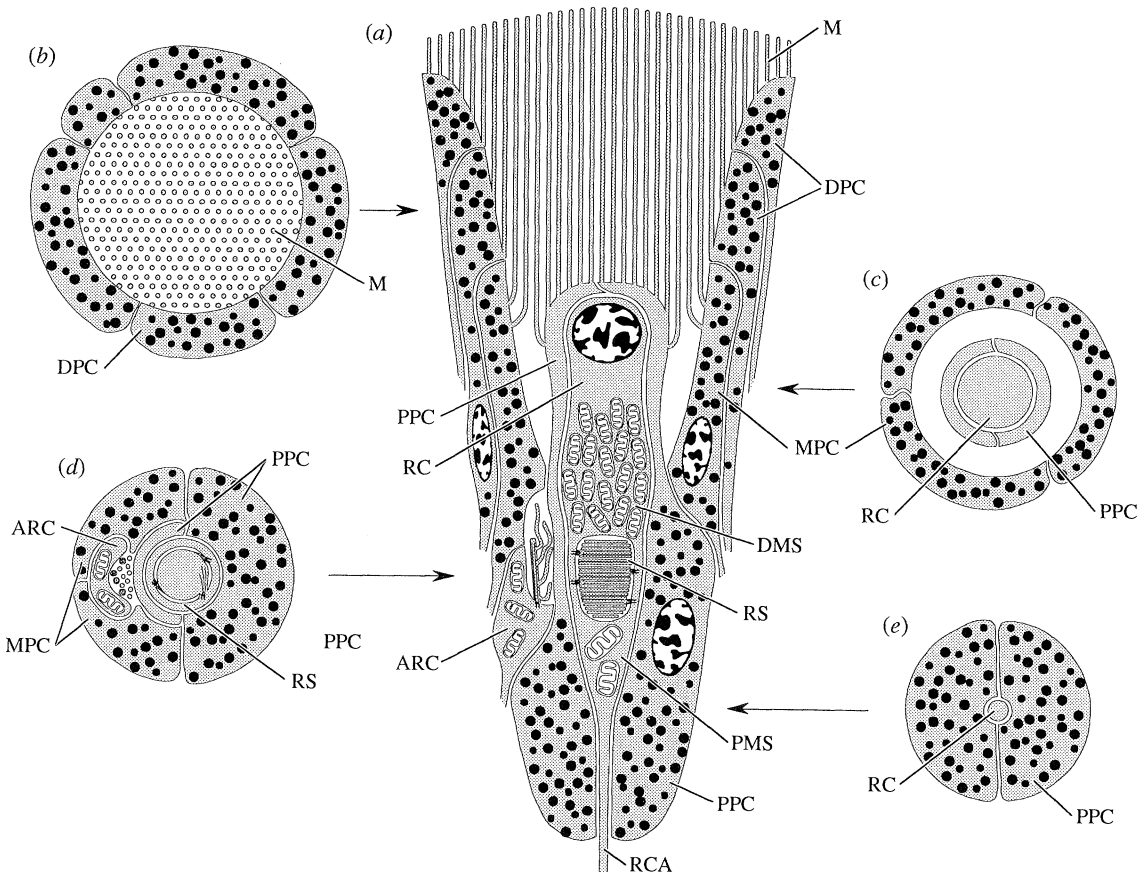

Figure 5. Semischematic diagram of an ommatidium of *Barbatia cancellaria*. The level of the cross-sections (*b–e*) are indicated by arrows. Cell nuclei, mitochondria and pigment granules are schematically illustrated. Abbreviations: DPC, distal pigment cell; MPC, medial pigment cell; PPC, proximal pigment cell; M, microvilli; RC, receptor cell with its distal mitochondrial segment (DMS), receptive segment (RS), proximal mitochondrial segment (PMS) and axon (RCA); ARC, accessory receptor cell with long cilia from which microvilli project.

sometimes swollen and appear to bud off vesicles at their tips, are similar in principle to the shorter epidermal microvilli which coat the animal. The middle segment of the pigment funnel is formed by three medial pigment cells, and distal to these there is an undetermined number of distal pigment cells arranged in two levels with 4–8 cells in each (figure 5). Both the medial and distal pigment cells contribute some microvilli to the content of the funnel. Between the ommatidia there is a small number of less-pigmented interstitial cells.

The photoreceptor cell is organized into four distinct segments lined up along the ommatidial axis: distally is a nuclear segment, followed by a segment with numerous small mitochondria, then the receptive segment, and finally a segment with a few large mitochondria (figure 6*a–c*). The axon emerges from the proximal tip of the cell, and joins the pallial nerve. In the periphery of the mitochondrial segments (figure 4*d*), there are vast numbers of minute (40–50 nm) spheres which resemble the photic vesicles of gastropod photoreceptors (see Eakin 1990).

The receptive structure is a cavity, or vacuole, into which short sensory cilia project (figure 4*d*). The membrane of each cilium gives rise to a few large flattened sacs. In total there are some 50 piled sacks originating from about half as many cilia. The membrane sacs, which may branch or fold, protrude from the side of the cilium (figure 6*d*), and not from the tip as in the sabellids. The cilia lack striated rootlets, and the axoneme has the complete $(9 \times 2 + 2)$ set of microtubules which, however, becomes disordered towards the tip of the cilium.

Every third or second ommatidium has a second sensory cell wedged in between the medial and proximal pigment cells (figures 5, 6*c*). Close to the receptive segment of the main photoreceptor cell, this accessory receptor cell carries a small bundle of cilia from which irregular microvilli project. These cilia also have two central microtubules. It is unclear whether this is another photoreceptor cell, but the possibility that it is a chemoreceptor or a mechanoreceptor can probably be ruled out because of its protected location.

Interference microscopy of preparations of disrupted fresh *Barbatia* eyes in sea water revealed no structures with significantly elevated refractive index. The microvillar body which fills the distal part of the pigment funnel, could frequently be identified in these preparations and it did, in fact, appear to have a lower refractive index than most other cellular

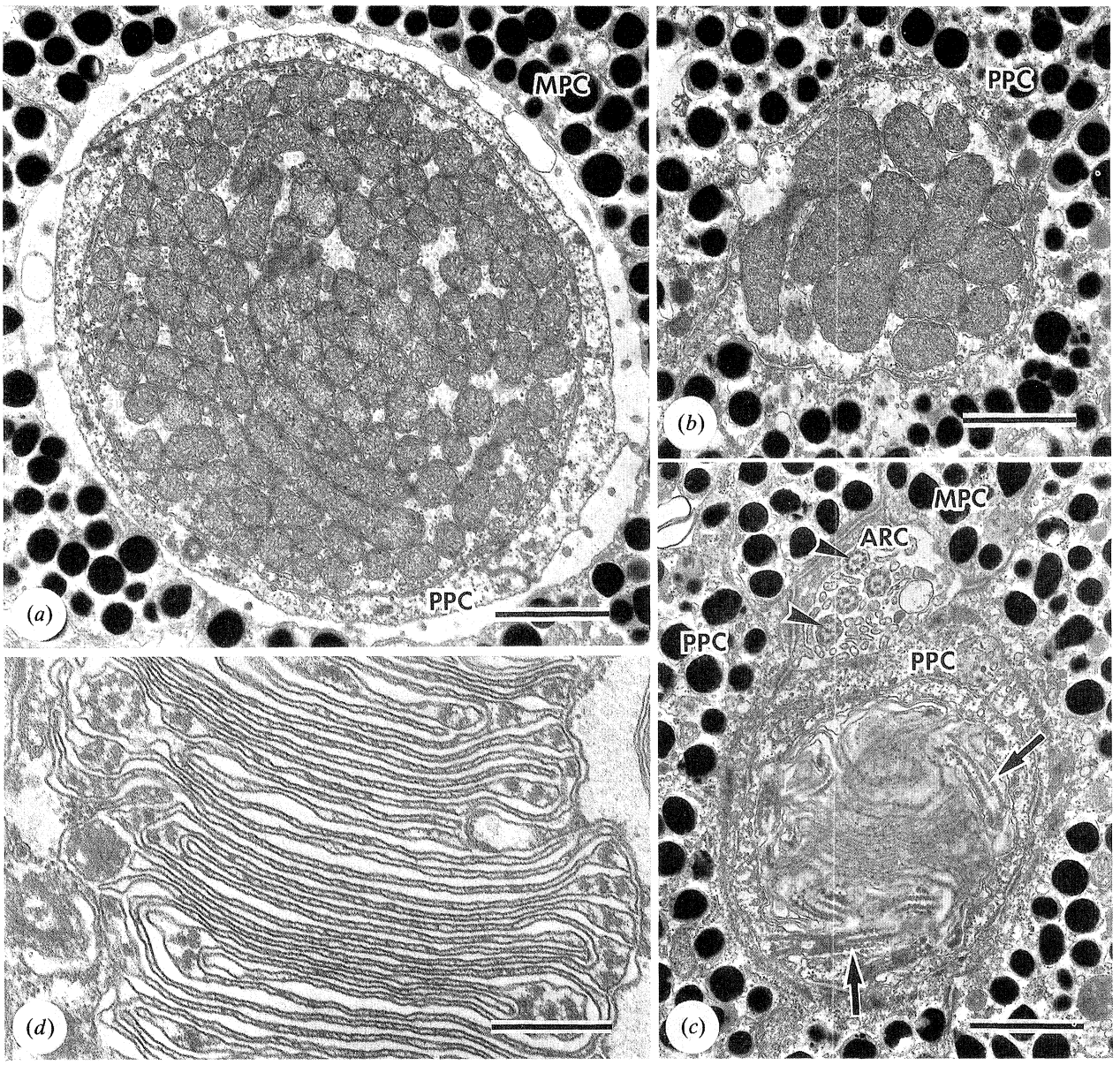

Figure 6. Electron micrographs of the receptor cell in ommatidia of *Barbatia cancellaria*. (*a*) Cross-section through the distal mitochondrial segment surrounded by unpigmented parts of the two proximal pigment cells and, in the periphery, the heavily pigmented medial pigment cells. (*b*) Cross-section of the proximal mitochondrial segment with its fewer and larger mitochondria. At this level, the receptor cell is surrounded by pigmented parts of the proximal pigment cells. (*c*) Ommatidial cross-section at the level of the receptive segment. Note the oblique projection of sensory cilia (arrows) into the receptor cavity. This ommatidium also has an accessory receptor cell, identified by the cross-cut cilia (arrowheads) and irregular microvilli. (*d*) Longitudinal section through part of the receptive segment, illustrating how the flattened membrane sacs project from the sides of the sensory cilia. Abbreviations: MPC, medial pigment cell; PPC, proximal pigment cell; RS, receptive segment; ARC, accessory receptor cell. Scale bars: (*a–c*) 1 μm; (*d*) 0.4 μm.

components. This demonstrates that the ommatidia are indeed without a lens. Lengths and widths of some optically important structures are given in table 1.

Behavioural experiments, identical to those performed on the sabellid polychaetes, were made also with *Barbatia cancellaria*. A moving black stripe of sufficient angular width caused the animal to close the shell. The response was not immediate but usually occurred 1–2 s after the stimulus. After closure, it took 10–30 min before the shell opened and the experiment could be repeated. A stripe subtending 6° of visual space caused a response in all tested animals whereas a stripe of 3° was only sufficient to cause a reaction in some of the animals. A stripe of 1.5° was not detected by any of the animals. These experiments, which were performed on only five individuals, and only repeated once for each stripe width, are indeed crude and preliminary, but they nevertheless indicate that *Barbatia* is unable to resolve spatial deails as fine as those resolved by *Sabella*.

