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The dorsal eye of the mayfly *Atalophlebia* (Ephemeroptera)

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[Plates 1–7]

The dorsal eye of *Atalophlebia* has two unusual features, the sensitivity only to ultraviolet (u.v.) light, and the candelabra-shaped rhabdom. In addition, the crystalline cone is surrounded to its tip by a yellow pigment, and the tip tapers gradually as a dense fibre. These details, particularly the pigment distribution, indicate that a superposition image cannot be formed by u.v. light. Also, there is no refracting or reflecting structure that could form a sharp superposition image. Instead, it is suggested that u.v. rays are sharply focused on the cone tip and conducted by the retinula cell columns acting as light guides across the clear zone. Light of longer wavelength, on the other hand, is partially focused through the yellow pigment, and, although it is not seen by the insect, it is available to photoregenerate the visual pigment. This method of boosting sensitivity is appropriate for a pure u.v. eye and does not require a sharp focus of the regenerative rays, although the clear zone is an essential part of the mechanism.

The rhabdom has an extraordinary shape like a flat 5-armed candelabra in cross section, with five posteriorly directed arms which are formed by six retinula cells. There is also a 7th retinula cell without a rhabdomere. This cell penetrates laterally the rhabdom of the other six, and also forms a sheath around half of its own ommatidium and half of the the adjacent ommatidium. The exceptional relations between this cell, and the other six, together with the orientated candelabra pattern of the rhabdom, and the large size of the 7th retinula axon, is interpreted as a way of enhancing the current flow down the 7th axon which runs direct to the medulla, by-passing the lamina.

Introduction

The turban-shaped dorsal eye of the male of the European ephemeropteran insect *Cloeon dipterum* L. projects from the top of the head of the imago as two golden-coloured cylinders. Although earlier general descriptions of this eye (Zimmer 1897; Priesner 1914) have suggested that it may be a superposition eye, the way it functions optically is not known. In an Australian species of *Cloeon* some unusual anatomical features have recently been explained by quite a different tentative theory (Horridge 1976). No peripheral optical system was found by which a superposition image could be formed by refraction, as occurs in skipper butterfly

eyes (Horridge, Giddings & Stange 1972), or by reflexion, as recently found by Vogt (1975) and Land (1976) in two species of Crustacea with square facets. With no alternative explanation available it was suggested that each ommatidium acts separately by focusing axial rays upon the end of the retinula cell column which functions as a light guide, while unfocused longer wavelengths pass through peripheral yellow pigments and increase sensitivity by the regeneration of photopigment. Details, such as the lack of a tracheal tapetum around the rhabdom region of each ommatidium, were consistent with this idea but not with superposition optics.

Enlarged dorsal eyes are also found in the males of quite a different group of mayflies, the Leptophlebioidea, of which the common Australian genus is *Atalophlebia*. The eye structure in this group is unlike that in *Cloeon* but equally unusual, so that *Atalophlebia* presents us with different adaptations which are presumably of selective advantage in the capture of females by male mayflies.

The Leptophlebioidea is the dominant group of mayflies in the Australian fauna and the genus *Atalophlebia* contains most of the common mayflies of slow streams and lakes. The genus is Australia-wide and occurs from inland billabongs to subalpine streams. Preliminary anatomical accounts of some of this material have already appeared (Meyer-Rochow 1971; Horridge 1975*a*).

Materials and methods

Larvae of three species of *Atalophlebia* were collected around Canberra and reared to subimago and then full imago in the laboratory. At this final moult *from the winged subimago*, the structure changes considerably. The systematics of this genus are in a bewildering state and therefore adult specimens from the populations studied are deposited with National Insect Collection, C.S.I.R.O. Black Mountain, Canberra, Australia. One species, *Atalophlebia* A, belongs to the *costalis* group of species, distinguished by its three caudal filaments and dark brown abdomen. A second species, *Atalophlebia B*, of the *australasica* group, also has three caudal filaments but is distinguished by its orange abdomen. The third and largest of the species we examined, *Atalophlebia C*, belongs to the *costalis* group but has only two caudal filaments. Its larva is broader and heavier than those of the other two species. These distinctions, while not enough to make specific determinations, serve reliably as field characters when collecting specimens in known areas around Canberra. The best systematic account is by Riek (1970).

Electron microscopy

Pieces of the eye were fixed at pH 7.4 at room temperature, left overnight at 4 °C, rinsed in buffer and post-fixed in 2 % OsO_4 in buffer for 2 h at room temperature. The fixative was 2 % paraformaldehyde and 2.5 % glutaraldehyde (both by mass) in modified Millonig's buffer, which consisted of 83 ml of 2.25 % sodium monobasic phosphate and 17 ml of 2.52 % sodium hydroxide (both by mass) in

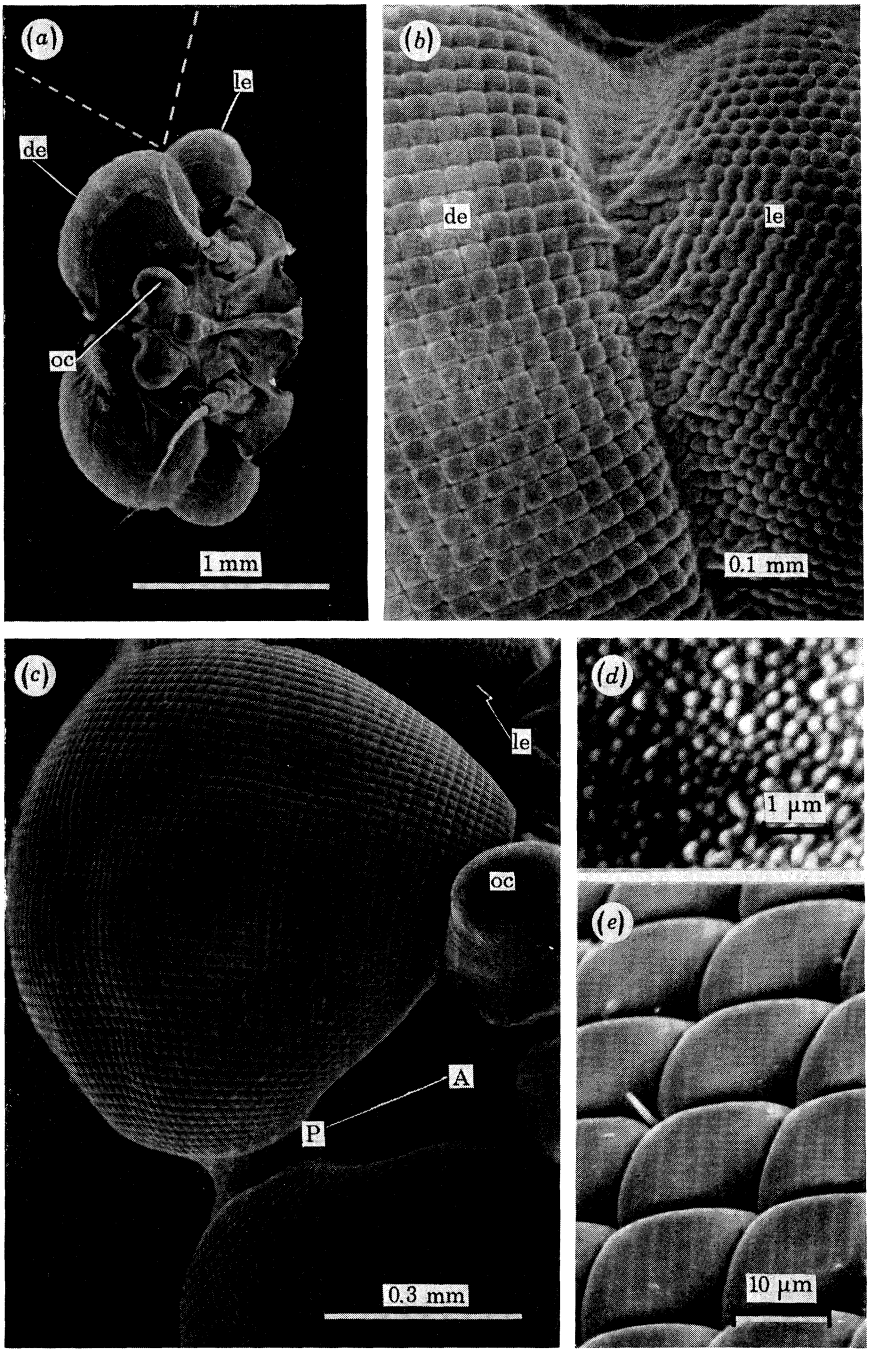

FIGURE 1. Scanning electron micrographs of the head and details of the eye surface. (a) Front view of the head showing dorsal and lateral eyes (de and le) and the prominent ocelli (oc). The dashed lines include the angle of the visual field that is seen by both lateral and dorsal eye on one side. (*b*) Detail of (*a*) where the square facets of the dorsal eye (left) meet the hexagonal facets of the lateral eye. (*c*) Facet lines of the dorsal eye. (*d*) Corneal nipples on the surface of a facet. (*e*) Dorsal eye facets including a small hair.

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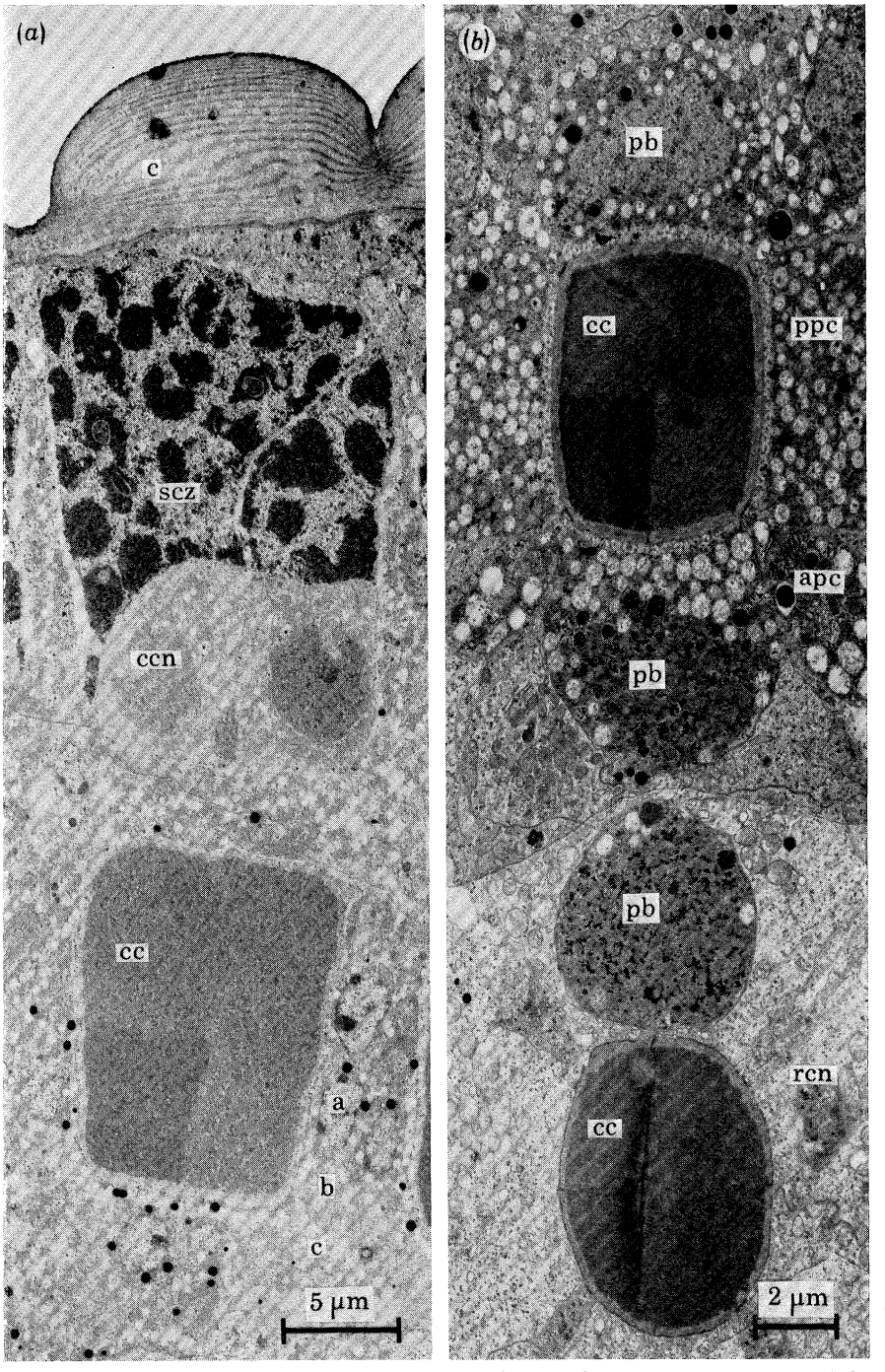

FIGURE 3. An oblique section through four ommatidia, starting at the cornea at top left of (*a*) and ending at the proximal end of the pigment bags at bottom right of (*b*). In the first ommatidium we see the subcorneal zone and the nuclei of the cone cells. In the second the square cone is surrounded by pigment cells that contain little pigment. In the third (top right) the cells surrounding the cone are densely filled by inclusions of several types. In the fourth the cone is round and one of the four bags of pigment (pb) stands out at this level.

