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STRUCTURE OF THE PHOTORECEPTORS IN THE COMPOUND EYESPOTS OF *BRANCHIOMMA VESICULOSUM*

F. B. KRASNE* AND P. A. LAWRENCE†
Department of Zoology, University of Cambridge

SUMMARY

Each photoreceptor unit within the eye is located immediately beneath the surface cuticle and is composed of 2 cells; a superficially placed lens cell and a large, deeply situated receptor cell which is composed of two segments. The deep segment of the receptor cell is filled by a large invaginated cavity containing a stack of some 450 disc-shaped membranous sacs; these are the expanded and flattened membranes of cilia, the basal bodies of which line the cytoplasmic wall of one side of the cavity. The basal bodies have a 9+0 arrangement of fibrils and lack striated rootlets and orthogonal centrioles. On the side of the cell opposite this field of basal bodies the cavity is continuous with a tunnel which passes through the superficial segment of the cell at one side and opens at its top. The tunnel is crescent-shaped in cross-section, and its inner wall is covered by an array of microvilli. The cytoplasm of the superficial segment of the receptor cell is mostly filled by some 3000 long, rod-shaped, hexagonally packed mitochondria, whose long axes lie normal to a plane dividing the basal body and tunnel sides of the cell. The arrays of mitochondria and microvilli correspond in number and spacing; and fibrils arising in the microvilli project into the cytoplasm running in the space between adjacent mitochondria.

INTRODUCTION

Vertebrate, arthropod and cephalopod photoreceptors are aggregated in eyes which are morphologically conspicuous and of obvious significance in life; this presumably accounts for the concerted analytical attack (see Moody, 1964) which has been made on their fine structure and physiology. Not surprisingly, the less conspicuous photoreceptors of other animal groups have been given less attention. This is unfortunate, because comparative analysis of fine structure may serve to bring out essential or primitive features of photoreceptor design. Only a few papers have appeared on the fine structure of annelid photoreceptors and none on those widespread among the sedentary polychaetes. The present paper helps to fill this gap.

The tubicolous polychaete genus *Branchiomma* has long been known for the remarkable compound eyespots which it bears on the tips of each filament of its branchial crown, and for the startlingly sensitive and rapid withdrawal reaction which it displays when disturbed by a passing shadow. Surprisingly, responsiveness to shadows

* Present address: Department of Psychology, University of California at Los Angeles, California, U.S.A.
† Present address: Department of Biology, University of Virginia, Charlottesville, Virginia, U.S.A.

remains if the eyes are removed (Hesse, 1899). But Nicol (1950) has shown that sensitivity to moving shadows is greater than that to the simple extinction of light, and it seems likely that it is for this ability to perceive movement that the eyes are responsible. Indeed, the early light-microscope investigations of Brunotte (1888) revealed a morphological organization well suited to the perception of motion. She described the eyes as being approximately spherical and composed of 40–80 clear conical sectors, separated from each other by dense pigmentation. At the base of each cone directly under the general body cuticle was a spherical lens and behind this a nucleus. Inferior to the lens complex was a 'granular protoplasmic region' sometimes containing a very large nucleus and behind this, filling the apical third of the cone, was a body of lamellar appearance formed by layers which were alternately clear and opaque. Hesse (1899) further recognized that the central core of the apex of the cone, which corresponded to Brunotte's lamellar body, was joined by radially directed fibrils to dense little rods distributed around part of the periphery of the cell. Finally, the cell tapered at its apical extremity to come into contact with the arborization of the branchial nerve. Our investigations with the electron microscope have allowed us to elaborate on and refine these essentially correct observations and have disclosed remarkable parallels between these photoreceptors and those of some other animals. A preliminary report on these structures has been published elsewhere (Lawrence & Krasne, 1965).

METHODS

Specimens of *Branchiomma vesiculosum* (Montagu) were collected from the Salcombe Estuary, Devon, and kept in cold, circulating sea water until needed.

Light-adapted (normal room illumination) eyes were removed from animals and fixed for 2 h at 4 °C in a solution containing 1% osmium tetroxide, 10% sucrose, and 8 mM calcium chloride, buffered at pH 7·5 with veronal. The material was embedded in Araldite epoxy resin and sectioned on a Porter–Blum microtome. Sections were stained for 35 min in a saturated solution of uranyl acetate in 50% alcohol, followed by 3 min in lead citrate (Reynolds, 1963). This staining method produced negligible contamination. The stained sections were viewed with a Philips EM 200 electron microscope.