(*c*) *Pigmented-cup eyes of ark clams*

Both *Arca zebra* and *Barbatia cancellaria* have large

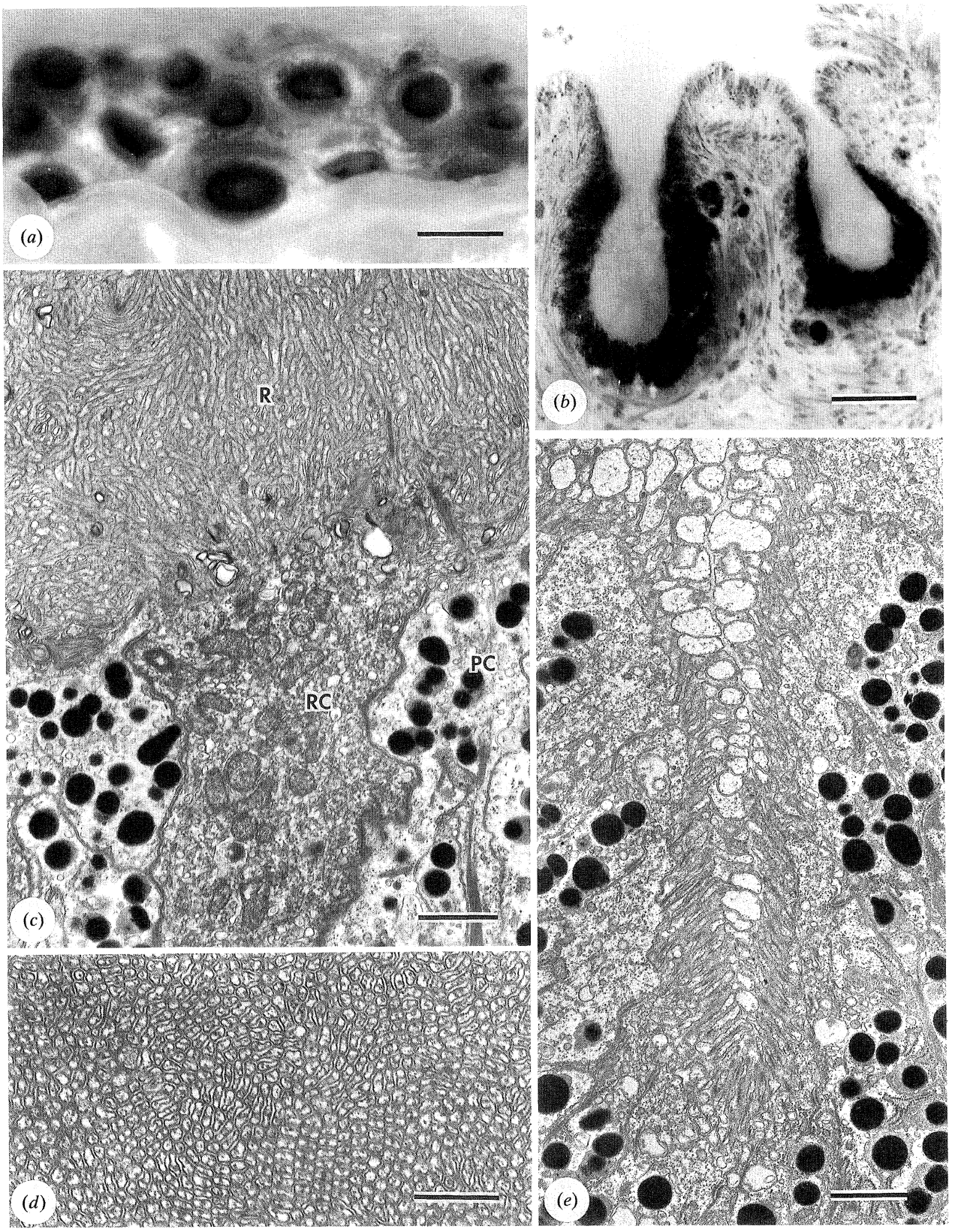

Figure 7. Pigment-cup eyes of ark clams. (*a*) The group of cup eyes on the anterior part of the mantle edge of *Anadara notabilis*, photographed in a freshly opened animal. (*b*) Semi-thin section through two cup eyes of *Anadara*. (*c*) Electron micrograph from the bottom of a large cup eye of *Barbatia cancellaria*, showing an unpigmented receptor cell wedged in between pigment cells. The receptor cell contains numerous mitochondria and produces a large plume of rhabdomeric microvilli into the lumen of the eye cup. (*d*) Rhabdomeric microvilli from a cup eye of *Anadara*, showing stout bundles of axial filaments in each microvillus. (*e*) One of the smaller pigmented pits of *Barbatia*. All cells are pigmented and contribute microvilli to the contents of the pit. It is questionable whether these small pits are sensory. Abbreviations: PC, pigment cell; RC, receptor cell; R, rhabdomeric microvilli. Scale bars: (*a*) 100 μm; (*b*) 40 μm; (*c*) 1 μm; (*d*) 0.5 μm; (*e*) 1 μm.

numbers of pigment-cup eyes close to the compound eyes on the mantle edge (figure 4*a,b*). In *Barbatia* the number of cup eyes is estimated to be about 2000. These eyes are epidermal pits formed by heavily pigmented cells and unpigmented photoreceptor cells. The shape and size of these pigmented cup eyes vary considerably. There is a continuous gradation from small weakly pigmented pits to large (80 μm wide) and densely pigmented eye-cups. The distinction between pigment and receptor cells is obvious in the larger eyes (figure 7*c*) but gradually disappears in the smaller eyes (figure 7*e*). It is unclear if the smaller pits really are eyes.

The interior of the eye cups are filled with densely-packed microvilli (figure 7*c*). In the larger eyes these come exclusively from the unpigmented cells which are undoubtedly sensory since they contain large numbers of mitochondria and send axons to the pallial nerve. There are no ciliary structures in any of these cells. The microvilli of neighbouring photoreceptor cells are contiguous, making it impossible to distinguish the individual rhabdomeres. In the smallest pigment pits, all cells produce microvilli identical to those of normal epidermal cells.

The third species of ark clam, *Anadara notabilis*, has no compound eyes and only about 40 pigment cup eyes clustered at the anterior part of the mantle edge (figure 7*a,b*). These invaginated eyes are similar to those of *Barbatia*. The photoreceptor cells are unpigmented, have no ciliary structures and produce large rhabdomeres of densely-packed microvilli (figure 7*d*). Some typical dimensions of pigment cup eyes of *Barbatia* and *Anadara* are given in table 1. None of the cup eyes have lenses or other focusing devices.

4. DISCUSSION

(*a*) *Ecological adaptations*

The animal species investigated in this paper differ in behaviour and habitat, and this may explain some of the differences in their visual organs. The most serious threat to sabellid polychaetes is probably fish predation, whereas ark clams are 'a la carte' items for birds, fish, gastropods and starfish, and their mantle cavity is often infested by small crabs. Sabellids are normally sessile but they are perfectly capable of crawling. Among the ark clams, some are burrowing forms (*Anadara*), some nestle in rock crevices (*Barbatia*) and some use their byssus to form colonies on sand flats (*Arca*). The lack of compound eyes in *Anadara* is certainly a result of their burrowing life-style. Surprisingly, the eyes of *Anadara* are grouped in the anterior part of the mantle edge, and not in the posterior end, around the siphons, as is commonly found in other burrowing bivalves (Morton 1987).

A discussion of the visual needs of these animals requires some information on the performance of their eyes. Such information, derived from anatomical data, is presented in table 2. An important value is the acceptance angle of individual receptor cells, $\Delta\rho$. The smaller this angle is, the more will the receptor signal be modulated by small moving objects. For an object of a certain size, the acceptance angle determines the distance at which it will be detected. The two species of sabellid polychaete have lenses (crystalline cones) in their ommatidia and this is the reason why their acceptance angles are only slightly more than 10°. The lensless ommatidium of *Barbatia* does considerably worse with an acceptance angle of about 30°. This correlates well with the simple

Table 2. *Measures of eye performance calculated from the anatomy.*

	Sabella melanostigma (compound eye)	*Dasychone conspersa* (compound eye)	*Barbatia cancellaria* (compound eye)	*Barbatia cancellaria* (cup eye)	*Anadara notabilis* (cup eye)
Optical blur-circle, $\Delta\rho_l$	2.2°[a]	5.2°[a]	32°[b]	35°[c]	19°[d]
Angular subtense of receptor at the nodal point, $\Delta\rho_r$	13.5°[e]	10.6°[e]	4°[f]	18°[g]	7°[h]
Acceptance angle[i], $\Delta\rho$	13.7°	11.8°	32°	39°	20°
Photoreceptor absorption[j]	7.7%	4.0%	4.7%	8.6%	4.6%
Sensitivity[k]	0.42	0.030	0.036	0.98	0.11

[a] Diffraction blur-circle calculated as λ/D (radians), where λ is the wavelength of light (500 nm) and D is the diameter of the distal aperture from Table 1 (Snyder 1979).
[b] Angular subtense of the aperture at the distal surface of the receptor (average values from Table 1).
[c] Angular subtense of the aperture at a nodal distance of 22 μm (to the estimated receptor centre).
[d] Angular subtense of the aperture at a nodal distance of 51 μm (to the estimated receptor centre).
[e] Angular subtense of the receptor diameter at the nodal distance from the centre of the cone to the centre of the receptor.
[f] Angular subtense of the receptor diameter at the plane of the distal aperture (average values from table 1).
[g] Angular subtense of the receptor diameter at a nodal distance of 22 μm.
[h] Angular subtense of the receptor diameter at a nodal distance of 51 μm.
[i] Calculated as the Gaussian convolution: $\sqrt{(\Delta\rho_l^2 + \Delta\rho_r^2)}$, Snyder (1979).
[j] Calculated for white light as $100 \cdot [kx/(2.5 + kx)]$, where x is the receptor depth (μm) and k is the absorption coefficient taken to be $0.035\,\mu m^{-1}$ for ciliary photoreceptors and $0.0067\,\mu m^{-1}$ for rhabdomeric photoreceptors (E. J. Warrant & D.-E. Nilsson, unpublished).
[k] The anatomical sensitivity calculated as $0.62(A)^2(\Delta\rho)^2[kx/(2.5 + kx)]$, where A is the light receiving aperture (the distal aperture in focused systems and the receptor diameter in lensless systems), $\Delta\rho$ is from note (i) but in radians, and $[kx/(2.5 + kx)]$ is from note (j) (see Land 1981; E. J. Warrant & D.-E. Nilsson, unpublished).

behavioural experiments, where *Sabella* responded to much finer stripes than *Barbatia* did. The crystalline cones of sabellids will thus allow these animals to detect approaching predators at long distance. The lack of optics in the ommatidia of ark clams is harder to explain. If the microvilli in the pigment tube were to secrete a refracting body, as in sabellids, the ark clams would significantly extend their distance range of vision. Either the compound eyes of ark clams are extremely young in evolutionary terms (which seems unlikely in view of the potentially rapid eye evolution calculated by Nilsson & Pelger 1994), or an extended distance of response would cause the clams to close when it is not necessary. I favour the latter alternative, because it has to be borne in mind that these animals are filter feeders and they will do better the longer they can stay open and feed. It thus seems possible that the acceptance angle of 30° could represent an optimum compromise between feeding efficiency and predator protection. The response delay of 1–2 s in *Barbatia* also indicates that the main threat is from relatively slow predators, for which an early warning is not necessary. Sabellids, on the other hand, have virtually no response delay, pointing to predation by fast-moving predators, against which the long response range (the small $\Delta\rho$) gives an earlier warning.

The estimated acceptance angles of receptors in the pigmented-cup eyes are not very impressive (table 2). This is again due to the lack of focusing structures. A comparison of $\Delta\rho$ in the compound and cup eyes of *Barbatia* demonstrates a small advantage for the compound eye (30° versus 40°), especially since the cup eye estimate comes from one of the larger eyes which have relatively smaller $\Delta\rho$. The calculated sensitivity, however, is almost 30 times higher for the cup eye. Since the sensitivity values are based on the assumptions that the absorption coefficients are the same as those measured in other animals (see footnotes of table 2), this comparison may be in some error. But it does allow for the speculation that the cup eyes and compound eyes are used under different conditions or for different tasks. The different sensitivity values of the compound eyes in *Sabella*, *Dasychone* and *Barbatia* are readily explained by their habitat. Both *Dasychone conspersa* and *Barbatia cancellaria* were collected in clear shallow water on coral rocks, whereas *Sabella melanostigma* were collected in brown turbid water among roots and mud in a narrow mangrove creek.