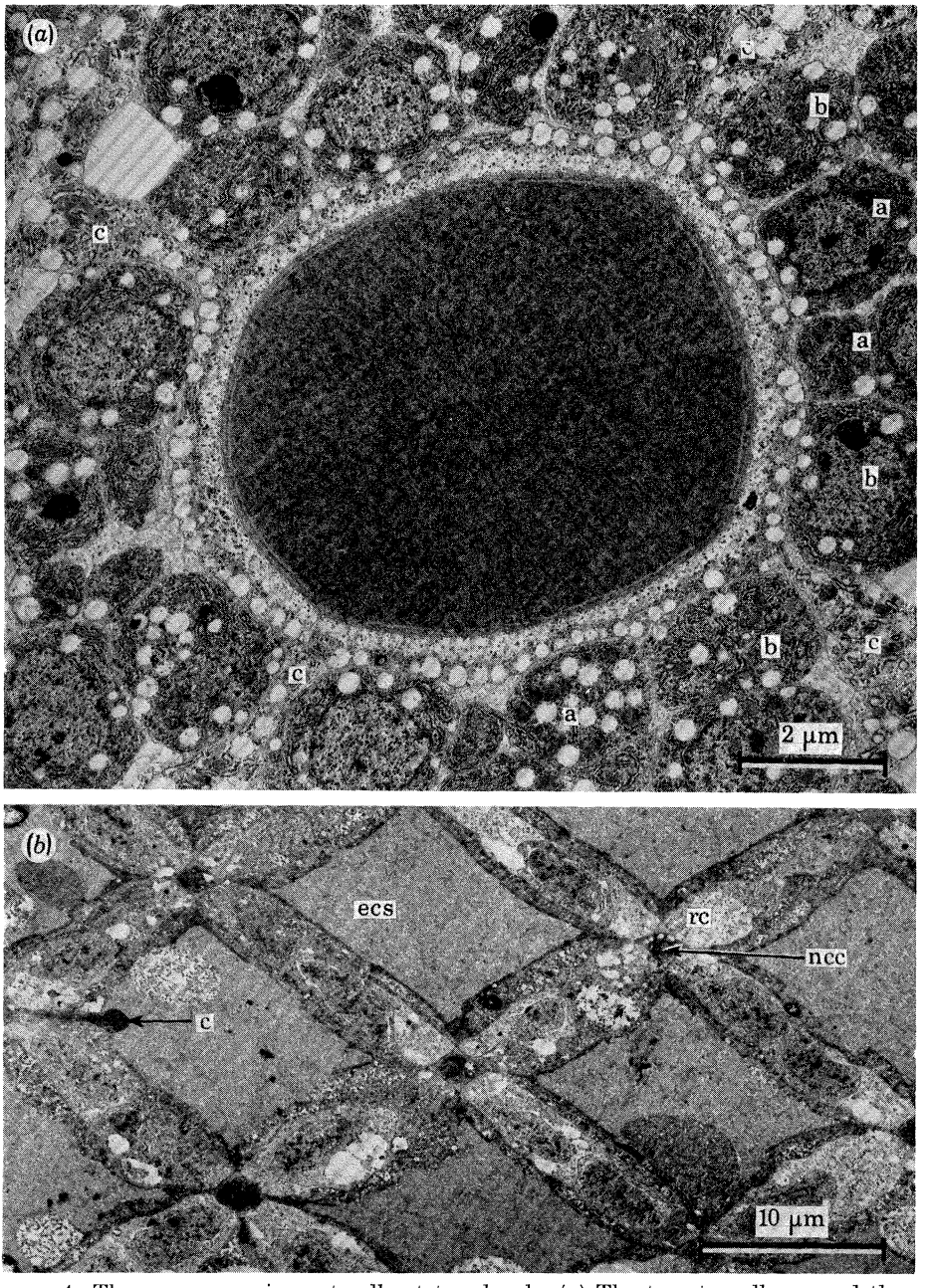

FIGURE 4. The accessory pigment cells at two levels. (*a*) The twenty cells around the cone near the level shown in figure 2*c*. The empty vesicles are believed to be the site of the yellow pigment. The cone in this region is homogeneous under both the light microscope and the electron microscope. (*b*) Transverse section at level (*g*) in figure 2, showing the penetration of the extracellular space of the clear zone into the lattice formed by the several types of accessory cells and retinula cells.

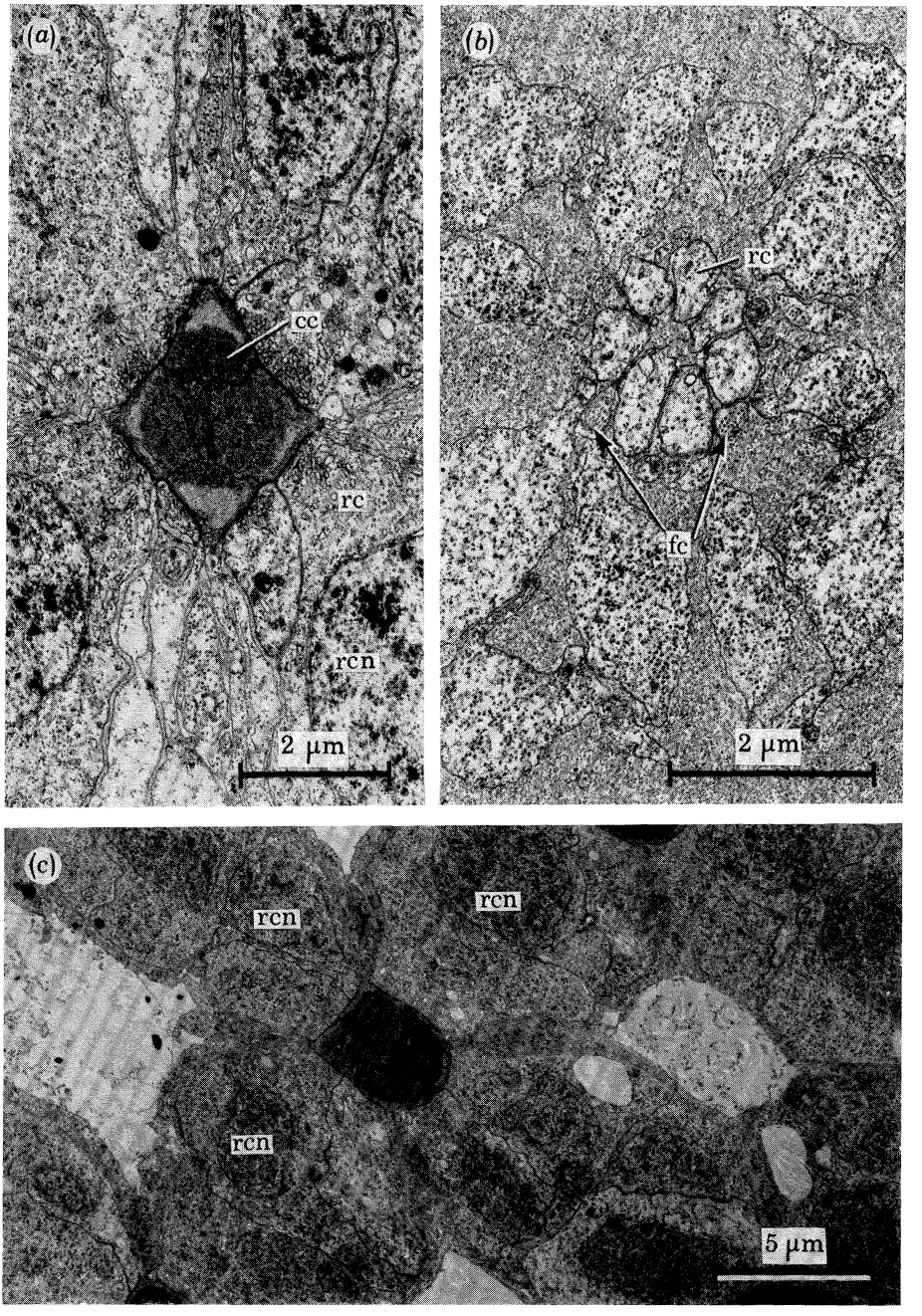

FIGURE 5. Regions of the proposed light guide. (*a*) Transverse section at the narrow part of the crystalline cone, where the accessory pigment cells change their positions between levels (*f*) and (*g*) in figure 2. Note the density and small diameter of the central region of the cone at this level. (*b*) The seven components of the retinula cell column in transverse section at level (*h*) in figure 2. (*c*) Retinula cell bodies 1–6 around the cone near level (*f*) in figure 2.

distilled water. After treatment in the OsO_4 the tissue was washed several times, dehydrated in an ethanol series, and embedded in Araldite or Taab resin. Sections were stained with uranyl acetate in methanol for 20–30 min, followed by lead citrate for 8–12 min according to the formula of Venable & Coggeshall (1965).

Results

Anatomy

In almost every feature the ommatidium is unusual compared with other insect groups but it consists of the same cell types and organelles. The facets of the dorsal eye are almost square (figure 1, plate 1), which at once suggests that we must look out for the reflecting optics described by Vogt (1975) and Land (1976). The pigment cells form a constant pattern across the eye but the arrangement is the most complicated yet described for a compound eye. The clear zone consists mainly of extracellular space which extends distally between the pigment cell, and one of the retinula cells has a unique form which is not found in any other insect. The general plan of the ommatidium, with sections at various levels, and (on the left) a key to the levels at which the electron micrographs are made, are set out in figure 2. The anatomical details refer to *Atalophlebia* A unless otherwise stated. For *Atalophlebia* B and C see figure 12.

The facets are square, of side 20 μm, with facet rows at 45° to the axis of the head (figure 1). The rows of facets are therefore unlikely to lie along the most common direction of relative motion of stationary objects seen in flight, as is often the case in diurnal insects. The inner corneal surface is almost flat; the outer surface forms a strongly convex lens which is coated with fine nipples at a density of about 16 μm^{-2} (figure 1*d*) like those on moth eyes, suggesting strong selection pressure to catch every possible photon. The cornea is composed of numerous layers caused by the arrangement of chitin micelles (figure 3*a*, plate 2), although, as in the Australian *Cloeon* species, the final moult to the imago takes place after only one day as a subimago so that these layers are unlikely to be zones of daily growth.

The cone is rather typical, being composed of four cells each of which extends as a long thread across the clear zone into the rhabdom column (figures 3, 4 and 5). The cone is densely filled with uniform fine granules (figure 4*a*, plate 3) similar to those identified as glycogen in the bee (Perrelet 1970). Unlike most insects, the cone is homogeneous right to its edge under the electron microscope (figure 4*a*) and most parts of it are homogeneous in sections of living material examined with the interference microscope. It is clearly much denser in solids and higher in refractive index than the immediately surrounding principal pigment cells, and could therefore conceivably act as a light guide, especially where it narrows. The extensions of the cone in the retinula cell column are only 0.2–0.3 μm in diameter (figure 5*b*, plate 4) which eliminates the possibility of there being separate light guides. Throughout their length into the rhabdom column, the cone extensions are filled with microtubules.

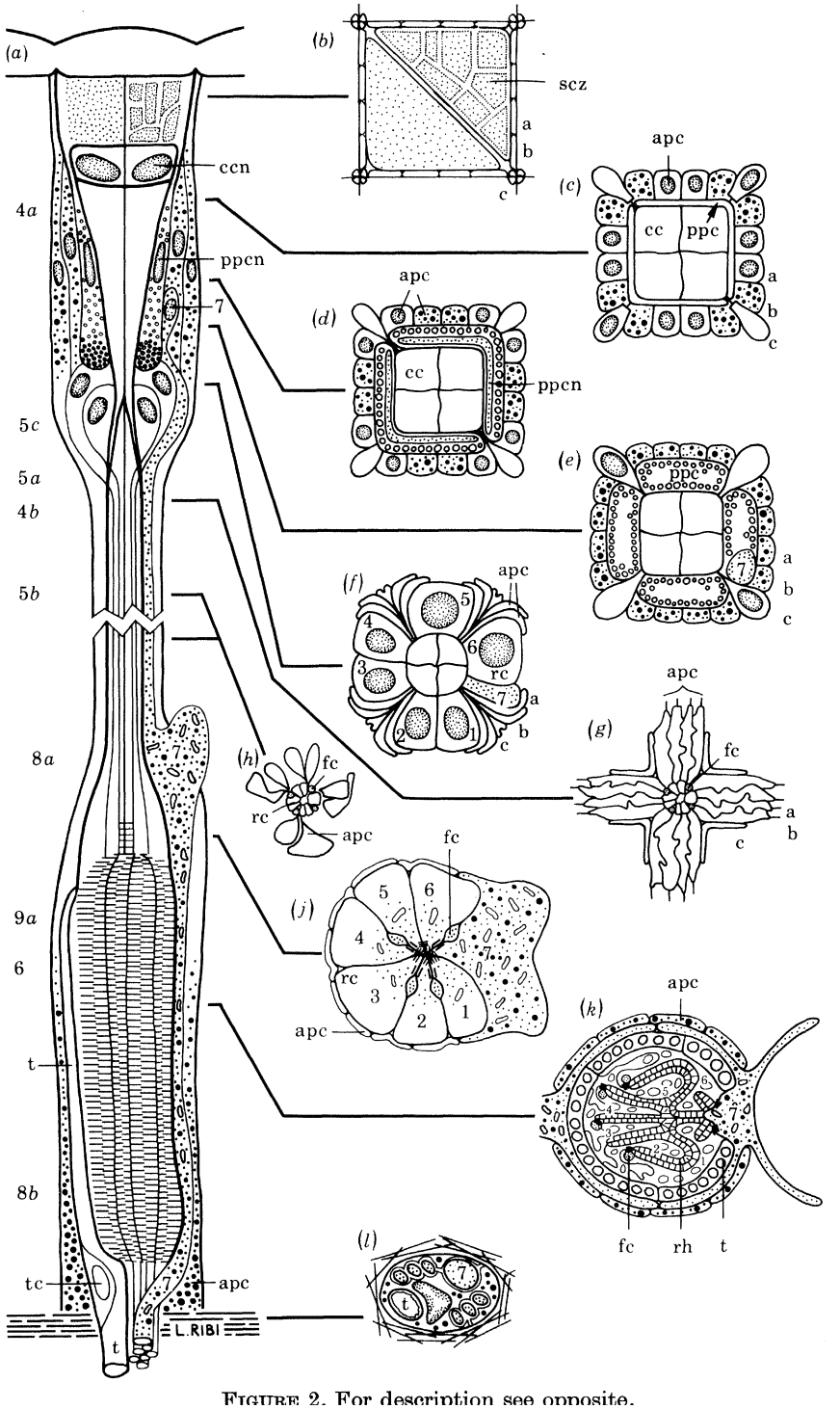

FIGURE 2. For description see opposite.

The principal pigment cells are complicated in shape and evidently serve several functions. Distally between the crystalline cone and the cornea in each ommatidium is a wide zone 10 μm deep, which we call the subcorneal zone (figure 2*b*). This was labelled pseudoconus in *Cloeon dipterum* and correctly identified by Priesner (1914) as a part of the two principal pigment cells. Although optically transparent in life, this region is seen under the electron microscope to be filled with granular particles which frequently collect into a pattern of clumps, perhaps as an artefact of fixation (figure 3*a*). In oblique sections the subcorneal zone is continuous with principal pigment cells; there are no nuclei unaccounted for at this level, and the subcorneal zone is divided into its two constituent cells along the same diagonal which separates them through the rest of the cone region. Extensive contact of the principal pigment cells with the cornea is typical of primitive insects and of the developmental stages of most insects.

The central region of the cone is surrounded by a narrow sheath formed by the two principal pigment cells, containing mitochondria, microtubules and characteristic dense grains 0.3 μm in diameter. The region around the cone itself has a low density of solids and inclusions suggesting a low refractive index. In the region where the sides of the cone are flat is a zone (ppc in figure 3*b*) of numerous vesicles up to 0.5 μm in diameter, which are usually washed out in our fixed material, but presumably contained the yellow pigment seen in life. There are also a few typical dense pigment grains in this zone. More proximally the principal pigment cells swell out into bags filled with unusual pigment grains on four sides of the cone. This complicated pattern is shown at several levels in figure 2. The pigment grains are of two types in these bags and again the whole of this region is yellow when examined in the light microscope.

As seen from the above account, the principal pigment cells are responsible for several of the optical features of the eye in that they form the curved corneal surface, determine the exact position of the focus relative to the tip of the cone by contributing the subcorneal space, provide the medium of low refractive index immediately around the cone, synthesize the distal screening pigments and hold them in position around the cone.

FIGURE 2. The ommatidium of *Atalophlebia* (*a*) longitudinal section with representative sections (*b*)–(*l*) at each level. The numbers on the left show the figure numbers of the electron micrographs. There are no anatomical changes upon adaptation. (*a*) The relative position of the pigment and main cell types. The distal part of retinula cell 7 is dotted to make it distinctive in the diagram: it is not pigmented until level (*j*). (*b*) The subcorneal zone, composed of the two principal pigment cells, with the other cells reduced to wisps. (*c*)–(*d*) Crystalline cone and pigment cells of four types in a constant pattern across the eye. (*e*) The region of the principal pigment cells where they are filled with yellow pigment. (*f*) Retinula cell somata 1–6 surround the neck of the cone. (*g*) the thin retinula cell column is surrounded by a cross of accessory pigment cells which join with those of neighbouring ommatidia to form a lattice permeated by extracellular space. (*h*) The retinula cell column and (*j*) its proximal end. (*k*) The main rhabdom column is sheathed by tracheae. (*l*) Seven axons of which no. 7 is the largest, are sheathed in a glial cell.

