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Retinal photoreceptor fine structure in the mallard duck *(Anas platyrhynchos)*

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Summary. The retinal photoreceptors of the mallard duck *(Anas platyrhynchos)* consist of rods, single cones and double (unequal) cones present in a ratio of about 1:2:1. The rods have relatively large cylindrical outer segments which in the light-adapted state reach to the retinal epithelial (RPE) cell bodies and are surrounded by the pigment-laden apical processes of these RPE cells. The inner segment displays an apically located ellipsoid of mitochondria and plentiful polysomes, some rough ER and Golgi zones. The rod nucleus is located within the outer nuclear layer and the synaptic pedicle displays both invaginated (ribbon) and superficial (conventional) synaptic sites. Single cones display a thin tapering outer segment, a large often heterogeneous oil droplet in the apical region of the inner segment, an ellipsoid of mitochondria and a prominent paraboloid of glycogen. Double cones consist of a larger chief member which shows a thin tapering outer segment, a large heterogeneous oil droplet and a prominent paraboloid. The small accessory cone shows a thin outer segment, a small granular oil droplet and a paraboloid. As in the single cone, polysomes, RER and Golgi zones are also present within the inner segment. Near the outer limiting membrane the two members of the double cone show a membrane specialization on their contiguous surfaces. Both single and double cones display several invaginated (ribbon) synapses as well as numerous superficial synaptic sites.

Key words: Photoreceptors, Electron microscopy, Mallard duck, *Anas platyrhynchos*

Introduction

The photoreceptors of the vertebrate retina are extremely active, highly polarized and greatly specialized cells in both structure and function. As the first neuron in the visual pathway, they have been studied in a variety of animals (Walls, 1942; Polyak, 1957; Cohen, 1972; Crescitelli, 1972; Young, 1974, 1976; Bok and Young, 1972; Braekevelt, 1975, 1983a, 1985). These studies have shown that all vertebrate retinal photoreceptors are constructed on an essentially similar plan consisting of an outer segment (light-sensitive area) joined to an inner segment (synthetic area - often further compartmentalized) by a nonmotile connecting cilium, a nuclear region and a synaptic ending (Cohen, 1963, 1972; Crescitelli, 1972; Rodieck, 1973). Phylogenetic and generic specialization such as glycogen deposits or oil droplets are often superimposed on this basic plan (Cohen, 1972; Fineran and Nicol, 1974, 1976; Braekevelt, 1982).

Traditionally, retinal photoreceptors have been classified as either rods or cones on the basis of morphological criteria (Walls, 1942; Cohen, 1972; Stell, 1972). While in some species the morphology can become somewhat ambiguous (Sjostrand, 1958, 1959; Pedler, 1965, 1969) and multiple receptors such as double or twin cones are sometimes encountered (Cohen, 1972; Rodieck, 1973; Braekevelt, 1975, 1985) for most species the classification of rods and cones adequately and accurately describes these cells (Crescitelli, 1972; Rodieck, 1973; Braekevelt, 1984, 1985).

The avian retina normally displays three types of photoreceptor namely rods, single cones and double (unequal) cones (Morris and Shorey, 1967; Morris, 1970; Meyer, 1977). Most studies on avian photoreceptors have however been carried out on readily available species like the chicken and pigeon with very few other birds having been examined. Consequently as part of a comparative morphological study of vertebrate photoreceptors, this report describes the fine structure of the rods and cones (both single and double) in the duplex retina of the mallard duck *(Anas platyrhynchos)*.

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Materials and methods

For this study the eyes from six adult, light-adapted mallards *(Anas platyrhynchos)* of both sexes were examined by light and electron microscopy. With the bird under deep anesthesia, the eyeballs were enucleated, opened at the equator and fixed for 5h at 4° C in 5% glutaraldehyde buffered to pH 7.3 with 0.1M Sorensen's phosphate buffer. The posterior half of the eyeball was then removed, washed in 5% sucrose in 0.1M Sorensen's buffer (pH 7.3) and cut into pieces less than 1mm^2, taking care not to detach the retina. The tissue was then postfixed for 2h in 1% osmium tetroxide in the same phosphate buffer, dehydrated through graded ethanols to methanol and propylene oxide and finally embedded in Araldite.

Pieces of plastic-embedded tissue were reorientated to desired angles by means of a wax mount and thick sections (0.5 μm) were cut, stained with toluidine blue and examined by light microscopy. Thin sections (60-70 nm) of selected areas were then cut and collected on copper grids. These sections were stained in aqueous uranyl acetate and lead citrate and examined and photographed in a Philips EM 201 transmission electron microscope.