(*b*) *Eyes or burglar alarms?*

The sabellid polychaetes and ark clams studied in this paper are equipped with an absurd number of eyes. Apart from the branchial eyes, sabellid polychaetes also have cephalic, segmental and pygidial eye spots (Ermak & Eakin 1976; Dragesco-Kerneis 1980*a*). These eye spots, however, guide locomotion and tube building (Dragesco-Kerneis 1980*b*) and the withdrawal response is probably triggered exclusively by photoreceptors on the branchial tentacles. In another sabellid, *Branchiomma vesiculosum*, which has one compound eye at the tip of each branchial tentacle, Hesse (1899) demonstrated that, after removal of the eyes, the animals still withdrew into their tubes in response to shadows. This implies that, in addition to the compound eyes, these animals have extraocular photoreceptors on the tentacles. Nicol (1950) argued that the compound eyes are visual motion detectors in contrast to the dermal light sensitivity which can only detect direct shadows. A total of 240 compound eyes with 50 ommatidia in each, as in *Sabella melanostigma*, still seems a bit extravagant for simple motion detection. The situation is even more remarkable in ark clams such as *Barbatia cancellaria*, which has the mantle edge covered in 300 compound eyes, each with some 130 ommatidia, and, in addition, about 2000 pigment cup eyes.

Triggering of the protective responses in fan worms and ark clams is a visual task quite different from that required for orientation behaviour. The main difference is that the protective response is an all-or-nothing behaviour and it is unidirectional: fan worms retract in exactly the same way irrespective of the direction of the visually-detected threat, and the same is true for shell closure in clams. Information about the direction of the stimulus is thus irrelevant. But the detection of movement of fine-image details remains as useful to clams and fan worms as it is to animals that orient visually. This leads to the somewhat perplexing conclusion that fan worms and bivalves may benefit from spatial resolution (the ability to detect objects subtending small angles) but without having spatial vision (the ability to visually reconstruct the environment). From this perspective, their photoreceptors are more analogous to burglar alarms than to eyes. The important point here is that this relieves their nervous systems from a great burden, since the processing of spatial information is one of the most neuron-intensive tasks that a nervous system can take on.

Having found the reason why they can cope neurally with such large numbers of eyes, we are still left with the question of whether the large numbers are really necessary. A shadow response does not require eyes at all, just photoreceptor cells. But the animals studied here respond to visual motion, which is far more reliable than a simple shadow response, since it allows for detection of threats from all directions. The motion-detector systems of vertebrate and arthropod visual systems rely on the spatial and temporal correlation of signals from neighbouring visual cells, to compute the direction and speed of motion (Franceschini *et al.* 1989). Clams and fan worms would have little use for this information. A moving object will cause a modulation of the signal in those receptors that point towards it, and this would be sufficient for direct triggering of the protective response. It would thus seem that the only requirement is a complete visual coverage of all directions in space. But *Barbatia* and *Sabella* have a massive over-coverage. In *Sabella melanostigma* the 240 compound eyes of, say, 50 ommatidia each, makes a total of 12 000 ommatidia, each monitoring a 13.7° field ($\Delta\rho$) in

the environment. The solid angle covered by a single ommatidium, Ω, can be calculated as:

$$2\pi[1 - \cos(\Delta\rho/2)],$$

which for *S. melanostigma* comes to 0.045 steradians. If we assume a coverage of all directions, then the full visual sphere, which has a solid angle of 4π steradians, is covered by 12 000 receptors seeing 0.045 steradians each. From this we can calculate that, at an average, each point in space is simultaneously seen by 43 different ommatidia. Performing the same calculation for *Barbatia*, which has a total of about 39 000 ommatidia and a $\Delta\rho$ of 32°, gives an impressive number of 755 ommatidia simultaneously monitoring any single direction in space.

It would thus seem that *Sabella* has 43 and *Barbatia* 755 times as many ommatidia as they would need to see in all directions. Do these numbers imply that there is a shocking redundancy in visual capacity? There are several reasons to trust that the large number of eyes is, in fact, part of their visual strategy. First, suspended particles or planktonic animals may cause false alarm if they happen to pass close to the distal aperture of an ommatidium. With a multiple visual coverage, such events can be discriminated from real threats. Second, if all receptor signals are pooled, the signal will increase by the factors 43 and 755 respectively, but the statistical photon noise will only increase by the square root of these figures. The result will be a much better sensitivity and a tremendous improvement of the signal-to-noise ratio of the visual signal. This will allow the animals to reliably detect objects of much lower contrast and also to operate at lower intensities. Third, the vulnerability to partial injury is much reduced by having many eyes covering the same visual field (especially in the fan worms, the risk of losing part of the tentacular crown is probably not insignificant). The large number of eyes thus provides for a robust alarm system designed to detect real threats reliably without causing false alarms. It is likely that this reasoning provides a general explanation for the large number of eyes often found in bivalves and fan worms (in the scallop *Pecten*, for instance, each point in space is viewed by one receptor in each of about 17 eyes: Land 1968).

(*c*) *Diversity in eye design*

A large number of fan worms are known to possess compound eyes. There is, however considerable variation in the placement of the eyes. In the genera *Branchiomma* and *Megalomma* each branchial tentacle (radiole) carries a single compound eye at the tip (Andrews 1891; Hesse 1899). Pairs of compound eyes, arranged at regular intervals along the radioles, occur in *Sabella* and *Dasychone* (see Carricaburu & Kerneis 1975). In *Potamilla*, a single row of somewhat asymmetrically-placed compound eyes occur along some of the radioles (Kerneis 1971). All the above species belong to the family Sabellidae, which are characterized by their soft tubes. Among the hard-tube worms (fam. Serpulidae) *Spirobranchus* has been shown to have large compound eyes at the base of two of the radioles (Smith 1984). Within both the Sabellidae and Serpulidae there are numerous species and genera that have no branchial eyes at all (see Fauchald 1977).

The ommatidial construction also shows variability among the fan worms (Krasne & Lawrence 1966; Kerneis 1966, 1968, 1971, 1975; Dragesco-Kerneis 1979; Smith 1984). In all species that have been investigated the ommatidium is a pigmented tube with focusing structures distally and receptive structures proximally, but the number of cells that contribute varies from one to at least three (figure 8). A uniting feature is the receptive structure, which invariably consists of a cavity into which flat membrane sacks of cilia project. In *Branchiomma* the lens is formed intracellularly in a single cell capping the ommatidium, whereas in all other examined species the lens (crystalline cone) is extracellular and consists of granular material penetrated by numerous microvilli (*Sabella, Dasychone, Potamilla, Eudistylia, Schizobranchia*). In most species a single cell produces both the lens and the receptive structure (*Potamilla, Eudistylia, Schizobranchia, Pseudopotamilla, Spirobranchus*). In *Branchiomma* there are two cells, one lens cell and one receptor cell. In *Sabella* and *Dasychone* there are three cells, two of which form the lens.

The anatomical variations, and the different position of the eyes on the branchial crown suggest that compound eyes have evolved independently several times in fan worms. Some of the sabellids have inconspicuous eyes that demonstrate how this may have happened: in *Protula*, receptor cells are loosely aggregated in small clusters and in *Vermilla* and *Hypsicomus*, ommatidia-like structures are found at some distance from each other on the radioles (Andrews 1891; Hesse 1899, 1908). The reason why the result is always a compound eye would thus be that scattered ommatidia preceded the clustering into eyes. Since the ommatidial pigment shield already provides a restriction of the angular sensitivity, there is no need to invaginate the epithelium to obtain directionality. The ommatidia of ark clams may likewise have preceded their compound eyes. Certainly, Patten's (1886) observation of scattered single ommatidia in addition to the compound eyes in *Arca barbata* provides some support for this hypothesis.

There is a surprising diversity and complexity in the anatomy of pigment-cup eyes on the mantle of bivalves (figure 9). Pigmented-cup eyes, similar to those of *Barbatia* and *Anadara* are found on the mantle edge of the file shells, *Lima* (Hesse 1900; Küpfer 1916) and the giant clam, *Tridacna* (Stasek 1966; Fankboner 1981; Wilkens 1986). The mantle eyes of cockles, *Cardium*, are different in that the photoreceptors lie in a reflector cup (Zugmayer 1904; Barber & Land 1967; Barber & Wright 1969). Reflectors are also employed in the much more advanced concave-mirror eyes of the scallop, *Pecten* (Patten 1886; Hesse 1900; Dakin 1910, 1928; Küpfer 1916; Barber *et al.* 1967; Land 1968). The nine stalked eyes around the siphon of the Pandora shell *Laternula truncata* are as sophisticated as scallop eyes but they lack a reflector and, presumably,

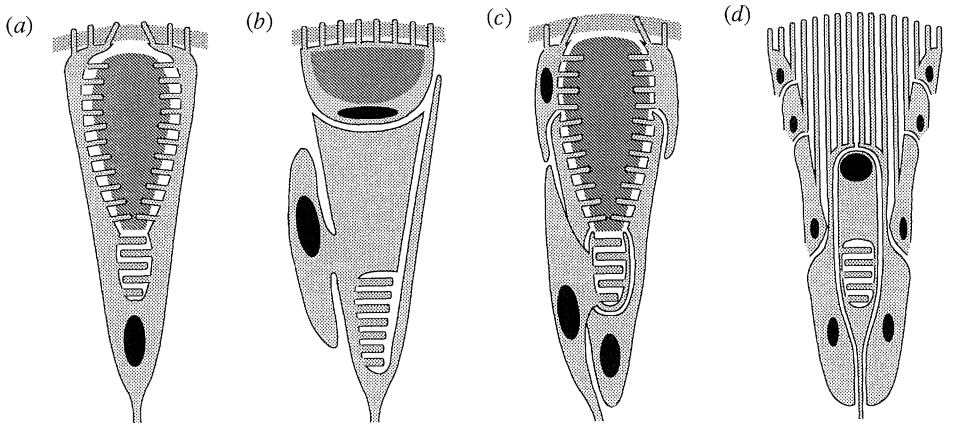

Figure 8. Schematic diagrams of the cellular composition of ommatidia in sabellid polychaetes and arcacean bivalves: (*a*) Single-cell ommatidium of *Potamilla*; (*b*) Two-cell ommatidium of *Branchiomma*; (*c*) Three-cell ommatidium of *Sabella*; (*d*) Multicellular ommatidium of *Barbatia*. Cell nuclei are indicated as black ovals. The polychaete ommatidia have lenses (darker shading) which are either extracellular (*a* and *c*) or intracellular (*b*), and the eyes are covered by a thin cuticle penetrated by microvilli. Ark clams (*d*), like other molluscs, have no cuticle, and their ommatidia contain no lenses. The receptive segments are formed by modified cilia in all four cases.

they rely on imaging with the well-developed lens (Adal & Morton 1973). All these cup-shaped eyes serve a purpose similar to the compound eyes of ark clams and fan worms: they are designed to provide directionality to the photoreceptors such that the animal's protective response can be triggered before a predator comes too close. Since the process of invagination is simple, and the selective advantage obvious (Nilsson & Pelger 1994), it is not hard to imagine that eye cups may have evolved independently in several lines of bivalves.

