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FINE STRUCTURAL ASPECTS OF THE DEVELOPING EYE
OF THE HONEY BEE

by
Judith Susan Eisen

A thesis submitted in partial fulfillment
of the requirements for the degree

of
MASTER OF SCIENCE

in
Biology

Approved:

Major Professor

Committee Member

Committee Member

Dean of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

1977

ACKNOWLEDGMENTS

My sincerest thanks go to Dr. Nabil N. Youssef, my major professor, who suggested my thesis problem and gave guidance and counsel throughout the entire investigation.

For further encouragement and advice during the course of my study, I would also like to extend my appreciation to Drs. Raymond T. Sanders, Hugh P. Stanley and William A. Brindley.

This investigation could not have been carried out without certain basic materials and equipment. Mr. William Nye was extremely generous in supplying me with bee brood. Mr. John Chidester did outstanding work in maintaining and repairing the necessary equipment.

Finally, I give my deepest love to Nabil and Judy Youssef and Chuck Harris, whose friendship and concern made the entire enterprise enjoyable.

Judith S. Eisen

This work is dedicated to the memory of the late Robert H. Whittaker.

I would like to acknowledge the honey bee, without whom all of this would not have been necessary.



This work is dedicated in loving memory to Nathaniel Herman Eisen.

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ABSTRACT

Fine Structural Aspects of the Developing Eye
of the Honey Bee

by

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Utah State University, 1977

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Department: Biology

The post-embryonic development of the compound eye of the worker honey bee was investigated with the light and electron microscopes. The cells of the optic primordium were reorganized into preommatidial cell clusters during the late third and early fourth larval instars. Each cluster contained nine prospective retinula cells, the ninth was centrally located and shorter than the other eight; four prospective cone cells; and an undetermined number of prospective pigment cells.

Rhabdomere development began in the eight peripherally located retinula cells just prior to pupation. Following pupation, each ommatidium elongated. During ommatidial elongation, the short ninth retinula cell moved from its central location to a peripheral location within the ommatidium and also developed a rhabdomere. The shape of each prospective crystalline cone also changed from teardrop-shaped to spherical to the typical cone shape of the adult during differentiation.

The involvement of junctional specializations of membranes and of microtubules in the processes of differentiation, including elongation, cellular migration, and cellular organization, have been raised. Also, the role of multivesicular bodies in the process of lens formation has been discussed.

(84 pages)

INTRODUCTION

The numerous morphological investigations on the compound eye of the adult honey bee have provided an excellent description of the spatial relationships between the different cell types forming the compound eye, but have failed to provide any description of the temporal relationships between these cells during post-embryonic development. Developmental studies on holometabolous insects (Phillips, 1905; Wolsky, 1949, 1955-56; Waddington and Perry, 1961; White, 1961, 1963; Perry, 1968; Ready et al., 1976) suggest that during the time between the appearance of primordial eye tissue and the emergence of an adult with a fully developed compound eye, there are remarkable changes not only within each cell but also in the relationships between cells of the optic region.

In the present study, the morphogenetic events during the post-embryonic development of the compound eye of the worker honey bee have been observed by means of the transmission electron microscope. An effort has been made to provide a precise description of each of the four cell types composing the compound eye and the relationships between them from the late third larval instar through the end of the pupal period.

LITERATURE REVIEW

In his extensive light microscopic investigation on the development and morphology of the compound eye of the worker honey bee, Phillips (1905) indicated that the eye consisted of several thousand ommatidia. Each ommatidium was composed of eight or rarely nine retinula cells surrounding a rhabdom, four cone cells, two corneal pigment cells, about 12 outer pigment cells, and covered by a corneal lens facet. He considered the rhabdom to be an intracellular secretion of the retinula cells, the crystalline cone to be an intracellular secretion of the cone cells, and the lens to be an extracellular secretion of the corneal pigment cells, possibly in conjunction with the outer pigment cells. He also stated that the only cells of the compound eye to receive innervation were the retinula cells. They were innervated by small fibrils which extended into the rhabdom from fibers located in the cytoplasm just peripheral to the rhabdom. He considered these fibers to be actual differentiations of the retinula cell cytoplasm which extended proximally from the retinula cells towards the supraesophageal ganglion.

No apparent elaboration on the morphology of the compound eye of the honey bee was reported in the literature until that of Goldsmith (1962). He investigated the morphology of the retinula of the adult honey bee worker adult eye at the level of the electron

microscope. He described the rhabdom as composed of numerous, closely-packed arrays of microvilli which originated from the cell membranes of the eight retinula cells. These microvilli were perpendicular to the long axis of the rhabdom, and each rhabdom was composed of four parts, one part from each of two adjacent cells. The microvilli in adjacent quadrants were mutually perpendicular. He also described a central region of the cytoplasm, just peripheral to the rhabdom, which contained membranous endoplasmic reticulum in an approximately radial orientation with respect to the axis of the ommatidium, and a more peripheral region which contained numerous mitochondria. Contrary to Phillips (1905), Goldsmith (1962) found each retinula cell to be innervated by an axon which arose from the proximal portion of the cell and pierced the basement membrane underlying the optic region, extending proximally towards the optic lobe of the supraesophageal ganglion.

Varela and Porter (1969), Skrzypek and Skrzypek (1971) and Gribakin (1967a, 1967b) also considered each retinula to be composed of only eight retinula cells. However, it was Perrelet (1970) who first suggested that the retinula of the worker was consistently composed of nine retinula cells, one of which was shorter than the other eight, and which Perrelet designated as the basal retinula cell. Subsequently, Skrzypek and Skrzypek (1974), Schinz (1975), Ribi (1975a, 1975b), Sommer and Wehner (1975), Wehner et al. (1975), Wehner (1976), and Gribakin (1975) have all recognized that each retinula is composed of eight long retinula cells and one short, basal retinula cell.

Fyg (1961) investigated the development of the honey bee crystalline cone at the light microscopic level and concluded that it arose as an intracellular accumulation of glycogen and protoplasmic ground substance during elongation and differentiation of the four cone cells. He also indicated that the cone cell nuclei were displaced to the distal cell borders. Electron microscopic investigations of the adult eucone by both Varela and Porter (1969) and Skrzypek and Skrzypek (1971) have further indicated that other cell organelles, such as mitochondria, were displaced peripherally and that the portion of the cone not occupied by organelles contained a granular-appearing substance.

Varela and Porter (1969) and Skrzypek and Skrzypek (1971) both indicated that each ommatidium contained three types of screening pigment cells. The long pigment cells extended from the cuticular lens overlying the eye to the underlying basement membrane. The principal pigment cells were associated with the crystalline cone. The basal pigment cells were located between the proximal end of each ommatidium and the underlying basement membrane. Gribakin (1975) suggested that the so-called basal pigment cells were, in fact, inflated, pigment granule containing portions of the cone cell processes, and not separate pigment cells.

Sommer and Wehner (1975) and Wehner et al. (1975) described two types of retinulae within the adult worker honey bee compound eye. The first type was composed of nine long retinula cells, did not exhibit twisting, and was restricted to the most dorsal 4-5

horizontal rows of ommatidia. The second type was composed of eight long and one short retinula cells, exhibited twisting, and composed the remaining ommatidia. Retinulae appeared to twist either clockwise or anticlockwise and the distribution of the two types of retinulae appeared to be random. Twisting has been hypothesized to be involved in polarized light detection by the short ninth retinula cell (Sommer and Wehner, 1975). Phillips (1905), at the light microscopic level, and Varela and Porter (1969), at the electron microscopic level, described the interommatidial bristles, found in conjunction with the honey bee worker compound eye, as being without innervation. In their electron microscopic investigation, Skrzipek and Skrzipek (1971) indicated that these bristles were innervated, and Nesse (1965) indicated that a scopale body was present.

The eight long retinula cells of the adult worker honey bee compound eye have been numbered in a variety of ways by different authors. These numbering systems have been summarized in Figure 1.

Goldsmith (1962) numbered each of the retinula cells from one to eight in the clockwise direction. Varela and Porter (1969) also numbered each of the retinula cells from one to eight, but in the anticlockwise direction. Because they based their numbering system on the location of the "eccentric" (ninth) cell and considered the retinula to consist of only eight retinula cells, retinula cells were numbered in two different ways (Figure 1).

Menzel and Snyder (1974) and Ribi (1975a, 1975b) used a numbering system based on that used by Perrelet (1970) for the

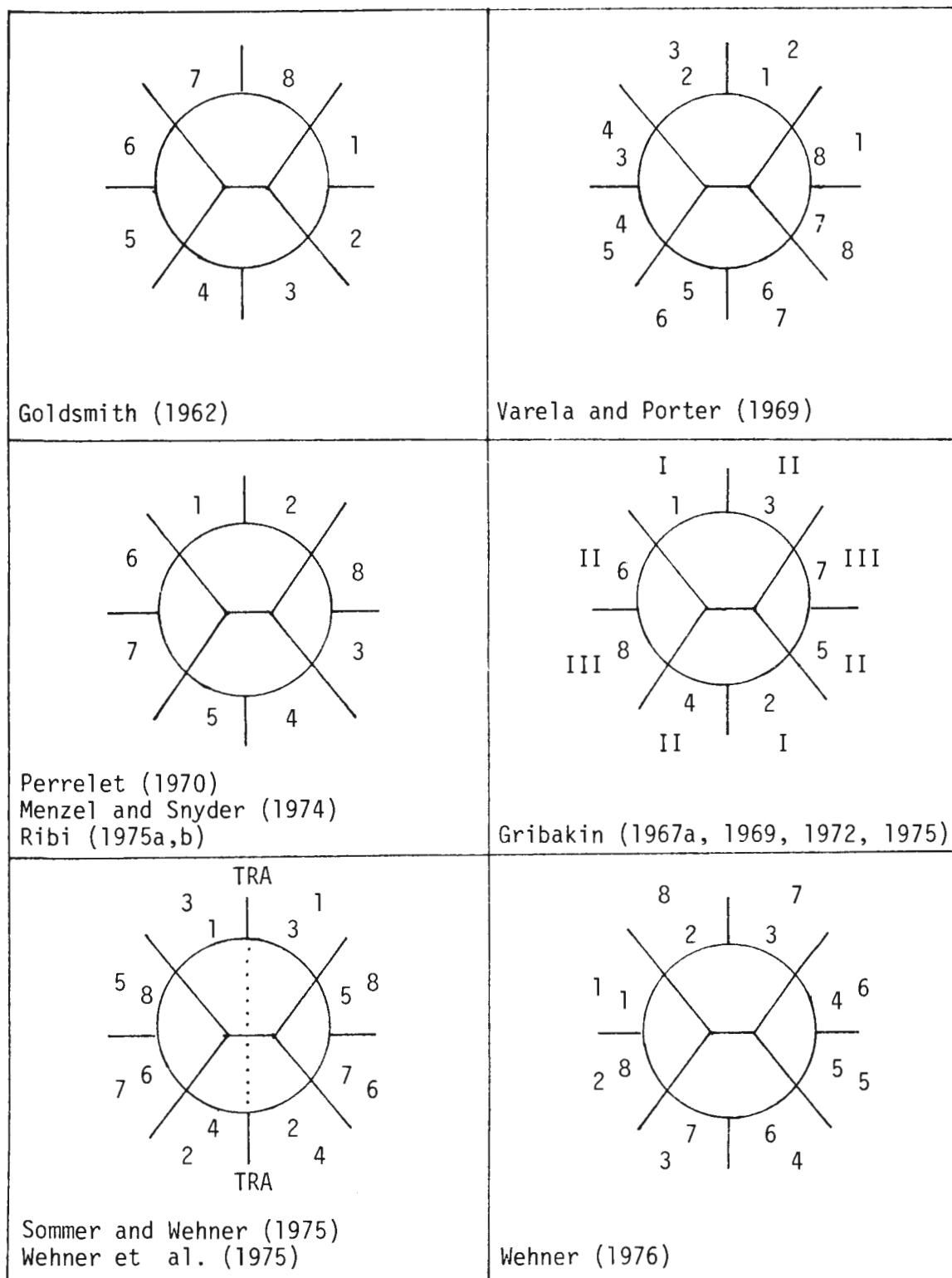


Figure 1. The numbering system used by various authors for the eight long retinula cells of the worker honey bee compound eye. For explanation, see text.

compound eye of the adult drone honey bee. Of the eight long retinula cells, six were observed to be larger and two to be smaller. The six larger cells were numbered one to six in the clockwise direction and the two smaller cells numbered seven and eight in the anticlockwise direction.

Gribakin (1967a) numbered the eight long retinula cells in pairs with the members of each pair being situated oppositely from one another. He also proposed that there were three distinct cell types based on electrophysiological considerations. Subsequently, Gribakin (1969, 1971, 1975) devised a numbering system based on both morphological and electrophysiological data. He divided the eight long retinula cells into the three following types: type I, two oppositely situated cells with parallel rhabdomeric microvilli which met along the ommatidial axis, having fewer pigment granules and mitochondria in the distal third of each of the cells, having the most distally located tier of nuclei, and sensitive to light of 340 nm; type II, four cells situated alternately with type I and type III cells, having the second tier of nuclei, and sensitive to light of 530 nm; type III, two oppositely situated cells with parallel microvilli which did not meet along the ommatidial axis, having the third tier of nuclei, and sensitive to light of 530 nm. The short ninth cell replaced one of the type III cells in the proximal third of the retinula.

Sommer and Wehner (1975) and Wehner et al. (1975) have defined their numbering system according to the following considerations:

1) Oppositely situated retinula cells having microvilli running in the same direction and having the same spectral sensitivity were numbered in pairs 1-2, 3-4, 5-6, 7-8;

2) A transverse axis (TRA) has been defined for the rhabdom, and cells 1 and 2 were defined by having microvilli parallel to the transverse axis and also by their location;

3) Numbering proceeding either in a clockwise or anticlockwise direction, depending on the direction of twisting of the retinula;

4) A coordinate system has been proposed for the eye and each retinula cell can be recognized by its position within the coordinate system;

5) In the proximal region of the retinula the ninth retinal cell replaced either retinula cell number 1 or number 2.

Wehner (1976) also proposed a simpler numbering system in which cell number 1 was the same as in the previously-described system, and the remaining cells, with the exception of the ninth, were serially numbered in either the clockwise or anticlockwise direction, depending on the direction of retinula twisting.

In several different groups of insects, both light and electron microscopic investigations of the developing compound eye have indicated that at a specified time during the larval period, a wave of cell proliferation followed by a wave of cell differentiation passed along the prospective eye tissue, leaving preommatidial cell clusters in its wake. This phenomenon was first described in Bombyx mori (Wolsky, 1949) at the light microscopic level. This was

followed by investigations on other insects including Ephastia, Nolenecta, Drosophila (Wolsky, 1955-56) and Aedes aegypti (White, 1961, 1963). Electron microscopic investigations of Drosophila (Campos-Ortega and Gateff, 1976; Ready et al., 1976) have indicated that the preommatidial cell clusters which arose just behind the wave of differentiation were not formed by a clonal mechanism but rather by cell recruitment at the morphogenetic furrow formed by the differentiation wave. Similar cell recruitment has been demonstrated in the eye of Oncopeltus fasciatus (Shelton and Lawrence, 1974; Green and Lawrence, 1975).

Electron microscopic investigations on the developing eye of Drosophila have revealed some of the specific cellular interactions of an eye with an open type of rhabdom and a pseudocone. Rhabdomere development appeared to be similar in both Drosophila (Waddington and Perry, 1961; Perry, 1968) and Bombyx (Eguchi et al., 1962), an insect with a closed type of rhabdom. In both cases, rhabdomere development began with irregular infoldings of the retinula cell plasma membranes along the ommatidial axis. As development progressed, the irregular infoldings were transformed into highly regular microvilli. Early in development the rhabdomeres of both types were fused. Separation of rhabdomeres occurred secondarily in Drosophila (Waddington and Perry, 1961).

According to Waddington and Perry (1961), the pseudocone of Drosophila developed either as an extracellular secretion, or as a degenerated region of the cone cells. Perry (1968) clarified this position by detailing the development of the cone cells and their

subsequent contraction away from the cuticular lens to form the pseudocone extracellular space. She indicated that the microtubules which were involved in the morphogenetic process persisted in the cone cell cytoplasm.

Elongate processes extending from the proximal tip of each cone cell to the basement membrane underlying the compound eye and located between adjacent retinula cells have been observed in the honey bee (Goldsmith, 1962; Varela and Porter, 1969; Gribakin, 1975; Skrzipek and Skrzipek, 1971) and in the locust (Horridge, 1965). Both of the aforementioned insects have compound eyes of the apposition type (Exner, 1891), in which the distal tip of the rhabdom contacts the proximal tip of the crystalline cone. Both also have closed types of rhabdoms, in which the tips of oppositely-situated rhabdomeric microvilli contact one another along the ommatidial axis and eucone types of crystalline cones. Varela and Porter (1969) and Horridge (1965) have speculated that the functions of these processes are mechanical support and anchoring of the dioptric system to the receptor system.

In several insect compound eyes of the superposition (Exner, 1891) or clear-zone (Horridge, 1971; Walcott, 1975) type, in which the rhabdom and crystalline cone do not contact one another at all times and in which there may be movement of either the cone cells or retinula cells during light/dark adaptation, crystalline tracts have been observed extending from the proximal tip of the crystalline cone towards the rhabdom (Horridge, 1968, 1971, 1975; Horridge and

Giddings, 1971a, 1971b; Døving and Miller, 1969; Walcott, 1975). It has been demonstrated that these tracts function as light guides (Horridge, 1971; Døving and Miller, 1969; Carricaburu, 1975) from the crystalline cone to the underlying rhabdom. The extensive literature on clear-zone eyes has been reviewed by Walcott (1975), Carricaburu (1975) and Horridge (1975).

Neville (1970) pointed out that both lamellate and nonlamellate types of cuticular lens facets lack pore canals. However, the adjacent cuticle may contain pore canals in abundance.