Results

Three distinct types of photoreceptors are found in the duplex retina of the mallard duck (*Anas platyrhynchos*). These are rods, single cones and unequal double cones (Figs. 1-3). These are present in a ratio of about 1:2:1 respectively. No regular pattern of arrangement or mosaic was noted for these photoreceptor types nor were retinal areas observed where one photoreceptor type was in obvious predominance.

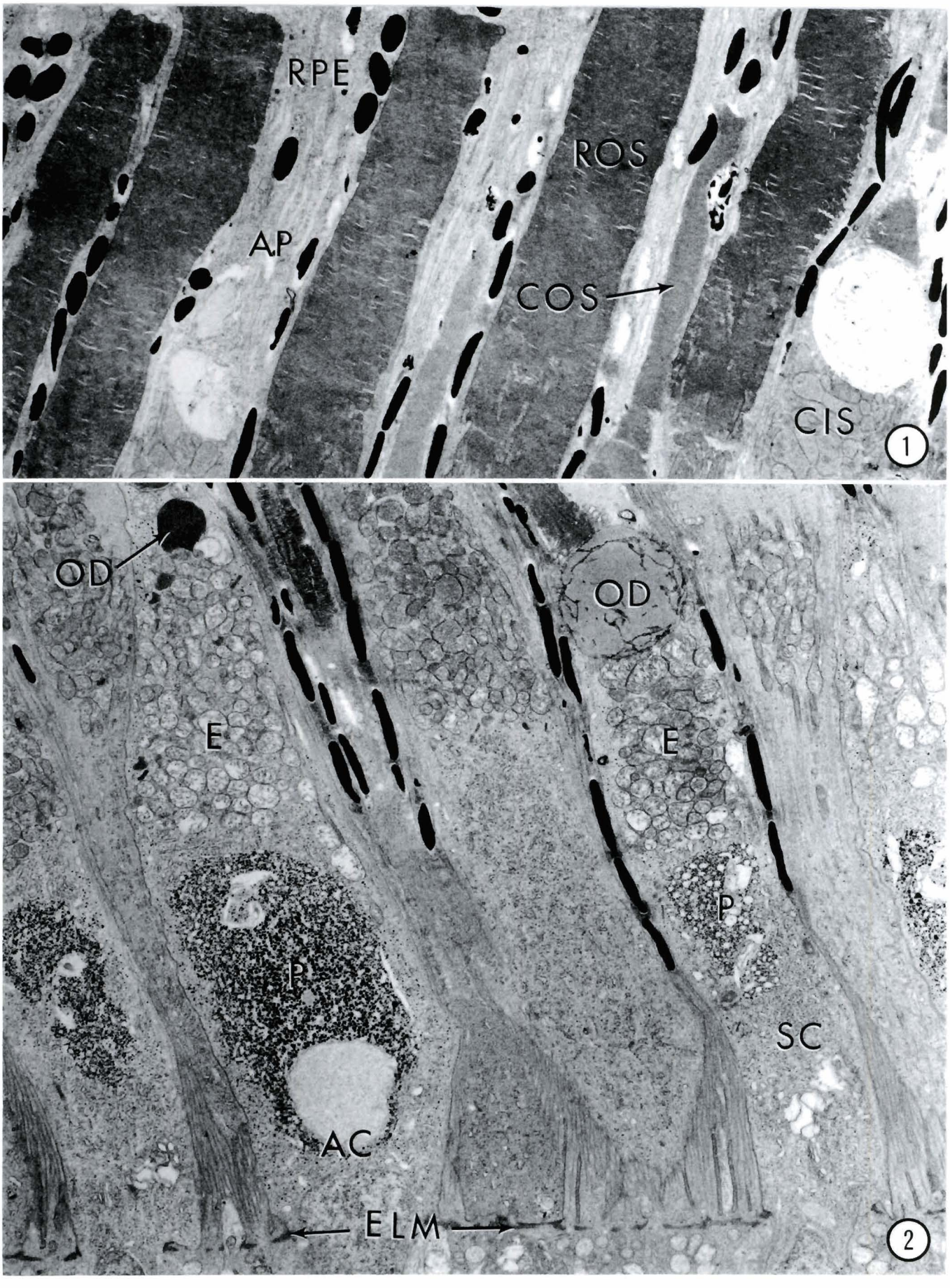
Rod photoreceptors are relatively large in this species with the outer segment measuring approximately 18-20 μm in length and 3 μm in width (Fig. 1). In the light-adapted condition, the tips of the rod outer segments reach to the body of the RPE cells while the rest of the outer segment as well as a portion of the inner segment is surrounded by the pigment-laden apical processes of the RPE cells (Fig. 1) which reach to within 7 or 8 μm of the external limiting membrane (ELM) (Fig. 2). In light-adaptation the rod myoid is very thin and difficult to locate amongst the cone photoreceptors and only near the ELM is the rod inner segment obvious when it measures about 3 μm in width (Fig. 7). The rod photoreceptors display a small ellipsoid of mitochondria immediately below the outer segment (Fig. 1). These mitochondria are small and for the most part rod-shaped and aligned with the long axis of the inner segment (Fig. 1). The rod inner segment shows no oil droplet or accumulation of glycogen as is noted for the cone photoreceptors (Fig. 1). Near the ELM however, polysomes and Golgi zones are plentiful as well as some profiles of rough endoplasmic reticulum (RER) (Fig. 7). Presumed autophagic vacuoles are also noted in the inner segment. As a rule the entire cytoplasm of rod photoreceptors is slightly more electron dense than that of the cones (Fig. 7). While cone nuclei are normally large, very vesicular and located close to the ELM, rod nuclei display more heterochromatin and are located closer to the outer plexiform layer (OPL) (Figs. 6, 9). The synaptic ending of the rod shows 3-4 invaginated (ribbon associated) synaptic sites as well as several of the more conventional synapses which show only a superficial membrane densification (Fig. 9).