RESULTS

General description

The receptive units of the compound eyespots in *Branchiomma* are bicellular (Figs. 1, 2); each consists of a receptor cell capped by a discrete lens cell which lies just under the general cuticle. These units are separated from each other by intervening pigment cells. The receptor cell proper has two sharply demarcated segments, a *superficial segment* which is packed with long rod-shaped structures, and a *deep segment* containing a large, extracellular, invaginated *cavity*, which is filled with a stack of closely packed membranous lamellae lying normal to the long axis of the cell. At

one side of this cavity (the *basal body side*) is a field of ciliary structures which project centripetally. On the opposite side the cavity is continuous with a *tunnel* which passes up the side of the superficial segment and opens at the top of the cell. The large nucleus

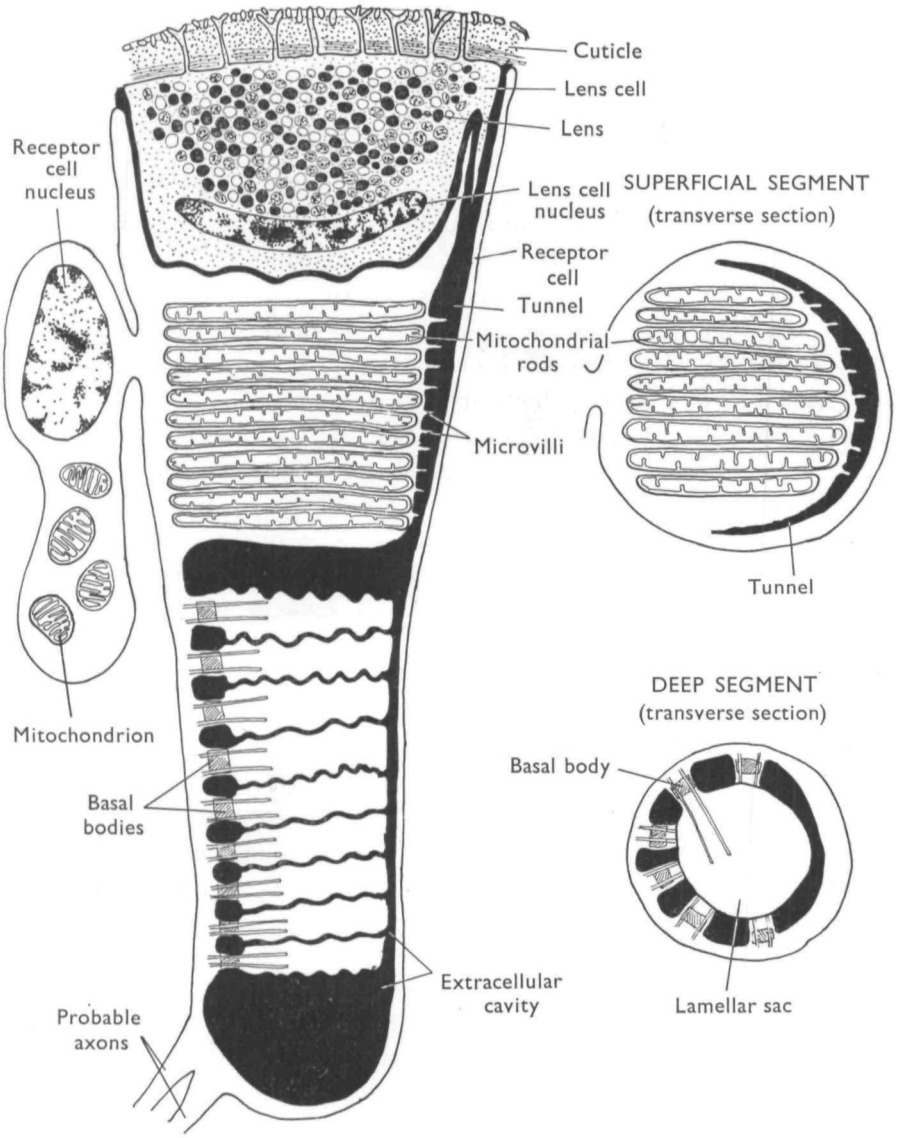

Fig. 1. Diagram of receptor and lens cells. The scale has been distorted to allow emphasis of certain relationships. Space which is continuous with extracellular space is drawn solid black.

and its adjacent cytoplasm are joined to the rest of the cell by a narrow isthmus on the basal body side (Fig. 1). A pouch of cytoplasm under the nucleus contains numerous mitochondria of typical appearance. The cell gives off one or more centrally directed processes from its basal body side; these are probably axons.

The lens cell

The lens (Fig. 2, *l*) is a large ovoid mass of vesicles, granular in substance and variable in size and electron density (Fig. 3). Below the lens there is a dish-shaped nucleus. Above, the cell associates closely with the two-layered cuticle (Fig. 3), into which it sends thin, branched cytoplasmic protrusions that reach the surface of the eye (Fig. 3, *cp*). Below, cytoplasm sometimes extends into the tunnel or over the sides of the receptor cell on which the lens cell is placed.

The tunnel

Transverse sections through the superficial segment show the tunnel to be a space, crescent-shaped in section and about 1 μ thick. The tunnel spans about half the circumference of the cell just below the plasma membrane on the side opposite the basal body side (Fig. 1). Favourable longitudinal sections show this space to be truly extracellular (Fig. 5). The difficulty of finding such sections indicates that the tunnel narrows near its mouth. Arms of both the lens cell and adjacent pigment cells enter the tunnel through this opening (follow *lc* and *pc*, Fig. 5). The tunnel contains fibres and strands of material (Fig. 5, *s*) which may be extensions of these lens and pigment-cell processes and which in some cases extend into the cavity of the deep segment.