Locke (1966) described the deposition of cuticulin, which arose from the tips of microvilli along the apices of the epidermal cells. Locke (1969, 1973) and Delachambre (1970, 1971a) both described plaque-like structures located at the tips of the apical microvilli and indicated that the plaque-like structures were involved both in cuticulin formation and in fibrous cuticle deposition. These two events were separated by a period during which secretory vesicles from the Golgi complexes discharged their contents into the extracellular space between the cuticulin layer and the epidermal cell apices by fusing with the plasma membrane between adjacent microvilli. Locke (1976) and Delachambre (1971a) also proposed that in periods during which the plaque-like structures of the apical microvilli were not involved in cuticulin or fibrous cuticle formation, the plasma membrane composing the microvilli flattened and then involuted. The plaque-like structures were apparent in the membranes of multivesicular bodies in the apical epidermal cell cytoplasm

during these periods. Locke (1976) also indicated that the appearance of apical microvilli with the plaque-like structures at their tips was a cyclical process, alternating with the appearance of multi-vesicular bodies with plaque-like structures in their membranes, during each moult/intermoult cycle.

MATERIALS AND METHODS

Combs of capped and uncapped bee brood were obtained from the Bee Biology and Systematics Laboratory ARS-USDA in Logan, Utah. To facilitate observation of gross developmental changes, some larvae and prepupae were isolated from the combs and placed in size 0 or 00 gelatin capsules. The combs, in retential frames, and the gelatin capsules were maintained at 32 ± 1 °C and 50 ± 5 percent relative humidity.

Larvae, prepupae, and pupae of various ages (Table 1) were removed from the gelatin capsules or from the comb according to stage characteristics defined in Table 1 and fixed immediately. Fixation was accomplished by decapitating insects under Karnovsky's fixative (Karnovsky, 1965), pH 7.2. Each head was then bisected sagittally and excess tissues including integument, muscles and glands, were removed from around the eye. Pupal eyes were cut into thirds (Figure 2) and only the portion with eight long and one short retinula cell (Schinz, 1975) was utilized by this study. Eyes remained in the fixative from 2.5 to 24 hours. Following fixation they were placed in cacodylate buffer at pH 7.2 for up to several weeks. Most of the eyes were, however, rinsed in three 5-minute changes of cacodylate buffer, post-fixed in cold 1 percent OsO₄ in cacodylate buffer, and then dehydrated in an ascending series of ethanols. They were cleared in propylene oxide, and embedded in

Table 1. The sequential stages in the development of the compound eye of the worker honey bee.

stage	1	2	3	4	5	6	7	8	9	10	11	12
name	active uncap- ped larva	defeca- ting larva	spin- ning larva	early pharate pupa	white eyed pupa	light-pink eyed pupa	pink eyed pupa	dark-pink eyed pupa	light-brown eyed pupa	brown eyed pupa	dark-brown eyed pupa	black eyed pupa
duration (hours)	12	12	12	48	36	12	24	12	24	36	24	24
period (hours)	0-12	12-24	24-36	36-84	84-120	120-132	132-156	156-168	168-192	192-228	228-252	252-276

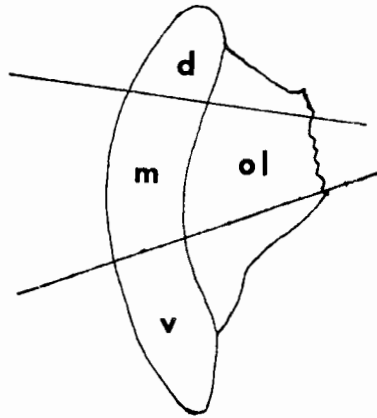


Figure 2. Schematic drawing of pupal honey bee eye. Only the middle area which contained ommatidia with one short and eight long retinula cells was used in the present investigation; d, dorsal region of eye; m, middle region of eye; v, ventral region of eye; ol, optic lobe.

Spurr's low viscosity embedding medium (Spurr, 1969) at 70 °C for 12 hours.

For light microscopy, serial one μm sections were obtained with glass knives on a Porter-Blum MT-2 ultramicrotome, picked up individually from the water surface, placed on glass microslides, and stained with Azure B-Methylene Blue.

For electron microscopy, gold to silver sections were also obtained with glass knives on a Porter-Blum MT-2 ultramicrotome, expanded with chloroform vapour, picked up on bare 200-mesh copper grids, stained with saturated uranyl acetate and Reynolds' lead citrate (Reynolds, 1963), and examined with a Zeiss 9A electron microscope.

In the course of the study, over 50 bees and more than 1000 micrographs representing samples from over 100 blocks were used as documentation.

RESULTS

Although morphogenesis is a dynamic process, its description is facilitated by dividing it into discrete stages. After reviewing the literature, it was concluded that the stages used by Daly (1964) in his description of the skeleto-muscular morphogenesis of the thorax and wings of the honey bee were most suitable for studying compound eye morphogenesis. Table 1 summarizes the characteristics of the different stages.

Cells differentiating into preommatidial cell clusters (Figures 5, 6, 7) were first recognized at the end of the third larval instar (stage 1) following reorganization of the cells of the optic primordium. This reorganization progressed across the optic primordium from posterior to anterior (Figure 5) and was similar in appearance to the morphogenetic furrow described by Ready et al. (1976) in Drosophila. Prior to this stage, the primordial visual cells were indistinguishable from one another, although the optic primordia were visible along the dorso-lateral portions of the head.

Prior to pupation (stage 4), preommatidial cell clusters were closely apposed to one another within the primordial optic region (Figure 7). After pupation and following the enlargement of the head to adult proportions (stage 5), the relative positions of the optic primordia were unchanged, although they had increased to their

final adult size. By this time, due to the increase in the size of the head and the optic primordia, ommatidia were observed to be less closely apposed to one another and were surrounded by extracellular space, not present prior to pupation. By stage 10 the ommatidia had reached their final, adult proportions (Figure 4f).

For the sake of clarity and brevity the cell types composing the dioptric system, the receptor system and the interommatidial bristle complex have been described separately.

Briefly, the dioptric system consisted of four cone cells, often referred to as Semper's cells (Goldsmith, 1964) which comprised the crystalline cone, and the two cone-adjunct pigment cells,* variously called principle pigment cells (Varela and Porter, 1969), primary or corneal pigment cells (Goldsmith, 1964) or corneagen cells (Phillips, 1905).

The receptor system consisted of the nine retinula cells which comprised the retinula and the 12 to 14 retinula-adjunct pigment cells,* variously called secondary pigment cells, accessory pigment cells, iris cells, or secondary iris cells (Goldsmith, 1964), outer pigment cells (Phillips, 1905) or long pigment cells (Varela and Porter, 1969).

*In the present study the terms cone-adjunct pigment cell and retinula-adjunct pigment cell have been introduced to replace numerous currently used terms which do not appear to describe these two cell types either morphologically or physiologically.

The interommatidial bristle complex was composed of four cell types including a sense cell, a neurilemma cell, a tormogen cell, and a trichogen cell.

The Dioptric System

Cone cells

The four cone cells were first recognized during the late third larval instar (stage 1) by their peripheral position within each newly formed preommatidial cell cluster (Figure 6). They surrounded the distal portion of the nine retinula cells of the prospective retinula and extended to the distal edge of the optic primordium. Following formation of preommatidial cell clusters over the entire optic primordium (stage 3), the cone was teardrop-shaped with the retinula protruding into the wide, proximal end (Figure 3). At this stage, each cone cell was shaped like a slightly flattened cone of approximately 20 μm in length, bulging in the region of the nucleus, and becoming narrower more distally. Two oppositely situated cone cells contacted one another in the central region of the cone distal to the retinula, while the remaining two cone cells did not (Figure 15). Each cone cell contained an ovoid nucleus of approximately 4 μm by approximately 7 μm . Nuclei were located in the proximal portion of each cone cell with the long axis of each nucleus parallel to the ommatidial axis (Figure 3). Extensive granular endoplasmic reticulum and some free polyribosomes were scattered throughout the cytoplasm along with numerous mitochondria, several multivesicular bodies, and a few Golgi complexes. Microtubules oriented

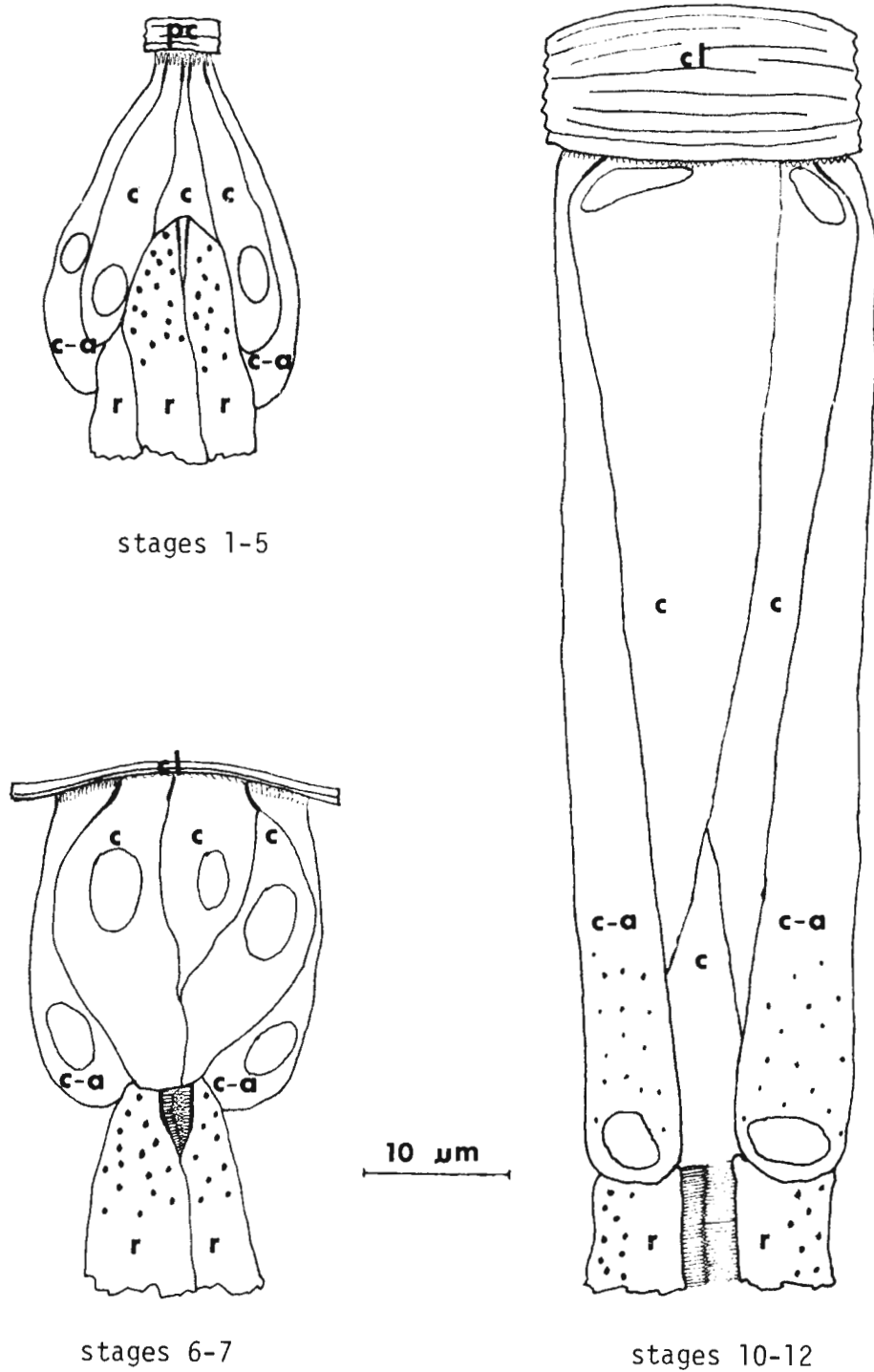


Figure 3. Diagrammatic representation showing the changes in the shape of the crystalline cone at different developmental stages. c, cone cell; c-a, cone-adjunct pigment cell; cl, corneal lens; pc, pupal cuticle; r, retinula cell.

perpendicularly to the ommatidial axis were observed in the peripheral region of the cone (Figures 15, 16). Longitudinally oriented microtubules were observed in the distal portion of the cone cell cytoplasm prior to pupation. They disappeared by the end of stage 4. Each cone cell was united to the three adjacent cone cells and also to the cells surrounding the cone by junctions of the adherens type, similar to those described by Farquhar and Palade (1963), located just proximal to the distal tips of the cells (Figure 8). Occasional septa were also apparent between the plasma membranes of the cone cells and the surrounding cone-adjunct pigment cells.

During formation of the fourth larval instar cuticle (stage 2), microvilli were observed along the distal end of each cone cell (Figure 8). Each microvillus had an electron-dense, plaque-like structure at its distal tip, similar to those described by Locke (1976) in Calpodes ethlius larvae. Vesicles, similar to the secretory vesicles also described by Locke (1976), were evident in the cytoplasm just proximal to the microvillous surface, and occasionally appeared to be fusing with the plasma membrane between adjacent microvilli. The microvilli persisted until the completion of cuticle formation when most of them disappeared (Figure 10), reappearing again at the beginning of cuticle secretion in the next instar. In the period preceeding apolysis, during which the old cuticle was being digested, few microvilli were evident along the apical cone cell surface (Figure 10). Multivesicular bodies which contained plaque-like structures embedded in their membranes

(Figure 9), similar to those described by Locke (1976), were observed within the distal cone cell cytoplasm in close proximity to the apical surface. These multivesicular bodies were visible during all stages of the moult/intermoult cycle, but were apparently more abundant during the digestive phase than during the secretory phase.

This apparent cycle of microvilli appearance, disappearance, and reappearance, coupled with the increased quantity of multivesicular bodies with plaque-like structures embedded in their membranes, was repeated during each larval moult/intermoult cycle. Following the larval/pupal moult, persistent microvilli were observed along the apical borders of the cone cells from stage 5 through stage 12, although these microvilli exhibited a more regular appearance after stage 8 (Figures 12, 14).

During stage 6, the shape of the cone changed from teardrop-shaped to spherical, and became located distal to the retinula (Figure 3). Each of the cone cells comprised approximately one quarter of the sphere, although two oppositely situated cone cells were still somewhat larger than the other two, and contacted one another in the central region of the cone.

During stage 6, the organization and distribution of cytoplasmic organelles also changed markedly from the preceding stages. The nuclei appeared to be migrating towards the distal portion of each cone cell. Organelles formerly located in the central region of the cone were now located more peripherally. The quantity of granular endoplasmic reticulum contained within each cone cell

appeared to be markedly reduced and the peripherally located microtubules observed during stage 5 were apparently absent.

The processes arising from the proximal end of each cone cell were first recognized near the end of stage 6 (Figures 23, 24). The four processes of each ommatidium extended proximally along the retinula periphery, lying in grooves between alternate adjacent retinula cells (Figure 23). In cross-section, each process was circular to ovoid and ranged from approximately 0.5-1.0 μm across. Processes contained numerous longitudinally oriented microtubules, at least some of which were continuous with microtubules located in the proximal portion of each cone cell (Figure 24), and an occasional vesicle, mitochondrion, or electron dense body (Figures 23, 24).

The shape of the cone continued to change during stages 7-8 from a sphere approximately 20 μm in diameter, to an elongate cone approximately 70 μm in length, approximately 20 μm across at its wide distal end, and approximately 4 μm across at its narrow proximal end (Figures 3, 33, 34, 35, 36, 37, 38). When viewed in cross-section, it was apparent that two of the cone cells, oppositely situated, contacted one another along the ommatidial axis, while the two remaining cone cells did not (Figures 34, 35, 36).

During stage 7, the nuclei continued their apparent distal migration, reaching the distal third of each cone cell (Figure 3). Mitochondria, granular endoplasmic reticulum, and free polyribosomes, with the exception of a few located distal to the nuclei, were all located near the cone periphery.

Concurrent with the elongation of the cone during stage 8, the distal migration of the nuclei reached completion. Each nucleus was kidney bean-shaped and lay along the periphero-distal border of its cone cell (Figures 33, 34). Also during stage 8 a granular appearing substance, glycogen according to Fyg (1961), began to accumulate in the central region of the cone.

Simultaneously with the narrowing of the proximal end of the cone, the cone cell processes were observed to be located more centrally within each retinula, between alternate adjacent retinula cells. Septate desmosomes were apparent between cone cell processes and adjacent retinula cells (Figure 27). Each process came to lie just peripheral to the junctional complex between the alternate adjacent retinula cells (Figures 26, 27, 29, 30, 31, 32). In cross-section, processes appeared to change shape during centerward movement from circular or slightly ovoid to distinctly ovoid (Figures 29, 30, 31). However, occasional circular processes were still observed during stage 12 (Figure 32).

Cone cell differentiation was nearly complete by stage 10. The granular substance had completely filled the cone interior, leaving only a narrow peripheral region of cytoplasm. This region contained the distally located nuclei, the peripherally located mitochondria, and free polyribosomes, and the proximally located longitudinally oriented microtubules, some of which appeared to extend farther proximally into the cone cell processes (Figures 3, 33). However, at this stage the cone did not exhibit the differential

staining observed by Varela and Porter (1969) and Skrzipek and Skrzipek (1971). The junctional complexes between adjacent cone cells disappeared, although at intervals around the entire periphery the cone remained joined to the surrounding cone-adjunct pigment cells by adherens junctions.

Following completion of crystalline cone differentiation, the proximal 8-10 μm of each cone cell process were observed to be inflated to a diameter of approximately 1.5 μm . Electron-opaque pigment granules, similar to those previously described by Gribakin (1975), were observed to be located within the inflated portion of each cone cell process.

Cone-adjunct pigment cells

During the prepupal period (stage 4) the cone cells were observed to be surrounded by two laterally located cone-adjunct pigment cells (Figure 15). These cells were very similar in appearance to the cone cells. They contained ovoid nuclei of similar size and orientation to those of the cone cells, abundant granular endoplasmic reticulum, some free polyribosomes, and mitochondria. Just proximal to the distal cell borders (Figure 8), the two cone-adjunct pigment cells of each ommatidium were united with one another and also with the four cone cells by junctions of the adherens type similar to those uniting the four adjacent cone cells. At the stage during which these cells were active in cuticle formation, microvilli similar to those described for the cone cells were observed along the apical borders of the cone-adjunct pigment

cells. The microvilli were observed alternately to appear, disappear, and reappear through the moult/intermoult cycle, in synchrony with those of the cone cells. Multivesicular bodies containing plaque-like structures embedded in their membranes became more numerous in the distal cone-adjunct pigment cell cytoplasm simultaneously with their increase in quantity in the cone cells.