The single cones in the mallard retina appear to be as plentiful as rod photoreceptors. The outer segment of the single cone is quite thin, measuring about 1.5 μm at its base and tapering slightly to about 1.0 μm near its tip (Fig. 1). The single cone outer segment measures about 10 μm in length (Fig. 1). In light adaptation the cone outer segments (both single and double) were located amongst the rod outer segments and were also more or less isolated by the pigmented apical processes of the RPE cells (Fig. 1).

Immediately below the outer segment of the single cone is a prominent oil droplet (about 4.0 μm in diameter) which varies in appearance from quite homogeneous and electron dense (Fig. 5) to less electron dense and quite heterogeneous, displaying strands of granular material within the droplet (Figs. 2, 4). Below the oil droplet is a prominent ellipsoid of mitochondria which again show a range of morphologies in size, shape and electron density (Figs. 2, 4, 5). Below the ellipsoid is a large accumulation of glycogen (the paraboloid) which varies in size and localization and which may reach almost to the ELM (Fig. 6). In the peripheral cytoplasm around the paraboloid are numerous polysomes, some short RER profiles, apparent autophagic vacuoles and prominent Golgi zones (Figs. 2, 5-7).

The inner segment of the single cones is usually widest in the ellipsoid/paraboloid region where it measures 7-8 μm in width (Figs. 2, 4) while near the ELM it narrows to 3-4 μm in width (Fig. 7). The nuclei of single cones are large and vesicular and often protrude slightly through the ELM in the light-adapted state (Figs. 2, 6). The synaptic spherules of the single cones display several (8-10) invaginated or ribbon synapses as well as numerous superficial membranous densifications which are felt to be conventional synaptic sites (Fig. 9).