Microvilli (see below) project into the tunnel from its inner wall (Figs. 5, 7). These contain internal filaments similar to those found in the villi of brush borders and which appear to extend centripetally into the superficial segment (see below). Microvillar fields of uncertain function have on several occasions been seen in association with light receptors, being borne either by the receptor cells themselves (Eakin & Westfall, 1964*c*) or by very closely associated supporting cells (MacRae, 1964; Yamamoto, Tasaki, Sugawara & Tonasaki, 1965).

The superficial segment

The superficial segment, which extends about half the length of the receptor cell, is characterized by a large array of parallel, rod-like structures, about 30 times as long as they are broad (Fig. 2, *mr*). The long axes of these rods are normal to a plane dividing the basal body side from the tunnel side of the cell, and when cut in such a plane the rods are seen to be hexagonally packed (Fig. 6). The spacing of the microvilli which project into the tunnel is the same as that of the rods, and the two are arrayed in a similar hexagonal pattern (Fig. 7). Fibrillar profiles are often found to run from the centre of a microvillus into the small gap between adjacent rods. The fibrils (Figs. 5, 7, *f*), which may extend some distance into the cell, can be seen in section at their outside termination in Fig. 7 and in longitudinal view in Fig. 5.

The rods are bounded by two membranes, the inner one of which is invaginated to form villus-like projections (Fig. 6, *cr*) into the body of the structures. These rods therefore meet electron-microscopic specifications for mitochondria (Rouiller, 1960). However, these mitochondria have few cristae compared to those found in the peri-nuclear cytoplasm. This, together with their large number (about 3000 per cell) and maximally close packing, suggests that they may have a special function.

Arranged around the remaining peripheral cytoplasm of the segment are Golgi bodies in association with small vesicles. Microtubules (Fig. 5, *mt*) having no obvious regularity of orientation are also frequent in the cytoplasm.

The deep segment

Longitudinal sections through the cavity of the deep segment show it to be filled by a pile of paired membranous lamellae whose surfaces are normal to the long axis of the cell (Figs. 2, 4, *pm*). Each membrane is 60–70 Å thick and separated from its partner by some 30–60 Å. Upon following these paired membranes to their lateral margins it becomes clear that each consists of the apposed walls of two adjacent, flattened, membranous sacs (Fig. 4). The cavity of the deep segment is filled by a stack of about 450 such sacs. Each is roughly disc-shaped and usually fills its section of the cavity; occasionally, however, sac edges have been observed about 1 μ central to the wall of the cavity. The thickness of the sacs is uneven due to (out-of-phase) undulations in the upper and lower membranes, which are in some places closely juxtaposed and in others separated by more than 0·1 μ.

Approximately half of the cytoplasmic cup in which the stack of discs lies is lined by a field of about 450 evenly spaced ciliary basal bodies. Favourable sections show that the lamellar sacs of the deep segment are modified cilia stemming from these basal bodies (Fig. 8). Study of pictures showing the origin of the sacs (Figs. 4, 8) suggests that each basal body contributes one sac (the ciliary membrane), and the correspondence between our rough counts of basal body and sac numbers confirms this conclusion.

The basal body structures start as a cartwheel arrangement of 9 triplets of clear outer fibres embedded in an electron-dense annulus (Fig. 9); there are no central fibres. We have seen no striated rootlets. Just before the cilium protrudes into the cavity of the deep segment one subfibre of each triplet is lost. As the cilium emerges, the previously clear core becomes electron dense and the fibrillar apparatus (now 9 doublets) becomes enveloped by a continuation of the plasma membrane of the cavity (Fig. 10). Adjacent to the membrane at this level are 9 components of tubular appearance (Fig. 10, *t*), each of which is linked to a corresponding member of the inner ring of 9 doublets. More distally the membrane comes very close to the inner ring of 9 doublets whose core is again clear. Finally, the membrane billows out to form one of the lamellar sacs of the deep segment, and the doublet filaments are here seen to be joined by single side-arms (Fig. 11). The 9 doublets extend into the lamellar sac (Fig. 8), becoming progressively disorganized, and terminating one by one when they have penetrated about a third of the disc diameter.

Multivesicular bodies (not figured) occur occasionally in the cytoplasm of the deep segment. Such bodies have been found in the cytoplasm of other photoreceptors (MacRae, 1964; Eakin & Westfall, 1965). Small clusters of vesicles (about 500 Å diameter), similar to those contained in the multivesicular bodies, are often contained in the cilium at the level where the membrane starts to billow out to become a sac. Vesicles have previously been found in ciliary receptor organelles (Eakin & Westfall, 1962*a*; Eakin, 1963; Horridge, 1964). Similar vesicles are also numerous at the bases

of protuberances which project a short distance into the cavity between emerging cilia (Fig. 4, *p*). Tangential sections just inside the cavity suggest that these 'protuberances' are in fact more or less extensive ridges which often join up with one another and on occasion span a substantial portion of the cavity wall.

DISCUSSION

Extensive elaborations of surface membrane occur in all photoreceptor cells whose ultrastructure has been examined (Eakin, 1963; Moody, 1964). While the precise configuration of these elaborations varies considerably from one kind of animal to another, all may be classed as fields either of lamellae or of tubular (villous) processes (see Table 1). The membranes thus formed are usually arrayed in an orderly manner, but not invariably so (e.g. *Pleurobrachia*, *Henricia*, Hesse and Joseph cells of *Amphioxus*, *Nereis vexillosa*). They are usually oriented across the path of impinging light, but on occasion are placed in line with it (e.g. *Henricia*, *Dugesia lugubrius*, and possibly *Sagitta*). Both microvillar and lamellar systems may arise either as apparently simple outfoldings of the plasma membrane or as elaborations of ciliary membranes (Table 1).