Accessory pigment cells, twenty in number, surround each ommatidium in a rigid pattern that changes at each level. There are three types, labelled a, b, and c in figure 2.

Eight cells labelled 'a' in figure 2 have more distal nuclei than the other eight, which are labelled 'b'. All 16 have narrow extensions which reach to the cornea (figure 2*b*) and proximally they contain pigment grains as far as the level of the retinula cell nuclei (figure 2*f*). Distally all 16 cells surround the principal pigment cells but where these fade out between levels (*e*) and (*f*) in figure 2, the accessory cells change their pattern, attach to the four edges of the cone and lie as leaves between the retinula cells (figure 5*c*). At level (*h*) they form an open square lattice (figure 4*b*) the cavities of which are filled by the intracellular fluid of the clear zone, and they carry a retinula cell column at each point of intersection of this lattice (figure 4*b*). Eight of these cells (figure 5*b*) continue with the retinula cell column as far as the basement membrane and proximally these same cells contain the dense pigment that lies between the rhabdom columns.

The cells labelled 'c' in figure 2 form the corners of a square pattern in the cone region (figure 5*c*). In the retinula cell region they lie in the angles between the sets of four cells of types a and b that form the sides of the lattice. In this zone of the eye the cells of type c stain more heavily than the others. Here and there one finds extensions of these cells into the intracellular space (figure 4*b*).

The retinula cell column, 120 μm long, crosses a clear zone which consists of extracellular space, so providing the lowest possible refractive index around the retinula cell columns. Only in mayfly dorsal eyes is such an arrangement known; where a clear zone occurs in other insects it is filled with parts of the accessory pigment cells. The cell column consists of 7 retinula cell extensions 0.5–0.8 μm in diameter, 4 cone cell processes of 0.2–0.3 μm and 10–16 loosely attached narrow mid-regions of the accessory pigment cells. There is no trace of pigment in any of these cell parts in this zone. The seventh retinula cell is indistinguishable from the others in the thin region. Desmosomes occur at intervals between the retinula cells, and between them and the cone cell processes.

The proximal part of the ommatidium consists of a candelabra-shaped rhabdom (figure 6*a*, plate 5) formed by 6 of the 7 retinula cells which are surrounded by a sheath of trachea. The seventh retinula cell differs in outline at each level (figure 7) and deserves detailed attention.

Retinula cells 1–6 contain numerous mitochondria between the arms of the rhabdom (figure 6*b*). Meandering membranes that separate them are developed into long desmosomes where they meet the rhabdom, as in most arthropod eyes. Each part of the rhabdom is formed by two adjacent retinula cells which form microvilli up against those of the other cell. The pattern is uniform across the eye, with the arms pointing *posteriorly*. The sheath of trachea surrounding the six retinula cells is continuous except where it opens to admit the 7th retinula cell along part of each anterior edge of the column, as shown by the sections at different levels in figure 7.

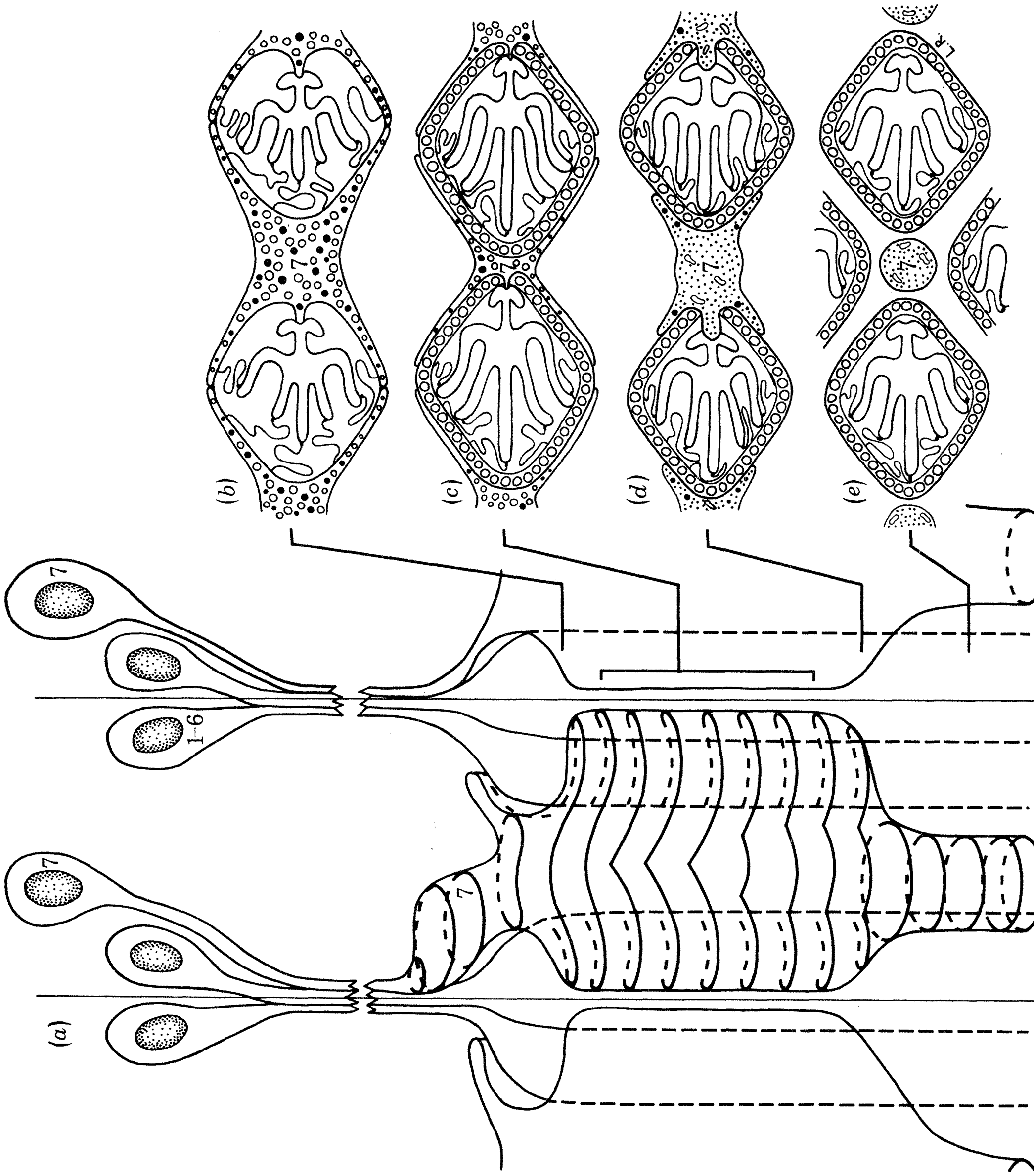

FIGURE 7. Retinula cells of two adjacent ommatidia showing the form of retinula cell 7 in transverse sections at different levels (*b*)–(*e*).

The seventh retinula cell has an extraordinary shape that has no parallel in any other insect eye. At one level it forms half of a longitudinal sheath around two adjacent ommatidia and penetrates to the rhabdom of one of them (figure 7). The cell body and nucleus lie far distally and asymmetrically between the cones, joined from there by a thin connection that has been traced by serial sections as far as the narrow extension along the retinula cell column. At one level of the distal ends of the rhabdoms (level (*j*) in figure 2) retinula cell 7 spreads out between the columns formed by the other six retinula cells (figure 8*a*, plate 6). Here its cytoplasm is crowded with pigment grains, mitochondria and empty vesicles, which presumably once contained the yellow pigment which is obvious in this region when examined under the dissecting microscope. In the central region of the rhabdom column, (level (*k*) in figure 2, and figure 9*a*, plate 7) cell 7 is pressed against the rhabdomeres of cells 1 and 6 but has no rhabdomere of its own. In this region it extends outside the tracheal sheath into four flat wings which curl round a half of its own rhabdom column and also half of the neighbouring one (figure 7). Proximally these wings become progressively smaller until the cell has transformed into a large axon filled with microtubules (figure 7). This axon runs outside the main ring of trachea which surround the main column of the ommatidium (figure 8*b*), passes through the basement membrane and then runs straight through the lamina to the medulla. It is the largest type of axon in the optic lobe and being 10 μm diameter could perhaps be found by a microelectrode. The unusual shape of this cell will be considered in the Discussion. The lateral eye has nothing comparable, having seven similar retinula cells and a simple columnar fused rhabdom (figure 9*b*).

Optics

Both cornea and crystalline cone are optically homogeneous, as seen in sections examined under the interference microscope. Therefore the first focus is formed principally by the outer convex surface of the corneal facets. There is available no second refracting region to form a second (superposition) image on the receptor layer. For a discussion of the refracting systems in clear zone eyes see Horridge (1975*b*).

When the eye is dropped into liquid nitrogen a small window can be cracked off one corner while it is still frozen. When it thaws, one can examine the receptor layer through the window where the cornea and cones are lacking. Under these conditions a parallel beam of white light shone on the eye gives a partially focused but broad distribution of yellow light on the receptor layers. Possibly the square sides of the cone participate in the partial focusing. The failure to see a sharp image was disconcerting, in view of the necessity for high resolution, until we discovered that the eye is not sensitive to *visible light.*

Spectral sensitivity

The spectral sensitivity was measured by recording the e.r.g. from the surface of the eye, with the indifferent electrode on the head between the dorsal eyes. At

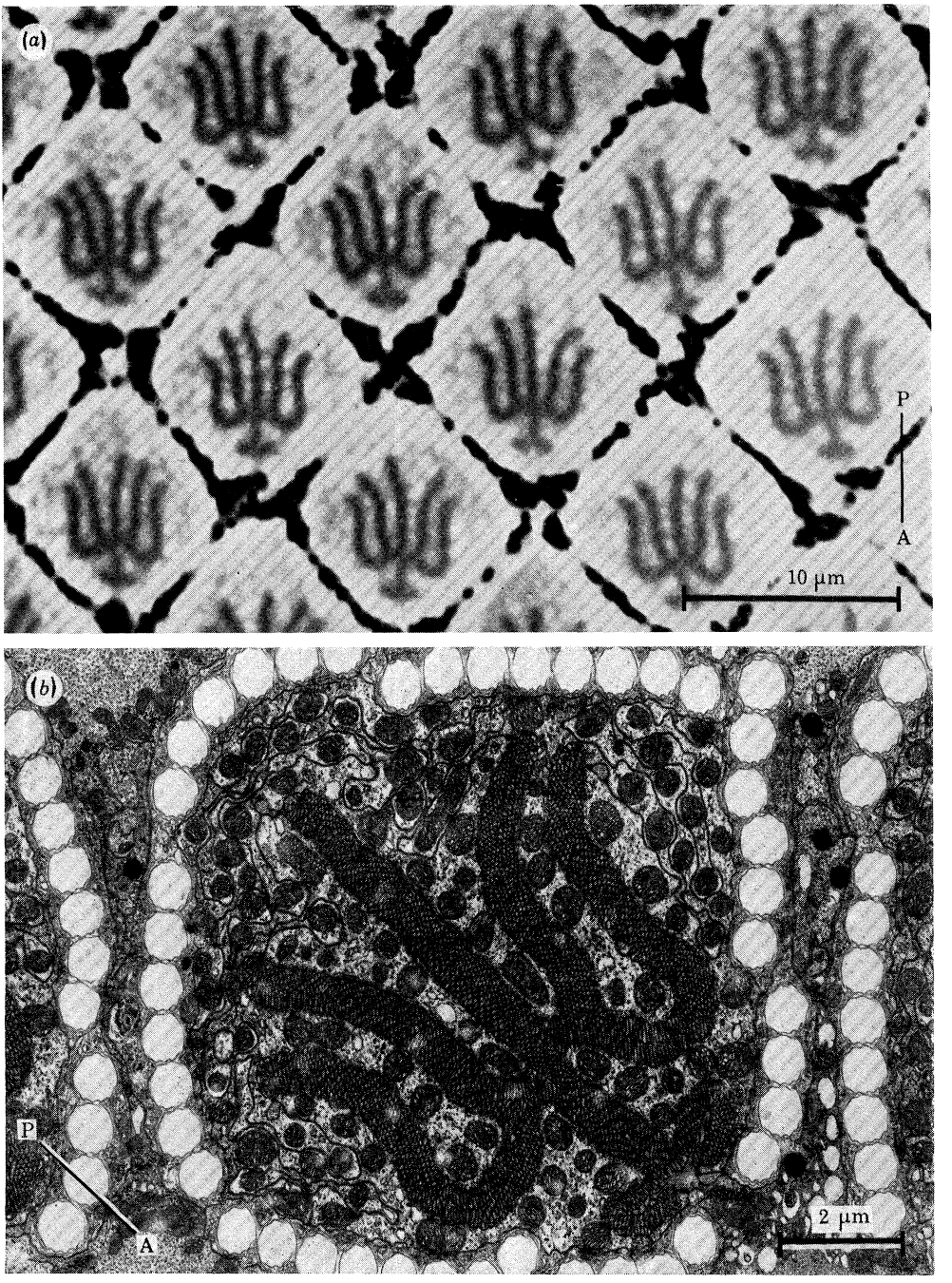

FIGURE 6. The central region of the rhabdom column (level (*k*), figure 2). (*a*) Light micrograph of a 1 μm section stained with toluidine blue. (*b*). Electron micrograph of one rhabdom surrounded by trachea. Note the numerous mitochondria the convoluted membranes between the retinula cells and the gap (bottom right) in the ring of trachea, where retinula cell 7 extends as shown in figure 9*a* and at level (*d*) in figure 7.