The double cones of the mallard are composed of two unequal cell types. The larger of the two members (chief cone) always displays a heterogeneous electron-lucent oil droplet which has strands of granular or membranous material within the droplet (Figs. 1, 3). The outer segment of the chief cone is very similar to that described for the single cone, measuring about 1.0 μm in width and about 10 μm in length (Figs. 1, 3). Below the prominent oil droplet is a large ellipsoid composed of round to oval mitochondria (Fig. 3). These mitochondria display a fairly homogeneous, moderately dense matrix (Fig. 3) and hence differ from the ellipsoid mitochondria of the single cones (Figs. 4, 5). Beneath the ellipsoid the chief cone displays a very large paraboloid of glycogen (Fig. 7) which as in the single cone is surrounded by polysomes, small profiles of RER and Golgi zones (Figs. 7, 8). The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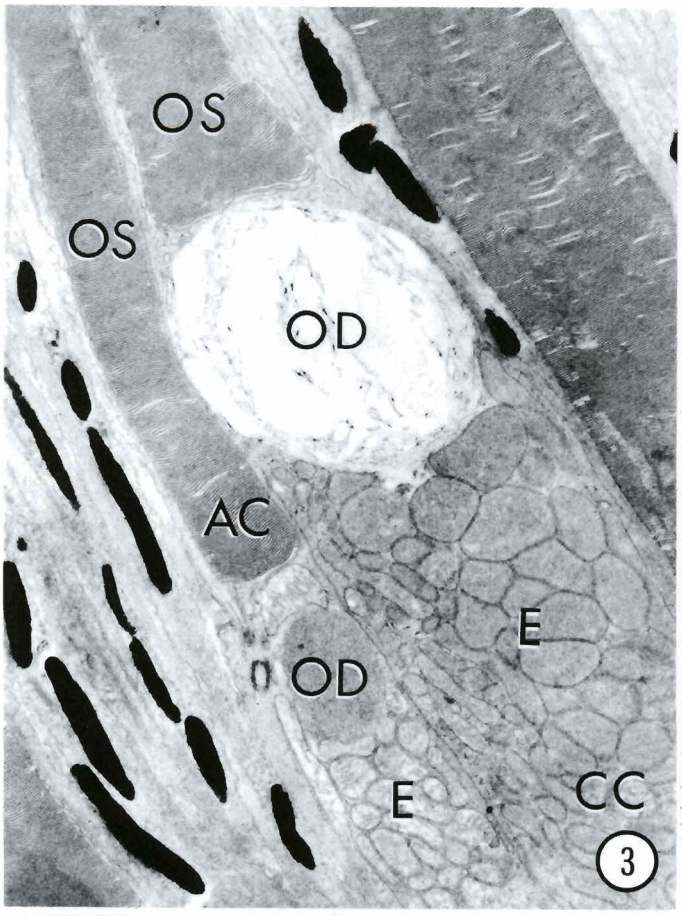
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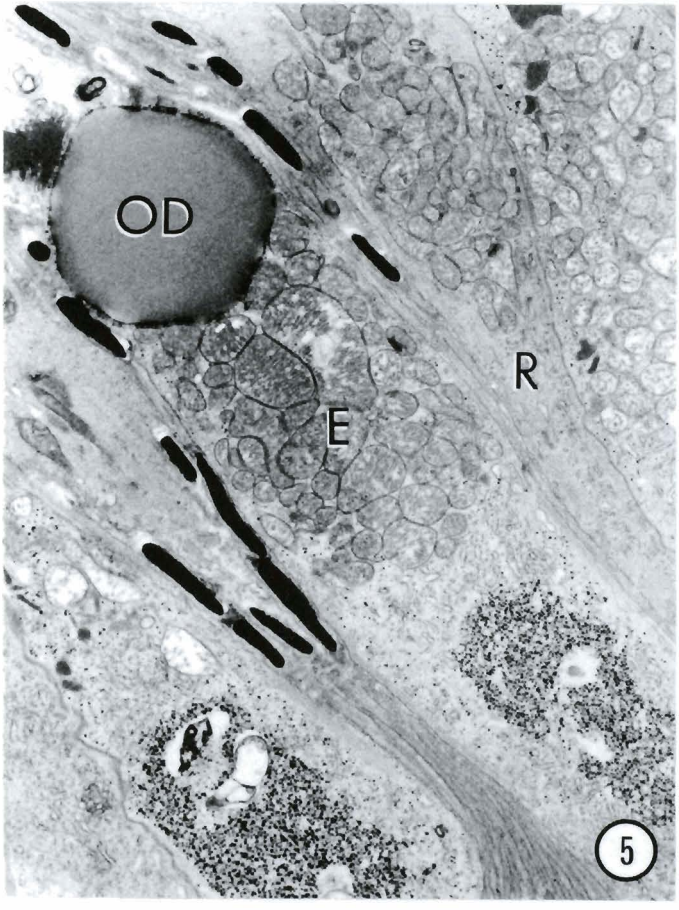
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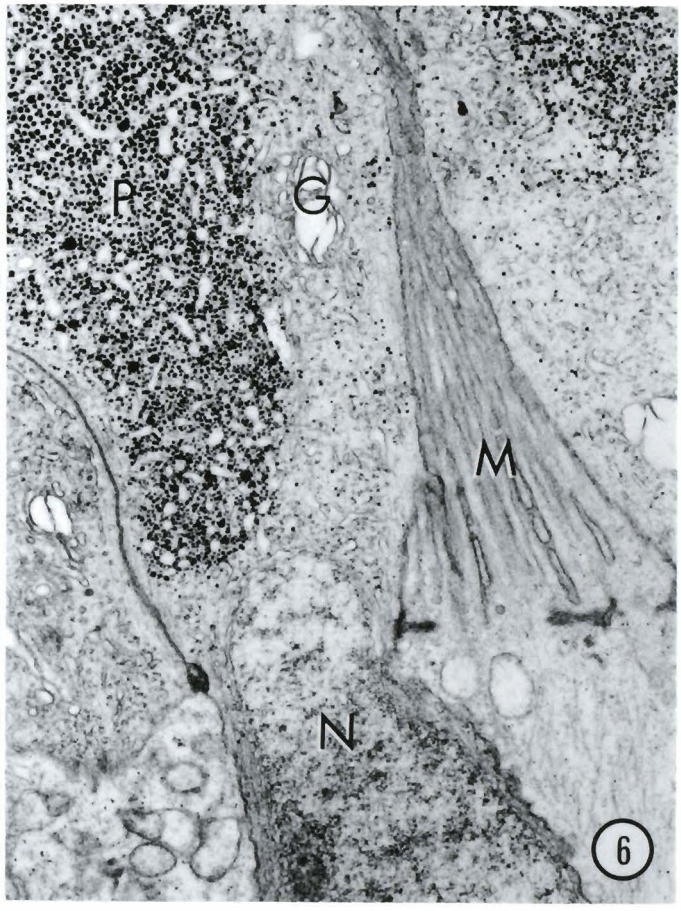
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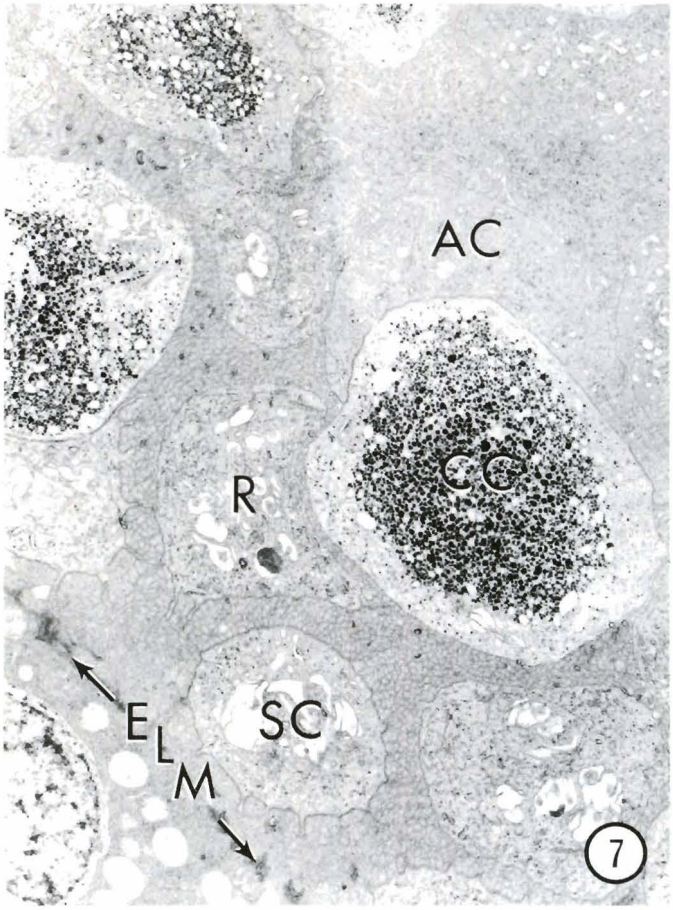