Comparing the eye anatomy of the five bivalves

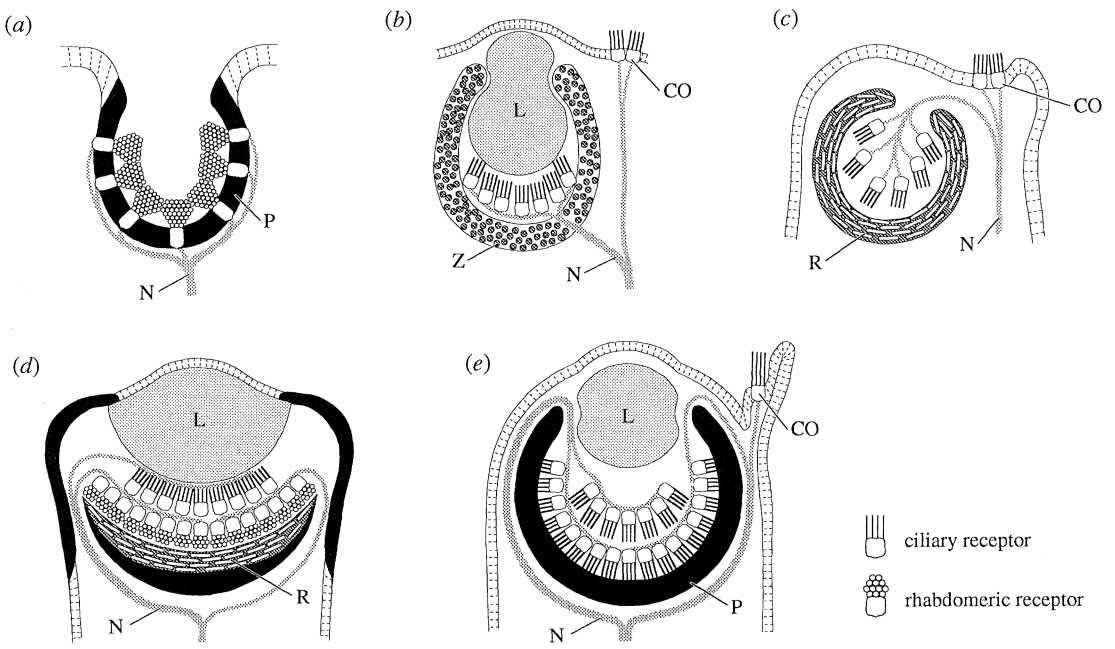

Figure 9. Schematic diagrams comparing cup eyes on the mantle edge of various bivalves. (*a*) The invaginated epidermal cup of ark clams has an everse retina of rhabdomeric photoreceptors. (*b*) In the giant clam *Tridacna* an everse retina of ciliary receptors is situated in a cup of zooxanthellae (symbiotic algae), and a presumably chemosensory organ of ciliary receptors is located close to the eye. (*c*) The eye of the cockle *Cardium edule* is a reflector cup with an inverse retina of ciliary photoreceptors. As in *Tridacna*, there is a ciliary sense organ close to the eye. (*d*) The concave mirror eye of the scallop, *Pecten*, has two inverse retinas: a distal ciliary retina and a proximal rhabdomeric retina. (*e*) A double inverse retina is also found in the pigment-cup eyes of the pandora shell *Laternula truncata*, but here both photoreceptor layers are ciliary and there is also a ciliary sense organ next to the eye. Abbreviations: P, pigment cup; R, reflector cup; Z, zooxanthellae; L, lens-like body; N, sensory nerve; CO, ciliary sense organ.

Arca, Lima, Tridacna, Cardium and *Pecten*, Salvini-Plawen & Mayr (1977) proposed that their cup eyes are homologous, and that they represent different stages on the same evolutionary line. However, the fact that ark clams have their eyes on the outer mantle fold whereas other bivalves have them on the middle fold (Waller 1980), speaks against a common ancestry of all mantle eyes. If we disregard the presence or absence of lenses and reflectors, and instead consider the rhabdomeric or ciliary nature of the photoreceptor cells, then three clear groups appear: (i) ark-clams, which have rhabdomeric receptors in the cup eyes, and ciliary receptors in the compound eyes; (ii) *Tridacna, Cardium* and *Laternula* which have ciliary receptors in their cup eyes and, close to the eye, a ciliary sense-organ of presumed chemosensory function; and (iii) *Pecten* and *Lima* which have cup eyes with a double layer of photoreceptor cells, the distal being ciliary and the proximal being rhabdomeric (Barber *et al.* 1967; McReynolds 1976; Mpitsos 1973).

Incidentally, this grouping coincides taxonomically with the three bivalve groups Taxodonta, Eulamellibranchiata and Anisomyaria. Given the limited number of permutations of a few optical designs and two photoreceptor types, it seems to me that there is not enough evidence to state that the cup eyes on the mantle edge of different bivalves are homologous. Neither is it possible to say that all are independent acquisitions. A speculation which carries at least some support is that mantle eyes evolved independently in the three orders of bivalves, and that they share so many features only because they evolved for similar reasons in similar eye-less ancestors.

It would be easy to conclude that if compound eyes originated from clustering of receptor cells that already had some means of achieving directionality, then, cup eyes may have resulted from clusters of non-directional photoreceptors that acquired directionality by invagination of the whole cluster. This is probably the way that most cup eyes have originated (Burr 1984; Nilsson & Pelger 1994), but it is not necessarily the way ark clams got their pigment-cup eyes. The continuous gradation in *Barbatia*, from small epidermal invaginations with only one type of cell, to large heavily-pigmented cups with a clear distinction between pigment cells and photoreceptor cells, points to the possibility that invagination preceded the photoreceptor cells. If invaginations of the epithelium already exist for, say, secretory purposes, these structures would constitute an ideal starting point for acquisition of directional photoreception.

(*d*) *The origin of photoreceptor cells*

The normal response to stimulus in sensory receptors is a depolarizing receptor potential. This general rule is broken by the rods and cones of vertebrates, and also by other photoreceptors where the receptive organelle is a modified cilium. In the early theories of photoreceptor cell evolution (Eakin 1963, 1966, 1968) two independent lines were identified: ciliary photoreceptors in deuterostomes and rhabdomeric photoreceptors in protostomes. Initially, this structural distinction seemed to correlate with hyperpolarizing and depolarizing responses respectively. Later studies revealed quite a number of taxonomic exceptions to Eakin's theory. Some of the animals that apparently have the 'wrong' type of photoreceptor are the fan worms and bivalves (ciliary type), and the echinoderms and cephalochordates (rhabdomeric). Exemplary reviews of photoreceptor types in the animal kingdom are given by Eakin (1972), Salvini-Plawen and Mayr (1977) and Vanfleteren (1982). Also, the correlation between photoreceptor structure and response sign is violated: the rhabdomeric photoreceptors of the thaliacean *Salpa* generate hyperpolarizing responses to light (Gorman *et al.* 1971) and the rhabdomeric photoreceptors (proximal retina) of the clam *Lima* produce depolarizing or hyperpolarizing responses, depending on light intensity and state of adaptation (Nasi 1991). There is at least one case of ciliary photoreceptor that is known to depolarize (in a lizard parietal eye: Solessio & Engbretson 1993), and the correlation between structure and electrical response is also weakened by the different ionic mechanisms involved in the hyperpolarizing response of vertebrate and bivalve ciliary photoreceptors (McReynolds & Gorman 1974; Cornwall & Gorman 1983). Hyperpolarizing responses may be functionally explained if the photoreceptor originated as a shadow receptor: depolarization in response to the relevant stimulus (intensity decrease) would lead to hyperpolarization in response to an intensity increase (Land 1968; Leutscher-Hazelhoff 1984).

Based primarily on ultrastructural information, photoreceptor cells have been considered to have a monophyletic, diphyletic or polyphyletic origin (Vanfleteren & Coomans 1976; Vanfleteren 1982; Eakin 1972, 1982; Eakin & Hermans 1988; Salvini-Plawen & Mayr 1977; Salvini-Plawen 1982; Clément 1980; Burr 1984). The tentacular eyes of fan worms and the mantle eyes of bivalves are special in that they clearly represent new acquisitions. The tentacular photoreceptor cells of fan worms are exclusively ciliary with only minor variations between species. The receptor cells of bivalve mantle-eyes include both ciliary and rhabdomeric types and the variation within each type is large. In contrast to this, the cephalic eyes of both annelids and molluscs are rhabdomeric. When the new eyes evolved on the tentacles and the mantle edge, the genetic program for making cephalic photoreceptors was obviously not just activated in a new location. The reason for this is, of course, that selection favouring a light response or shadow response does not 'know' if there are unexpressed genes that could possibly do the job. Selection will work exclusively on phenotypically expressed features in the cells where a photic response makes an advantage to the animal.

There are a number of prerequisites for a functional photoreceptor: a photopigment, a large membrane area, all the steps of a transduction cascade and a synaptic connection to the nervous system. Genes coding for photopigment are ancient in eukaryotic

cells and they must have been useful long before multicellular organisms appeared (Goldsmith 1990). G-proteins and other transduction components are also standard eukaryote features that are involved in many kinds of signalling (see Wilson & Applebury 1993). Likewise, cilia and microvilli are standard eukaryote organelles serving a multitude of different functions. The basic building blocks, necessary for making a photoreceptor, are thus generally available to eukaryotic cells.

The distinction between two photoreceptor types, ciliary and rhabdomeric, is a result of the definition of ciliary and non-ciliary parts of the cell membrane. Since photoreception requires a large membrane area, cilia and microvilli are natural targets for recruitment. Membrane sacs, discs, whirls and microvilli can project from a cilium, and the cell membrane proper can produce microvilli, and even disc-like lamellae. All of these possibilities are realized in various photoreceptors (Salvini-Plawen & Mayr 1977; Duelli 1978). Within the limits set by the eukaryotic cell, we cannot possibly expect photoreceptor cells to vary more than they do. Since even the response polarity and ionic mechanisms vary, it is indeed possible that photoreceptor cells have evolved independently numerous times in the animal kingdom. Based on different arguments, Salvini-Plawen and Mayr (1977) concluded that photoreceptor cells are polyphyletic.

The branchial photoreceptors of fan worms and the photoreceptors on the mantle edge of bivalves offer particularly compelling evidence for independently-evolved photoreceptor cells. The epidermal cells of these animals are normally equipped with both microvilli and cilia (Bubel 1984; Welsch *et al.* 1984). In *Barbatia*, there is even a continuous gradation, from the microvilli of normal integumental cells to the large rhabdomeres of the cup-eye photoreceptors. Although perfectly plausible, it is not necessary that these fan worm and bivalve photoreceptor cells originated directly from non-sensory cells. An alternative possibility is that they evolved as modifications of other sensory cells. Just as in photoreceptors, the receptive organelles of chemoreceptors and mechanoreceptors are microvilli or cilia (Vinnikov 1982). With a transduction mechanism and synaptic connections already in place, such a shift of sensory modality would require relatively minor modifications. A speculative but possible scenario would be a chemoreceptor which is inhibited by light through the presence of small amounts of a rhodopsin-metarhodopsin system. A shadow would thus remove the inhibition and cause a depolarization. If the function of the chemoreceptor was to signal the presence of predators, it would make possible a rather straightforward transformation to a shadow receptor ('off' receptor) as in the distal retina of *Pecten* (McReynolds & Gorman 1970) or the compound eyes of *Branchiomma* (Leutscher-Hazelhoff 1984).