During stage 6, the distribution and organization of cytoplasmic organelles changed from that of the preceding stages. The nuclei, mitochondria, free polyribosomes, and granular endoplasmic reticulum appeared to be more concentrated towards the proximal portion of the cytoplasm.

The cone-adjunct pigment cells maintained their relationship with the elongating cone, forming a complete, elongating cylinder around it during stages 7-8. As the shape of the cone changed from a sphere to an elongate cone, the shape of the cone-adjunct pigment cells changed as well. The outside diameter of the cylindrical sheath remained fairly constant, while the cone-adjunct pigment cells became inflated proximally and narrower distally (Figures 3, 33).

Pigment granules, similar to those described by Varela and Porter (1969) in the adult honey bee compound eye, were first observed in the proximal portion of the cone-adjunct pigment cells during stage 8. Also during this stage a granular-appearing substance, similar to that of the cone cells but more diffuse, began to appear in the distal region of the cytoplasm. Accumulation of this granular material continued through stage 9, but the material remained diffuse, never becoming as concentrated as in the cone cells.

By stage 10 the dioptric apparatus was essentially fully differentiated. It was approximately 70 μm in length and had an almost uniform outside diameter of about 25 μm . The cone-adjunct pigment cell cytoplasm was concentrated in the proximal third of each cell and contained the nucleus, mitochondria, pigment granules, free polyribosomes, and granular endoplasmic reticulum. The nucleus was kidney bean-shaped and extended almost completely around the cone-adjunct pigment cell periphery. Distally the cone-adjunct pigment cells became narrower, and the distal two-thirds of the cytoplasm contained granular material similar to that of the cone cells, but less concentrated in appearance.

Lens formation

The synchronous appearance of microvilli, vesicles, and multivesicular bodies in the cone, cone-adjunct pigment, and retinula-adjunct pigment cells suggests that the cuticle covering the eye was secreted jointly by cells of these three types. The mechanism of cuticle secretion appeared to be similar in each of the three cell types, and closely resembled that described by Locke (1969, 1976) and Delachambre (1970, 1071a).

The first indication of cuticle formation was the appearance of a trilaminar structure of approximately 25 nm thickness (Figure 11). This constituted the cuticulin layer which arose at the surface of specialized plaques located on the distal tips of the apical microvilli (for details, refer to sections on the cone, cone-adjunct pigment, and retinula-adjunct cells). Following

cuticulin deposition, coated vesicles ranging in size from approximately 180 nm to 240 nm in diameter were evident in the distal cytoplasm of all three cell types. These vesicles occasionally appeared to fuse with the plasma membrane at the base of adjacent microvilli and to discharge their contents into the extracellular space between the microvilli and the cuticulin layer. Microvilli with apical plaques and coated vesicles which appeared to fuse with the plasma membrane between adjacent microvilli persisted from stages 5-12 (Figures 12, 13, 14).

Although each cuticular lamella of the corneal lens was continuous over the entire eye surface, its thickness was not constant. Cuticle was thickest at the center of each hexagonal lens facet and was thinnest in the interlens regions. It was observed that for the first several lamellae (approximately 10), the portion of each lamella over the cone cells was 5 μm thick and that the thickness of this cuticle graded to 7 μm over the retinula-adjunct pigment cells. During this period the microvilli of the cone-adjunct and retinula-adjunct pigment cells were more pronounced than those of the cone cells (Figures 12, 14). As a consequence of the shape of these lamellae, each lens facet was meniscus-shaped and the interlens regions were located more proximally than the lens regions, forming distinct boundaries between adjacent lens facets.

In the remaining lamellae, the central portion, overlying the cone cells, was 8 μm thick and graded to 5 μm over the retinula-adjunct pigment cells. During this period, the microvilli of the

cone cells were not distinguishable from those of the cone-adjunct and retinula-adjunct pigment cells (Figure 14). After several of these lamellae had been secreted, each lens facet was biconvex in shape. In interlens regions the lamellae still formed distinct boundaries between individual lens facets and appeared as though they were compressed.

It is of interest to note that the developing cuticular lens lacked pore canals and the cuticle of the lens was not differentiated into endocuticle and exocuticle. However, pore canals were observed in the cuticle surrounding the eye.

The Receptor System

Retinula cells

These cells were first recognized during the late third larval instar (stage 1) as a group of nine cells occupying the central portion of each preommatidial cell cluster surrounded by the four cone cells (Figure 6). One of these cells was centrally located, while the other eight cells were concentrically arranged around the central one. The entire group of nine retinula cells appeared spindle-shaped in longitudinal section (Figure 4a). The nucleus of the centrally located cell was located near that cell's middle region, while the nuclei of the eight concentrically arranged cells were generally more proximally located (Figure 4a), although occasionally a nucleus was observed to be more distally located. The portion of each cell containing the nucleus was larger in diameter than the remaining portion (Figures 6, 7).

To facilitate description of the retinula, each of the retinula cells has been numbered according to the system used by Gribakin (1969, 1971, 1975) as either a type I, type II, type III, or ninth cell (Figure 16). Also the retinula has been divided into three regions along its longitudinal axis: a distal region, a middle region, and a proximal region. Each region comprised approximately one-third of the length of the retinula.

Following formation of preommatidial cell clusters over the entire optic primordium (stage 3), the three regions were distinguished by the following characteristics. The distal region of each retinula contained only the eight concentrically arranged retinula cells which were observed to extend more distally than the ninth retinula cell (Figure 16). The middle region contained eight retinula cells concentrically arranged around the centrally located ninth retinula cell (Figure 17). In the proximal region the two oppositely situated type III cells became narrower and gave rise to axons which extended proximally along the retinula periphery, leaving six retinula cells concentrically arranged around the centrally located ninth cell, and two peripherally located axons (Figure 18).

Just prior to pupation (stage 4) the distal region was characterized by the beginning of rhabdomere development. This was evident by: 1) the presence of irregular indentations in the portions of the plasma membranes along the ommatidial axis (Figure 16), 2) the development of an ommatidial cavity along the ommatidial axis into which the plasma membrane infoldings extended, and 3) the appearance in the proximity of the invaginating plasma membranes

of cytoplasmic vesicles, which ranged in diameter from approximately 0.8 μm to 2.0 μm (Figures 16, 21).

In conjunction with the development of irregular plasma membrane indentations, screening pigment granules, similar to those described by Varela and Porter (1969) in the adult, appeared in the distal cytoplasm of six of the eight retinula cells. Few or no screening pigment granules were observed in the distal cytoplasm of the two type I cells (Figure 16).

At this stage the distal retinula cell cytoplasm also contained free polyribosomes, a few mitochondria, and numerous longitudinally oriented microtubules which were concentrated near the retinula periphery (Figure 16). The eight concentrically arranged retinula cells were connected to one another by junctional complexes of the adherens type located just peripheral to, and extending the entire length of, the developing rhabdomeres (Figure 16, 19). Adherens junctions also connected each of the eight concentrically arranged cells to the ninth centrally located cell at that cell's distal tip (Figure 19). Occasional septa were observed both between the plasma membranes of adjacent retinula cells and between the plasma membranes of the retinula cells and the surrounding retinula-adjunct pigment cells (Figure 16, 19, 21).

The nuclei of all nine of the retinula cells were contained within the middle region. The two type III cell nuclei were located in the more distal part of the middle region, while in the remaining seven retinula cells the nuclei were more proximal.

Homogeneously electron dense structures, similar in appearance to lipid droplets, were located just distal and proximal to each nucleus (Figure 18). These droplets ranged from approximately 0.3 μm to approximately 1.0 μm in diameter and were not membrane bound.

The majority of the retinula cell mitochondria were contained within the cytoplasm of the middle region of the cell. Although they were distributed throughout the middle region cytoplasm, the mitochondria exhibited a slight tendency to congregate in the peripheral portion of this region (Figures 17, 19).

Randomly distributed free polyribosomes and granular endoplasmic reticulum were abundant in the middle region (Figure 17). Occasional Golgi complexes were also observed. Vesicles, possibly portions of agranular endoplasmic reticulum, were also scattered throughout the cytoplasm of the middle region.

Paired, parallel centrioles (Figure 22), similar to those of the epipharyngeal sense organ of the honey bee (Youssef, personal communication), were observed in appropriately oriented sections of the retinula cell cytoplasm along the distal border of the middle region (Figures 21, 22). Several multivesicular bodies were located in the middle region cytoplasm of each retinula cell (Figures 17, 19, 21, 22), and some of them contained plaque-like structures in their membranes similar to those of the cone, cone-adjunct, and retinula-adjunct pigment cells. Longitudinally oriented microtubules concentrated near the periphery of the middle region appeared to be continuous with those of the distal retinula

cell cytoplasm (Figures 17, 21).

At the distal border of the proximal region the two type III cells became narrower, giving rise to axons which contained abundant longitudinally oriented microtubules. Most of these microtubules were not continuous with those of the middle and distal regions. Axons also contained a few polyribosomes, occasional mitochondria, and some vesicles (Figure 18). Longitudinally oriented microtubules were also located within the other seven axons. The nine axons from each retinula formed an axon bundle, just distal to the basement membrane, which pierced the basement membrane and extended proximally towards the optic lobe of the supraesophageal ganglion.

As the retinulae continued to differentiate, elongation, twisting, and proximal movement (sinking) took place (stage 6). In conjunction with elongation, the distal cytoplasm of the eight concentrically arranged retinula cells began to reorganize. This reorganization was evidenced by the migration of mitochondria and pigment granules from the cytoplasm directly surrounding the developing rhabdomeres towards the retinula periphery. Simultaneously, microtubules became more concentrated in the central portion of the cytoplasm.

During stage 6, the formation of the rhabdomeres continued in the distal portion of the retinula. The plasma membrane infoldings began to exhibit more regularity, appearing more similar to irregular microvilli.

During elongation, there was an approximately three-fold increase in the number of microtubules throughout the retinula cell cytoplasm

(Figure 23). These microtubules were oriented along the longitudinal axis of each cell.

During the process of elongation, the retinula cell nuclei appeared to become stratified within the middle region of the retinula, forming four tiers. The most distal tier contained the nuclei of the type III cells, the second tier contained the nuclei of the type II cells, the third tier contained the nuclei of the type I cells, and the most proximal tier contained the ninth cell nucleus.

During the later part of the period of proximal sinking (stage 6), cone cell processes extended in grooves between alternate adjacent retinula cells (Figure 23). See the section on the cone cells for a more complete description of these processes.

During stage 7 the cellular activity appeared to be concentrated in the middle region of each retinula. To allow for cellular rearrangement, junctional complexes between each of the eight concentrically arranged cells and the ninth cell disassociated. The distal tip of the centrally located ninth cell began to move laterally into the position formerly occupied by the one of the two type III cells (Figure 26), while the more proximal portion remained centrally located (Figure 27). One of the type III cells remained adjacent to the distal portion of the ninth cell; more proximally both of the type III cell axons extended in grooves along opposite sides of the retinula periphery.

The distal portion of the ninth cell moved laterally, followed

by the proximal portion. The entire ninth cell was situated lateral to the ommatidial axis by the beginning of stage 9 (Figures 31, 32). Lateral movement of the ninth cell was probably mediated in part by pressure exerted by the other eight cells.

Rhabdomere development in the ninth retinula cell began, as in each of the other eight retinula cells, with irregular indentation of the distal portion of the plasma membranes along the ommatidial axis (Figure 26). Rhabdomere development in all nine of the cells followed ninth cell lateral migration, starting at the distal tip and extending proximally. Each rhabdomere ended just distal to the region where its retinula cell gave rise to an axon.

The junctional complexes connecting the distal portions of adjacent retinula cells, with the exception of those associated with the two type III cells, all extended along the developing rhabdomeres into the middle region of the retinula. The junctional complexes connecting type III cells with adjacent cells ended where the type III cells gave rise to axons. Junctional complexes developed just peripheral to the rhabdomeres along the point of contact between the ninth cell and its two adjacent cells (Figure 26).

Simultaneously with the cellular rearrangements occurring during this stage, the elongating cone cell processes began to move between the alternate adjacent retinula cells and halted just peripheral to the junctional complexes (Figure 26). See the section on cone cells for further details.

During stage 8, the proximal, axon-like portion of each retinula cell elongated (Figures 4d, 28). It is possible that this

elongation, coupled with the sinking of the retinulae, was instrumental in pushing the underlying basement membrane towards the optic lobe of the supraesophageal ganglion. Elongation of the retinula was completed during stage 9.

Rhabdomeres began to have the appearance more typical of adults as previously described by Goldsmith (1962), Gribakin (1967a, 1975), Skrzipek and Skrzipek (1971), and Varela and Porter (1969) during stages 10-12. This was apparently accomplished by the organization of the irregular infoldings of the plasma membrane of each retinula cell into regular microvilli oriented perpendicularly to the long axis of the rhabdom.

During stages 10-12 the differentiation of the retinula cytoplasm into central and peripheral regions, first observed during stage 6, was apparent along the entire length of the retinula. The majority of the retinula pigment granules, mitochondria, granular endoplasmic reticulum, and other organelles migrated from the central cytoplasm to the retinula periphery (Figures 29, 30, 31, 32). The microtubules, previously abundant in the central and peripheral cytoplasm, were much reduced in number.

Portions of agranular endoplasmic reticulum were observed to have enlarged in the central region cytoplasm, forming the inflated cisternae previously described in the adult (Goldsmith, 1962; Gribakin, 1967b, 1975; Varela and Porter, 1969). Also during stages 10-12, adjacent retinula cells separated from one another near the retinula periphery, often extending as far centrally as the

junctional complexes. Leaf-like processes from the retinula-adjunct pigment cells, previously described in the adult (Gribakin 1967b), invaded the spaces between adjacent retinula cells (Figures 29, 31). The lipid-like droplets previously located distally and proximally to each retinula cell nucleus were no longer apparent during stages 10-12.

Retinula-adjunct pigment cells

The retinula-adjunct pigment cells were not discernible from other cell types of the optic primordium until the beginning of the pupal period (stage 5). During this period the retinula-adjunct pigment cells appeared, in cross-section, as a ring of 12 to 14 cells surrounding both the dioptic and receptor systems of each ommatidium (Figure 18). These cells extended from the distal edge of the optic primordium to the underlying basement membrane and completely ensheathed each ommatidium.

Each retinula-adjunct pigment cell contained a spheroidal nucleus of approximately 8-9 μm in diameter, located in the distal half of the cell. Numerous mitochondria, some free polyribosomes, and occasional vesicles and multivesicular bodies, some with plaque-like structures in their membranes, were scattered throughout the retinula-adjunct pigment cell cytoplasm. Septa were occasionally apparent between the plasma membranes of adjacent retinula-adjunct pigment cells.

Probably the most striking feature of the cytoplasm was the extensive arrays of granular endoplasmic reticulum, concentrically

arranged around the nucleus (Figure 19). Although the majority of the granular endoplasmic reticulum was located around the nucleus, some parallel arrays were also located in more distal and proximal portions of the cytoplasm.

Microvilli, similar to those of the cone and cone-adjunct pigment cells, appeared along the retinula-adjunct pigment cell apices during the secretion of pupal cuticle. These microvilli, along with multivesicular bodies located in the distal cytoplasm, appeared to cycle in synchrony with those of the cone and cone-adjunct pigment cells. Junctional complexes of the adherens type just proximal to the microvillous surface joined retinula-adjunct pigment cells to one another and to adjacent cone-adjunct pigment cells.

As elongation of the retinulae progressed during stage 6, the retinula-adjunct pigment cells also elongated, but maintained their position both relative to the retinulae and relative to the axis of elongation.

During stage 7 the retinula-adjunct pigment cell cytoplasm often appeared to contain large vacuoles surrounded by glycogen (Figures 26, 27). It is not known if these vacuoles were actual features of the retinula-adjunct pigment cell cytoplasm, or were artifacts resulting from poor fixation. Other cell types appeared to be adequately fixed even when the vacuoles were present in the retinula-adjunct pigment cells (Figures 26, 27). By stage 8 the extensive arrays of granular endoplasmic reticulum were no longer apparent within the retinula-adjunct pigment cell cytoplasm.

Screening pigment granules, similar in appearance to those described in the adult eye by Varela and Porter (1969), were first observed in the retinula-adjunct pigment cell cytoplasm during stage 10 (Figure 32). At this stage, after the completion of elongation, the retinula-adjunct pigment cells appeared to form a cylindrical sheath surrounding the dioptric system and only the distal portion of the receptor system. At the level of the middle region of the retinula each retinula-adjunct pigment cell became narrower so that these cells no longer contacted one another around the retinula periphery (Figure 28).

During stages 10-12, leaf-like processes of the retinula-adjunct pigment cells extended into the spaces between adjacent retinula cells. See the section on the retinula cells for more details.

The Interommatidial Bristles .

Although the interommatidial bristles were not directly part of the visual system of the honey bee compound eye, it was felt that in light of their spatial relationship to the other elements of the eye a brief description of their development would be appropriate.

Interommatidial bristle-forming complexes were first recognized at the beginning of stage 6. Each complex was located at the junction of three ommatidia and was surrounded by the retinula-adjunct pigment cells of the adjacent ommatidia. It is of interest to note that bristle-forming complexes were not located at all such junctions and appeared to be randomly distributed.

In cross-section each complex appeared as a group of four cells, two large cells of approximately 6-10 μm diameter and two small cells, one of which was ensheathed by the other (Figures 44, 45). The centrally located small cell has been recognized as a sensory cell, similar to those of other insect sensilla (Lawrence, 1966). The cell ensheathing the sense cell has been recognized as a neurilemma cell. The two large cells were adjacent to one another. The complex formed by the two small cells extended in a groove along the length of one of the large cells (Figures 44, 45), which has been recognized as a trichogen or bristle-forming cell. The remaining large cell has been recognized as a tormogen or socket-forming cell.