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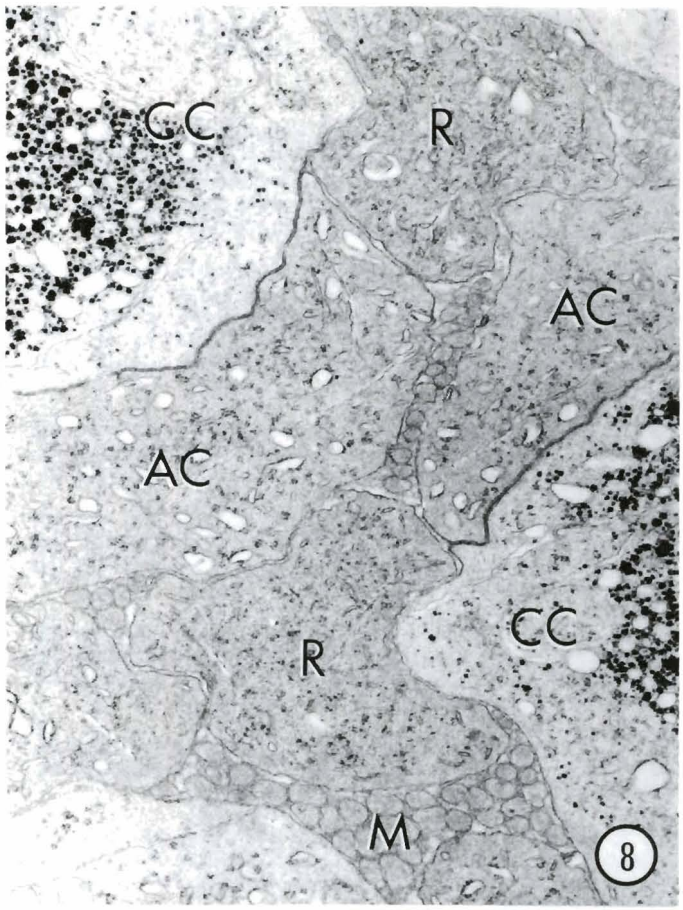
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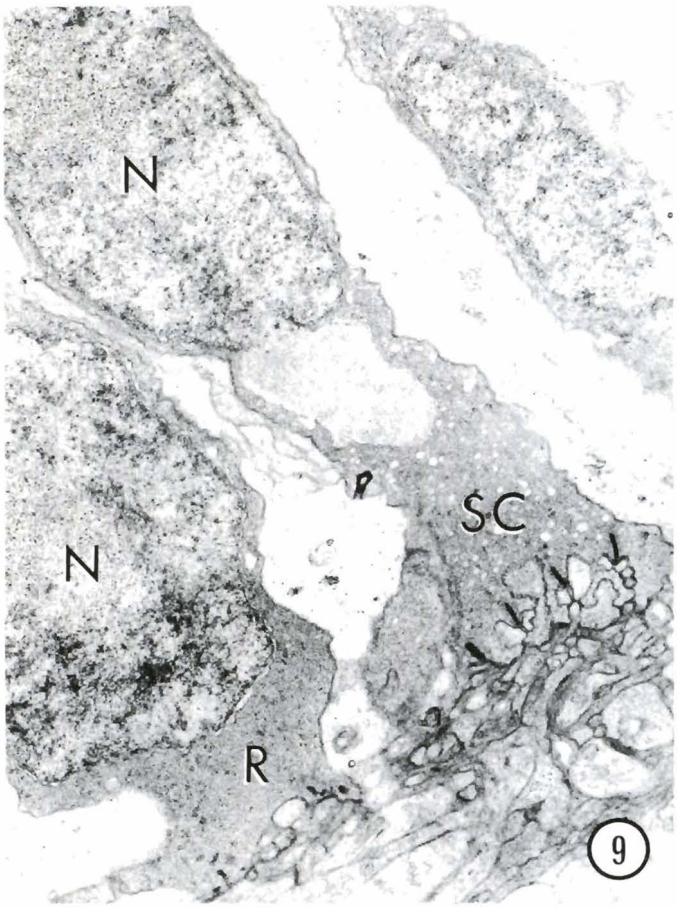
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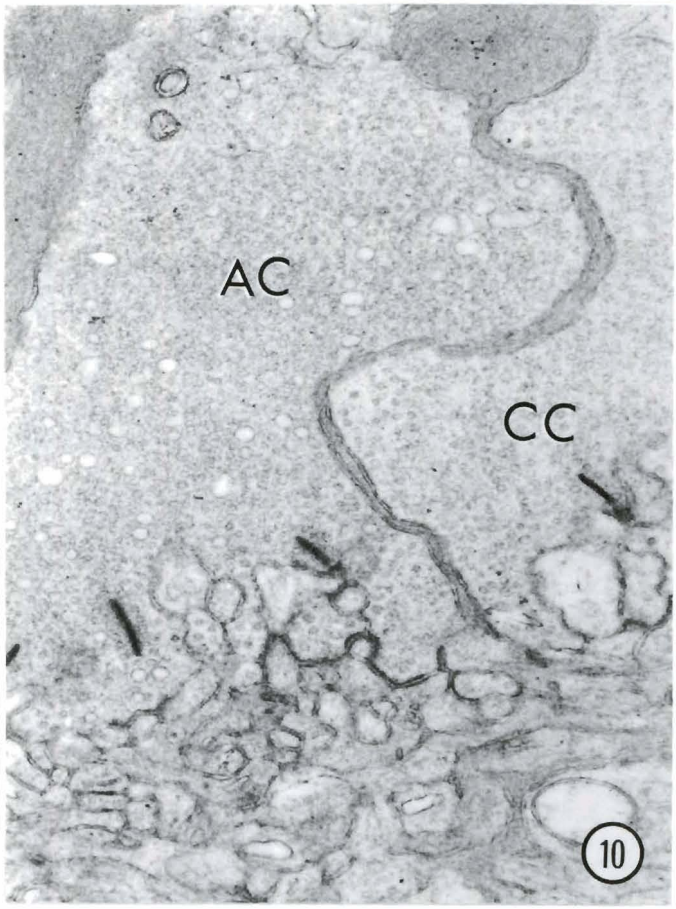
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Fig. 1. Low power electron micrograph of the retinal epithelium (RPE) and photoreceptor outer segments from a light-adapted mallard. Rod outer segments (ROS), single cone outer segments (COS) and the apical processes (AP) of the RPE cells as well as the inner segment of the chief member of a double cone (CIS) are all indicated. × 5,600