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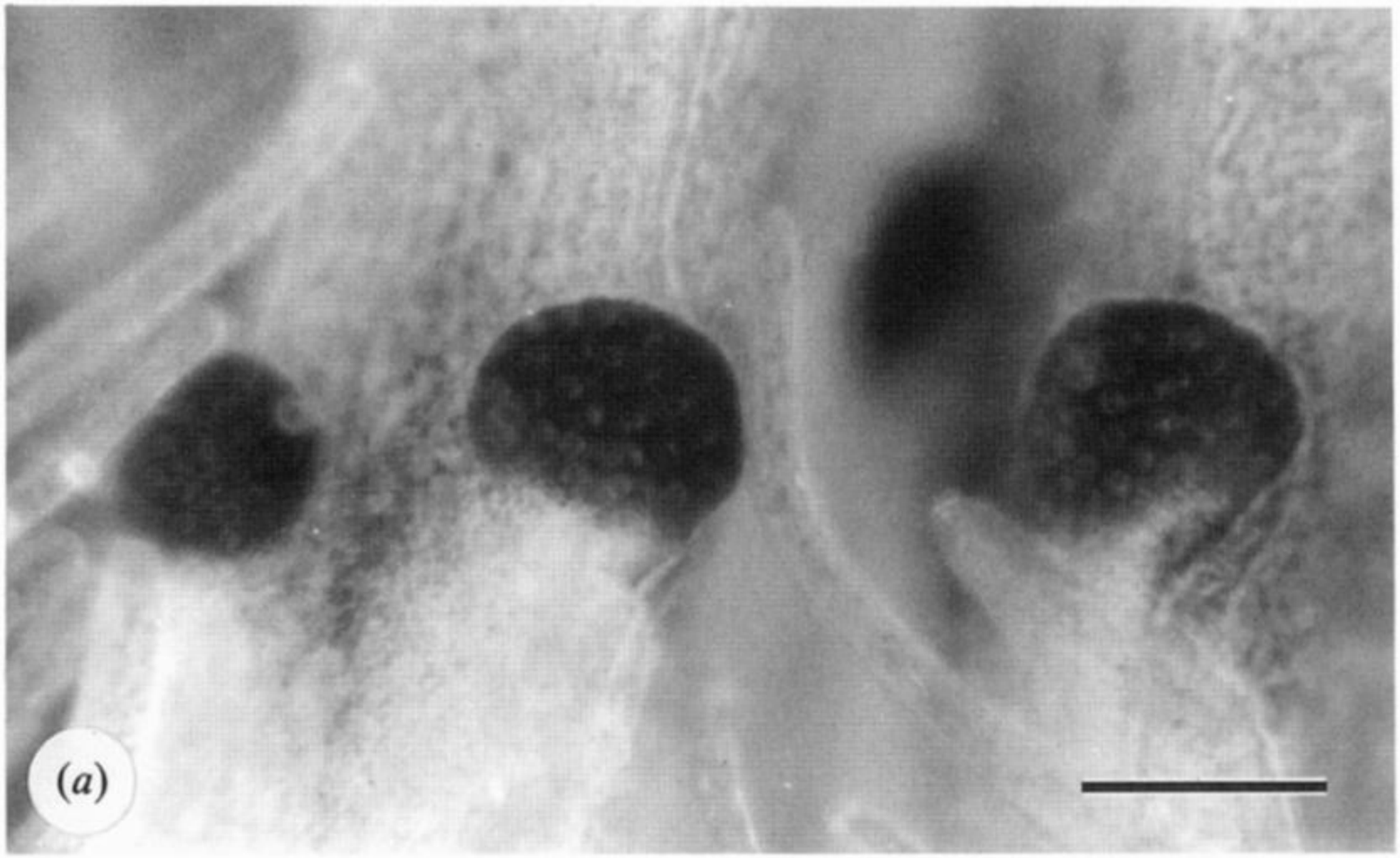
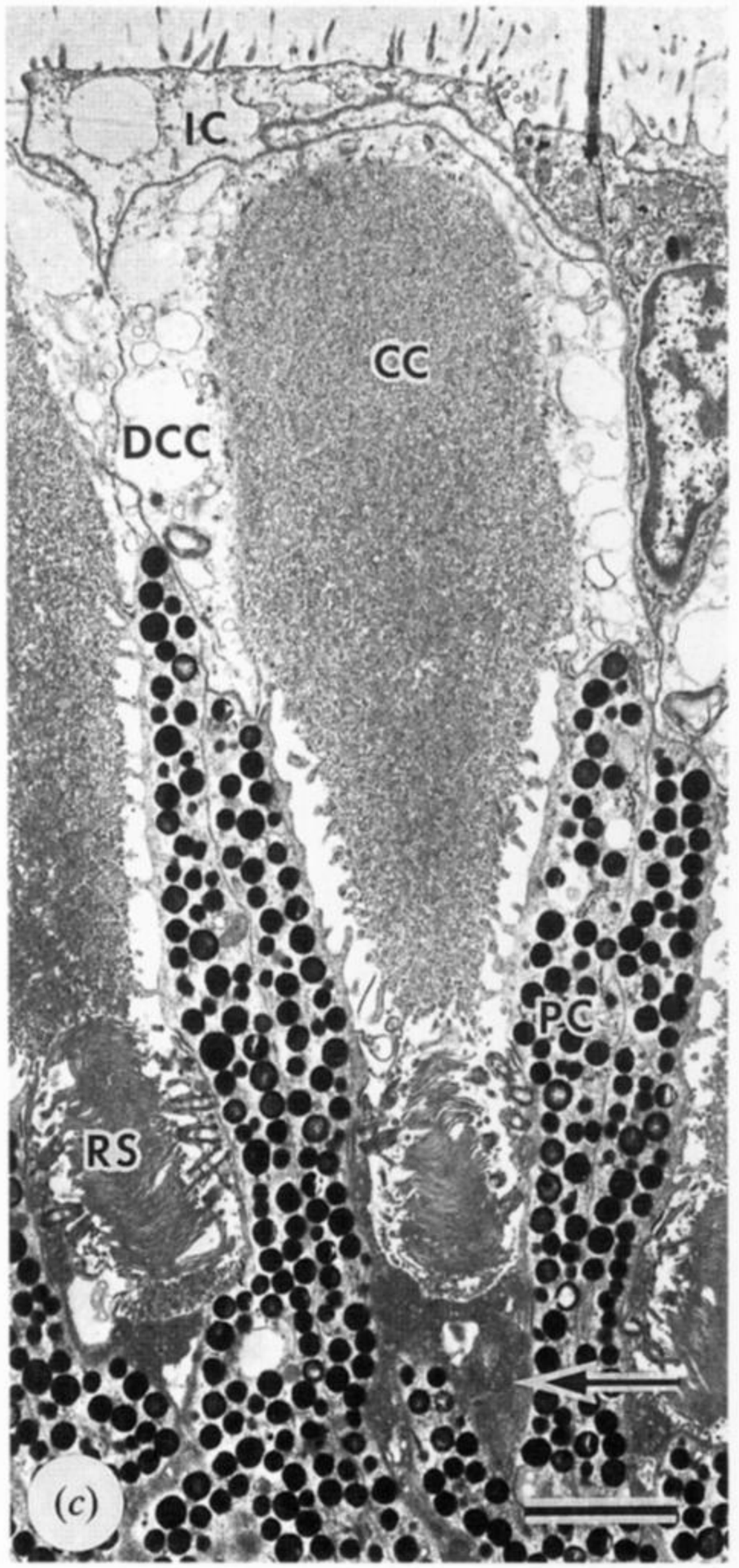




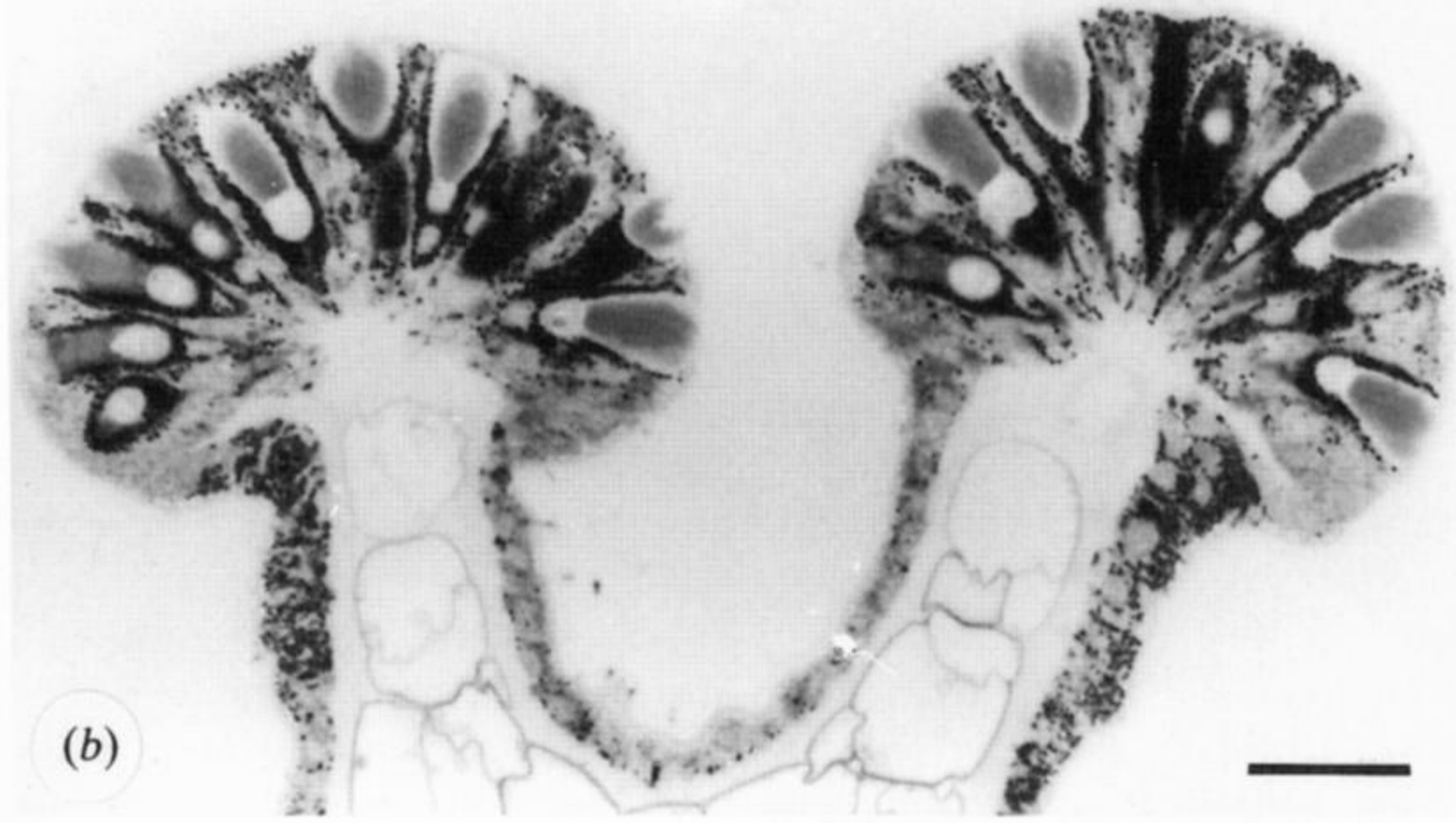


Figure 1. Compound eyes of sabellid polychaetes. (*a*) Part of two radioles of a live *Sabella melanostigma*, showing three compound eyes in focus. (*b*) Semi-thin section through a pair of compound eyes of *Sabella melanostigma*. The eyes sit at the distal end of a pair of ridges on the radiole, giving the false impression of eye stalks in the section. (*c*) Electron micrograph of an ommatidium in the compound eye of *Dasychone conspersa*. Note the density gradient in the crystalline cone, the cilium on one of the interstitial cells and the mitochondria (arrow) below the receptive segment. Abbreviations: CC, crystalline cone; DCC, distal cone cell; IC, interstitial cell; PC, pigment cell; RS, receptive segment of receptor cell. Scale bars: (*a*) 100 μm; (*b*) 25 μm; (*c*) 2 μm.

(a)

RC

CC

PC

(c)

RC

SC

(b)

RC

PC

(d)

Figure 3. Electron micrographs of the compound eye of *Sabella melanostigma*. (*a*) High magnification micrograph across the crystalline cone, showing the density gradient and the crystalline packing of granules in the central core. Microvilli (arrowheads) invade the periphery of the cone. (*b*) Longitudinal section through the receptive segment of the receptor cell and the proximal tip of the crystalline cone. The receptor cell forms a cytoplasmic cup around the stack of flattened ciliary membrane-sacs. (*c*) Cross-section through the proximal part of the crystalline cone enveloped by the pigment cell. (*d*) Cross-section through the receptive segment of the receptor cell showing the connection (between arrows) to the cell body. Abbreviations: CC, crystalline cone; PC, pigment cell; RC, receptor cell; SC, sensory cilium. Scale bars: (*a*) 0.5 μm; (*b*) 1 μm; (*c*,*d*) 2 μm.