The neurilemma and sense cells both contained numerous longitudinally oriented microtubules, several mitochondria, and a few vesicles. The neurilemma cell also contained some free polyribosomes (Figure 44). The somata of these two cells were not distinguished from among the surrounding retinula-adjunct pigment cells and neither was ever located. It is possible that these somata were located below the level of the basement membrane.

The tormogen and trichogen cells contained spheroidal nuclei in the proximal portion of each cell, numerous ovoid mitochondria, free polyribosomes, and extensive arrays of granular endoplasmic reticulum. In the trichogen cell the granular endoplasmic reticulum was arranged in concentric layers located either just lateral to the nucleus or surrounding it (Figure 44).

Extensive cellular rearrangements of the four bristle-forming cells occurred during stage 7. The trichogen cell appeared to extend laterally around the small cell complex and surrounded it completely (Figure 42). Simultaneously, the tormogen cell appeared to extend laterally around the complex formed by the other three cells, completely ensheathing it (Figure 42). As these rearrangements were occurring, longitudinally oriented microtubules appeared in the cytoplasm of both the trichogen and tormogen cells (Figure 42).

Following cellular rearrangements, septate desmosomes connected each of the cells of the bristle-forming complex to the adjacent bristle-forming cells and also to the adjacent retinula-adjunct pigment cells (Figure 43).

Microvilli, similar in appearance to those described for the cone, cone-adjunct pigment, and retinula-adjunct pigment cells, appeared along the apical surface of the tormogen cell during stage 8. The multivesicular bodies with plaque-like structures embedded in their membranes, characteristic of the other three cuticle secreting cells of the compound eye, were only occasionally observed in the tormogen cell.

The trichogen cell also developed microvilli along its apical surface. Simultaneously it began to protrude through the ring-shaped apical region of the tormogen cell. Longitudinally oriented microtubules extended from the distal trichogen cell cytoplasm into the protruding portion of the cell.

The sense cell elongated simultaneously with the elongation of the trichogen cell. Because cross-sections of the bristle distal to the level of the developing lens were not observed, the extent to which the sense cell extended into the bristle was not known. The neurilemma cell did not appear to extend distally beyond the level of the socket (Figure 40).

An electron-dense material, similar in appearance to that of insect sensillum scolopale, began to accumulate around the periphery of the sense cell in the region of the socket and just distal to it (Figures 39, 40, 41) during stage 8.

As the bristle increased in length during stage 9, the diameter of the entire bristle-forming complex decreased. Both the trichogen and the tormogen cells appeared smaller and the diameter of the complex, approximately 12 μm during stage 6, was reduced to approximately 8 μm at the level of the distal region of the cone.

By stage 12 the bristle had attained its final length. The size of the bristle-forming complex continued to decrease to approximately 5 μm in diameter. Although the somata of the neurilemma and sense cells continued to elude observation, solitary neurite-like structures were occasionally observed at the level of the proximal region of the retinula (Figure 30). These may possibly represent dendrites or axons of the bristle sense cells.

DISCUSSION

The results of the present investigation on the development of the compound eye of the worker honey bee suggest that the genesis of the relationships between the cells of the dioptric and receptor systems involved numerous morphogenetic events which occurred in a precise temporal sequence.

When the cells composing each preommatidial cell cluster first appeared during the late third larval instar, they were distinguishable from the surrounding epidermal cells primarily by their location and spatial arrangement. There were no pronounced cytoplasmic or membrane specializations to distinguish them from the adjacent epidermal cells. Following formation of preommatidial cell clusters over the entire optic primordium, the precise morphogenetic movements and elongation of the primordial optic cells were mediated by the sequential appearance of both cytoplasmic and membrane specializations. These specializations included membrane junctions, microtubules, microvilli, vesicles, and multivesicular bodies.

Junctional specializations of the plasma membrane first appeared in the cells of the worker honey bee optic primordium following the formation of preommatidial cell clusters over the entire region. The adherens type of junctions between the eight concentrically arranged retinula cells, just peripheral to the developing rhabdomeres, probably served to anchor these cells to one another. Attachment of adjacent cells by specialized junctional

regions of their plasma membranes has been demonstrated to be an important process during vertebrate (Campbell and Campbell, 1971; Staehelin, 1974) and invertebrate (Gustafson, 1963; Wolpert and Mercer, 1963) ontogenetic development. Junctions of the adherens type have been generally considered to be involved in mechanical attachment (Farquhar and Palade, 1963; Gilula, 1974; Staehelin, 1974), rather than in isolation of separate extracellular compartments. Perrelet's (1969) work on the drone honey bee has demonstrated that adherens junctions did not function to isolate the extracellular compartment surrounding the rhabdom from the extracellular compartment between adjacent retinula cells. It is probable that adherens junctions played a similar role in the developing eye of the worker honey bee.

Junctional regions similar to those attaching adjacent concentrically arranged retinula cells to one another also appeared to anchor these cells to the centrally located ninth cell, at that cell's distal tip. These junctions were observed to disappear just prior to the period of ninth cell lateral migration. Disappearance of these junctions accordingly freed the ninth cell from those surrounding it, allowing it to migrate laterally. Disappearance of cell junctions has been reported to be a normal occurrence during vertebrate ontogenetic development (Campbell and Campbell, 1971) and probably plays a similar role during ontogenetic development of the honey bee compound eye. Following migration, new junctions formed between the ninth cell and the two adjacent cells, probably anchoring it into its lateral position within the retinula.

The junctional specializations observed along the distal points of contact between adjacent cone cells and between cone and cone-adjunct pigment cells probably served to anchor these cells to one another during the reorganization and elongation of the dioptic system. Each developing cone was apparently strongly anchored to the surrounding cone-adjunct pigment cells distally by junctional specializations of adjacent membranes, and to the retinula proximally by the cone cell processes. Each cone cell was also anchored distally to the three adjacent cone cells by membrane junctional specializations. As the retinulae continued to move proximally, the cone cells elongated. It is probable that the distally located adherens junctions prevented the cone cells from being pulled free from the surrounding pigment cells, and held the distal portion of the cone essentially rigid with respect to the cells adjacent to it. The portion of the cone proximal to the membrane junctional specializations was apparently neither held in place by attachments to the surrounding cells nor stabilized by an internal microtubular cytoskeleton. This portion of the cone was apparently stretched by the proximal movement of the underlying retinula, becoming narrower proximally. It is of interest that the volume of the cone did not change during elongation.

In the developing eye of the worker honey bee septate desmosomes were not present in the early preommatidial cell clusters. They were first observed between adjacent retinula cells, retinula and retinula-adjunct pigment cells, and cone and cone-adjunct pigment cells following formation of preommatidial cell clusters over the

entire optic primordium. Their appearance was irregular, usually consisting of only a few isolated septa between adjacent plasma membranes. They remained throughout the course of development and were still apparent between retinula cells and adjacent cone cell processes just prior to adult emergence.

Septate desmosomes appeared to be involved in cellular adhesions in the developing honey bee compound eye. Eley and Shelton (1976) have postulated a similar role for septate desmosomes during the development of the compound eye of Schistocerca gregaria. However, the course of septate desmosome development in Schistocerca gregaria was similar to that of the honey bee only during the early stages of development. During the later stages, septate desmosomes were still apparent in the ommatidia of the honey bee, but had disappeared from the ommatidia of Schistocerca gregaria (Eley and Shelton, 1976). Although the development of septate desmosomes between adjacent cells suggests that they functioned in cell-to-cell adhesions, the irregularity of their appearance seemed to indicate that their role in adhesions was not so precise as that of the adherens junctions.

Microtubules were observed to sequentially appear and disappear within both the retinula and the cone cells. Prior to the pronounced ommatidial elongation, the acquisition of a 180° clockwise or anti-clockwise twist, and the proximal movement of the retinulae, longitudinally oriented microtubules appeared within the peripheral and central regions of the retinula cytoplasm. These microtubules persisted throughout elongation, twisting, and proximal movement, but showed approximately a 2.5-fold decrease in quantity following

these events. Although the spatial distribution of microtubules was somewhat different in the honey bee from that described by Perry (1968) in the developing retinula cells of the Drosophila compound eye, the temporal sequences of microtubule appearance and disappearance were similar in the two insects.

As the retinulae moved proximally, the distal tip of each retinula no longer extended into the proximal end of the overlying group of cone cells. It is probable that the presence of microtubules oriented perpendicularly to the ommatidial axis and arranged around the cone periphery mediated a contraction of the proximal region of the cone and a bulging of the middle region, as the retinula moved proximally. When the retinula was located entirely proximal to the group of four cone cells, the cone was nearly spherical in shape and the cone cell microtubules had disappeared.

Elongation of the cells of both the dioptric and receptor systems was probably accomplished with the aid of microtubules. The development of a process containing numerous longitudinally oriented microtubules, from the proximal tip of each cone cell, was also probably mediated by the assembly of the microtubules. The role of microtubules in elongation has also been postulated in sperm (Porter, 1966; Tilney, 1971; Bloodgood, 1974; Wilkinson et al., 1974; Youssef et al., 1974), in protozoan axostyles (Porter, 1966; Tilney, 1971; Bloodgood, 1974), and in cilia (Porter, 1966; Tilney, 1971; Bloodgood, 1974).

Although there is no direct physiological evidence to indicate

which cell types of the developing compound eye were involved in cuticle secretion, indirect morphological evidence suggests that the cone, cone-adjunct pigment, and retinula-adjunct pigment cells were all involved in cuticle secretion. While larval and pupal cuticle were being formed, microvilli were apparent on the apical surfaces of the cone, cone-adjunct pigment, and retinula-adjunct pigment cells. The microvilli appeared to participate in membrane recycling with cytoplasmic multivesicular bodies and vesicles, similar to that ascribed to cuticle secreting cells by Locke (1969, 1976) in his description of cuticle secretion in Calpodes ethlius and by Delchambre (1970, 1971a) in Tenebrio molitor.

Contrary to the hypothesis of Phillips (1905), the cone cells did appear to participate in cuticular lens secretion along with the cone-adjunct pigment and retinula-adjunct pigment cells. The thickness of each cuticular lens facet appeared to be controlled by two factors: the degree of rotation of each cuticular lamina with respect to those adjacent to it, determined by the number and thickness of chitin-protein microfibrils composing each lamina (Bouligand, 1965; Locke, 1967; Neville, 1969, Neville and Luke, 1969a, 1969b), and the morphology of the apical microvilli of the cone, cone-adjunct pigment, and the retinula-adjunct pigment cells. During the secretion of the first several cuticular lamellae the apical microvilli of the cone cells were apparently shorter, less regular, and less dense, than those of the pigment cells. Less apical surface area and therefore probably fewer plaque-like structures were available to participate in fibrous cuticle deposition by the cone

cells during this period. Thus, the portion of each cuticular lamella overlying the cone cells was not as thick as the portion overlying the two types of pigment cells. During the secretion of the remaining lamellae the apical microvilli of the cone cells were observed to be morphologically similar to those of the pigment cells and the portion of each cuticular lamella overlying the cone was also of a similar thickness to the portion overlying the pigment cells. The underlying mechanism(s) which determined the degree of lamina rotation and the morphology of the apical microvilli have not yet been elucidated.

During the course of the present investigation, several questions were raised. First, pore canals, abundant in the cuticle adjacent to the honey bee worker compound eye, were not present in the cuticle of the lens facets. It is conceivable that pore canals might interfere in some manner with light perception, or that the cells of the optic region have become so specialized for other functions that the ability to form pore canals has been lost. Second, the cone cell processes of the honey bee compound eye resembled the crystalline tracts of some insects having eyes of the clear-zone type. These tracts have been demonstrated to act as light guides, conveying light to the rhabdom (Horridge, 1971; Døving and Miller, 1969; Carricaburu, 1975). Whether the cone cell processes of the honey bee function in a similar manner is still to be determined.

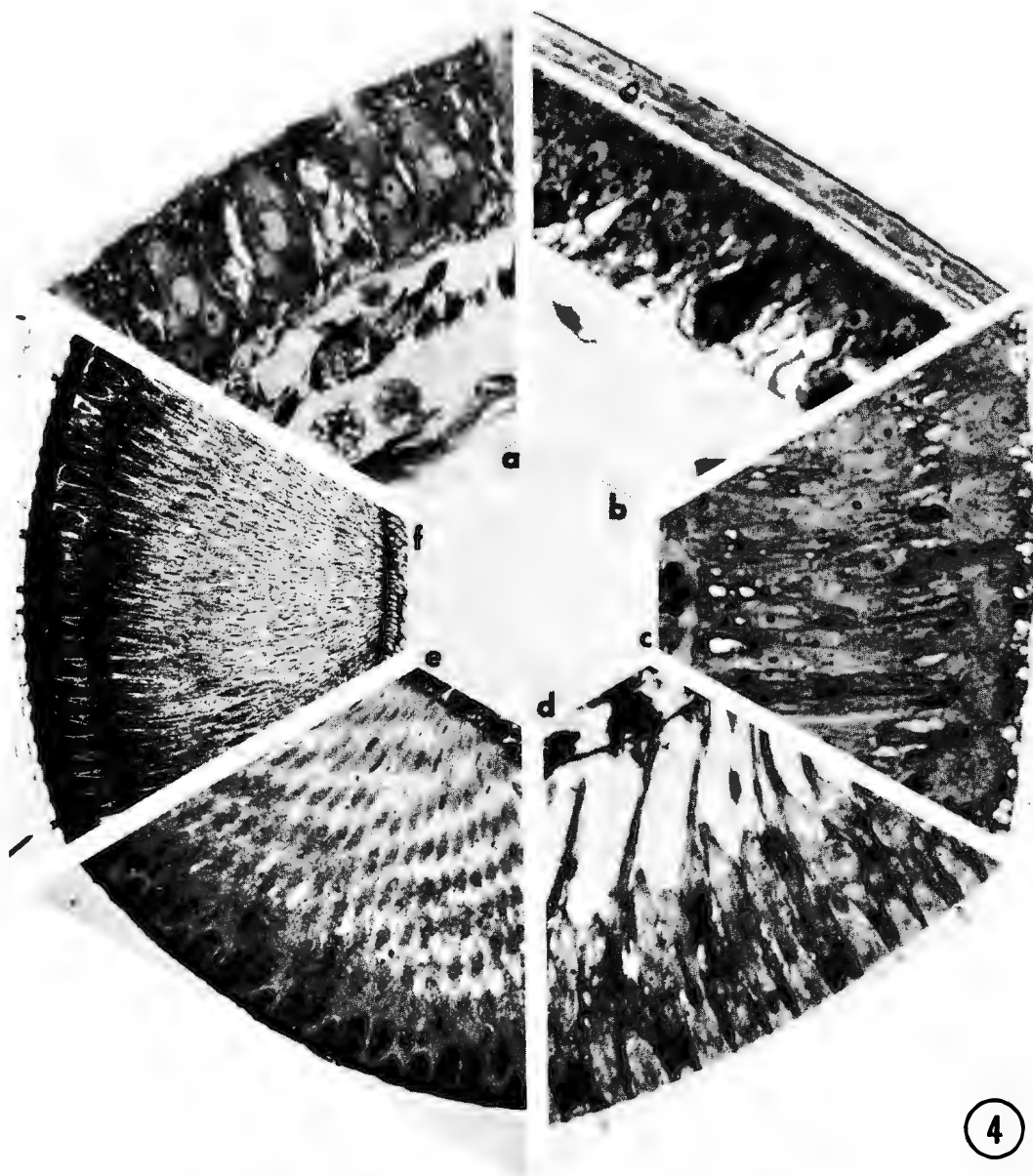
In conclusion, the differentiation of indistinguishable primordial optic cells into adult ommatidia represented a striking

example of the precise timing of cellular processes during development. Cell membrane junctions served to anchor adjacent cells to one another, while junction disappearance allowed for free cell migration. Transient microtubules appeared to be involved in elongation in both the dioptic and receptor systems, while persistent microtubules within the cone cell processes appeared to function in anchoring the dioptic and receptor systems together.

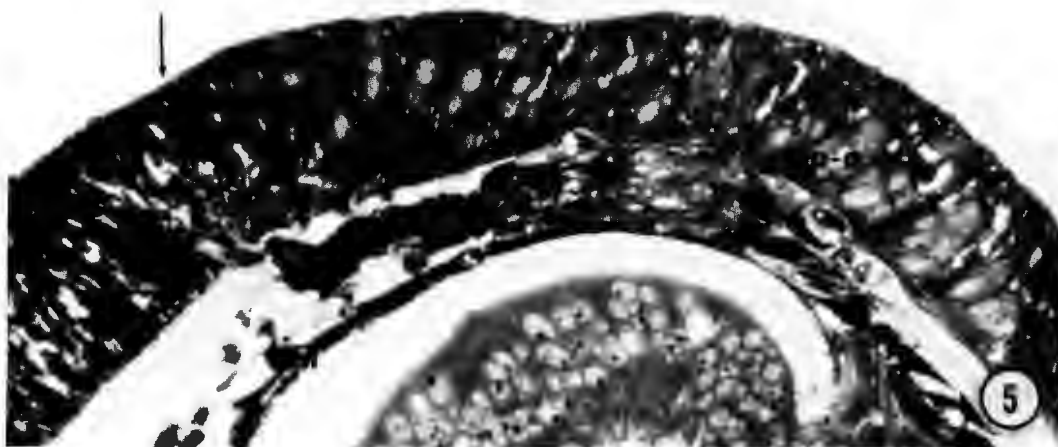
Figure 4. Longitudinal sections of portions of the worker honey bee compound eye at different developmental stages.