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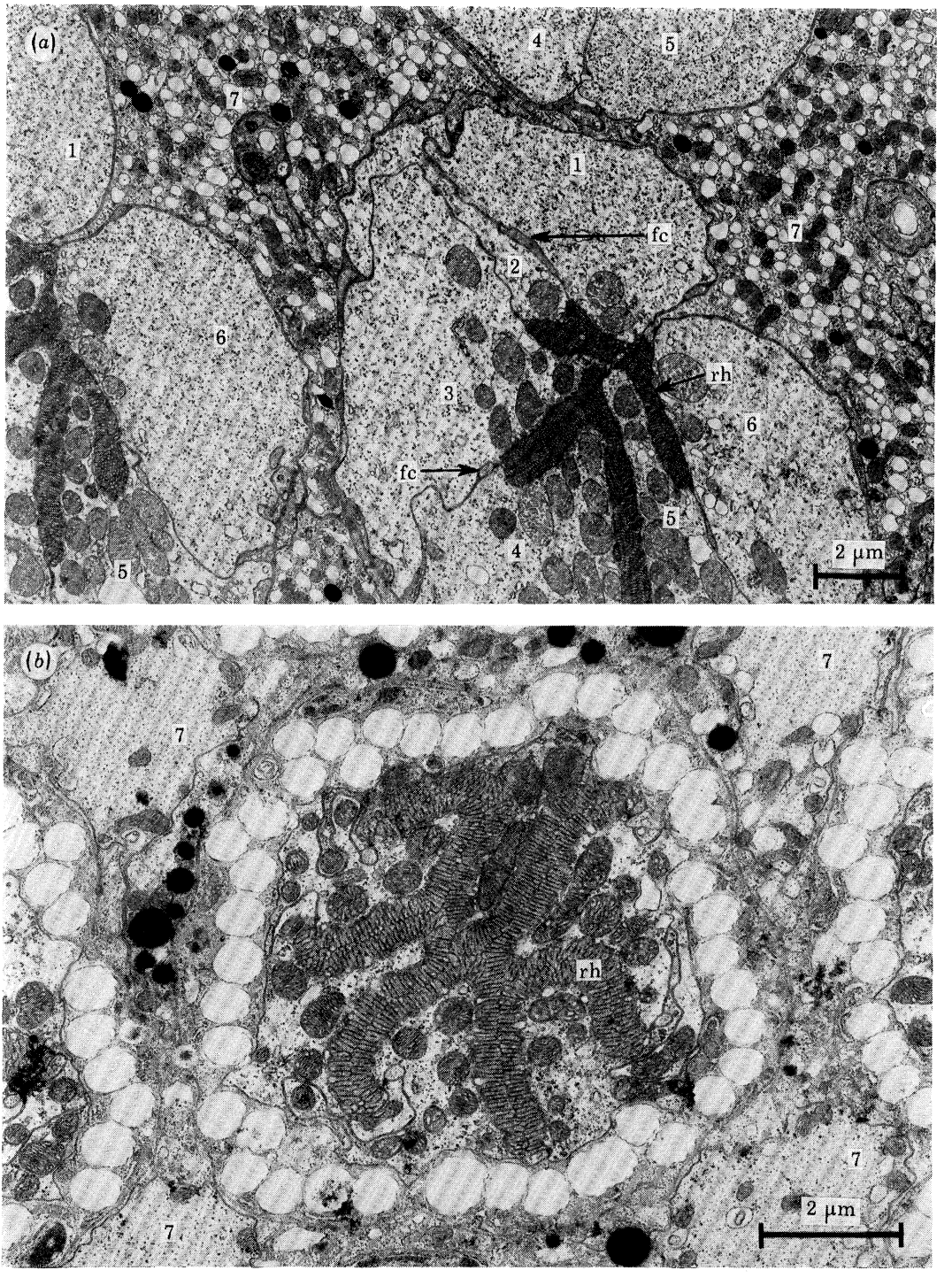

FIGURE 8. For description see opposite.

Description of plate 6

Figure 8. The rhabdom column at other levels. (*a*) Level (*j*) in figure 2, where retinula cell 7 is extensive and crowded with pigment grains, some of which are yellow in life. (*b*) Level (*e*) in figure 7, where the column is completely surrounded by a ring of trachea, and cell 7 forms a separate axon outside the ring.

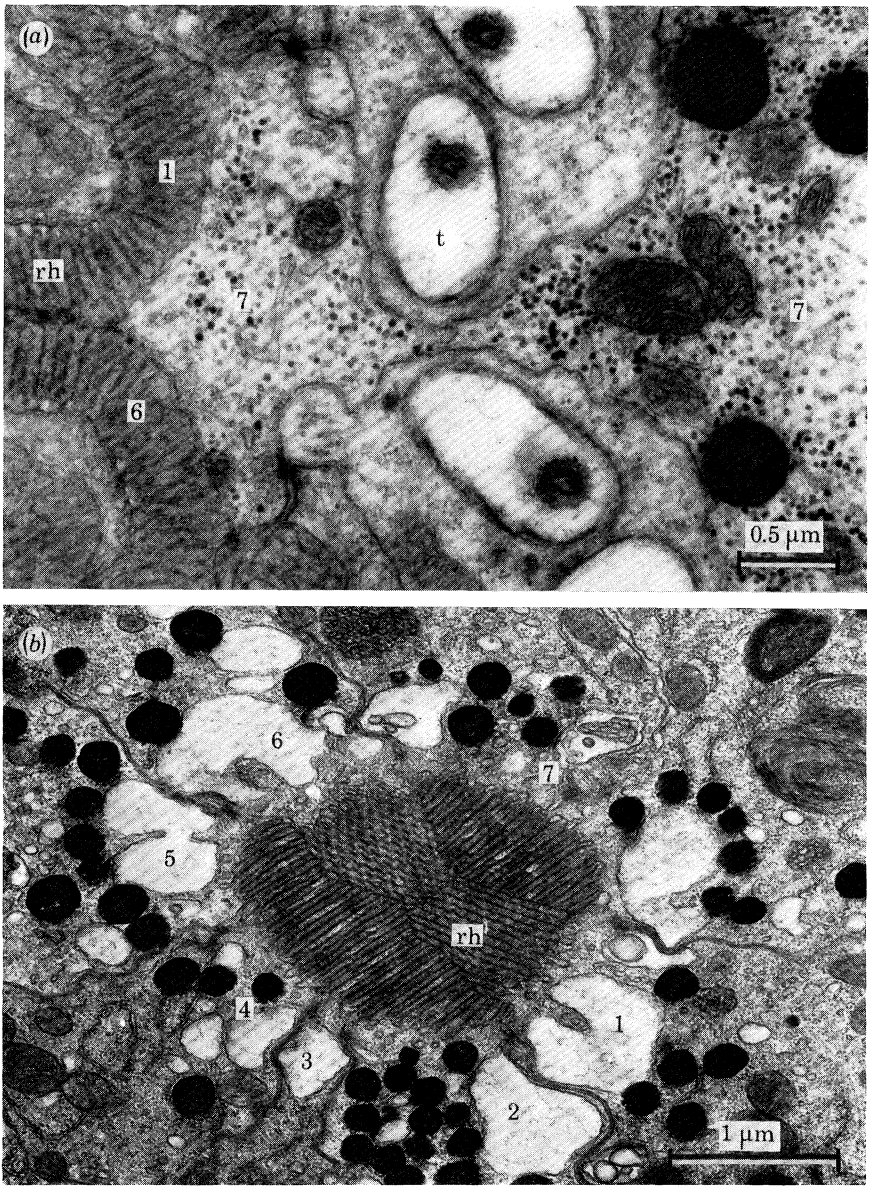

FIGURE 9. (*a*) Retinula cell 7 enters the ring of trachea by a narrow neck and presses up against the rhabdomeres of cells 1 and 6. This transverse section is from level (*c*) in figure 7. The transverse sections of contracted tracheal tubes within the trachea show that this is a subimago that has not completed its final moult. (*b*) Tranverse section of the rhabdom of the lateral eye of *Atalophlebia* A. All seven retinula cells contribute to the rhabdom, which is surrounded by a palisade of endoplasmic vacuoles, which in turn are surrounded by dense grains of screening pigment.

each wavelength, obtained by narrow band interference filters, a response was recorded over a wide range of intensities, obtained by neutral density filters. Care must be taken to exclude a response contribution from the lateral eye, which is sensitive to visible light. This is excluded more easily by covering it with black paint than by placement of the indifferent electrode. The sensitivity was then calculated

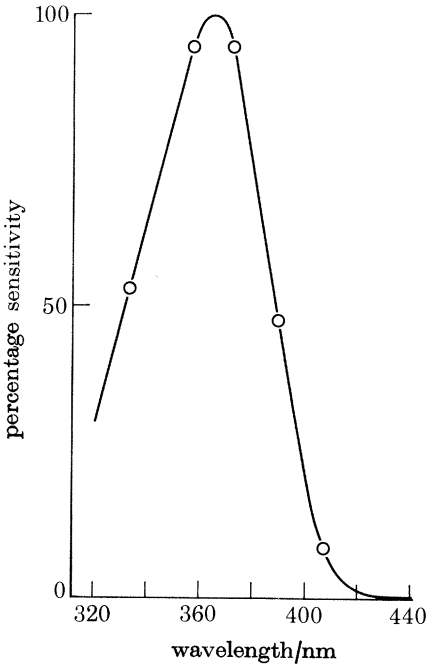

FIGURE 10. Spectral sensitivity of *Atalophlebia* C (points) compared with the theoretical curve for a rhodopsin with a peak at 365 nm (smooth curve).

at each wavelength from the known intensity of the light falling on the eye after passing each filter. Sensitivity is defined as the reciprocal of the number of photons required to give a small constant response. The measured points fit exactly on the theoretical curve for a rhodopsin with a peak at 360 nm (figure 10). The sensitivity at 410 nm is only 1 % of peak and therefore the eye has relatively little sensitivity in the wavelength range visible to man. The sensitivity, reduced by stimulation at maximum intensity for 10 s, is restored to normal by illumination by visible light, as described by Hamdorf, Paulsen & Schwemer (1973) for the owlfly *Ascalaphus* (Neuroptera). In figure 11 the spectral sensitivity is compared with the relative numbers of photons at different wavelengths that are emitted from the blue of the sky at various angles to the sun.

Differences between species

Atalophlebia A is the only species we found which has the candelabra-shaped rhabdom in transverse section (figure 6). This species is the one figured in this

paper. In *Atalophlebia* B and C the arms of the rhabdom are directed radially and the pattern in which retinula cell 7 wraps itself around neighbouring ommatidia is different (figure 12). Despite the different arrangement, the number 7 retinula cells of *Atalophlebia* B and C join to make a continuous layer between the rhabdom columns and the extracellular fluid of the clear zone. They also form a sheath around the distal parts of the rhabdom column, the significance of which is discussed below. We did not notice any other major differences between the species.

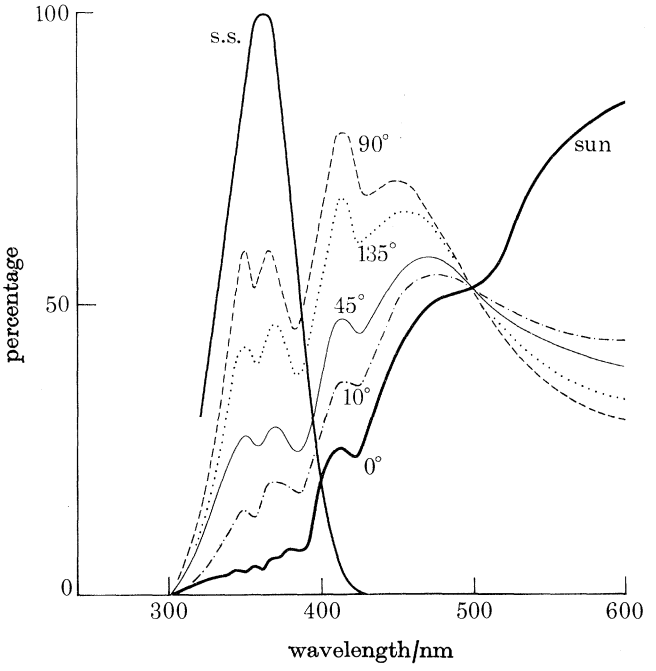

FIGURE 11. Relative numbers of photons at each wavelength in light from the blue of the sky at various angles to the sun. The curve marked 0° is of direct sunlight. The curves are brought to the same value at 500 nm. They are plotted from data given in energy units by Rosenberg (1966). The curve marked s.s. is the spectral sensitivity curve from figure 10.

DISCUSSION

Rhabdom shape, a generic character

We find a major difference in rhabdom form between species A in the *costalis* group on the one hand, and species B and C in the *australasica* group on the other. All three have been placed in the genus *Atalophlebia*. In other groups of insects the shape of the rhabdom is a character that differs between genera but not between species. When a systematic revision of *Atalophlebia* is made, additional reasons may be found to split the genus.

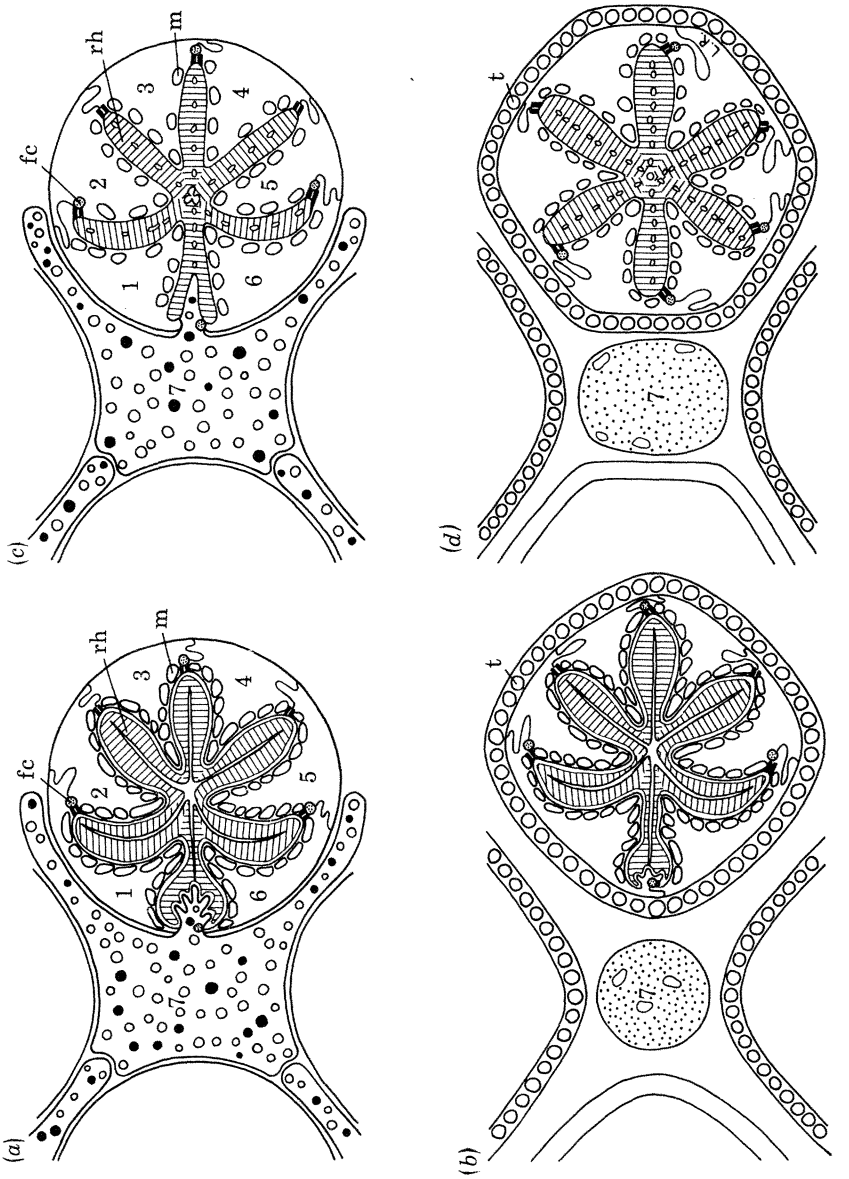

FIGURE 12. Transverse sections though the rhabdom column of other species. (*a*), (*b*) *Atalophlebia* B (*australasica* group). (*c*), (*d*) *Atalophlebia C* (*costalis* group). In (*a*) and (*c*) the level of the section corresponds to that in figure 9 *a* (between (*j*) and (*k*) in figure 2). In (*b*) and (*d*) the level corresponds to that in figure 8 *b* (between (*k*) and (*l*) in figure 2).

Yellow pigment around the cone tip

The bright yellow pigment densely arranged around the cone tip, combined with the sensitivity only to ultraviolet light, shows that the eye cannot have a superposition mechanism which operates by light freely crossing the clear zone. A yellow pigment also surrounds the distal end of the retinula cell column in the dorsal eye of the owlfly *Ascalaphus* (Schneider & Langer 1975), and again in that eye we find a sensitivity to u.v. light.