In the few annelid (including some polychaete) eyes which have been studied, receptor organelles of microvillar type have been the rule. While parts of isolated ciliary structures have often been found (Table 1), their relationship, if any, to the microvilli has remained obscure. Thus, the system of stacked membranous sacs, unmistakably derived from cilia, which occurs in *Branchiomma* is so far unique among the annelids. However, it is a condition closely resembling that typical of vertebrates, which shows (as do several other entries of Table 1) that the form of light-receptor organelles within a phylum need not be homogeneous. This emphasizes the possibility of independent but parallel evolution at the level of ultrastructure, and thereby demonstrates the dangers of using ultrastructural features to infer phylogenetic kinship (see Grimstone, 1959).

While ciliary photoreceptor organelles seem to be characteristic of some taxonomic groups and to be occasionally (though not typically) present in other groups, their specific morphology exhibits considerable diversity of detail. Thus, the cilia of the receptor cells of *Branchiomma* lack central fibres; while this is usually considered a feature characteristic of sensory cilia, variations such as $8+1$, $9+1$ and $9+2$ patterns have been observed in the sea star, *Leptasterias*, in the presumably photosensitive ependymal cells of *Branchiostoma*, and in the hydromedusan *Polyorchis* (Eakin, 1963). It is most common for receptor cells of the ciliary type to bear a single cilium-like outgrowth, presumably the photosensitive organelle, which has near its basal body (c_1) a second centriole (c_2), oriented roughly orthogonally to the first, and which does not itself give rise to a cilium; both centrioles usually have a striated rootlet. *Branchiomma* photoreceptors are unusual in possessing many cilia per cell and in lacking orthogonal centrioles and striated rootlets; they share these features with the presumed photoreceptors of the ctenophore, *Pleurobrachia* (Horridge, 1964). The two classes of ciliary receptors thus formed are not, however, exhaustive. The chaetognath *Sagitta*

Table 1. *Distribution of basic configurations of photoreceptor organelles*

Animal	Configuration	Reference
Coelenterates		
Polyorchis	T C	Eakin & Westfall, 1962*a*
Ctenophores		
Pleurobrachia	L C	Horridge, 1964
Platyhelminths		
Dugesia	T D	Röhlich & Török, 1961; MacRae, 1964
Dendrocoelum	T D	Röhlich & Török, 1961
Philophthalmus	T D	Isseroff, 1964
Fasicola	T D	Kümmel, 1960
Aschelminths		
Asplanchna	L D	Eakin & Westfall, 1965
Molluscs		
Pecten	L C	Miller, 1958
Viviparus	T ?	Clark, 1963
Helix	T ?	Röhlich & Török, 1963; Schwalbach, Lickfeld & Hahn, 1963
Sepia	T D	Wolken, 1958
Loligo	T D	Zonana, 1961
Octopus	T D	Yamamoto *et al.*, 1965
Annelids		
Platynereis	T D	Fischer, 1963
Nereis	T ?	Eakin, 1963
Neanthes	T ?	Eakin & Westfall, 1964*b*
Branchiomma	L C	Present paper
Helobdella	T ?	Clark, 1963
Enchytraeus	T ?	Bradke, 1962
Onychophorans		
Peripatonder	T ?	Eakin & Westfall, 1964*a*
Arthropods generally	T D	Eakin, 1963; Moody, 1964
Chaetognaths		
Sagitta	T C	Eakin & Westfall, 1964*c*
Echinoderms		
Leptasterias	T C	Eakin, 1963
Henricia	T C	Eakin, 1963
Asterias	T ?	Vaupel-von Harnack, 1963
Urochordates		
Ciona	L C	Dilly, 1964, and quoted by Eakin, 1963
Cephalochordates		
Branchiostoma		
Ependymal cells	T C	Eakin, 1963
Infundibular cells	T C	Eakin, 1963
Joseph cells; Hesse cells	T D	Eakin, 1963; Eakin & Westfall, 1962*b*
Vertebrates generally	L C	Eakin, 1963; Moody, 1964

Tubular (microvillar) types are indicated by T, lamellar types by L. Those in which photosensitive membranes are believed to arise directly from the plasma membrane are called 'direct', D, and those deriving from a cilium are indicated by C; ? means that a basal body has been found in the receptor but that no relationship to the presumed photosensitive membranes has been traced.

illustrates, for example, that a single rooted cilium can occur in absence of a second orthogonal centriole (c_2) (Eakin & Westfall, 1964*c*). Finally, the character of the membrane elaborations themselves is not uniform. The lamellar type system found in *Branchiomma* is found also in all the vertebrate eyes with which we are familiar, in the lamellibranch mollusc *Pecten*, and in the ctenophore *Pleurobrachia*. But villous or tubular systems are also common; they are found among the chordates in the infundibular appendage of *Branchiostoma* and occur in the echinoderms *Leptasterias* and *Henricia*, in the hydromedusan *Polyorchis*, and in the chaetognath *Sagitta* (see Table 1).