Fig. 2. Low power electron micrograph of various photoreceptors in the mallard retina. A single cone (SC) and the accessory member of a double cone (AC) are indicated as is the external limiting membrane (ELM). Note the oil droplet (OD), ellipsoid (E) and paraboloid (P) within the cone inner segments. The pigment-laden apical processes of the RPE are obvious. × 5,600

Fig. 3. Electron micrograph of the chief (CC) and accessory (AC) members of a double cone. Note the difference in outer segment (OS), oil droplet (OD) and ellipsoid (E) mitochondria morphology. × 9,300

Fig. 4. Electron micrograph of a single cone from the mallard. Compare and contrast the morphology of the oil droplet (OD) and ellipsoid (E) mitochondria with the single cone in figure 5 and the double cone in figure 3. × 10,300

Fig. 5. Electron micrograph of a single cone from the mallard. Compare the morphology of the oil droplet (OD) and mitochondria of the ellipsoid (E) with that shown in figures 3 and 4. A rod photoreceptor (R) is also indicated. × 6,200

Fig. 6. Electron micrograph of a cone photoreceptor near the ELM. The paraboloid (P), a Golgi zone (G) and the cone nucleus (N) are indicated as are Müller cell (M) processes. × 10,300

Fig. 7. Electron micrograph of several photoreceptors near the external limiting membrane (ELM). A rod (R), a single cone (SC) and the accessory (AC) and chief (CC) members of a double cone are all indicated. × 6,000

Fig. 8. Electron micrograph of two double cones to indicate the denser membrane between the chief (CC) and accessory (AC) members. Two rods (R) and Müller cell (M) processes are also indicated. × 13,200

Fig. 9. Electron micrograph of the synaptic region of a rod (R) and a single cone (SC). The nucleus (N) of each photoreceptor is indicated. Both ribbon and superficial synapses are present on both photoreceptor types. × 9,300

Fig. 10. Electron micrograph of the synaptic pedicle of the accessory (AC) and chief (CC) members of a double cone in the mallard. Both ribbon (invaginated) and conventional (superficial) synaptic sites are obvious on both members. × 22,300

chief cone is widest in the ellipsoid/paraboloid region measuring 8-10 μm in width (Fig. 7) and is more electron lucent than the accessory cone (Figs. 7, 8).

The smaller or thinner member of the double cone (the accessory cone) usually displays a slightly longer outer segment than the chief cone as it arises beside or below the oil droplet of the chief cone and extends with the outer segment of the chief cone (Fig. 3). The outer segment of the accessory cone (as is the case for both rods and the other cone types) is joined to the inner segment by an eccentrically located ciliary process (Fig. 3). At the tip of the outer segment the accessory cone displays a small (1.2-1.4 μm) granular droplet which is often incorporated amongst the mitochondria of the ellipsoid (Figs. 2, 3). These mitochondria are smaller and show a more electron lucent matrix than those of the chief cone (Fig. 3). Below the ellipsoid, the accessory cone contains a paraboloid of glycogen and flattens out to partially clasp the chief cone (Figs. 7, 8). In this location it is more electron dense than the chief member and displays numerous polysomes, profiles of RER and an occasional Golgi zone (Figs. 7, 8).

Near the ELM localized areas of the adjacent membranes of the two members of the double cone are more electron dense with only a very narrow intercellular space (Figs. 7, 8). Also near the ELM all the photoreceptor types are surrounded by numerous villous-like processes of the Müller cells which protrude through the ELM for 3-5 μm (Figs. 2, 6). In this region the rods, single cones and accessory members of the double cones show lateral, vertical fins of cytoplasm which interdigitate with these numerous processes of the Müller cells (Fig. 7).

The nuclei of both members of the double cone are large and vesicular and are located close to the ELM. The synaptic endings of the two members of the double cone are often separated by Müller cell cytoplasm and are rich in synaptic vesicles (Fig. 10). Both the accessory and chief members of the double cone display several invaginated (ribbon) synapses as well as numerous superficial synaptic sites (Fig. 10).

The external limiting membrane (ELM) in the mallard is composed of a series of zonulae adherentes between the photoreceptors (all types) and the Müller cells (Figs. 2, 6). Due to the numerous processes of the Müller cells which reach almost to the apical processes of the RPE cells, in the light-adapted state at least, the photoreceptors of the mallard are almost completely isolated from one another (Figs. 2, 6).

Discussion

Most birds are highly active diurnal animals and their retinas are characterized by the presence of numerous cones (both single and double) which can be as plentiful as rods (Walls, 1942; Crescitelli, 1972; Meyer and May, 1973). The avian retina normally displays three types of photoreceptor cell; rods, single cones and double (unequal) cones (Meyer, 1977) with some investigators further subdividing the single cones into two or three different classes (Morris and Shorey, 1967; Morris, 1970; Mariani and Leure du Pree, 1978; Mariani, 1987). Avian cones are also characterized by the presence of an oil droplet which may be coloured (in diurnal species) or clear (in nocturnal species) (Meyer, 1977; Yew et al., 1977).

In the mallard duck *Anas platyrhynchos*, three distinct types of photoreceptor are noted, namely, rods, single cones and double cones (consisting of two unequal members).