Refraction within the cone, as found in many superposition eyes, or reflection from the flat sides of a square cone, as recently found by Vogt (1975), requires that the cone tip is free from pigment. For this reason alone we are thrown back to the conclusion that rays parallel to the axis are focused on the end of a light guide. Following this line of thought, we see that reflection from the square sides of the cone may help to concentrate the yellow rays which filter past the pigment round the cone tip. The recovery of sensitivity caused by long wavelength light shows that the absorption peak of the metarhodopsin is on the long wavelength side of the peak for the rhodopsin, as it is for the u.v. rhodopsin of *Ascalaphus*, with a peak at 345 nm (Hamdorf *et al.* 1973). Therefore we appear to have found an eye which sees with a high resolution u.v. mechanism that depends on light guides but takes advantage of the visible light to keep the visual pigment in the rhodopsin state.

Why rely on ultraviolet vision?

The shorter wavelength of u.v. light allows greater resolution but this could apply only in an apposition eye. The complex optics of superposition eyes are too sensitive to small aberrations of the components to reach the fundamental limit set by wavelength. Relying on u.v. rays could improve resolution if a high-quality corneal lens is focused on a thin tip of a light guide. Then, given that receptor fields are small, to see a small object against a light background the feature of interest is the modulation of light in the receptor. In the case of a male mayfly seeing a female against the background of the sky, little can be done about the brightness of the female, which will appear black against the background. The contrast is increased by *matching the spectral sensitivity of the photoreceptors to the colour of the background.* For most animals, including insects, the most common backgrounds are green foliage and the blue of the sky, but this is not necessarily true of twilight insects.

The distribution of wavelengths in the twilight sky is increased in relative intensity in the ultraviolet at progressively greater angles to the sun, because the mean angle of scattering depends strongly upon wavelength (figure 11). When the sun is near the horizon there is more ultraviolet overhead, relative to the total, than there is near the sun (Rozenberg 1966). This pattern moves round with the sun but is more significant at and after sunset because the direct sunlight then disappears and with it the visible light scattered from objects on the ground. The ultraviolet, measured in photon numbers, not energy units, becomes a significant part of

the spectrum for animals which see objects against the twilight sky. Although in absolute terms there are few photons available in twilight, an insect living by mountain streams with an eye that is specialized to use u.v. may have a trick that defeats predators and competitors with normal eyes.

A comparable u.v. sensitivity has been found in the dorsal eye of the neuropteran *Ascalaphus* (Hamdorf *et al.* 1973). This insect catches insect prey against the background of the blue sky in bright daylight, when relatively more visible light is available.

The form of the rhabdom in cross section

At least three totally different types of explanation offer themselves for the unique and striking form of the rhabdom in cross section, as a mechanical, optical or electrogenic structure. As a mechnical explanation, the special form of the rhabdom allows mitochondria of the cytoplasm to mingle closely with the microvilli, and axoplasm to flow from the distal cell body past the rhabdomeres to the axon terminal in the lamina; also the complex angle girder which is so formed can contribute mechanical rigidity.

An optical explanation, proposed previously (Horridge 1975*a*), is that the deep grooves between the rhabdomeres provide a trap for visible light entering from above and behind the eye. Significantly, the arms of the rhabdom are plates 1 μm thick so that each might act partially independently as a light guide, but at present we have no optical theory to guide us in this interpretation.

A more likely explanation is that the rhabdomeres are so shaped and constantly orientated that they channel the extracellular currents into the seventh cell. The general form of the insect retina, with electrogenic columns at right angles to the basement membrane, is readily interpreted as a structure which channels current *vertically* in the retina and along the retinula axons, which transmit excitation by electrotonic spread. The relatively large axon of retinula cell 7, and its extension without a rhabdomere into the throat of the rhabdom, suggests that it collects current from all six rhabdomeres and conducts it through the basement membrane directly to the medulla. This interpretation is strengthened by the fact that the star-shaped or candelabra-shaped rhabdom has only one lateral outlet, at the seventh cell. In addition there may be lateral interactions, for example between the pairs of ommatidia that are sheathed by one cell 7, but it appears more likely that the lateral opening of the rhabdom into an abnormally large axon that runs direct to the medulla is a way of concentrating the light-induced current for maximum effect at a distance. As the structures are quite unique, direct physiological tests will no doubt be made.

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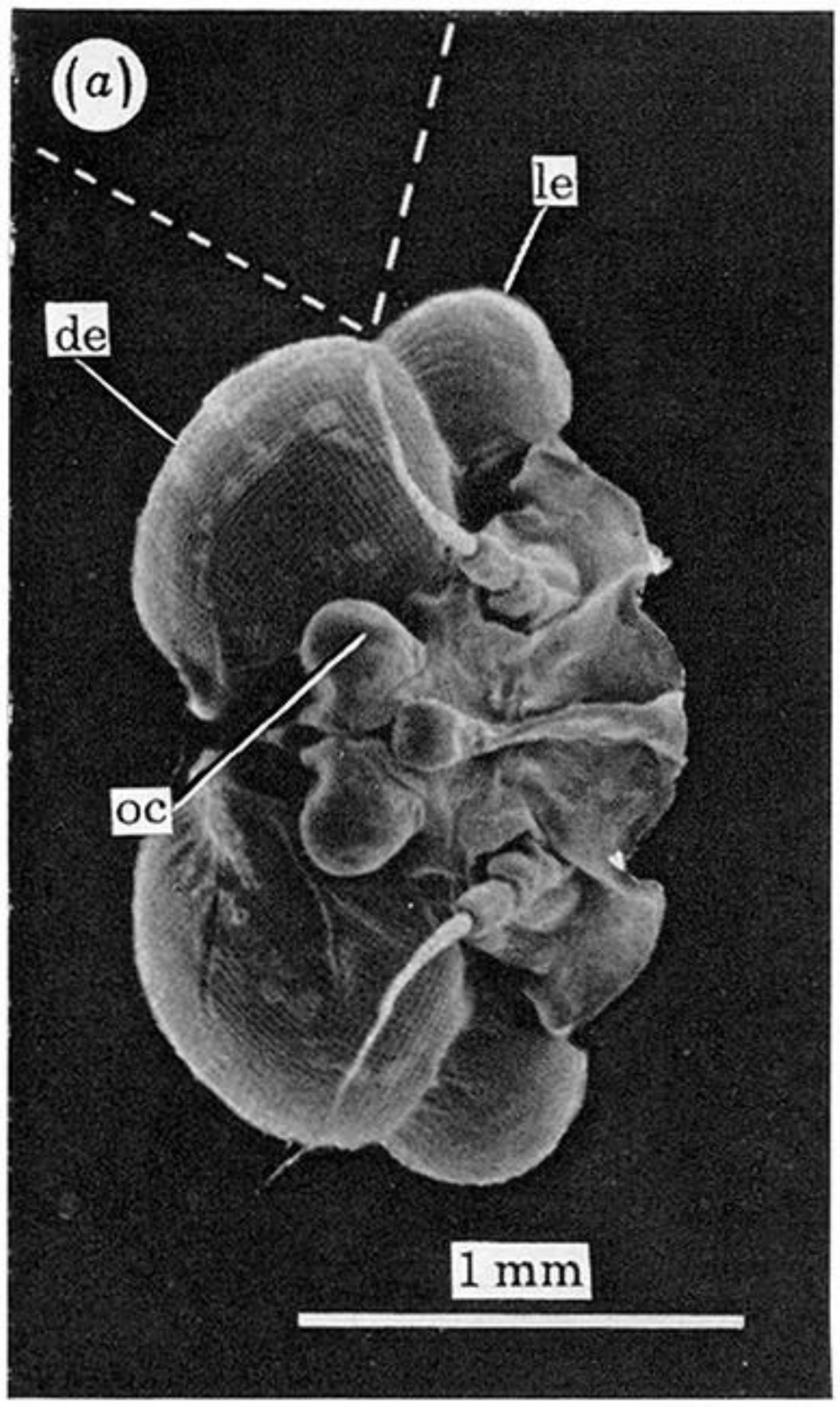
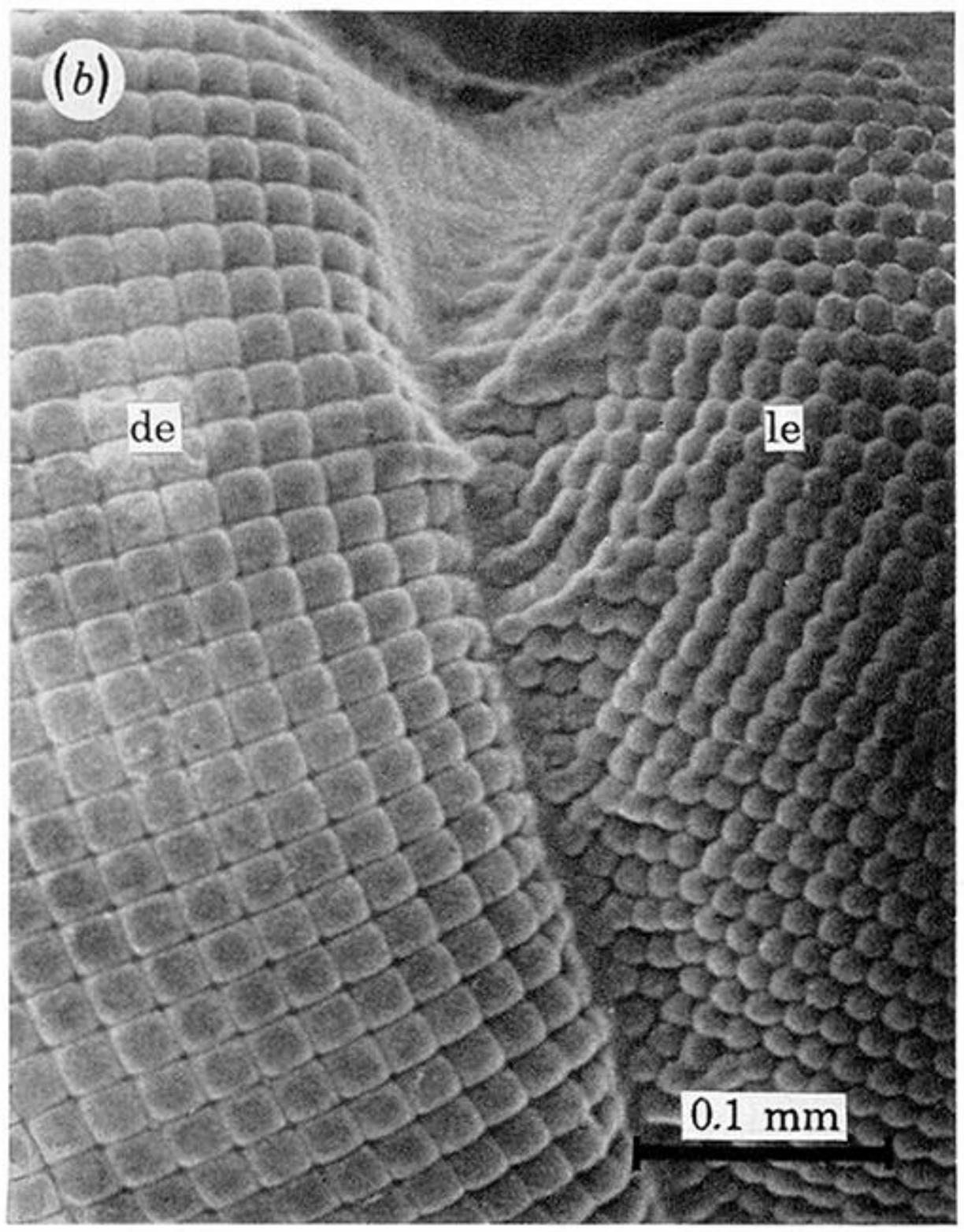
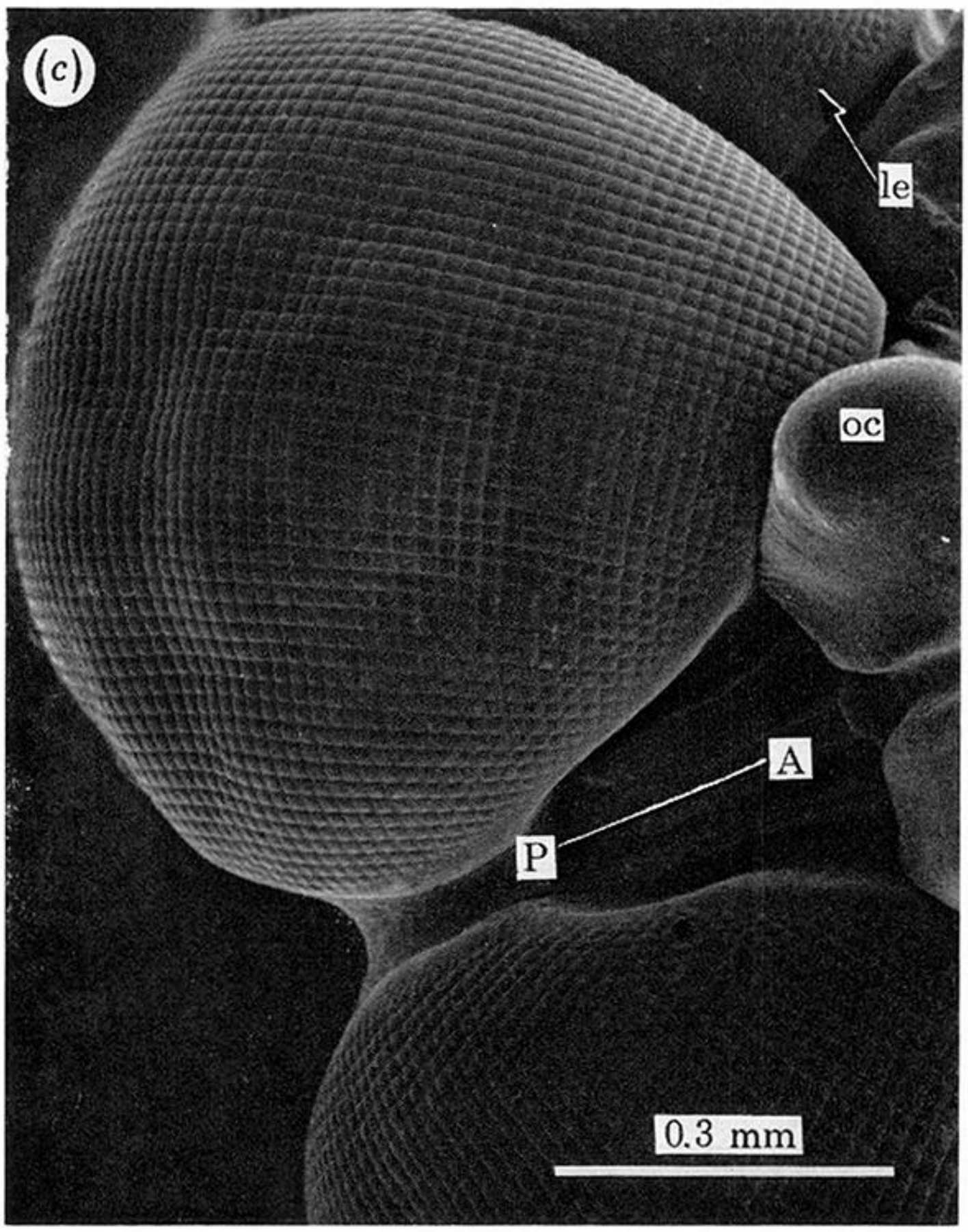
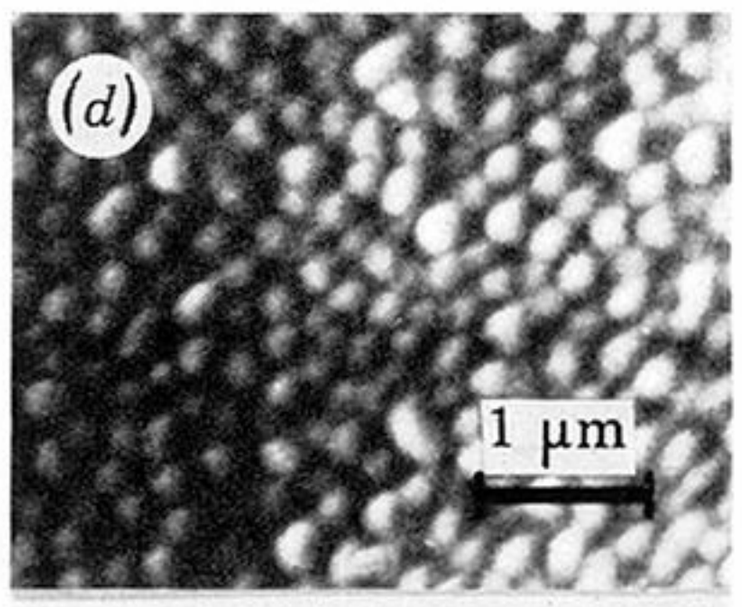
Explanation of abbreviations used on figures