(a)

(b)

M

DPC

PPC

RCN

MPC

(c)

DMS

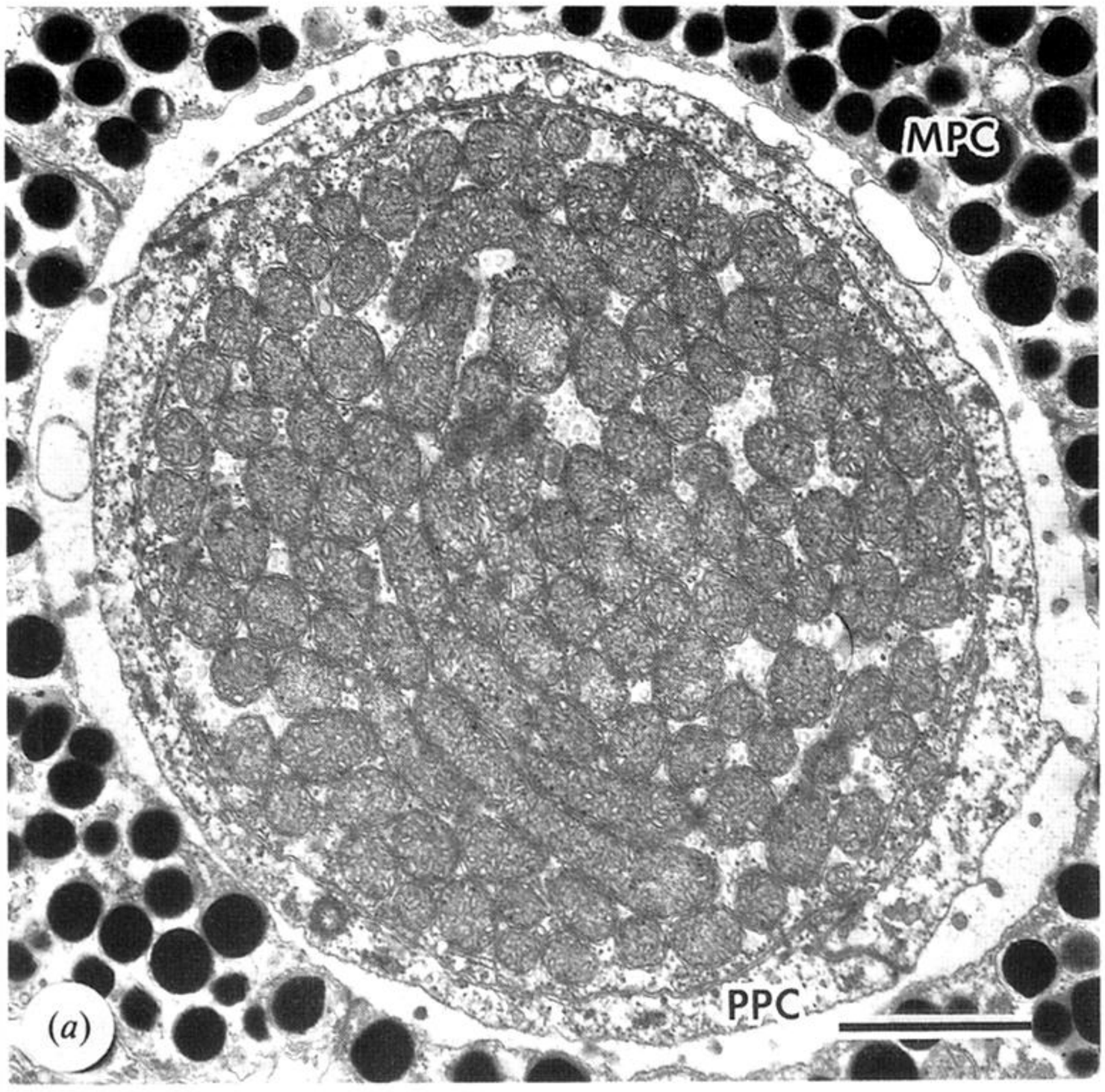
PV

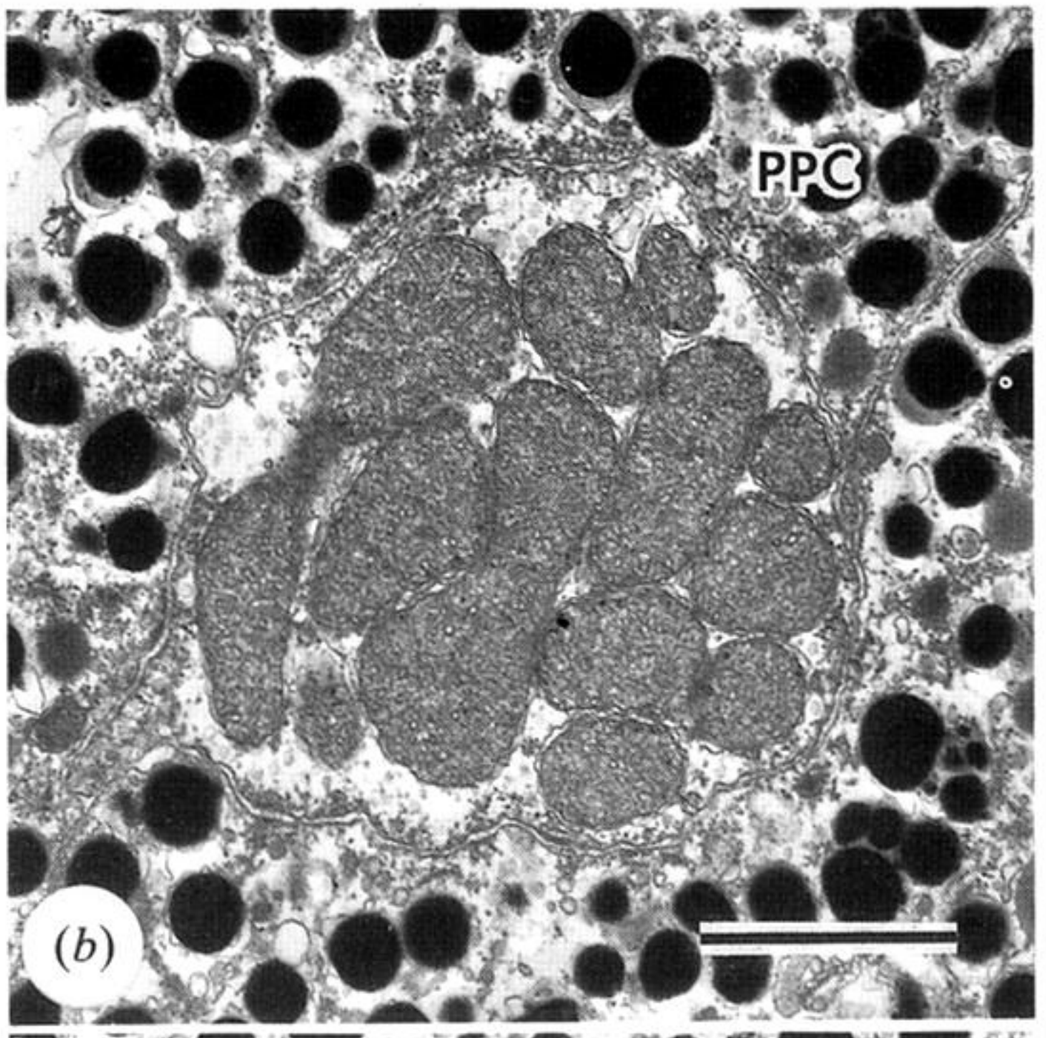
PMS

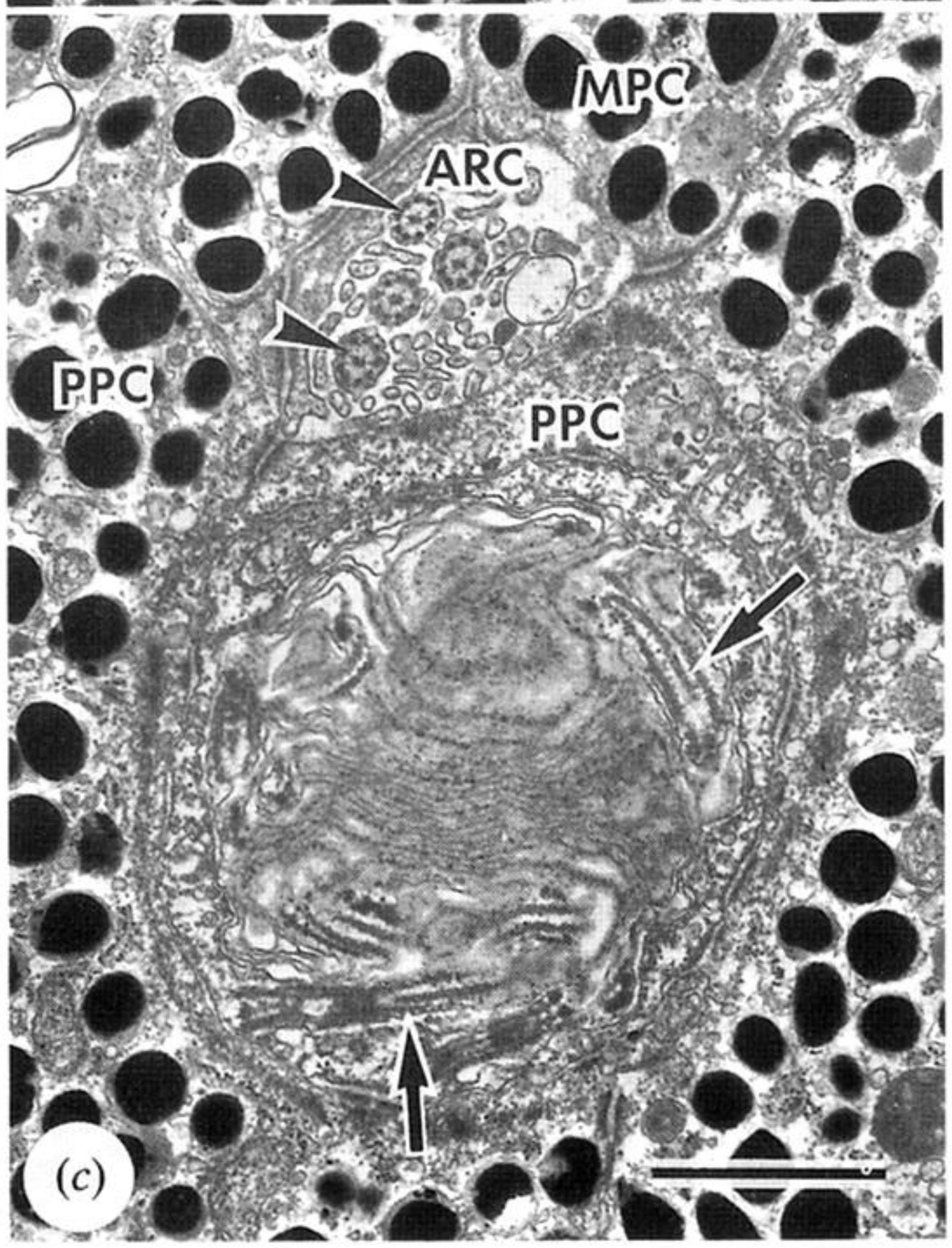
PPC

(d)

Figure 4. For description see opposite.