In comparing the photoreceptors of *Branchiomma* with those of other forms it may be important to recognize that the extreme sensitivity of this species to shadows contrasts with a complete behavioural indifference to increases of illumination (Nicol, 1950; Krasne, unpublished observation). It is thus possible that the sensory cells described here have the singular property of being triggered by reduction, rather than increase, of illumination, and this possibility should be borne in mind by anyone attempting a physiological interpretation of their ultrastructure.

A remarkable feature of these photoreceptors is the densely packed mitochondrial rods of the superficial segment. It is especially striking that these inclusions are interposed between the lens and the presumed photosensitive membranes. The possibility that they invest the superficial segment with dichroic properties which would allow it to act as an analyser for polarized light should be considered. A generous endowment of mitochondria is almost typical of photoreceptor cells and these are very often, as here, placed where they are subject to illumination. However we know of no other invertebrate receptor in which there are so many mitochondria arrayed in so orderly a way.

Finally, a note of caution is necessary. It must be recognized that the photosensitive nature of the lamellae of the deep segment is merely presumed on the basis of their apparent analogy with the receptor organelles of vertebrate eyes. Also unproved, but surely correct, is the assumption that the organs whose cells we have described are in fact eyes. This can hardly be doubted when their gross as well as their fine structure is considered. Their role in life, however, is less certain. For we know from the work of Hesse (1899) that the worm still reacts smartly to shadows after all these eyes have been cut off. Although we have confirmed this observation, it was our impression that the mutilated worms were less responsive to moving shadows than intact specimens. The eyes seem well designed for the perception of movement, and the above observation may show that this is indeed their function. However, such a conclusion would be premature, since within 72 h of operation new eyes have developed far enough for them to be externally conspicuous as dark swellings at the tip of each filament of the branchial crown. Reactions must therefore be tested very shortly after the eyes are removed. At this time, however, the worm is surely suffering from generalized post-operative trauma. Furthermore, since cutting the nerves of the branchial filaments would probably cause them to discharge a barrage of injury potentials, the central synapses of the escape reflex, which are at best highly labile (Nicol, 1950), may well be in a fatigued state at the time that the tests must be made. Thus, a quantitative analysis

of the relationship between the recovery of the shadow reflex and the anatomical organization of the regenerating eyes will be required to clarify the functional significance of the elaborate structures which we have described.

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Fig. 2. Low-power micrograph of the entire lens receptor cell complex. The receptor cell nucleus lies out of the plane of section. Note that the tunnel (*t*) through the superficial segment does not open to interstitial space in this section. Uninterrupted longitudinal sections of the rod-like mitochondria (*mr*) of the superficial segment are seen at the bottom of the segment (*bb*, basal bodies; *cp*, cytoplasmic processes; *ds*, deep segment; *l*, lens; *ln*, lens cell nucleus; *p*, pigment granules; *ss*, superficial segment).