- a) stage 4 The retinula is spindle-shaped and the cone cells surround the distal portion. X 723
- b) stage 5 The retinula is still spindle shaped and the cone cells surround the distal portion. The optic primordium has expanded and the retinulae are not as closely apposed to one another as in the preceding stage. X 613
- c) stage 7 The retinulae have elongated and have sunk proximally. The cone is spherical. X 591
- d) stage 8 Note the elongate, axon-like portion of the distal region of the retinulae. X 324
- e) stage 10 Oblique section, differentiation is essentially complete. X 193
- f) adult Note biconvex shape of each lens facet. X 148

Figure 5. Region of the optic primordium in which cells are reorganizing to form pre-ommatidial cell clusters. The area of the morphogenetic furrow is indicated by an arrow, pre-ommatidial cell clusters (p-o) are located to the right, and the entire region is underlain by a basement membrane (bm). X 385



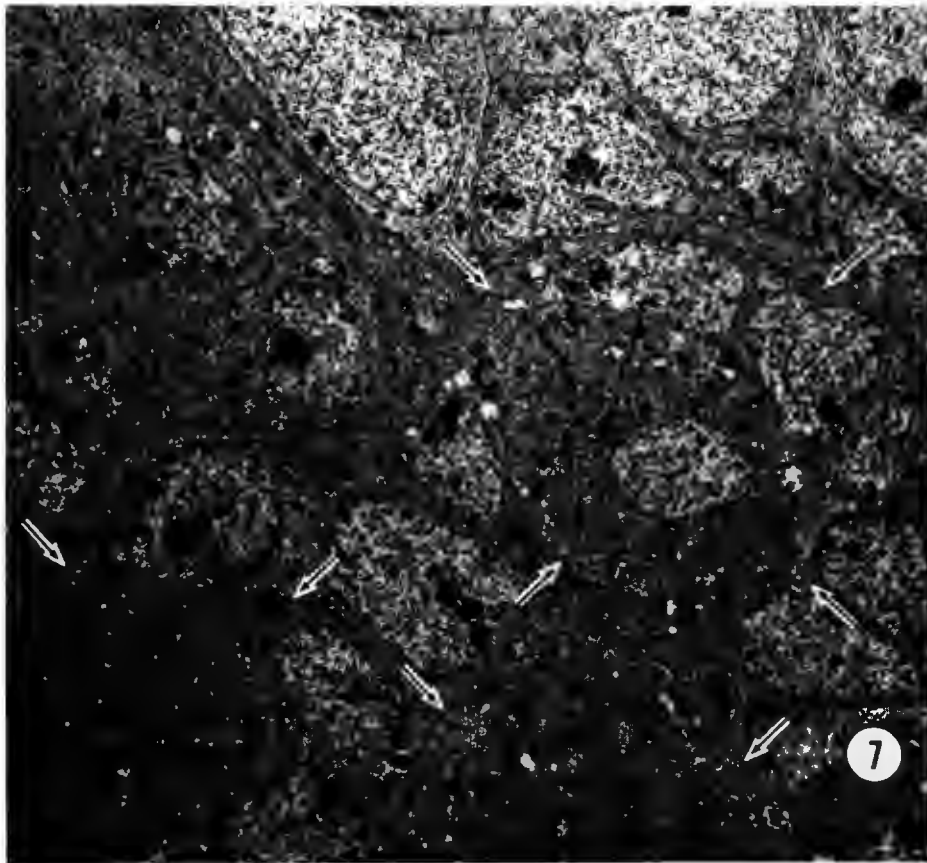
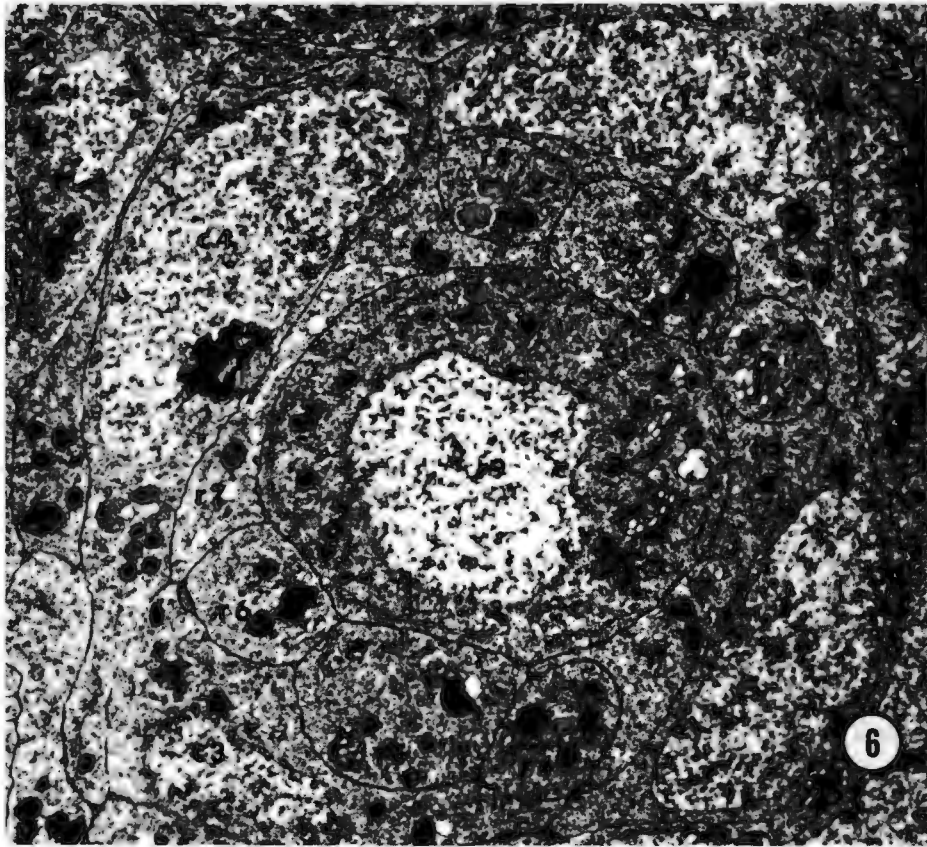
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Figure 6. Stage 1. Cross-section through a preommatidial cell cluster composed of one centrally located and eight concentrically arranged retinula cells (r1-9), surrounded by four cone cells (c1-4). X 10073

Figure 7. Stage 1. Cross-section through the optic primordium showing portions of several preommatidial cell clusters (arrows). X 5348



Figures 8-14. Cuticle secretion

- Figure 8. Stage 2. Apices of cone (c) and cone-adjunct pigment (c-a) cells showing microvilli with plaque-like structures at their tips. Note: adherens junctions between adjacent cone and those between cone and cone-adjunct pigment cells are (single arrow). X 22000
- Figure 9. Stage 3. A multivesicular body (mvb) with a plaque-like structure in its membrane (arrow). Similar multivesicular bodies are abundant in the distal cytoplasm of cone, cone-adjunct pigment, and retinula-adjunct pigment cells during this stage. X 36250
- Figure 10. Stage 3. Microvilli have disappeared from the apical surfaces of the cone and cone-adjunct pigment cells, and multivesicular bodies with plaque-like structures in their membranes (mvb) have appeared in the distal cytoplasm. X 9300
- Figure 11. Stage 6. Cuticulin deposition. Note the trilaminar structure formed by deposition of material by the plaque-like structures of the apical microvilli. X 35325
- Figure 12. Stage 8. Microvilli along the cone cell (c) apex, underlying the developing cuticular lens (cl). Microvilli are smaller than those of the cone-adjunct and retinula-adjunct pigment cells. X 63000
- Figure 13. Stage 8. Microvilli along the cone-adjunct (c-a) and retinula-adjunct (r-a) pigment cell apices underlying the interlens (il) portion of the cuticle. Microvilli are larger than those of the cone cell. X 40000
- Figure 14. Stage 11. Microvilli along the apices of the cone (c) and cone adjunct (c-a) pigment cells. Microvilli are similar in size in both cell types X 49000

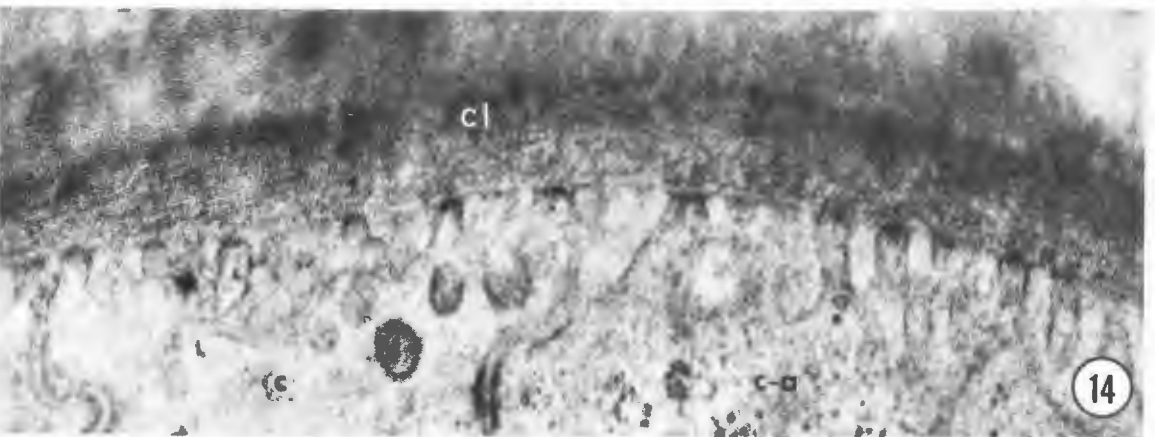
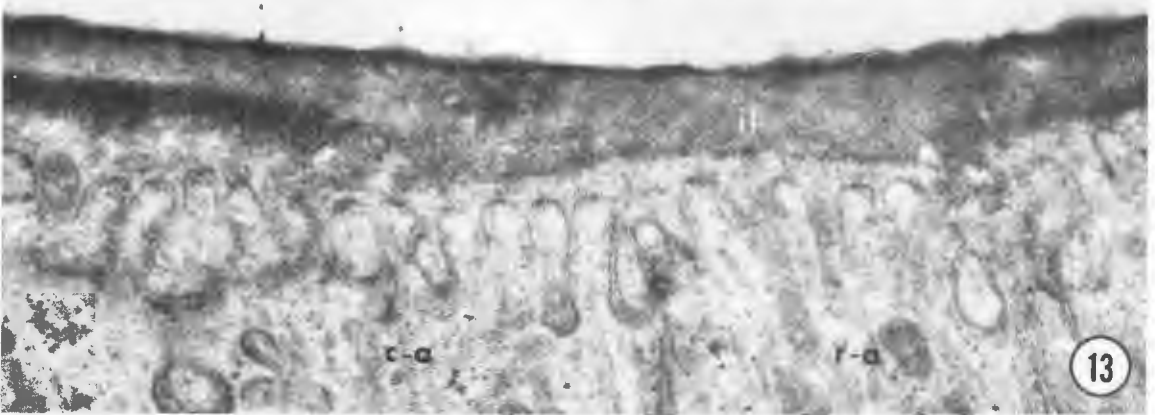
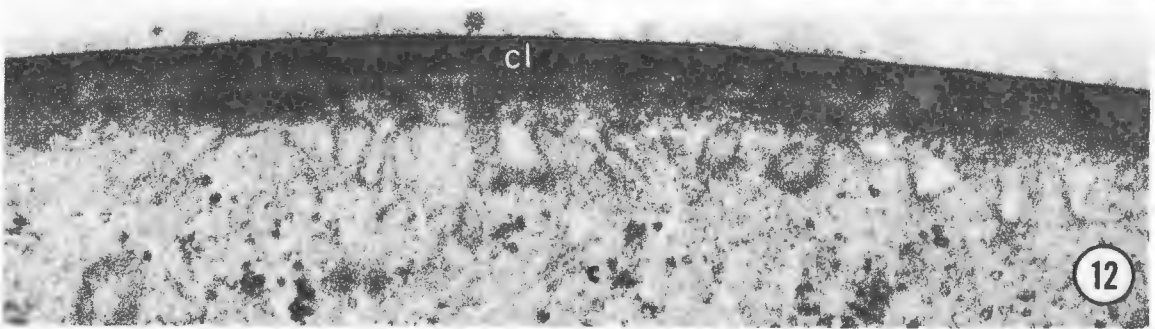
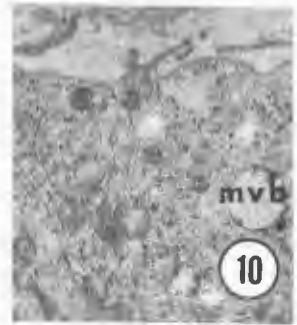
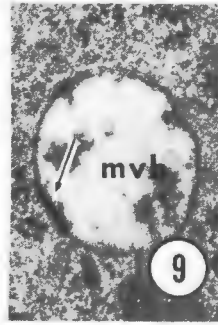
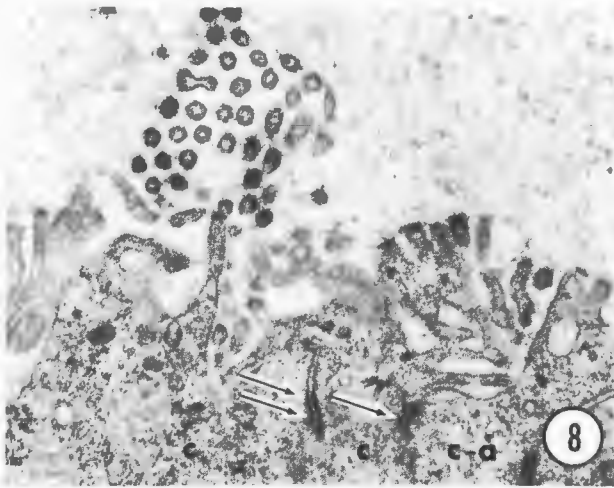


Figure 15. Stage 5. Cross-section through the dioptric system showing the four cone cells (c) surrounded by two cone-adjunct pigment (c-a) cells. Two of the cone cells meet along their inner surfaces. X 8266

Figure 16. Stage 5. Cross-section through the distal region of the retina. The eight concentrically arranged retinula cells are surrounded by four cone cells (c) which contain microtubules oriented perpendicular to the ommatidial axis. The rhabdomeres of the eight retinula cells contain few pigment granules (pg). Numerous longitudinally oriented microtubules are contained in the peripheral portion of the retinula cytoplasm. Several multivesicular bodies (mvb) with plaque-like structures in their membranes are seen within the retinula cells. Numbering of the retinula cells is according to the scheme of Gribakin (1967a, 1969, 1972, 1975). X 10913

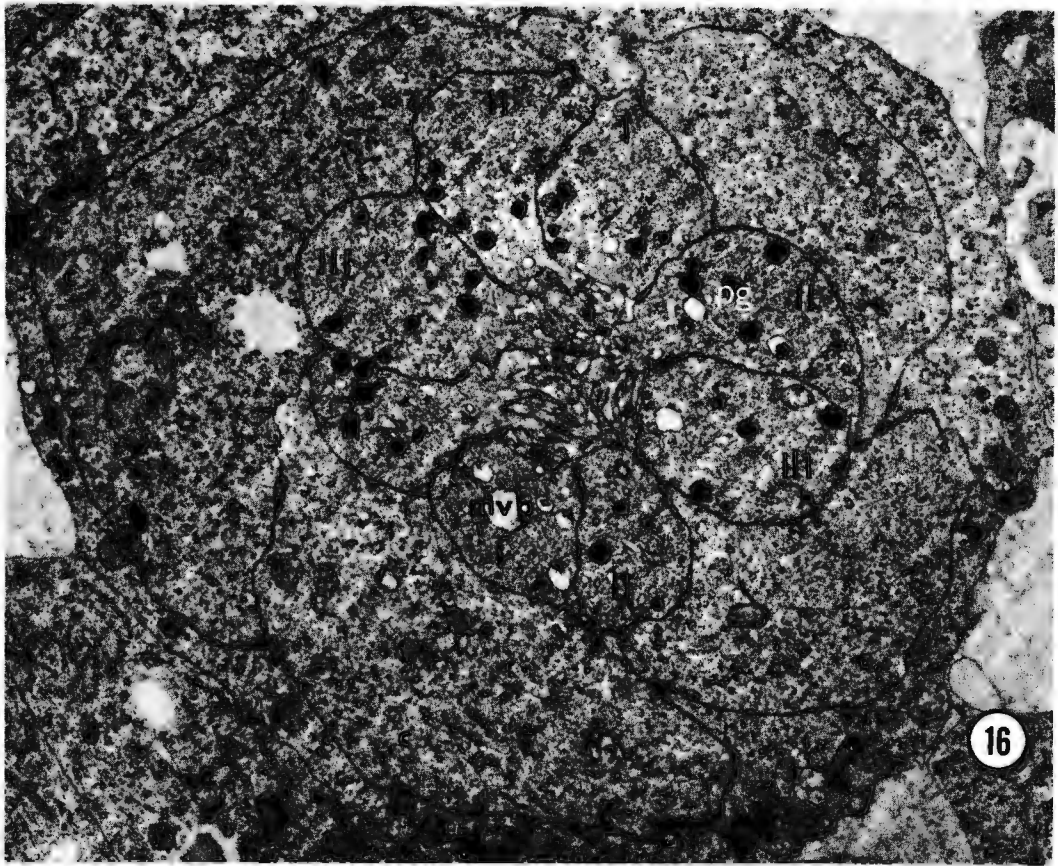
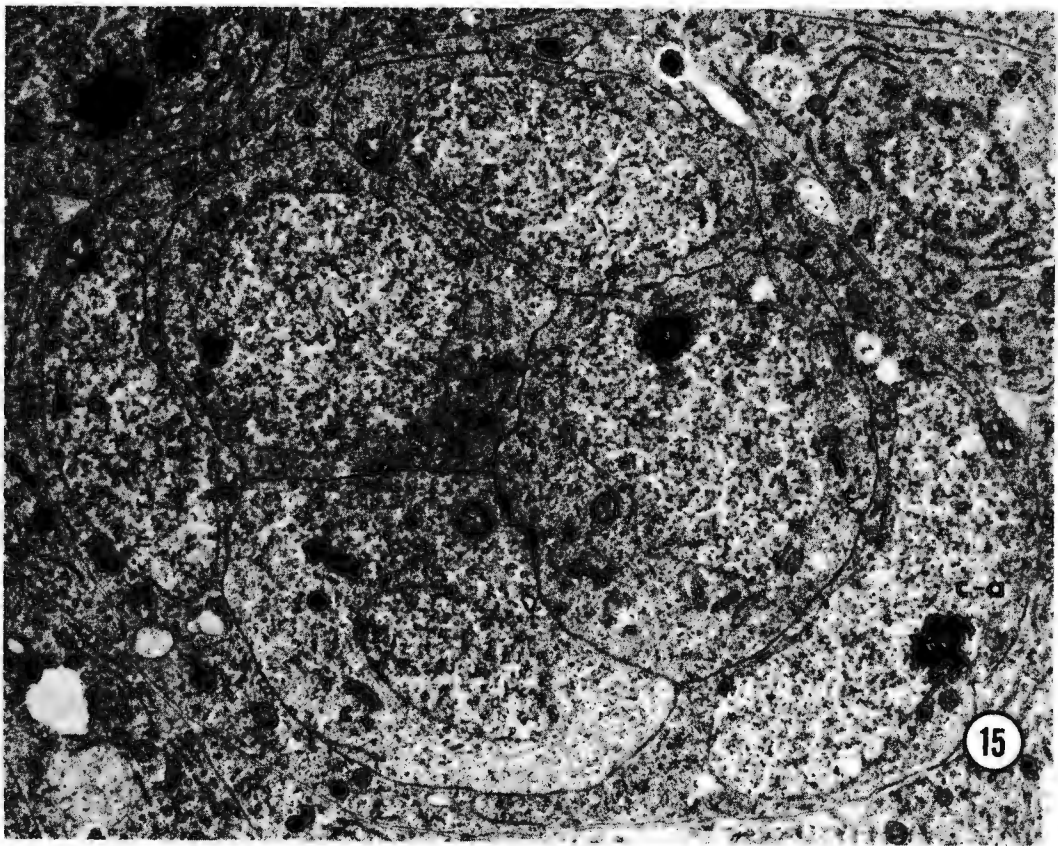