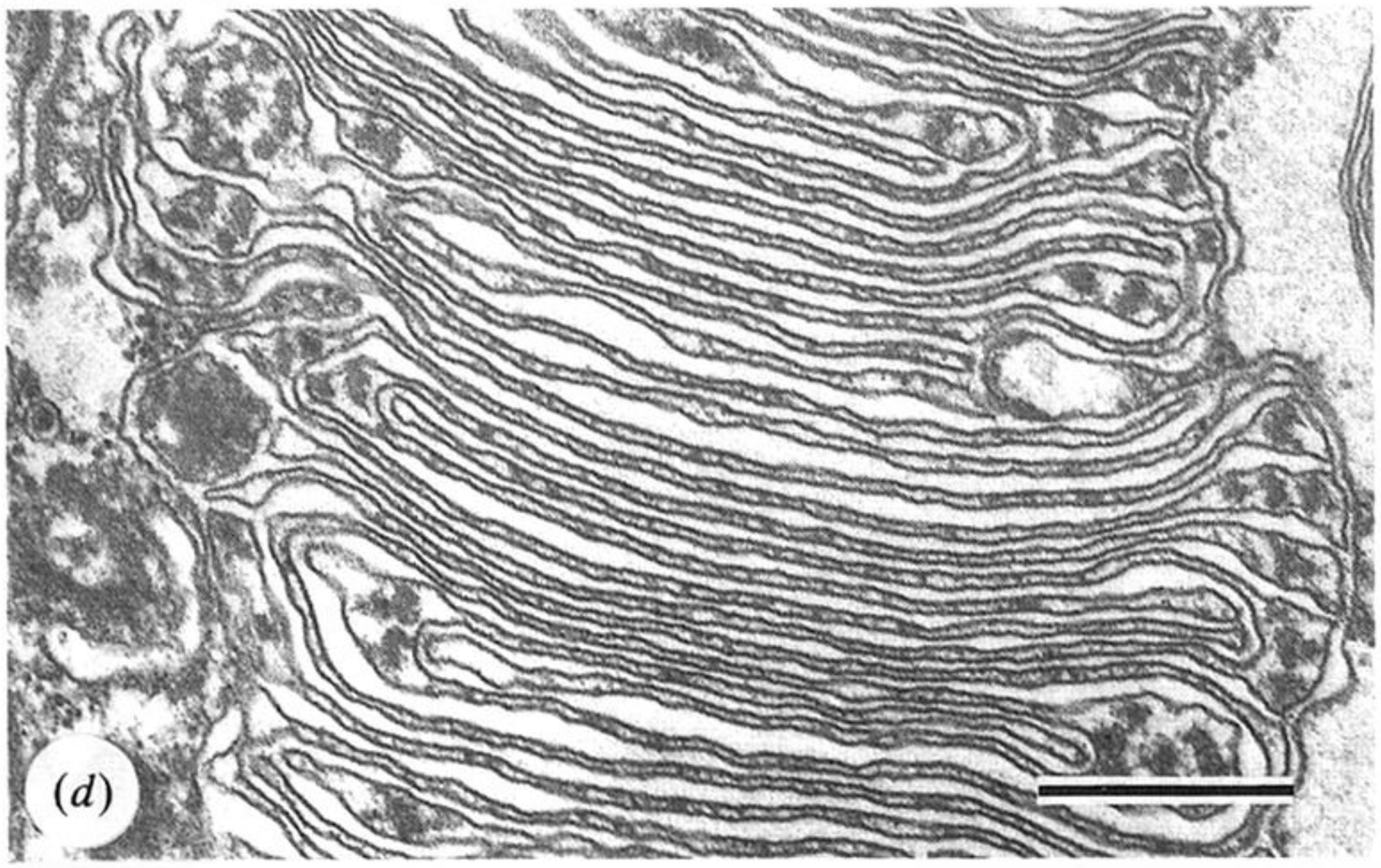
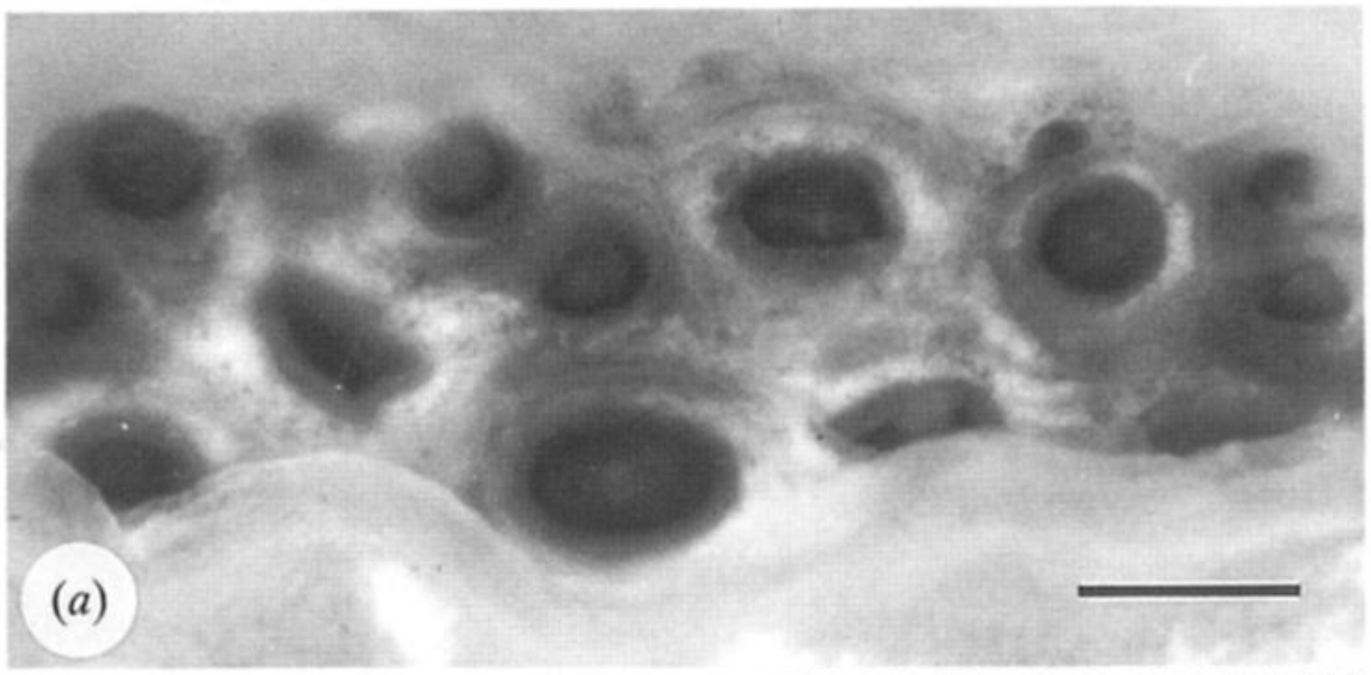
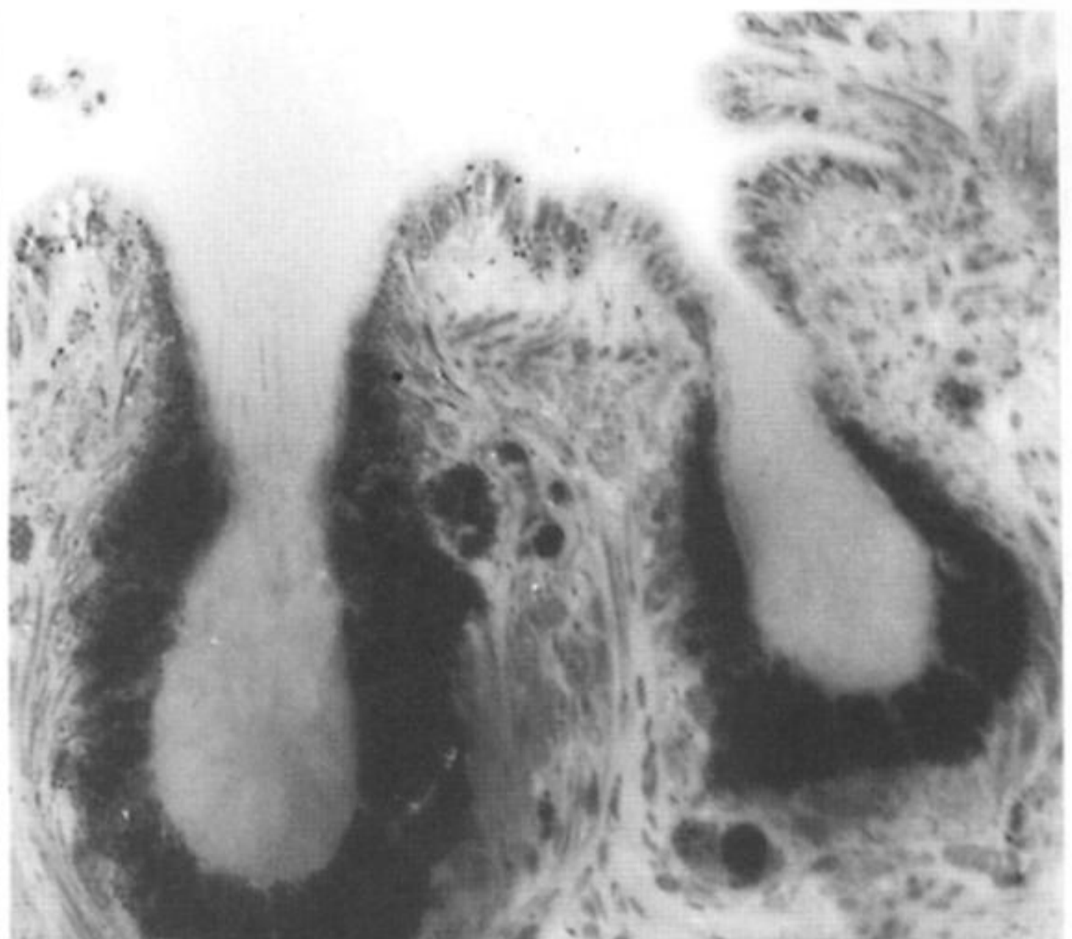
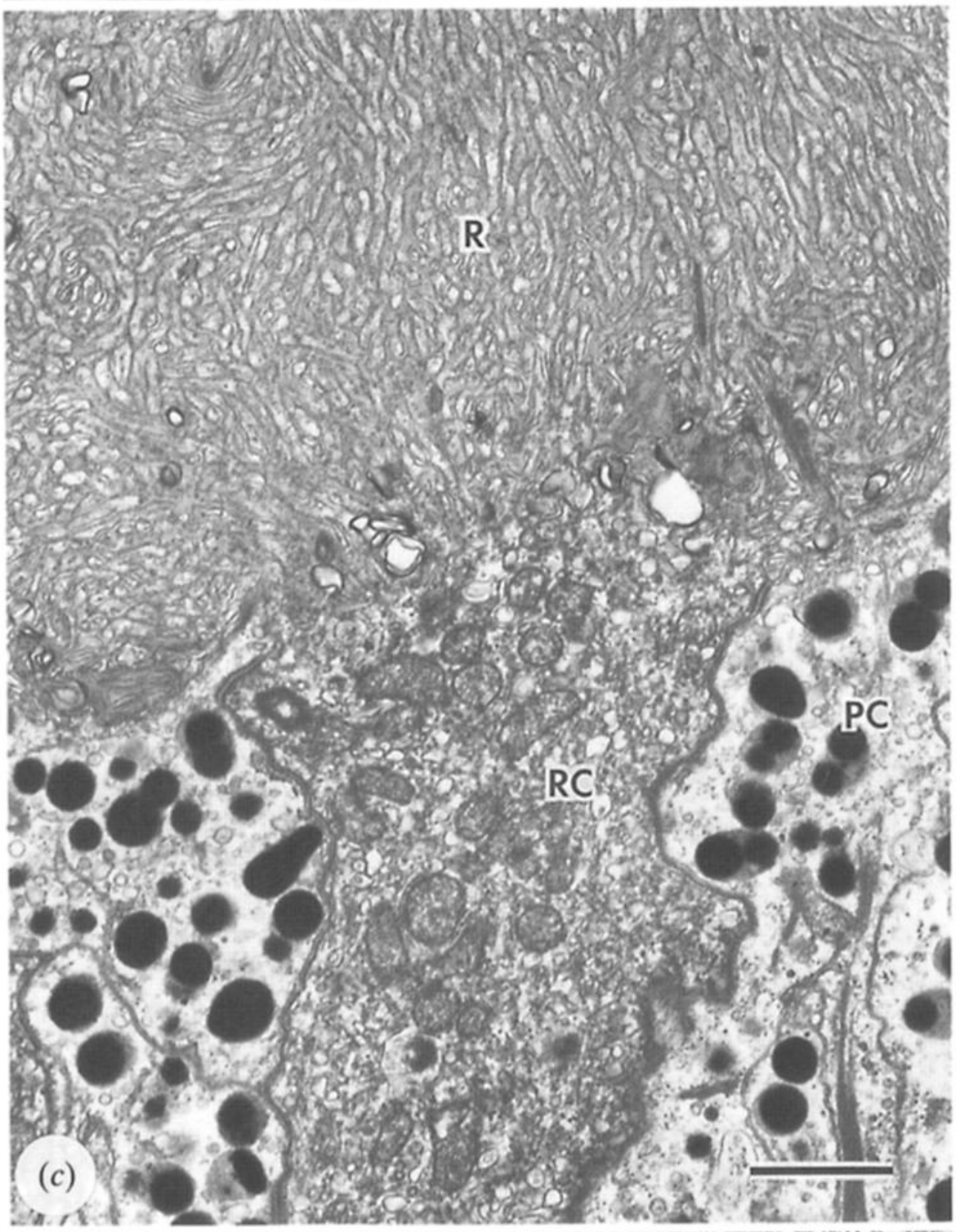
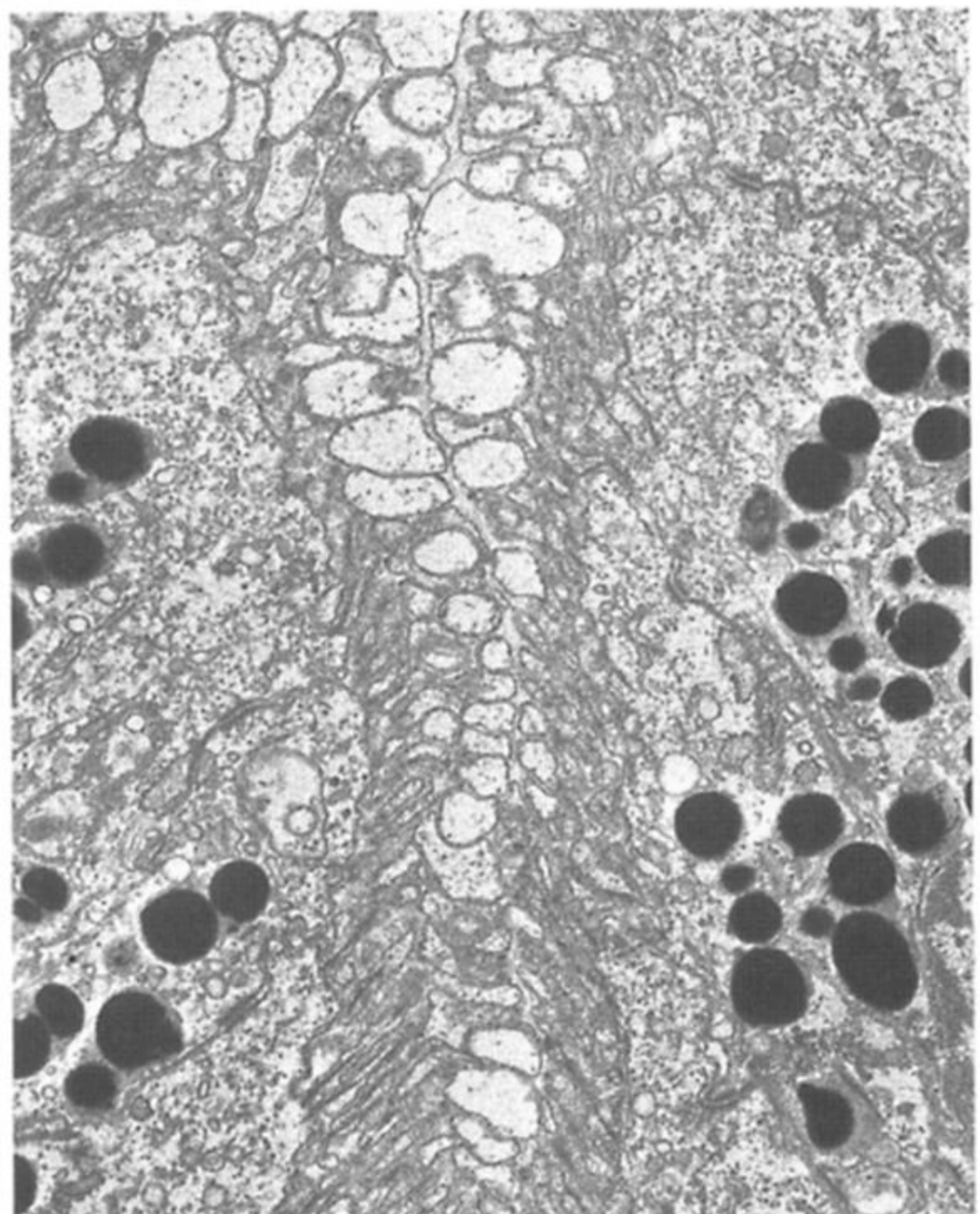