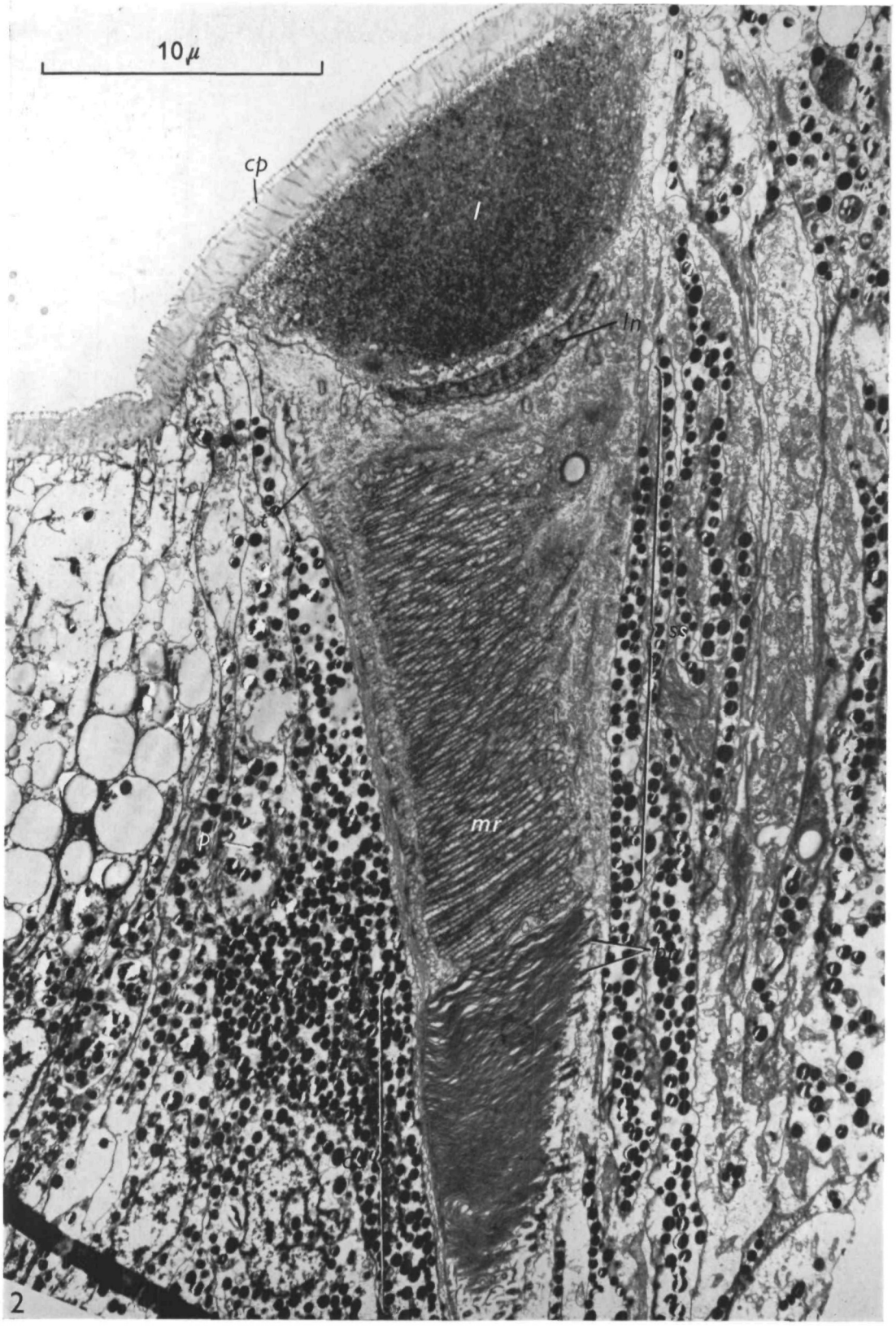

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Fig. 3. Micrograph showing the structure of cuticle (top) and lens (centre) (*cp*, cytoplasmic process; *lc*, lens cell; *p*, a process of the lens cell; *rc*, receptor cell; *1*, outer layer of cuticle; *2*, inner layer of cuticle).

Fig. 4. The lamellae formed by the flattened membranous sacs of the deep segment. This was taken from an approximately longitudinal section cut parallel to the mitochondrial rods of the superficial segment; the page should be rotated 90° clockwise for correct orientation of the section (*cyt*, receptor cell cytoplasm; *e*, extracellular space of the deep segment cavity; *pm*, paired membranous lamellae; *v*, vesicles in a protuberance (*p*) from the cavity wall).