Figure 17. Stage 5. Cross-section through the junction of the distal and middle regions of the retinula showing the centrally located ninth retinula cell surrounded by the eight concentrically arranged retinula cells. Note: adherens junctions between the ninth retinula cell and the surrounding eight. Numerous microtubules are located near the retinula periphery. X 11257

Figure 18. Stage 5. Cross-section through the junction of the middle and proximal regions of the retinula showing the two type III cells narrowing to form axons. X 7619

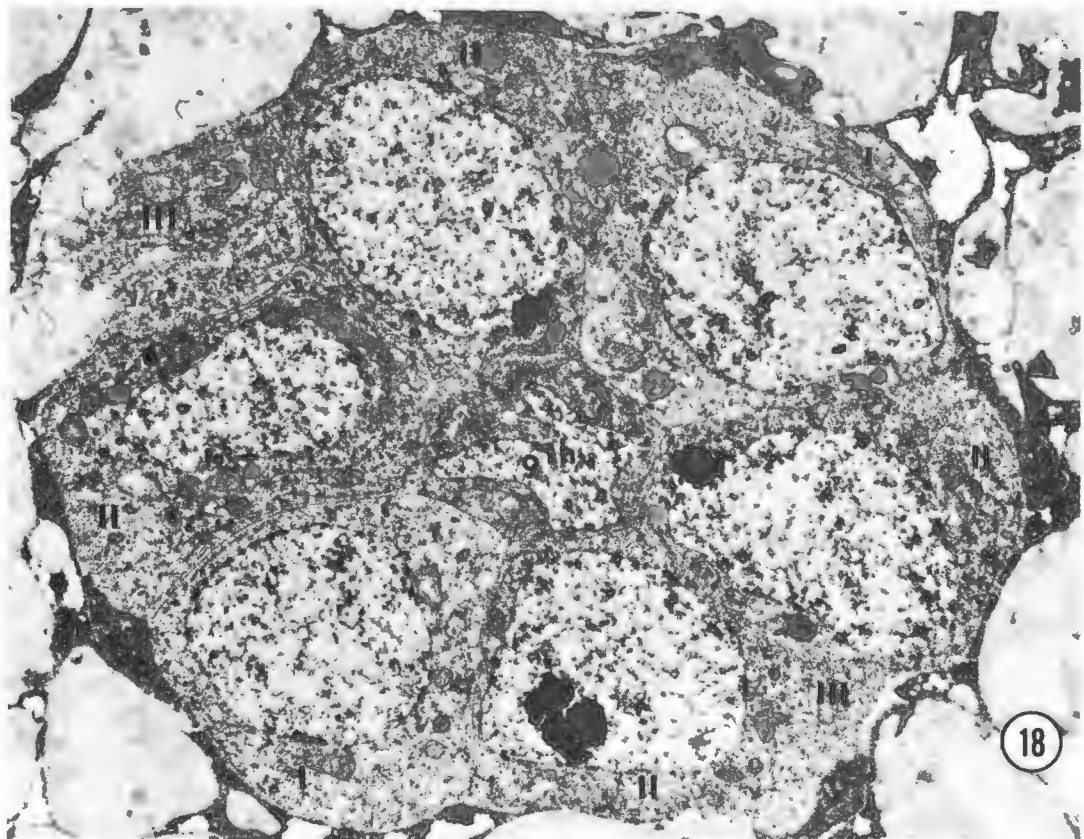
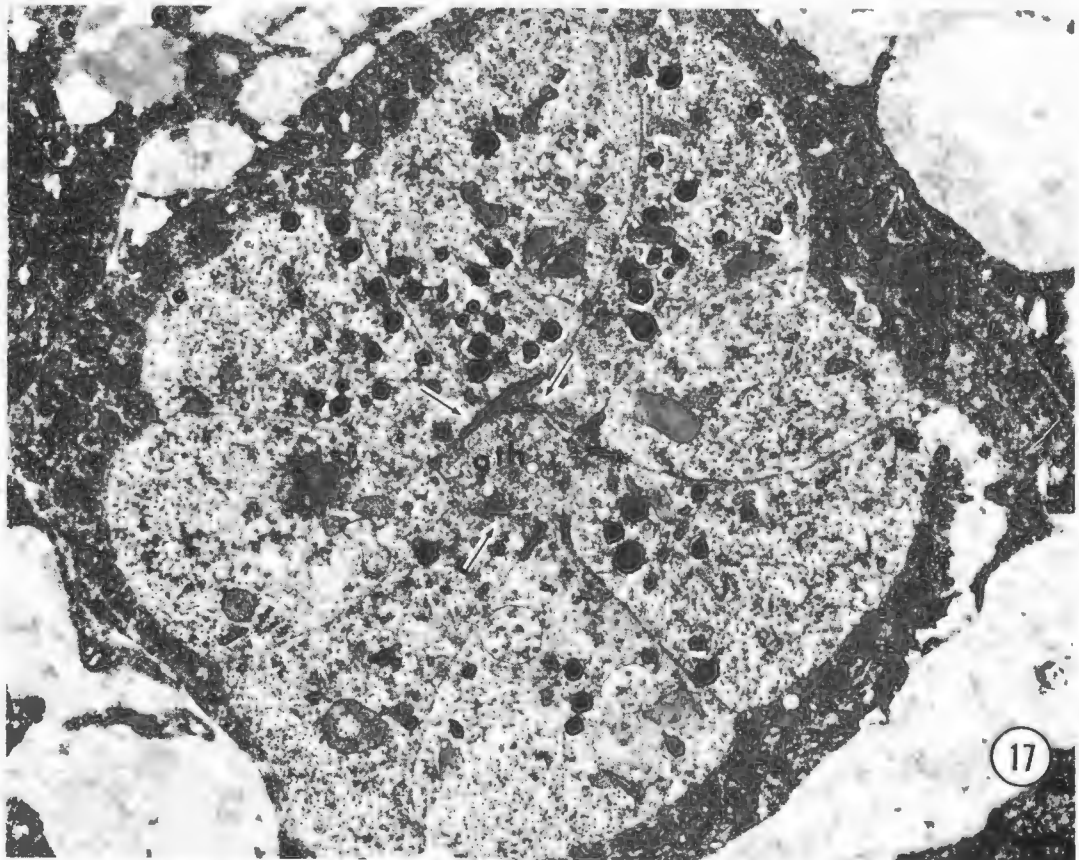


Figure 19. Stage 6. Cross-section through the retinula and surrounding retinula-adjunct pigment cells (r-a) at the level of the boundary between the distal and middle levels. The tip of the ninth retinula cell is present only at this level. X 8250

Figure 20. Stage 5. Cross-section through several retinula-adjunct pigment cells at the level of their nuclei showing the concentric arrays of granular endoplasmic reticulum (ger). X 5931

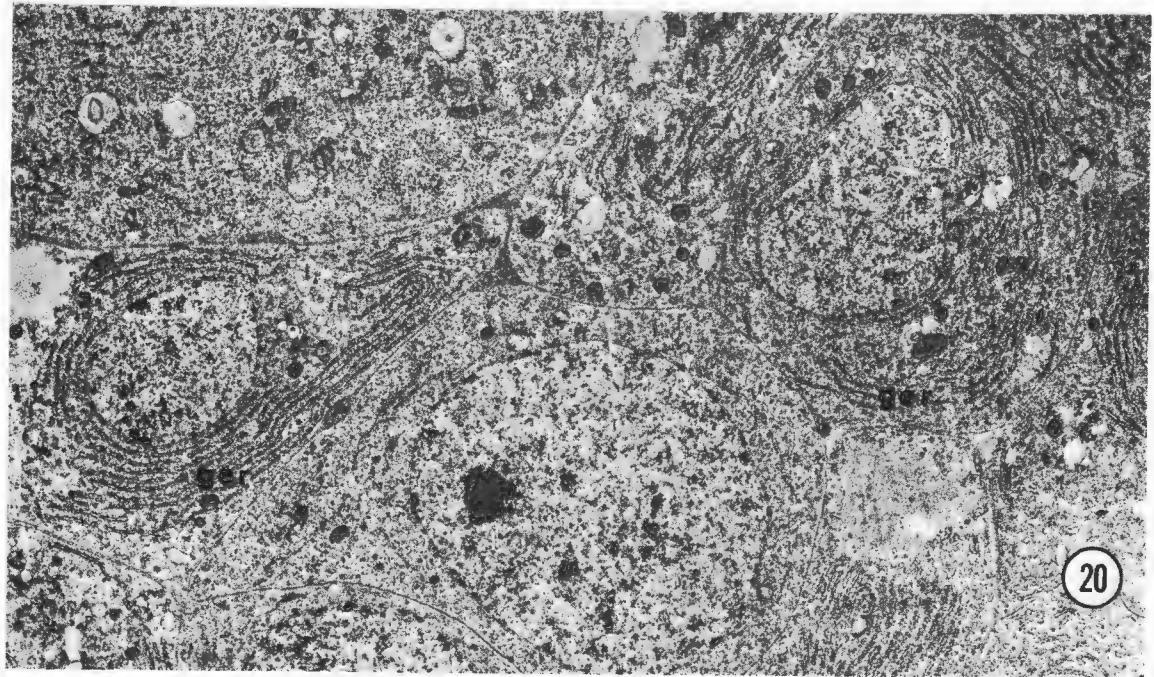
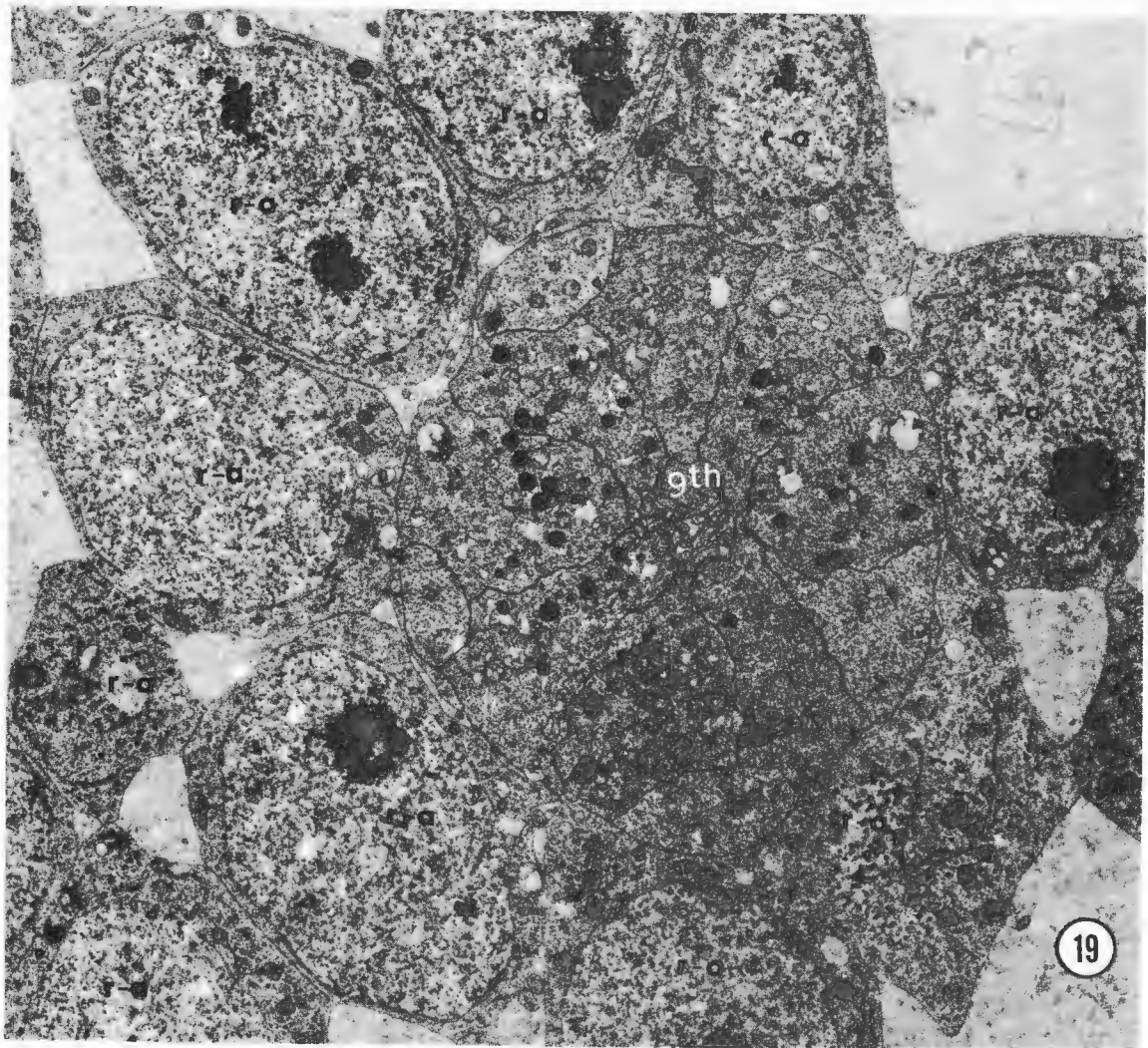
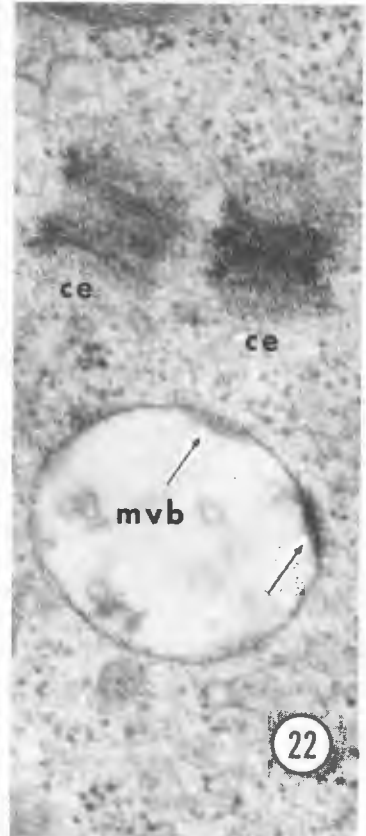
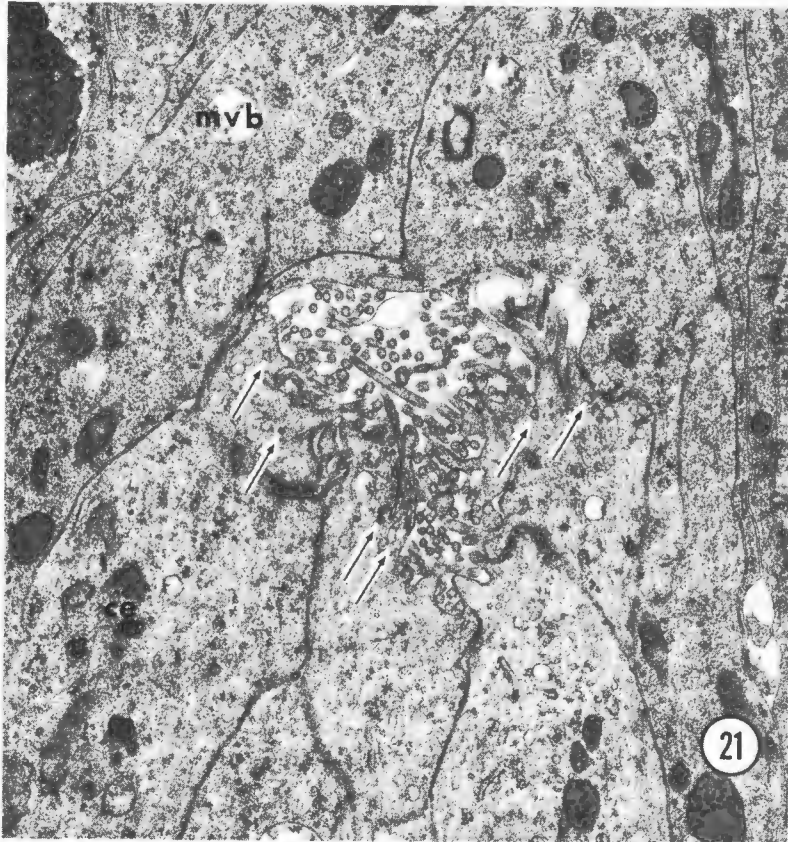


Figure 21. Stage 5. Oblique-section through the retinula. Note vesicles (single arrow), centrioles (ce) and multivesicular bodies (mvb) in the cytoplasm surrounding the developing rhabdomeres. X 13035

Figure 22. Stage 5. A multivesicular body (mvb) shown at high magnification with several plaque-like structures in its membrane (arrows) and parallel paired centrioles (ce) from the retinula cell cytoplasm. X 65250