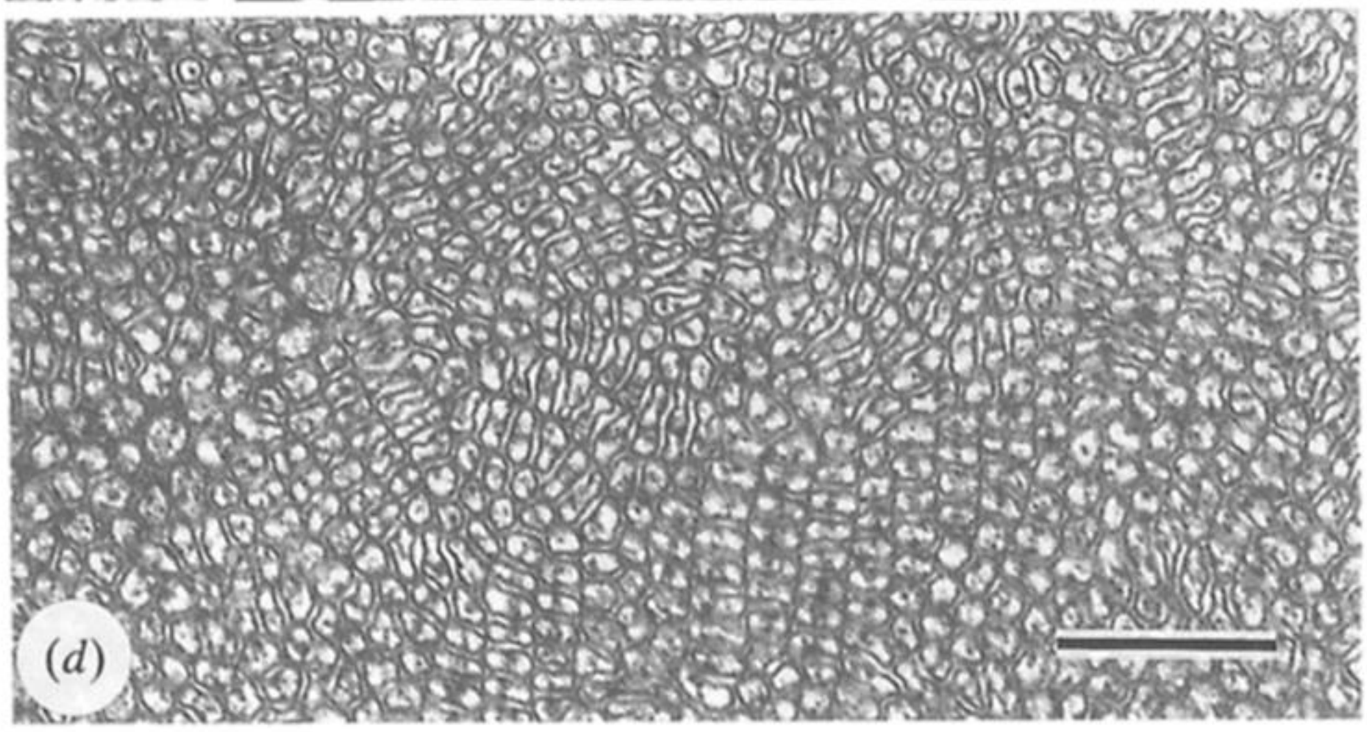
Figure 6. Electron micrographs of the receptor cell in ommatidia of *Barbatia cancellaria*. (*a*) Cross-section through the distal mitochondrial segment surrounded by unpigmented parts of the two proximal pigment cells and, in the periphery, the heavily pigmented medial pigment cells. (*b*) Cross-section of the proximal mitochondrial segment with its fewer and larger mitochondria. At this level, the receptor cell is surrounded by pigmented parts of the proximal pigment cells. (*c*) Ommatidial cross-section at the level of the receptive segment. Note the oblique projection of sensory cilia (arrows) into the receptor cavity. This ommatidium also has an accessory receptor cell, identified by the cross-cut cilia (arrowheads) and irregular microvilli. (*d*) Longitudinal section through part of the receptive segment, illustrating how the flattened membrane sacs project from the sides of the sensory cilia. Abbreviations: MPC, medial pigment cell; PPC, proximal pigment cell; RS, receptive segment; ARC, accessory receptor cell. Scale bars: (*a–c*) 1 μm; (*d*) 0.4 μm.











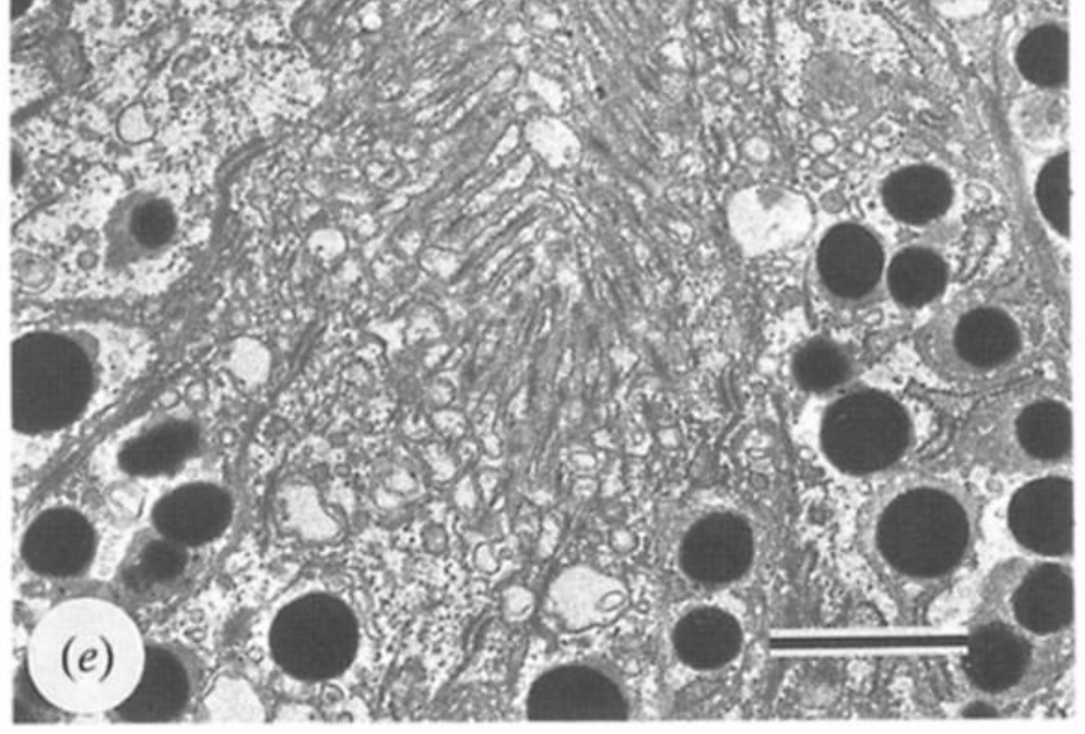


Figure 7. Pigment-cup eyes of ark clams. (*a*) The group of cup eyes on the anterior part of the mantle edge of *Anadara notabilis*, photographed in a freshly opened animal. (*b*) Semi-thin section through two cup eyes of *Anadara*. (*c*) Electron micrograph from the bottom of a large cup eye of *Barbatia cancellaria*, showing an unpigmented receptor cell wedged in between pigment cells. The receptor cell contains numerous mitochondria and produces a large plume of rhabdomeric microvilli into the lumen of the eye cup. (*d*) Rhabdomeric microvilli from a cup eye of *Anadara*, showing stout bundles of axial filaments in each microvillus. (*e*) One of the smaller pigmented pits of *Barbatia*. All cells are pigmented and contribute microvilli to the contents of the pit. It is questionable whether these small pits are sensory. Abbreviations: PC, pigment cell; RC, receptor cell; R, rhabdomeric microvilli. Scale bars: (*a*) 100 μm; (*b*) 40 μm; (*c*) 1 μm; (*d*) 0.5 μm; (*e*) 1 μm.