A	anterior	P	posterior
a,b,c,	types of accessory pigment cells	pb	pigment bag
apc	accessory pigment cell	ppc	principal pigment cell
c	cornea	ppcn	principal pigment cell nucleus
cc	crystalline cone	ncc	neck of the cone cells
ccn	cone cell nucleus	rc	retinula cell
ecs	extracellular space	rcn	retinula cell nucleus
de	dorsal eye	rh	rhabdom
fc	filament of the cone	scz	subcorneal zone (ppc)
le	lateral eye	t	trachea
oc	ocellus	tc	tracheal cell









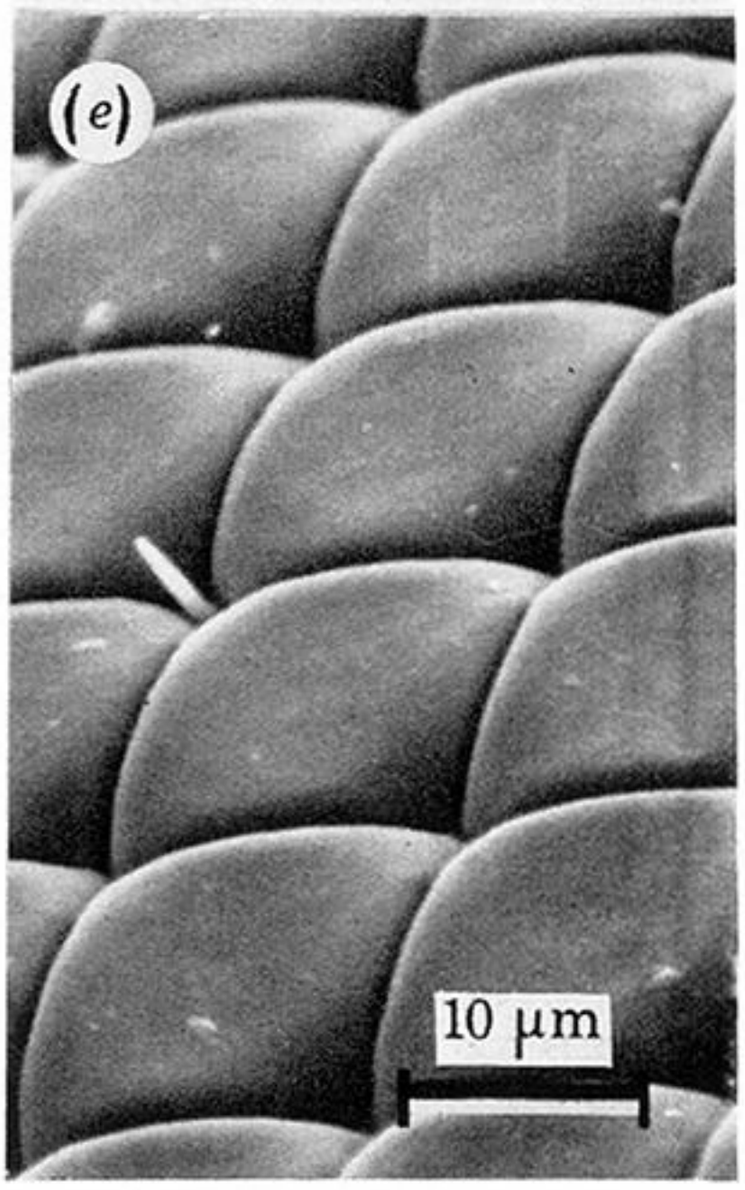


FIGURE 1. Scanning electron micrographs of the head and details of the eye surface. (a) Front view of the head showing dorsal and lateral eyes (de and le) and the prominent ocelli (oc). The dashed lines include the angle of the visual field that is seen by both lateral and dorsal eye on one side. (*b*) Detail of (*a*) where the square facets of the dorsal eye (left) meet the hexagonal facets of the lateral eye. (*c*) Facet lines of the dorsal eye. (*d*) Corneal nipples on the surface of a facet. (*e*) Dorsal eye facets including a small hair.

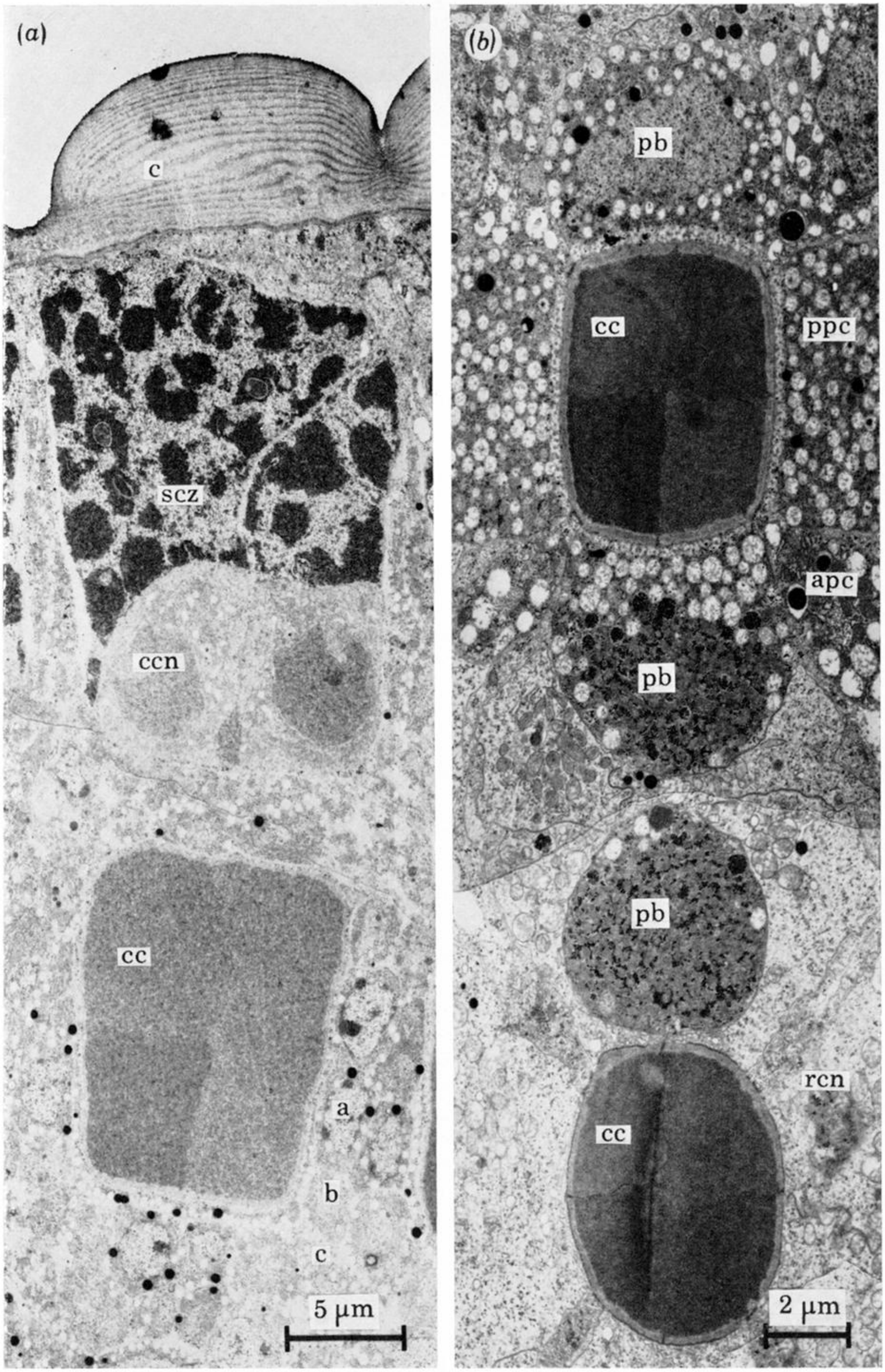
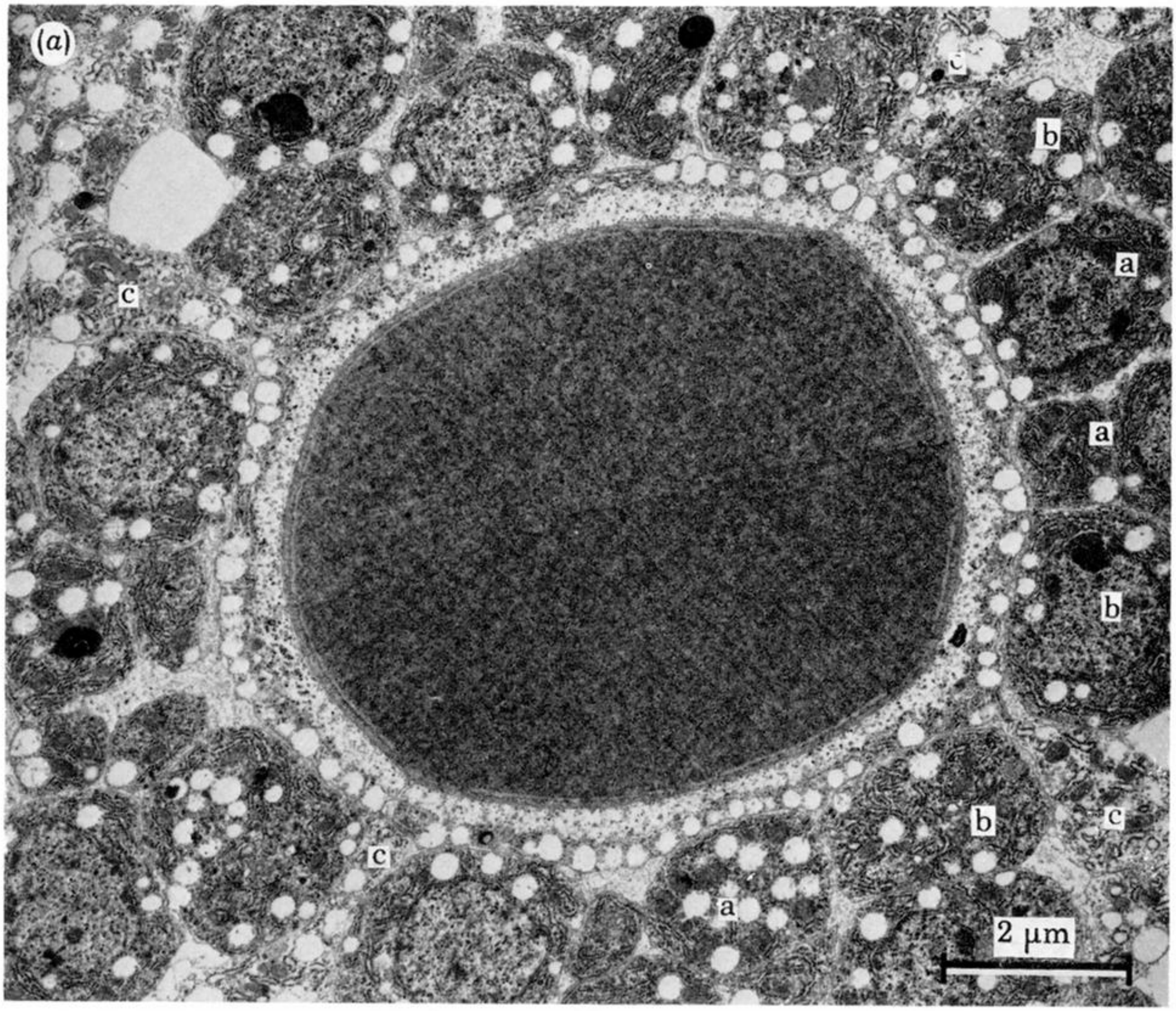


FIGURE 3. An oblique section through four ommatidia, starting at the cornea at top left of (*a*) and ending at the proximal end of the pigment bags at bottom right of (*b*). In the first ommatidium we see the subcorneal zone and the nuclei of the cone cells. In the second the square cone is surrounded by pigment cells that contain little pigment. In the third (top right) the cells surrounding the cone are densely filled by inclusions of several types. In the fourth the cone is round and one of the four bags of pigment (pb) stands out at this level.