- Figure 23. Stage 6. Slightly-oblique section through the retinula distal region showing the cone cell processes (cp). Note the numerous longitudinally oriented microtubules located within both the peripheral and central retinula cytoplasm.
X 13035
- Figure 24. Stage 6. Longitudinal section through the proximal region of a cone cell showing the cone cell process (cp) containing numerous longitudinally oriented microtubules.
X 7244
- Figure 25. Stage 6. Cross-section through the boundary between the middle and distal regions of the retinula showing the peripherally located cone cell processes (cp). Structures similar in appearance to lipid droplets (li) are present at this stage within the retinula cell cytoplasm.
X 6944

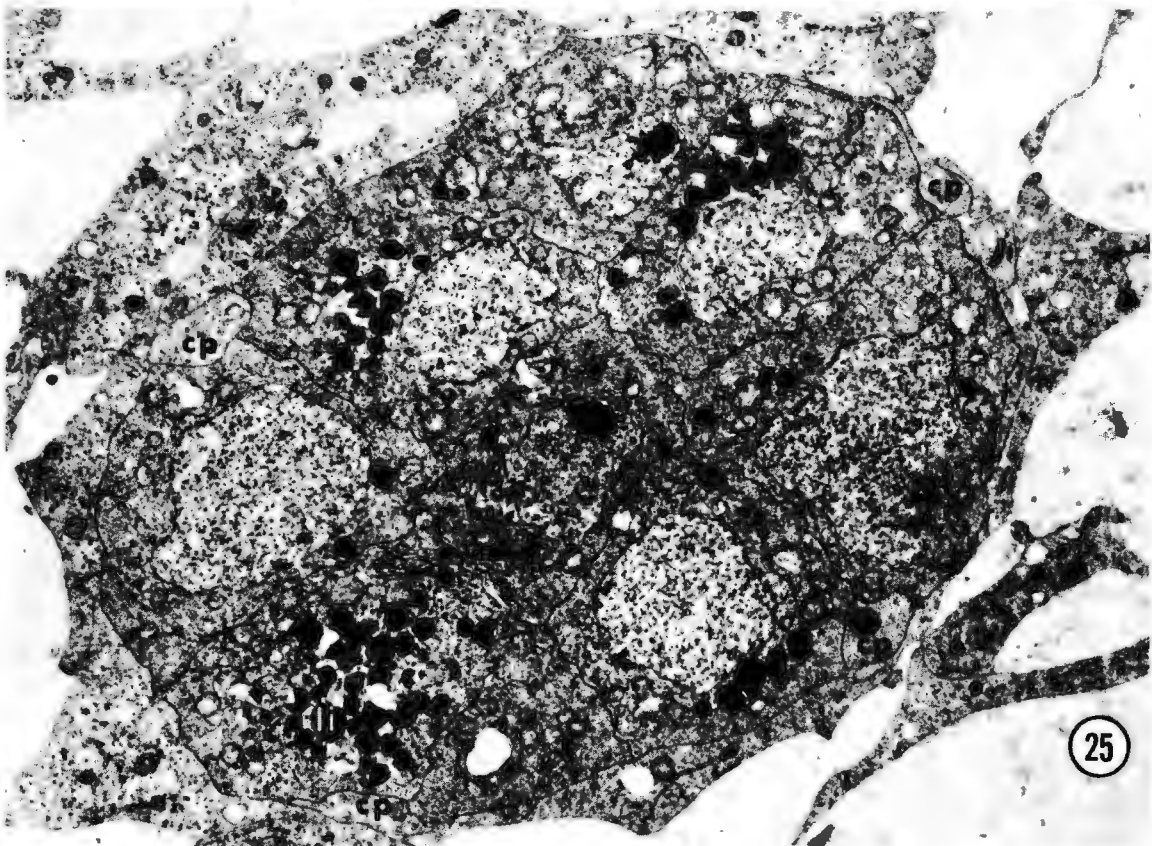
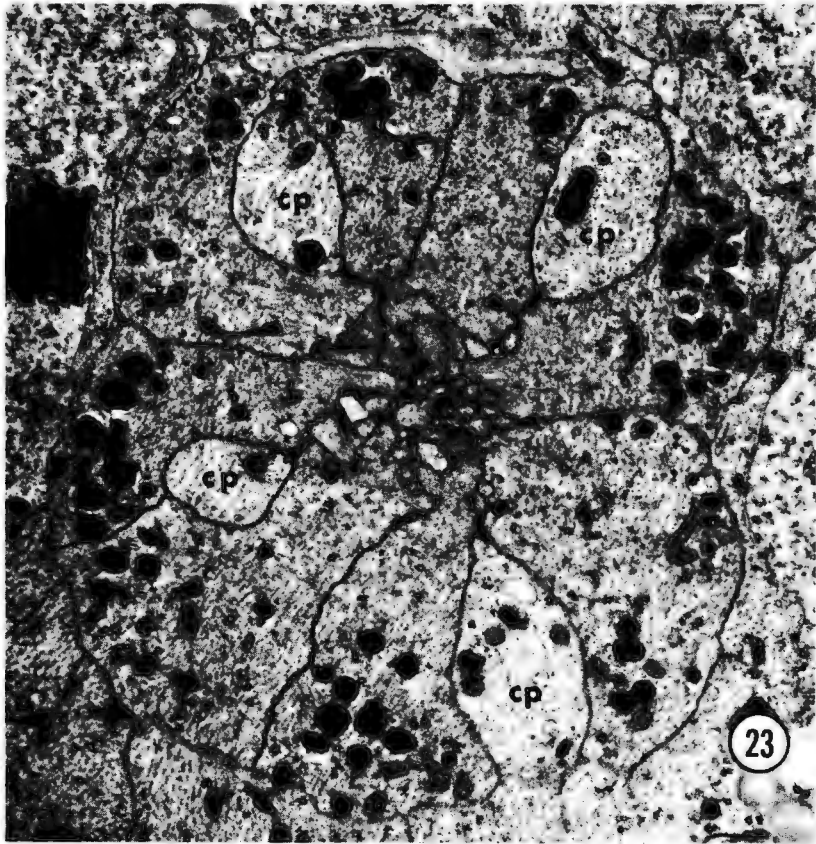


Figure 26. Stage 7. Cross-section through the middle region of the retinula showing the cone cell processes (cp) located just peripheral to the junctional complexes between adjacent retinula cells. The ninth retinula cell is no longer centrally located, and is beginning to develop a rhabdomere. Numerous longitudinally oriented microtubules are located in the peripheral and central regions of the retinula cytoplasm. X 9844

Figure 27. Stage 7. Cross-section through the middle region of the retinula below the level of the developing rhabdom. The ninth retinula cell is located more laterally than in preceding stages, and the cone cell processes (cp) are more centrally located. X 6256

Figure 28. Stage 8. Cross-section through the proximal, axon-like portion of the retinula showing the nine retinula cells, the four cone cell processes (cp) and the surrounding retinula-adjunct pigment cells (r-a). X 8838

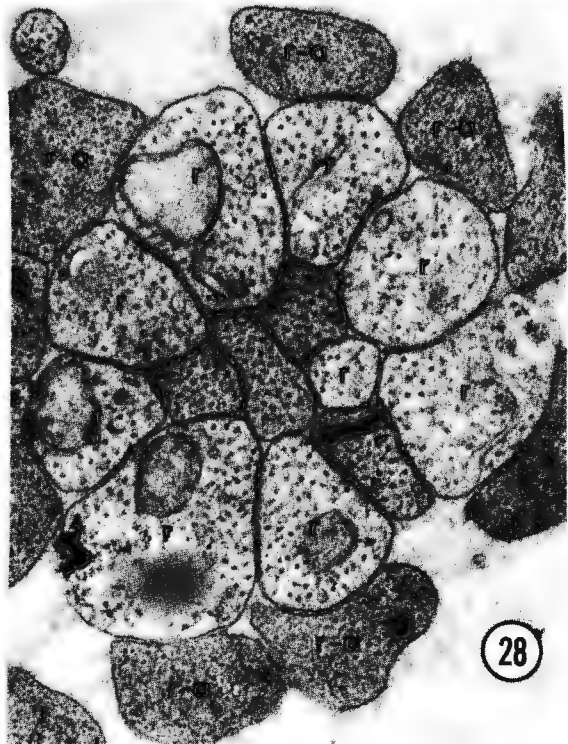
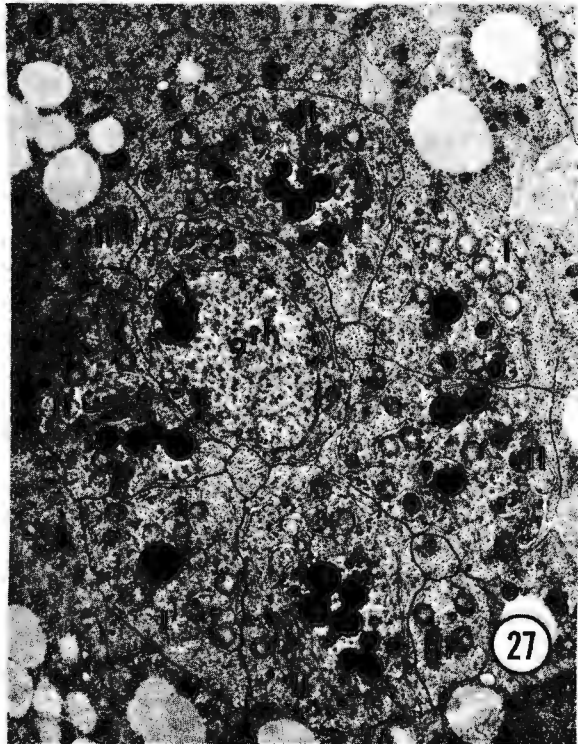
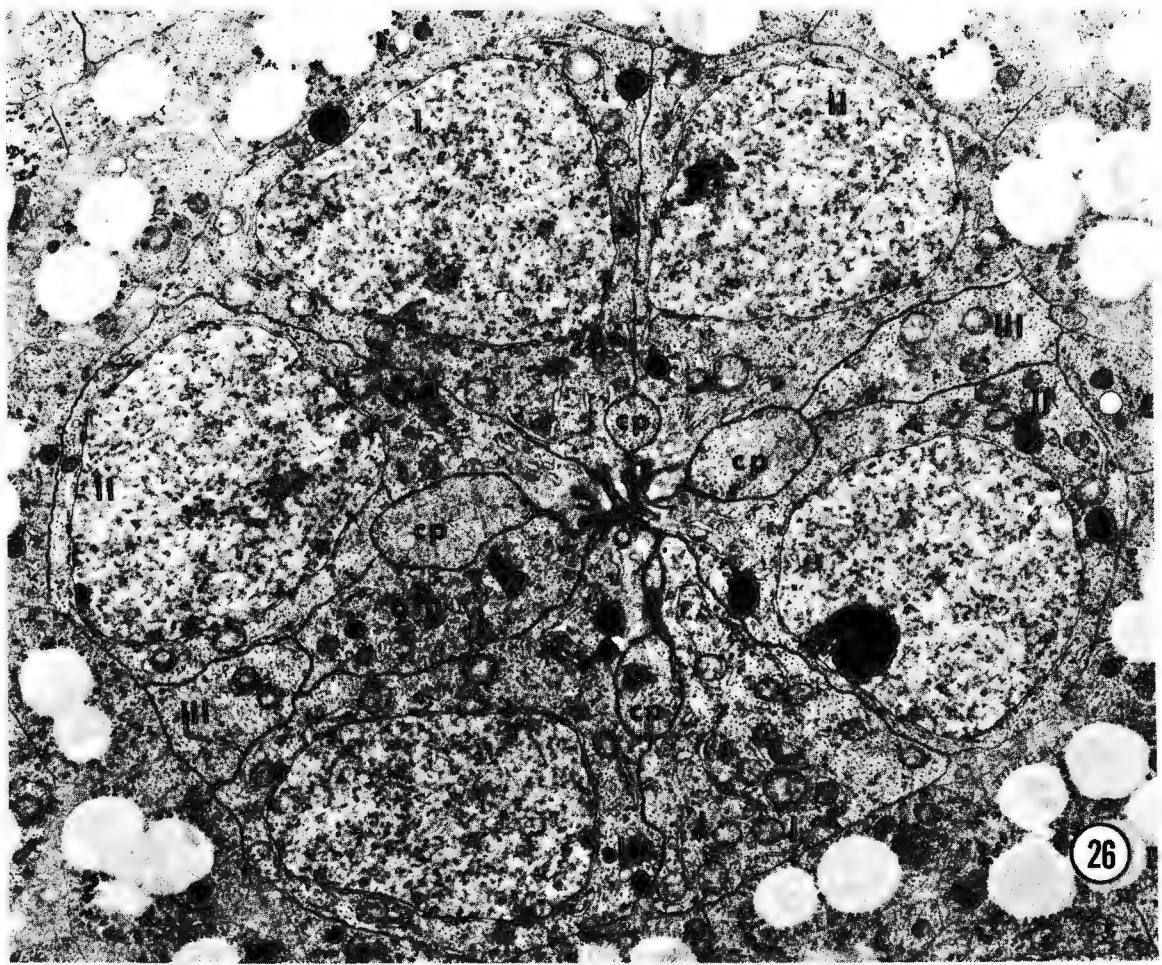


Figure 29. Stage 11. Cross-section through the distal portion of the retinula showing the ovoid cone cell processes (cp) located close to the junctional complexes between adjacent retinula cells. Inflated cisternae (arrows) of the endoplasmic reticulum are located in the central retinula cytoplasm, while most of the mitochondria are more peripherally located. Fewer microtubules are seen within the retinula cell cytoplasm than in preceding stages. Leaf-like processes of the retinula-adjunct (r-a) cells are located the space between adjacent retinula cells. X 12443

Figure 30. Stage 11. Cross-section through the middle region of the retinula at the level where the two type III cells have formed axons. An axon-like structure, possibly a bristle sense cell neurite (bn) is located adjacent to the retinula. X 13944