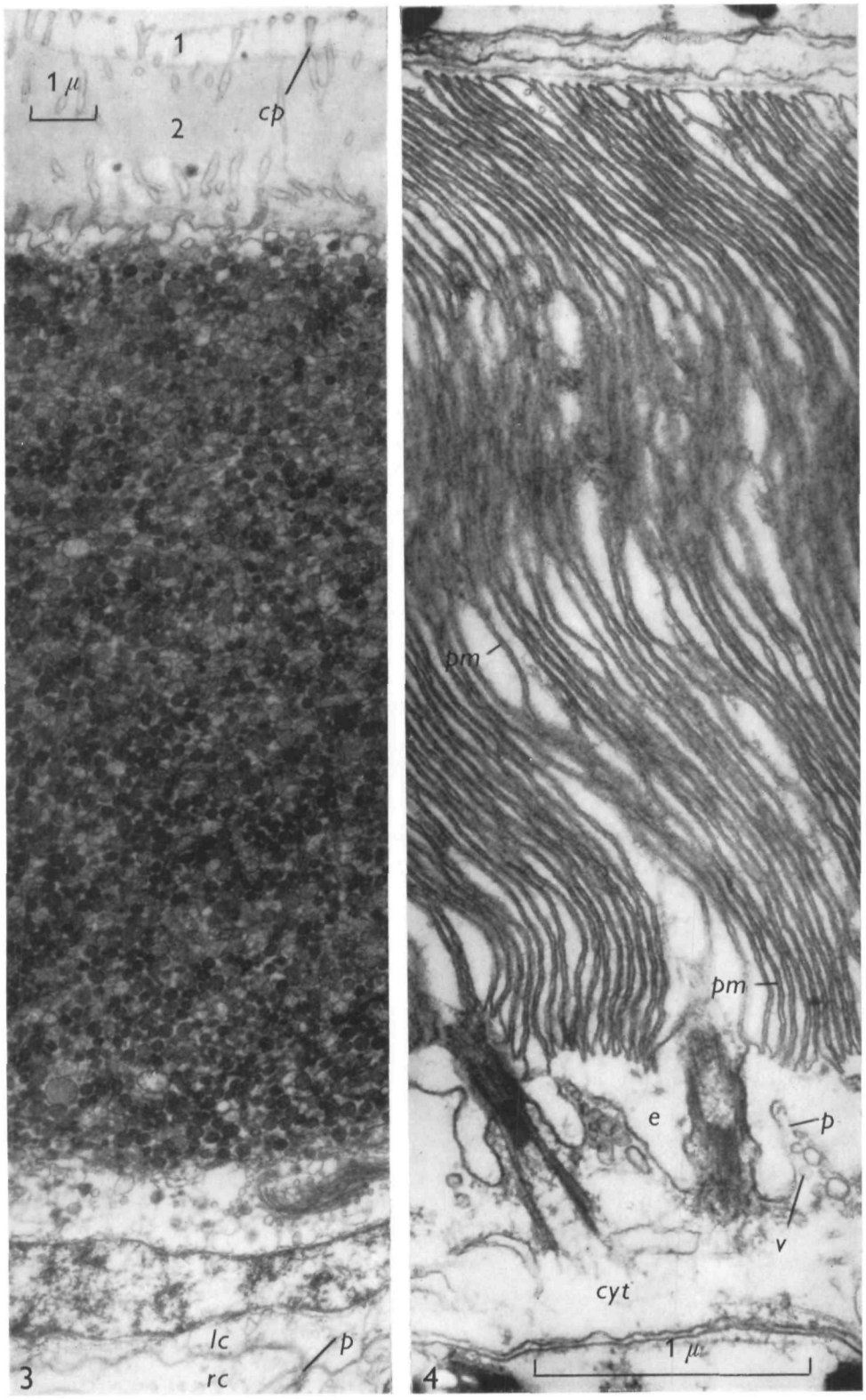
1
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Fig. 5. Micrograph demonstrating that the tunnel is continuous with interstitial space. This is a longitudinal section tilted 45° clockwise from the vertical. The tunnel (*t*) runs from the lower left and opens at the upper right of the plate. Notice the lens cell (*lc*) sending an extension into the tunnel; to the left of this an extension of a pigment cell (*pc*), which lies out of the plane of section, also protrudes into the tunnel. The microvilli of the tunnel appear to send filaments (*f*) between the mitochondrial rods (*mr*) (*mt*, microtubule; *mv*, microvilli; *pm*, plasma membrane of receptor cell; *s*, strands of material possibly continuous with lens or pigment cells).