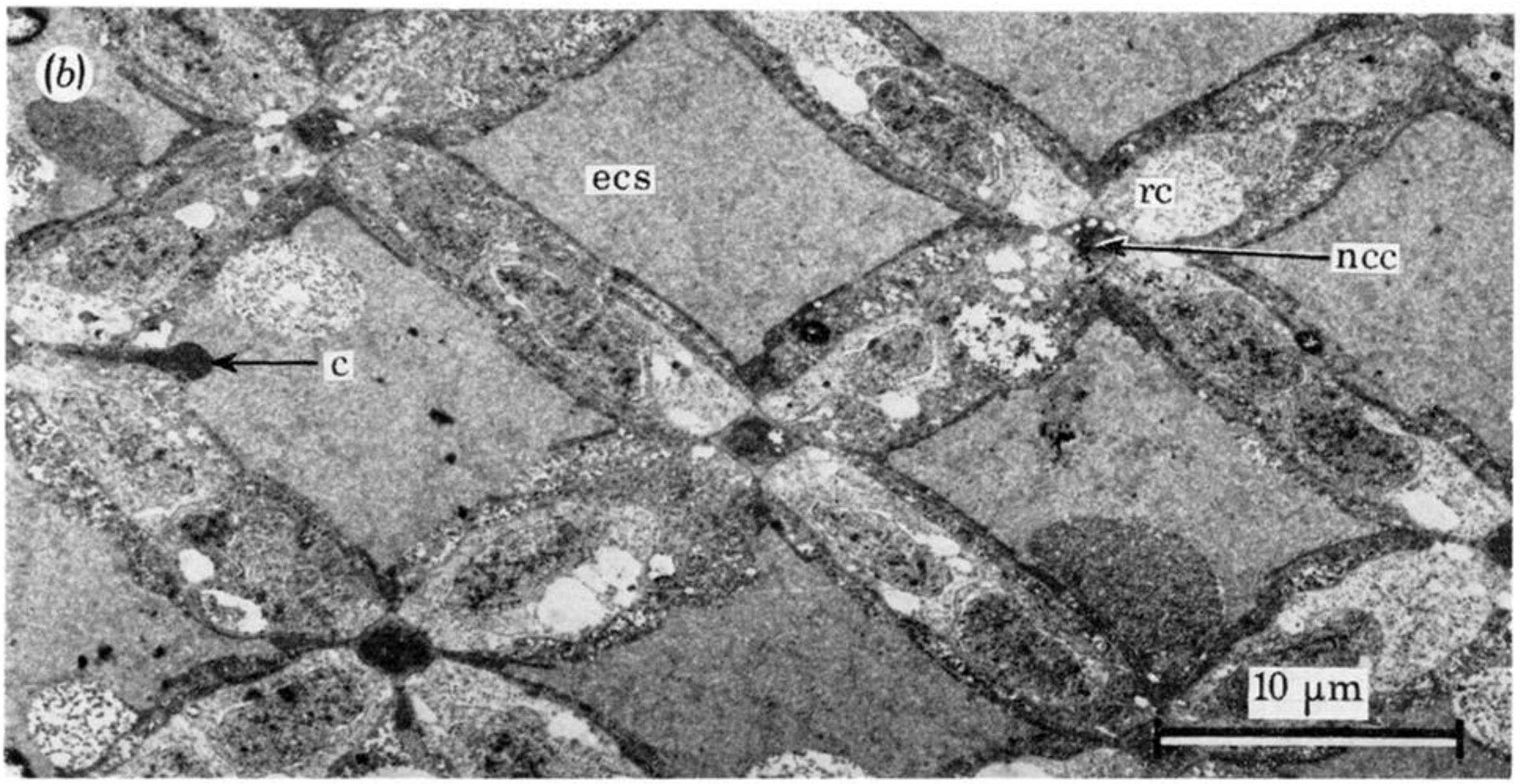
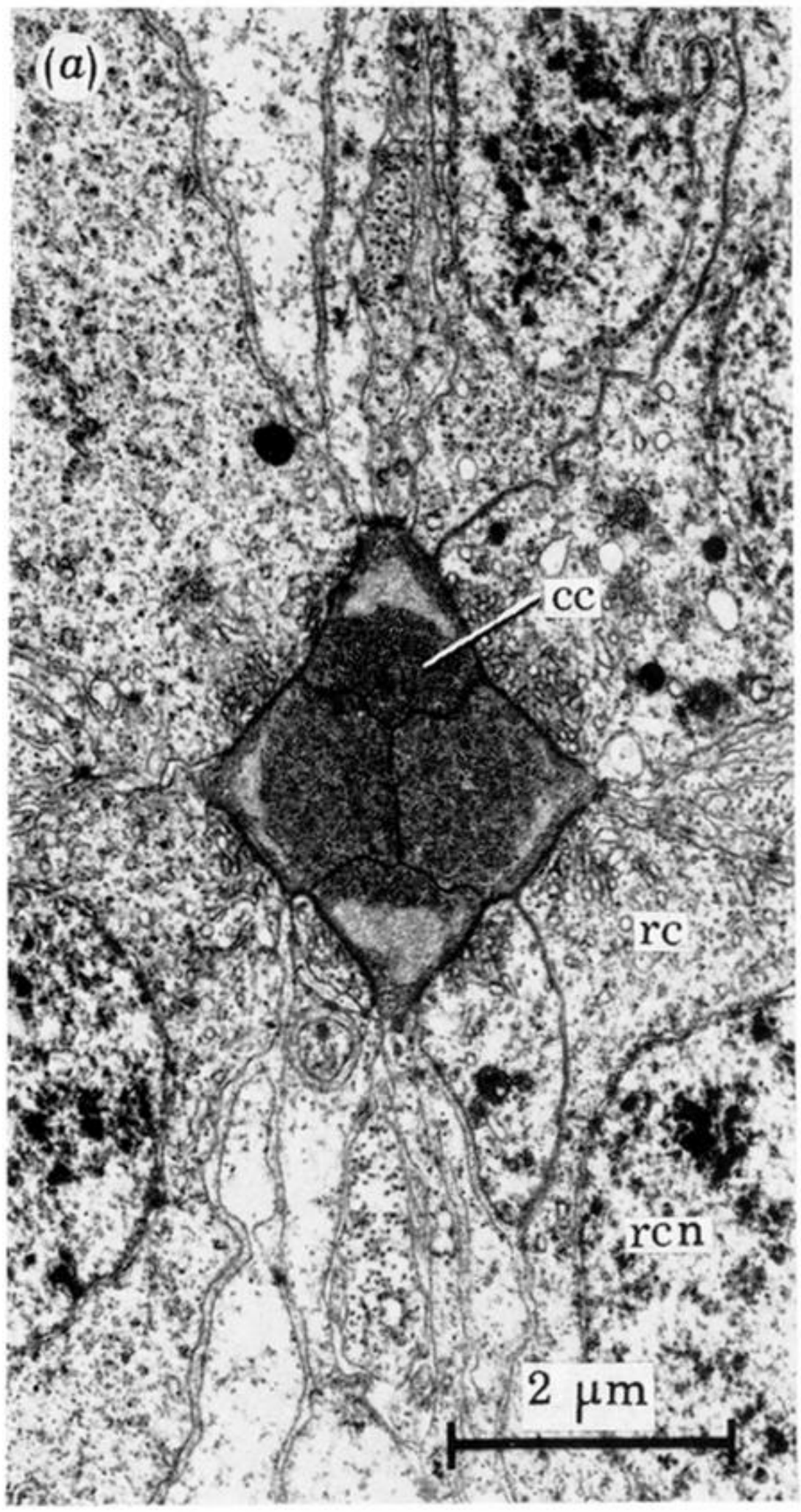
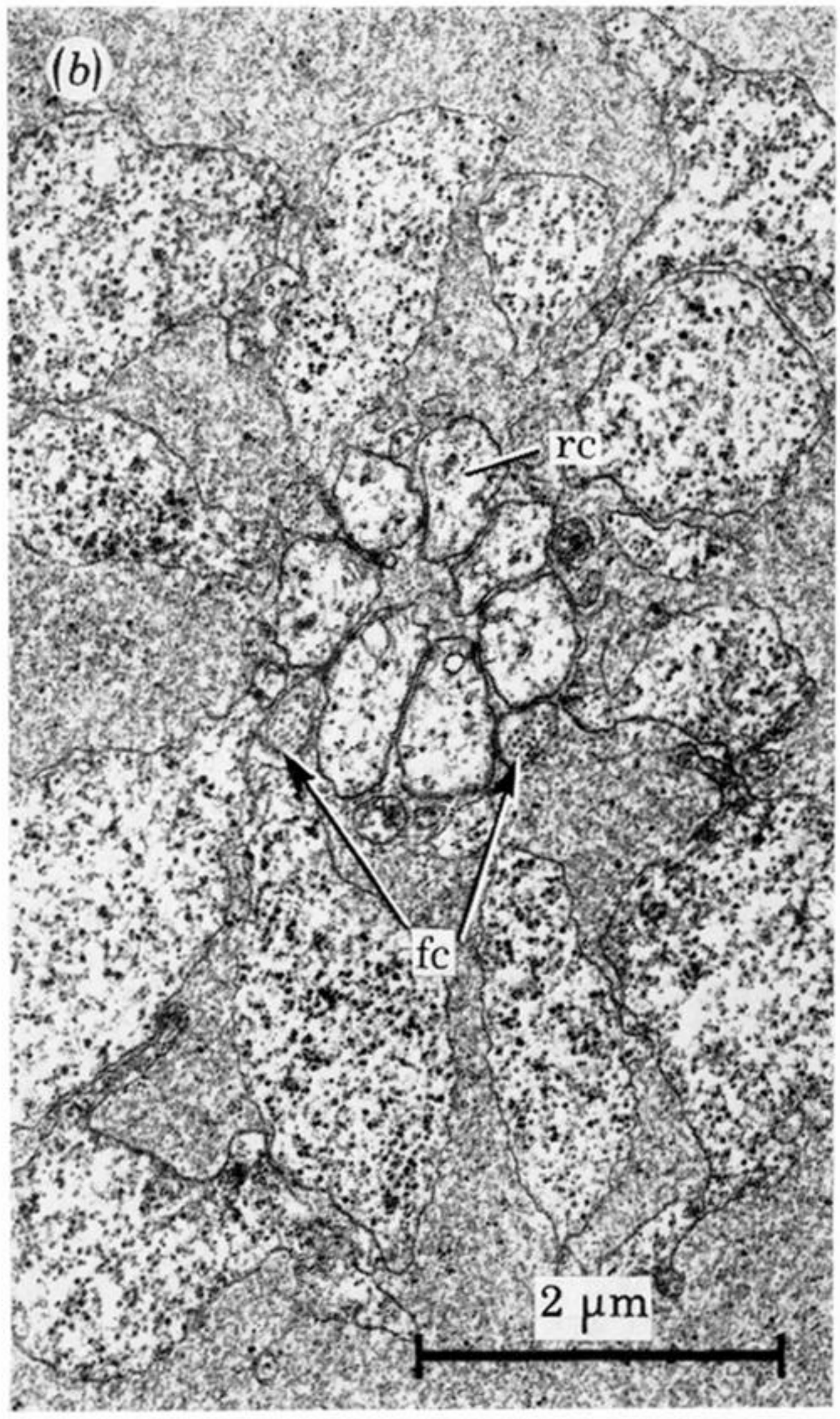


FIGURE 4. The accessory pigment cells at two levels. (*a*) The twenty cells around the cone near the level shown in figure 2*c*. The empty vesicles are believed to be the site of the yellow pigment. The cone in this region is homogeneous under both the light microscope and the electron microscope. (*b*) Transverse section at level (*g*) in figure 2, showing the penetration of the extracellular space of the clear zone into the lattice formed by the several types of accessory cells and retinula cells.





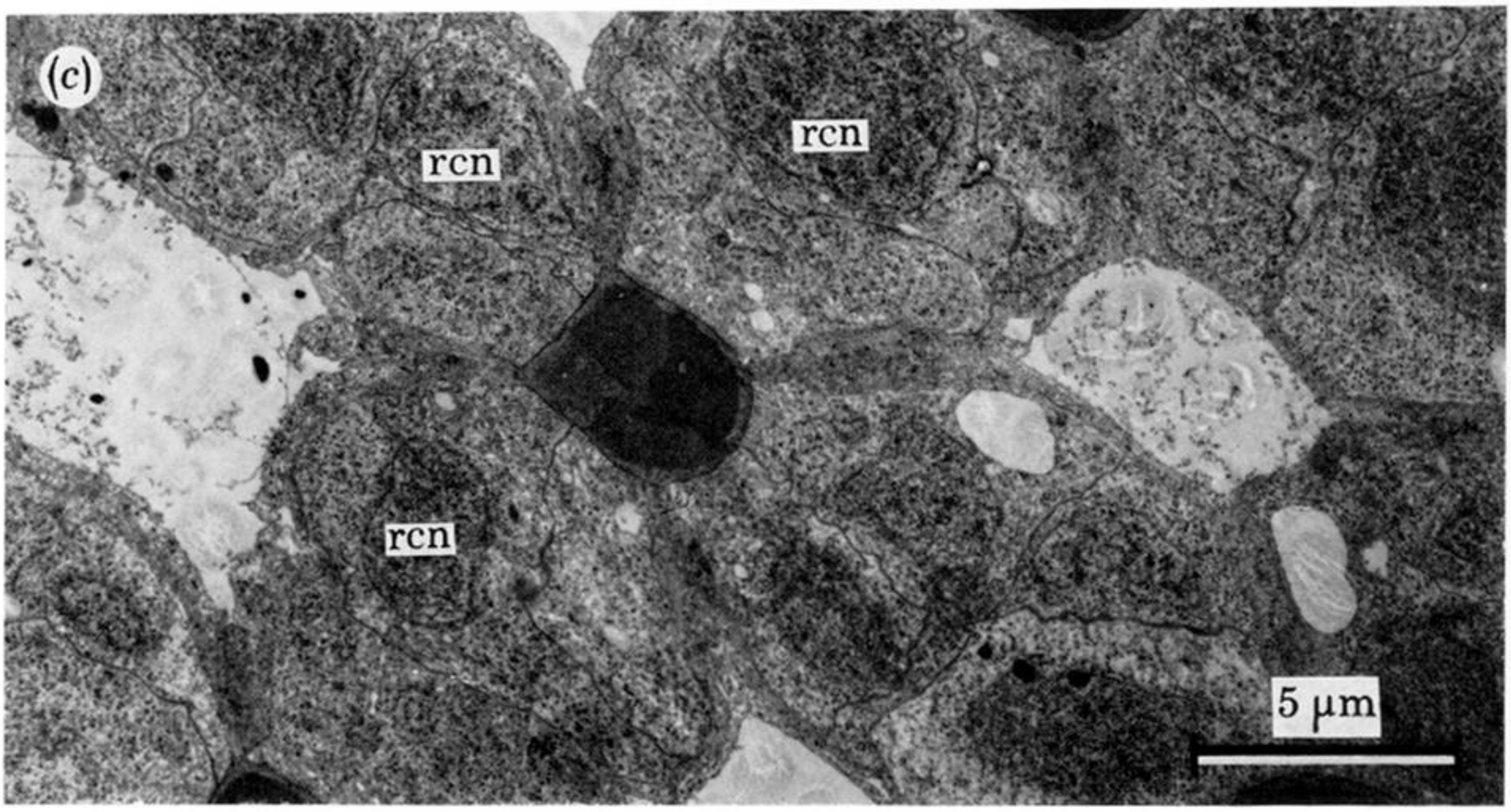
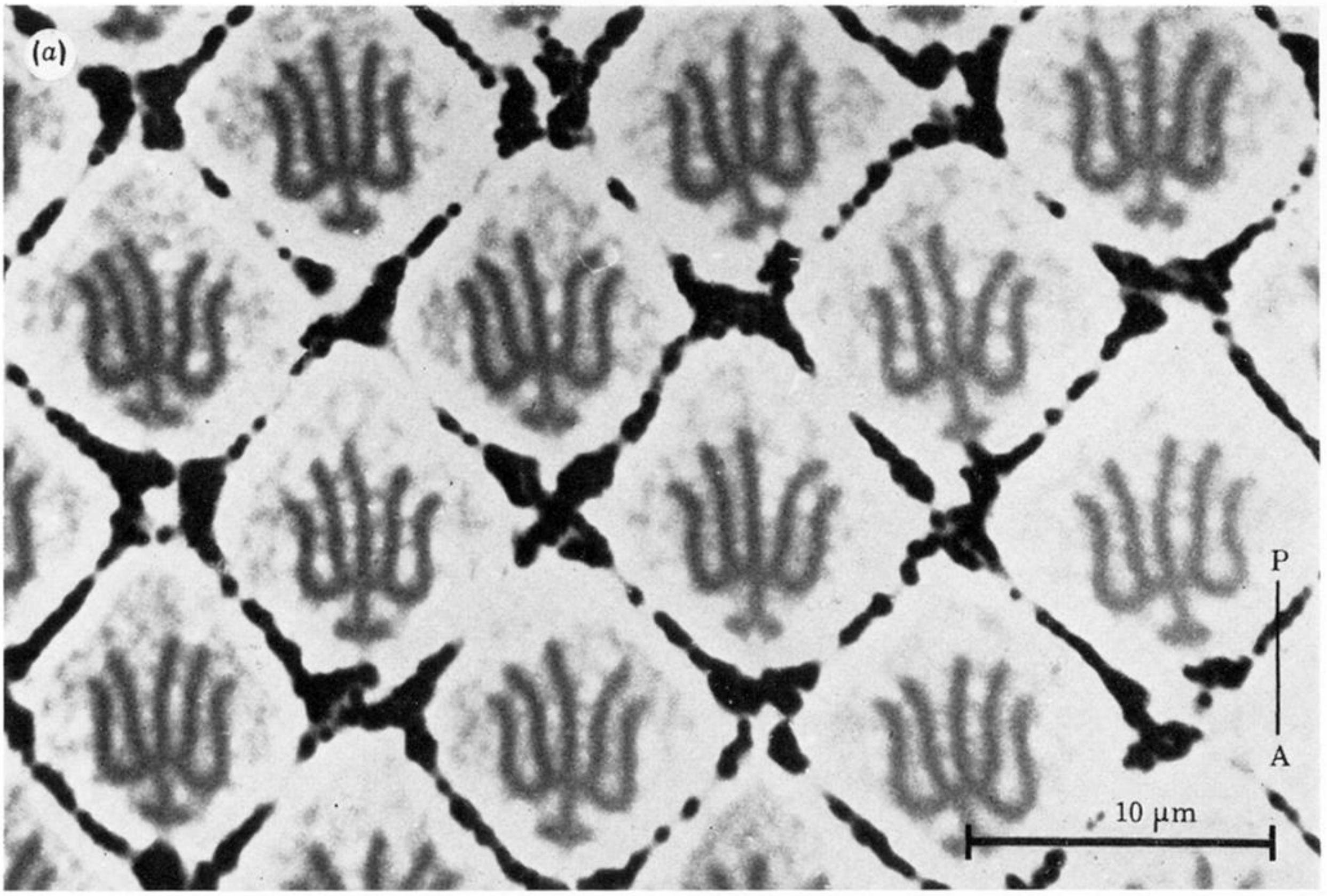