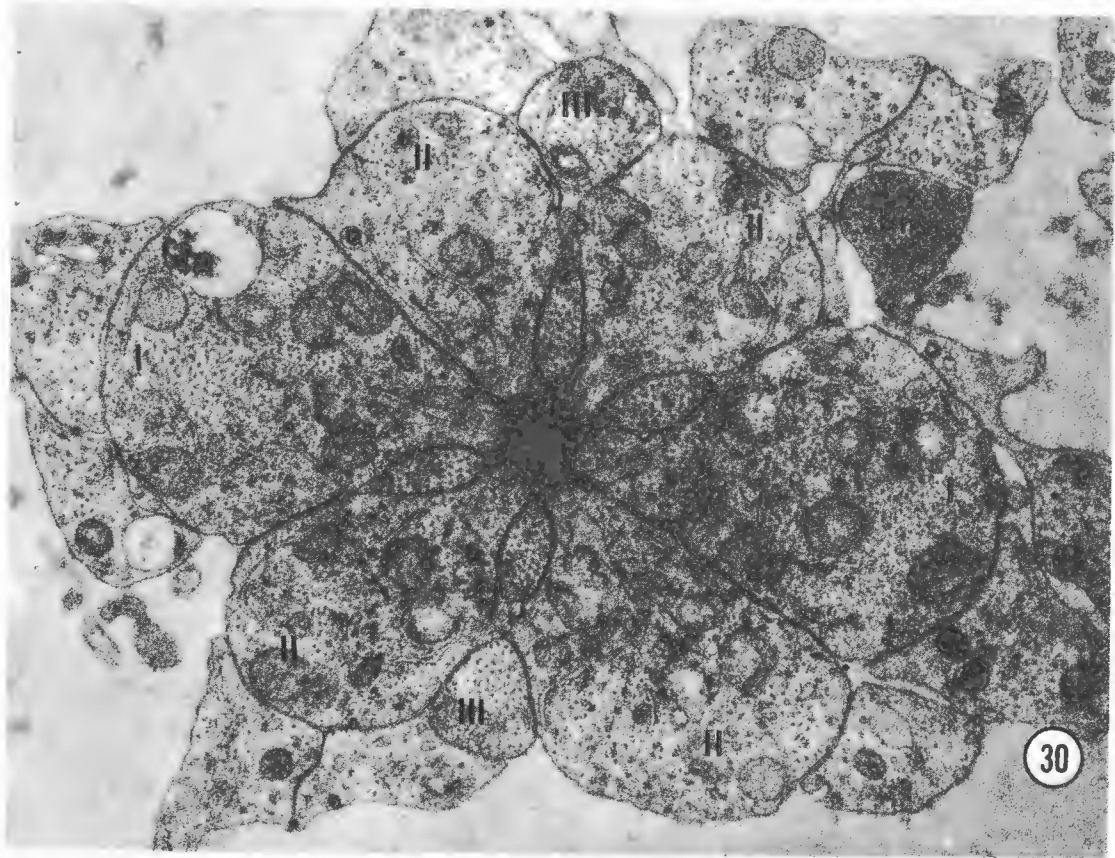
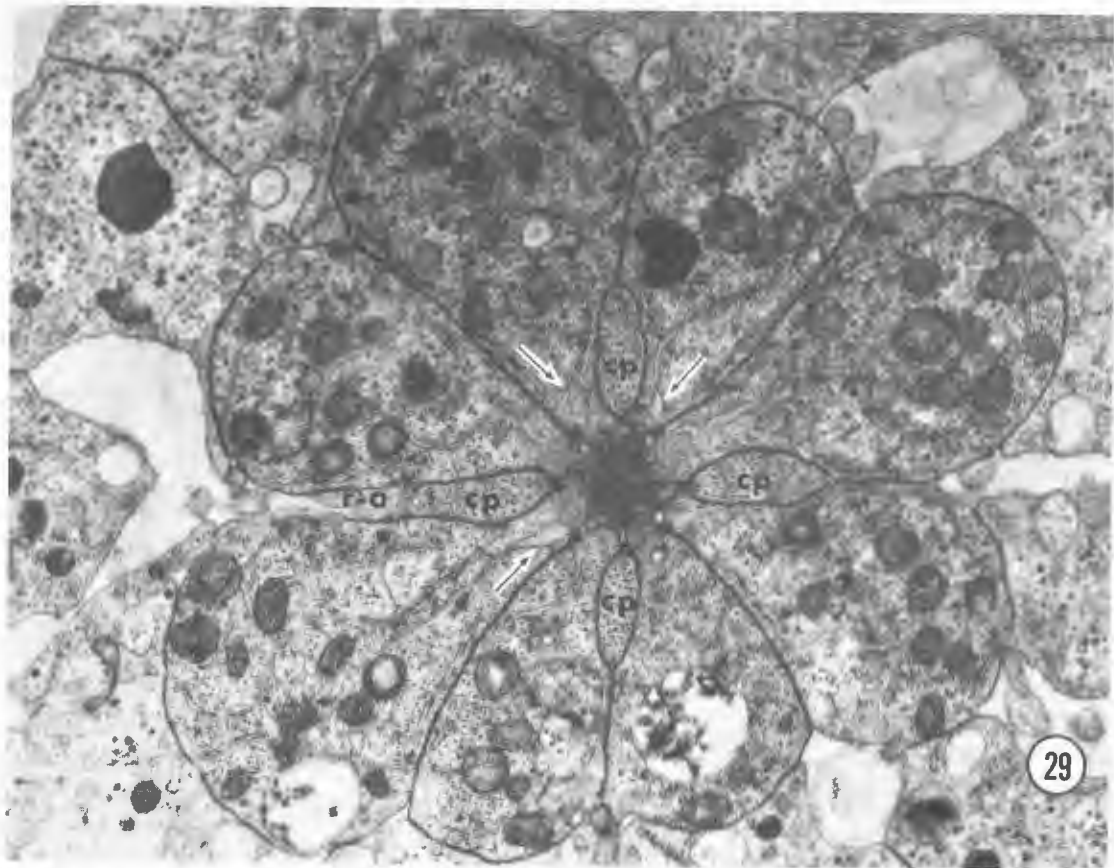
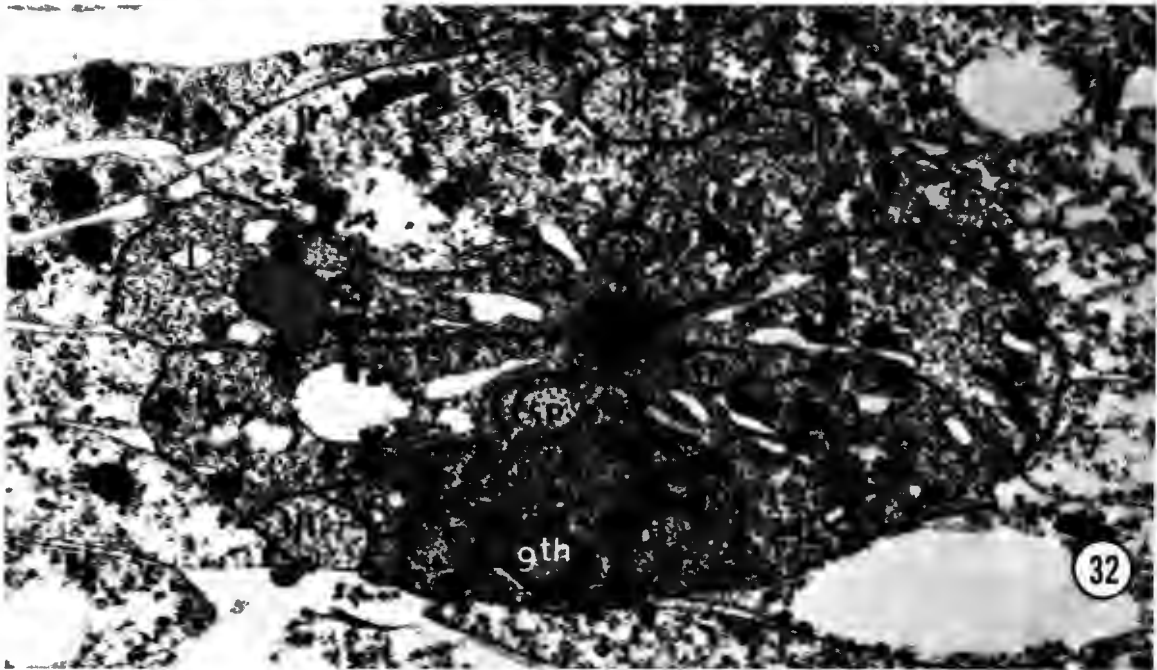
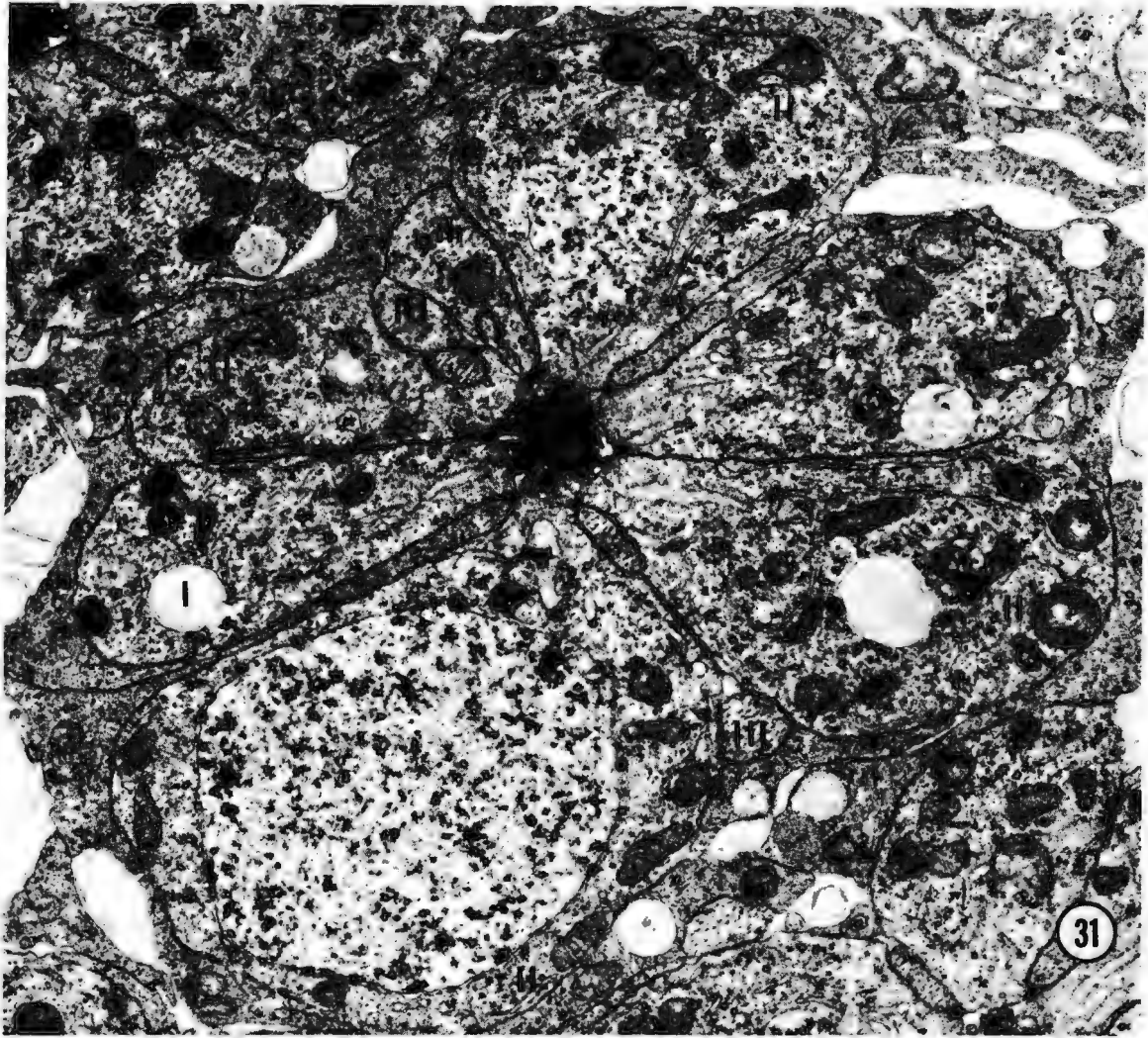


Figure 31. Stage 12. Cross-section through the middle region of the retinula at the level of the distal tip of the ninth retinula cell. X 13035

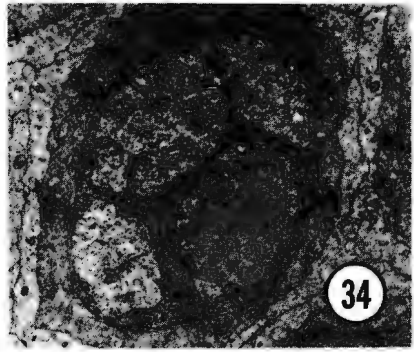
Figure 32. Stage 12. Cross-section through the proximal region of the retinula showing the two type I, four type II, and ninth cells contributing to the rhabdom. At this stage, the two type III cells have formed peripherally located axons. Note that the cone cell processes (cp) are almost round in cross-section. X 16590



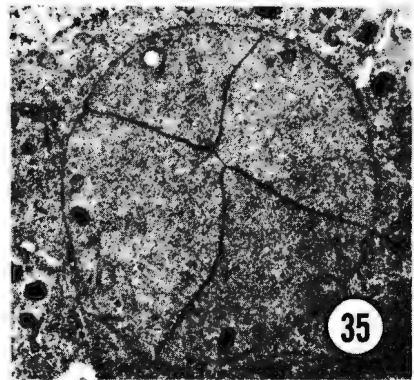
- Figure 33. Stage 11. Slightly-oblique-section through the crystalline cone. Lines indicate approximate levels of cross-sections. X 5088
- Figure 34. Stage 11. Cross-section through the cone at level a. Note the location of the cone cell nuclei along the distal cone cell periphery. X 3214
- Figure 35. Stage 11. Cross-section through the cone at level b. Two of the cone cells meet along the ommatidial axis. X 5925
- Figure 36. Stage 11. Cross-section through the cone at level c. X 5925
- Figure 37. Stage 11. Cross-section through the cone at level d. X 5925
- Figure 38. Stage 11. Cross-section through the cone at level e. Junctional complexes can be seen where the retinula cells contact one another, and where they contact the proximal tip of the cone (arrow). X 9813



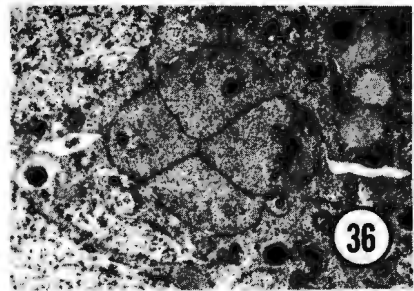
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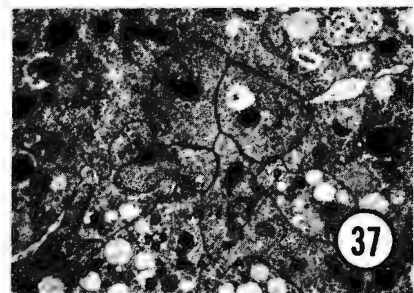
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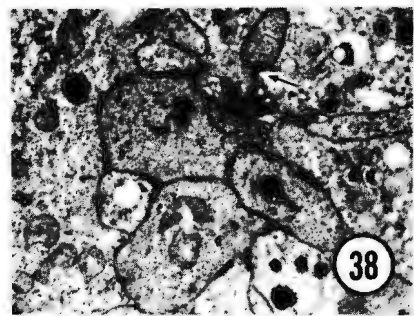
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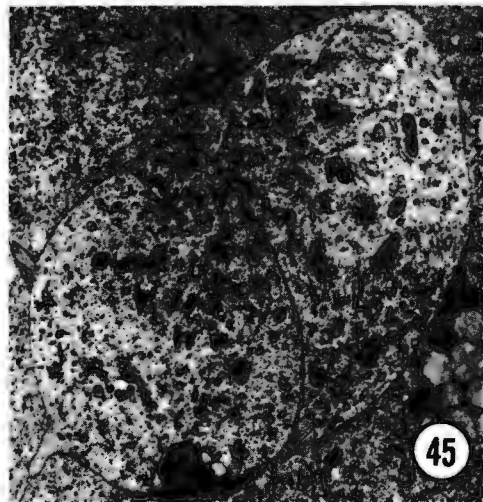
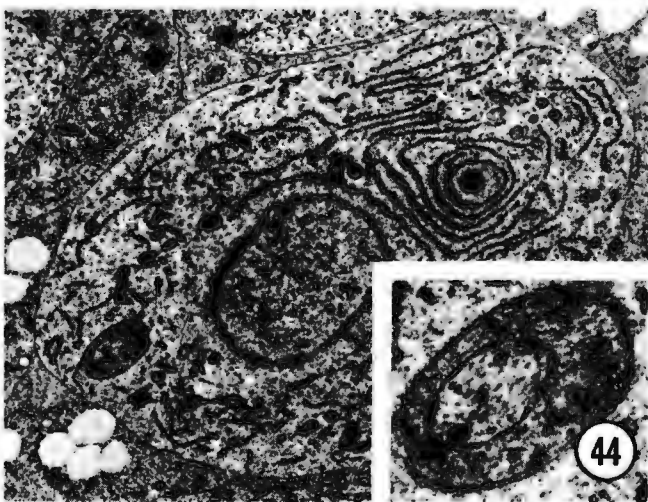
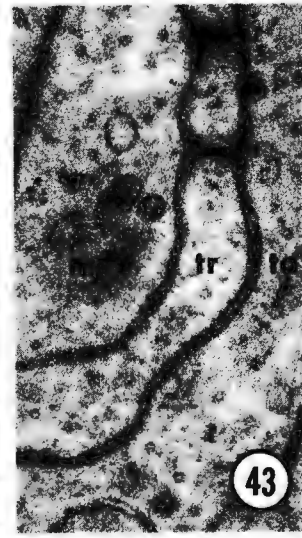
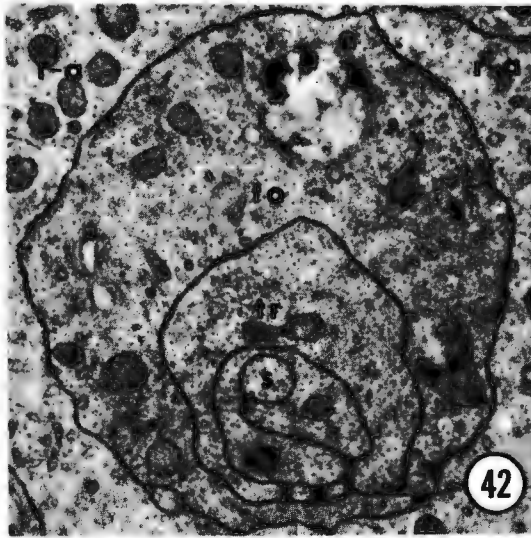
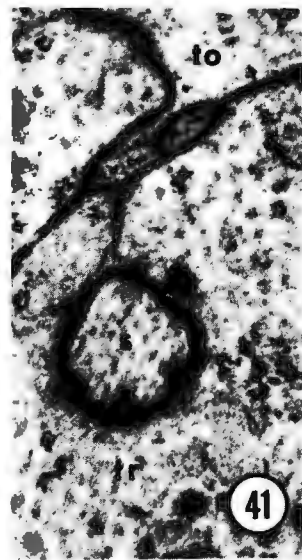
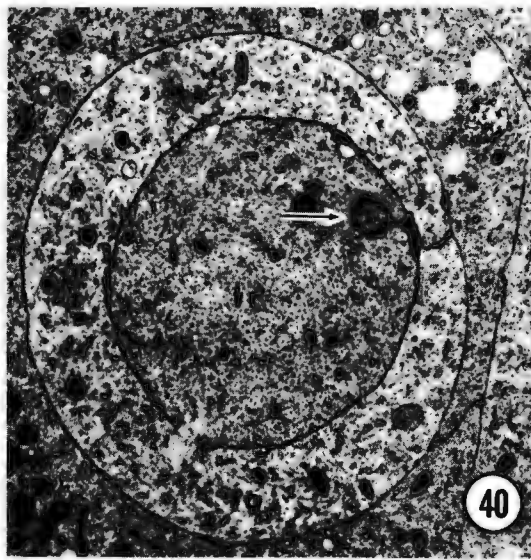
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Figures 39 - 45. Bristle - forming complex.

- Figure 39. Stage 11. Longitudinal section (tangential) through an interommatidial bristle. The bristle is located at the junction of three ommatidia and pierces the cuticle in the interlens region, between adjacent corneal lens (cl) facets. Scolopale indicated by arrow. X 7300
- Figure 40. Stage 11. Cross-section of a bristle-forming complex just proximal to the socket. The neurilemma cell does not extend this far distally. The sense cell (s) is surrounded by the trichogen (tr) and tormogen (to) cells. The scolopale is indicated by an arrow. X 888
- Figure 41. Stage 11. Enlargement of a portion of figure 40 showing the sense (s), trichogen (tr) and tormogen (to) cells. X 35550
- Figure 42. Stage 11. Cross-section of a bristle-forming complex at the level of the distal portion of the crystalline cone. The sense (s) cell is surrounded by neurilemma (n), trichogen (tr), and tormogen (to) cells. The entire bristle-forming complex is surrounded by several retinula-adjunct pigment (r-a) cells. X 17000
- Figure 43. Stage 11. Enlargement of a portion of figure 42 showing the septate desmosomes between the neurilemma (n), trichogen (tr), and tormogen (to) cells. X 60000
- Figure 44. Stage 8. Cross-section of a bristle-forming complex proximal to the level of the tormogen cell. The sense (s) and neurilemma (n) cells are surrounded by the trichogen (tr) cell which contains extensive concentric arrays of granular endoplasmic reticulum (ger). X 5400
Inset. Enlargement of sense (s) and neurilemma (n) cells. X 19800
- Figure 45. Stage 6. Cross-section of a bristle-forming complex showing the adjacent trichogen (tr) and tormogen (to) cells. The sense (s) and neurilemma (n) cells extend in a groove along the trichogen cell. X 5700



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