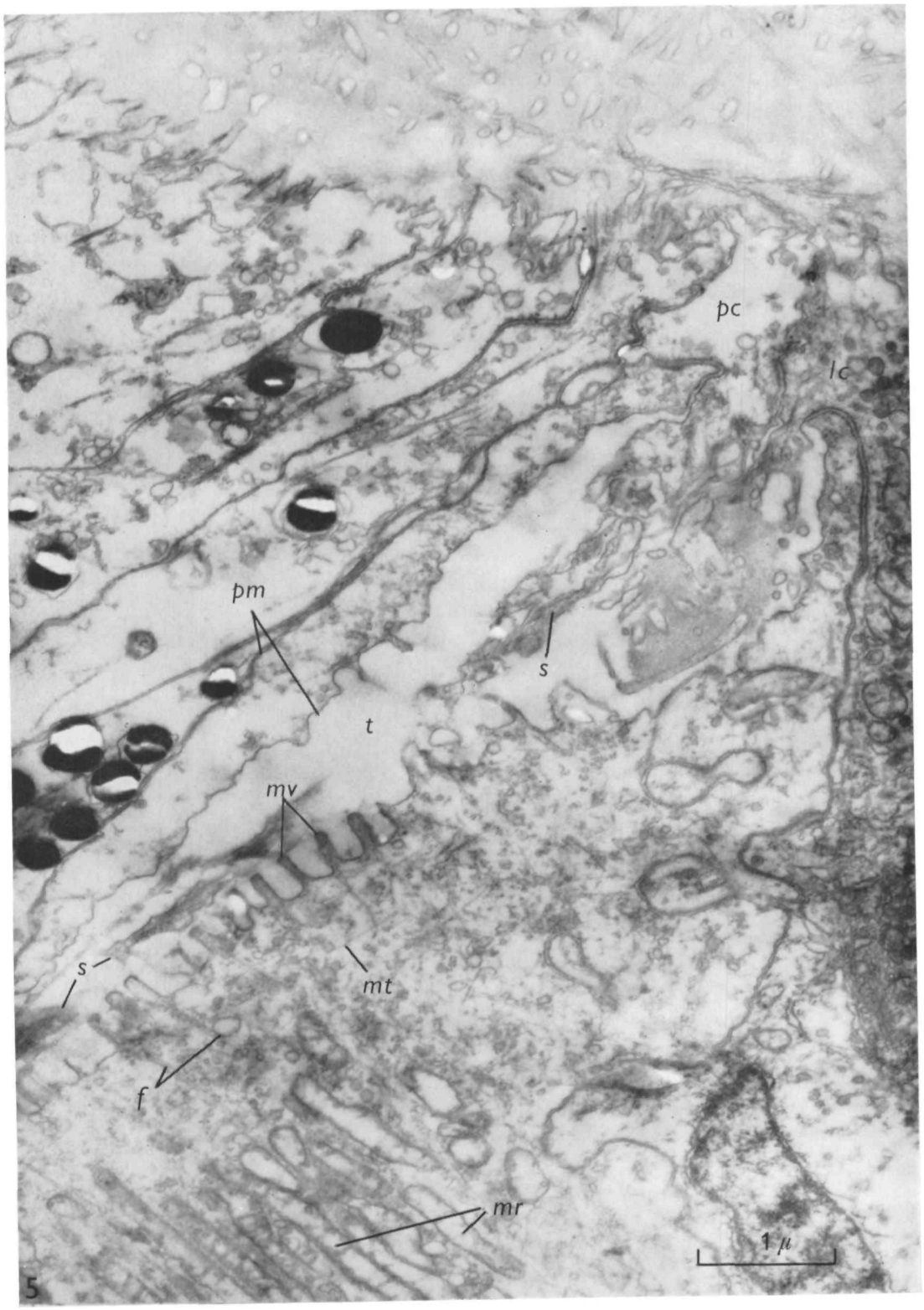

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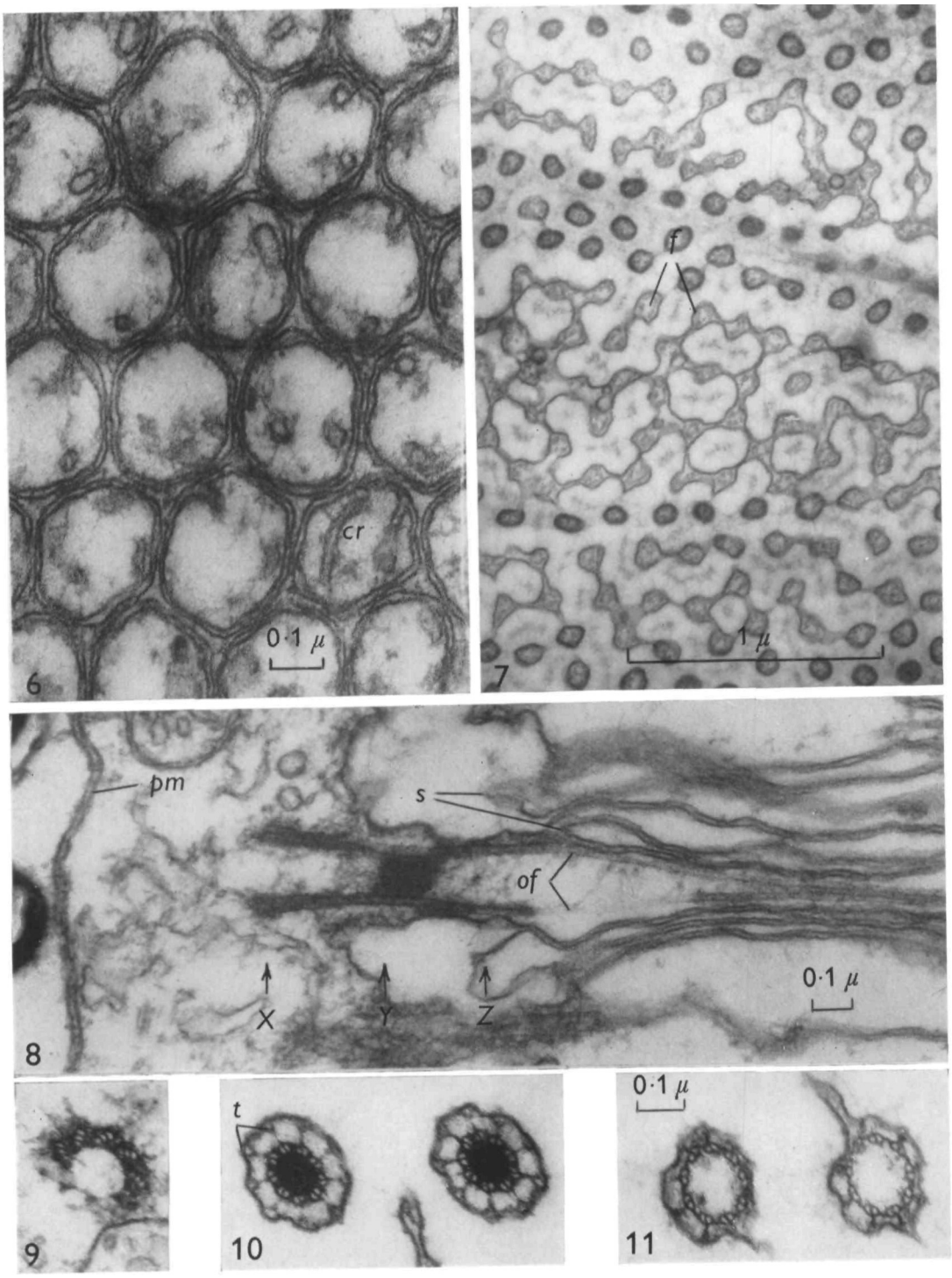
Fig. 6. Section through the superficial segment transverse to the axes of its hexagonally packed mitochondria. A crista is seen to be an invagination of the inner membrane at *cr*.

Fig. 7. This section cut tangentially to the microvillar side of the superficial segment shows the microvilli in cross-section. Each villus contains a number of fibrils (*f*).

Fig. 8. Micrograph of a cilium emerging from the cytoplasmic wall (left) of the deep segment cavity (toward the right). The membrane of the cilium and two of its outer fibres (*of*) can be followed into the lamellar region. Above and below this cilium are the edges of sacs (*s*) associated with other basal bodies (*pm*, plasma membrane). The arrows *X*, *Y*, and *Z*, indicate approximately the levels from which the transverse sections below (Figs. 9–11 respectively) were taken.

Figs. 9–11. Transverse sections of deep segment cilia (*t*, tubular profiles adjacent to membrane).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