FIGURE 5. Regions of the proposed light guide. (*a*) Transverse section at the narrow part of the crystalline cone, where the accessory pigment cells change their positions between levels (*f*) and (*g*) in figure 2. Note the density and small diameter of the central region of the cone at this level. (*b*) The seven components of the retinula cell column in transverse section at level (*h*) in figure 2. (*c*) Retinula cell bodies 1–6 around the cone near level (*f*) in figure 2.



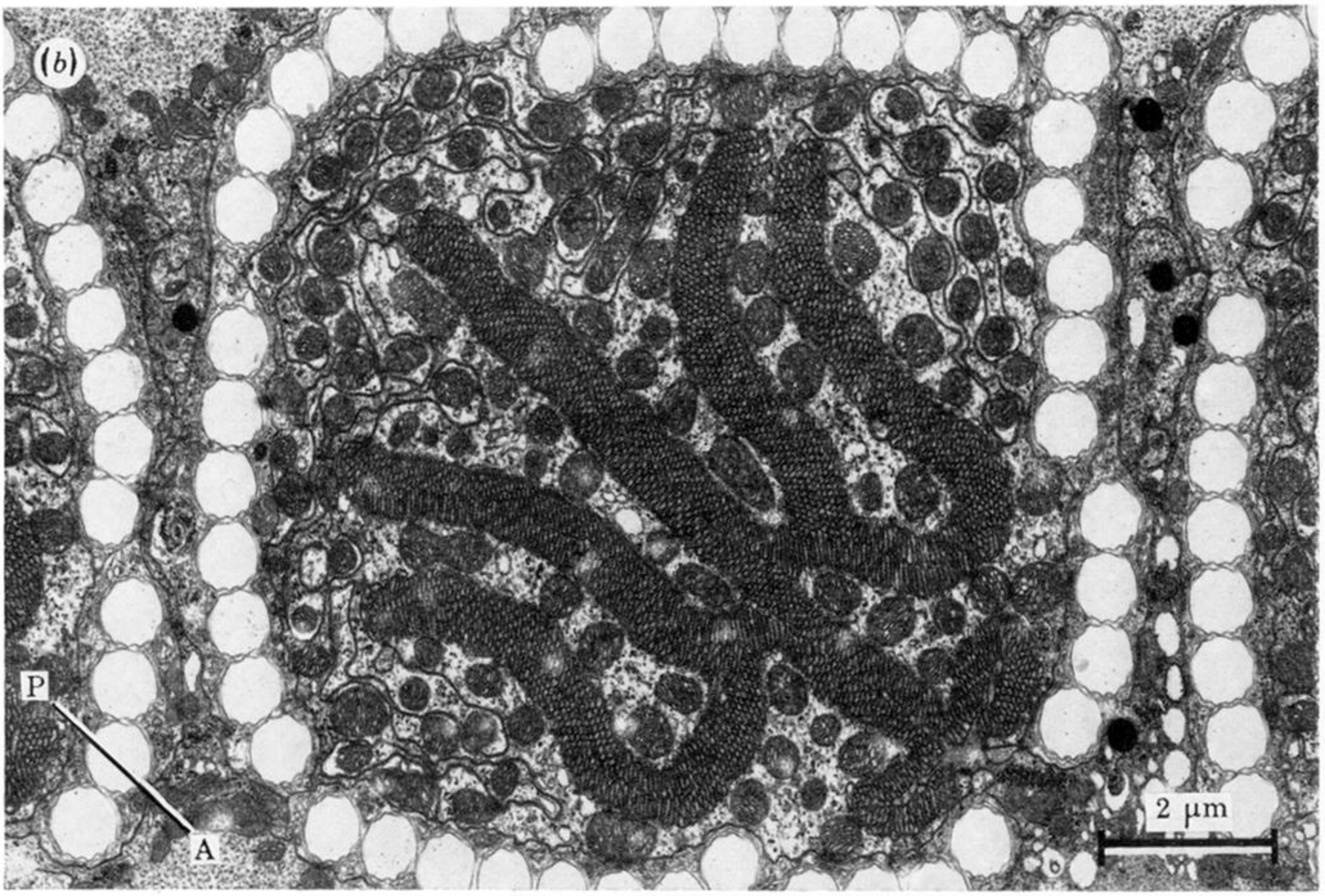


FIGURE 6. The central region of the rhabdom column (level (*k*), figure 2). (*a*) Light micrograph of a 1 μm section stained with toluidine blue. (*b*). Electron micrograph of one rhabdom surrounded by trachea. Note the numerous mitochondria the convoluted membranes between the retinula cells and the gap (bottom right) in the ring of trachea, where retinula cell 7 extends as shown in figure 9*a* and at level (*d*) in figure 7.

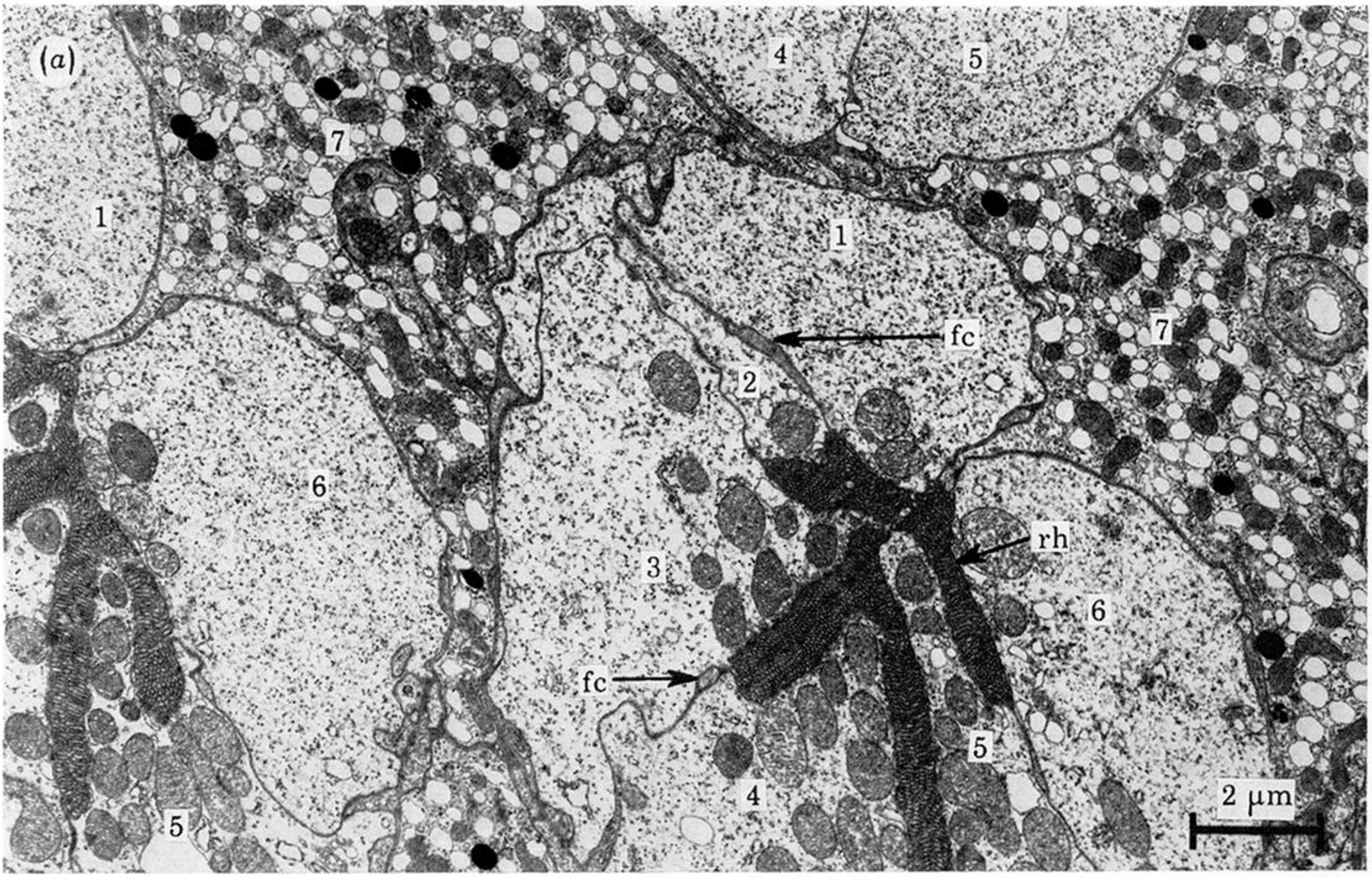


FIGURE 8. For description see opposite.

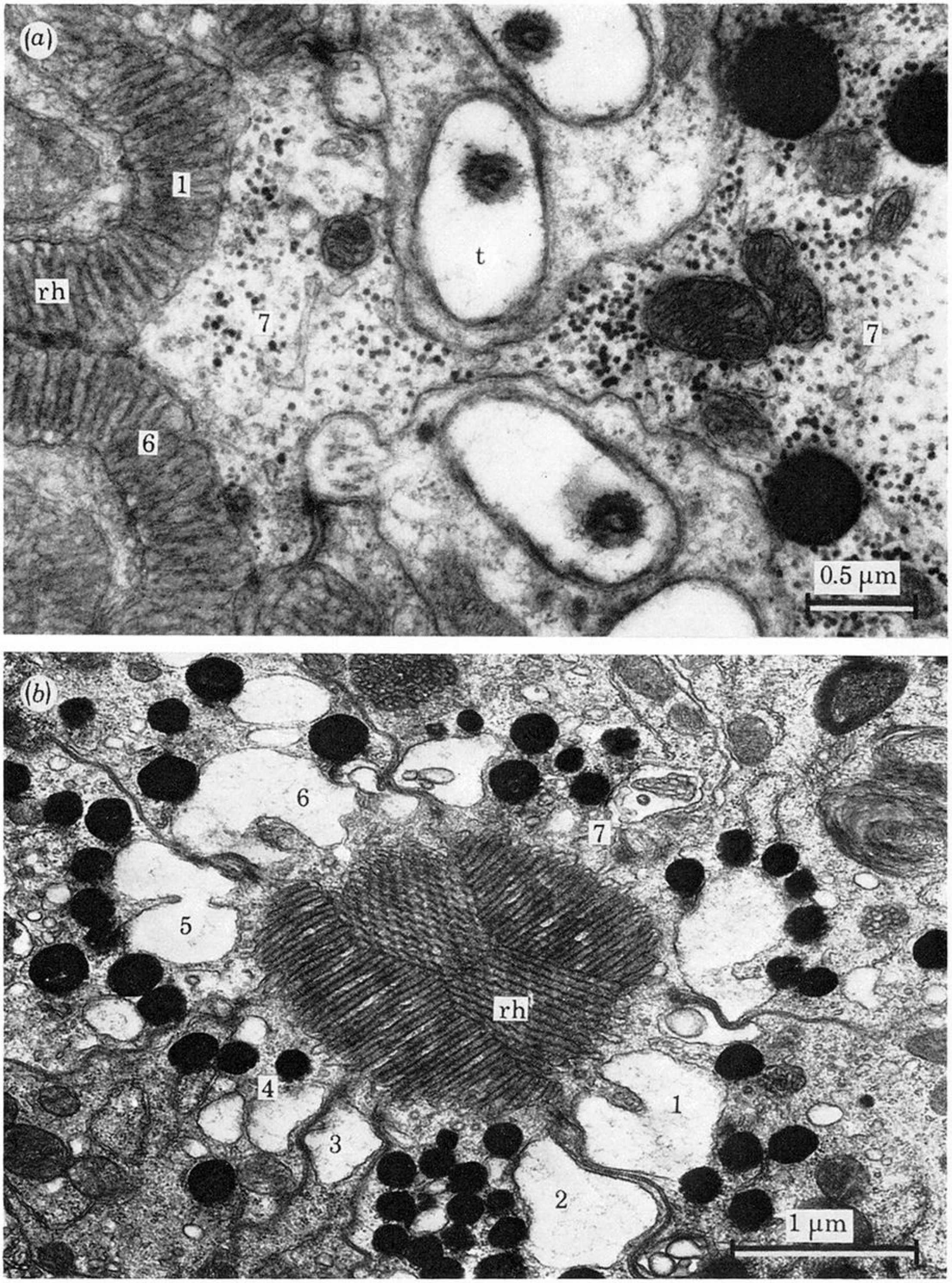


FIGURE 9. (*a*) Retinula cell 7 enters the ring of trachea by a narrow neck and presses up against the rhabdomeres of cells 1 and 6. This transverse section is from level (*c*) in figure 7. The transverse sections of contracted tracheal tubes within the trachea show that this is a subimago that has not completed its final moult. (*b*) Tranverse section of the rhabdom of the lateral eye of *Atalophlebia* A. All seven retinula cells contribute to the rhabdom, which is surrounded by a palisade of endoplasmic vacuoles, which in turn are surrounded by dense grains of screening pigment.