In light-adaptation, the rods are the most elongated cells, reaching to the RPE cell body. This probably indicates that they undergo extensive retinomotor or photomechanical responses. Rods are about equal in number to double cones, slightly less numerous than single cones and appear to be fairly equally distributed throughout the retina.

The outer segment of both rods and cones consist of a stack of bimembranous discs (Cohen, 1972). In rods,

outer segment discs are usually all of the same diameter while in the cones the more apical discs are smaller than those of the basal region giving the outer segment a tapering or conical shape (Cohen, 1963, 1972). In the mallard the rod outer segments are the largest in both length and diameter which may be an attempt to enlarge their light-capture area. The outer segments of single cones and chief cones of the double variety do taper distally while that of the accessory cone does so only minimally. In many species, cone discs display a circular outline while rod discs very often have a scalloped or lobulated perimeter due to the presence of one or more incisures (Cohen, 1963; Nilsson, 1965; Braekevelt, 1983a,b). The lobulation of rod outer segments is felt to be another attempt to increase surface area and is noted in the mallard while the cones show no such incisures.

The connecting cilium located between inner and outer segments is a constant feature of all vertebrate photoreceptors described. In this species the cilium is typical in that it is eccentrically located and displays the peripheral arrangement of nine pairs of microtubules and lacks the central pair found in motile cilia (Dowling and Gibbons, 1961; Cohen, 1963).

The inner segment of a photoreceptor cell is known to be the synthetic center of the cell and it is here that the materials for new outer segment discs (as well as for other metabolic requirements) are produced (Young, 1976).

In the mallard, at the apex of the inner segment of single cones and both members of the double cone, but not in the rod, is located a single oil droplet. Such oil droplets have been reported in amphibians, reptiles, birds and non-placental mammals (Rodieck, 1973; Braekevelt, 1973, 1989; Meyer, 1977; Kolb and Jones, 1982). Oil droplets apparently selectively filter light and in so doing probably enhance contrast, reduce glare and lessen chromatic aberration (Meyer, 1977).

While all investigators report a large oil droplet in avian single cones and the chief member of double cones (Morris, 1970), some controversy exists as to whether or not the accessory member of the double cone displays an oil droplet (Meyer, 1977). It has been reported most convincingly in the chicken and pigeon (Meyer and May, 1973; Mariani and Leure du Pree, 1978) and an oil droplet is present within the accessory cones of the mallard.

Cone oil droplets can display a variety of colours which can be observed with light microscopy of fresh retinal preparations (Meyer and May, 1973). Diurnal birds normally display coloured oil droplets (most often red, orange, yellow or green) while nocturnal species more usually show only colourless (or pale yellow) droplets (Meyer and Cooper, 1966; Morris and Shorey, 1967; Yew et al., 1977). No attempt was made in this study to determine the colour of the oil droplets in the mallard cones.

Morris (1970) distinguished three different types of single cone in the chicken based on oil droplet and ellipsoid mitochondrial densities in electron micrographs. While this study also notes differences in these parameters, it is not known if this indeed signifies different single cone types or merely reflects a difference in metabolic activity or chemical composition of these single cones. Pedler and Boyle (1969) have reported the presence of numerous small oil droplets within some single cones of the pigeon but this was not observed in the mallard.

The large accumulation of mitochondria at the apex of the inner segment (the ellipsoid) is a constant feature of all vertebrate photoreceptors (Cohen, 1972; Rodieck, 1973). The paraboloid which is an accumulation of glycogen found in the inner segment of the cones of some birds, fish, amphibians and reptiles (Cohen, 1972) is noted in the mallard in single cones and both members of the double cone. This differs from other reports where the accessory cone displays a paraboloid but the chief membrane does not (Morris and Shorey, 1967; Meyer, 1977). Also while other reports note a glycogen deposit in the inner segment of avian rods (the so-called hyperboloid) (Meyer and Cooper, 1966; Meyer, 1977) that structure was not noted in the rods of the mallard. The presence of large numbers of mitochondria (the ellipsoid), large amounts of glycogen (paraboloid of cones), numerous polysomes and some RER, several Golgi zones and autophagic vacuoles as noted in the inner segments of vertebrate photoreceptors are all indicative of metabolically very active cells (Cohen, 1972; Remé and Sulser, 1977).

In some avian species, a regular arrangement or mosaic of the single and double cones is reported (Engstrom, 1958; Morris, 1970). No such mosaic was noted in the mallard nor was anything like the «red area» of the pigeon (Mariani and Leure du Pree, 1978) observed where one cone type was in a preponderance. The lack of a mosaic in the mallard may reflect the nonpredaceous and nongranivorous feeding habits of this species.

The region between the ellipsoid and the cell nucleus is often referred to as the myoid as it is this region which changes in length during retinomotor movements (Cohen, 1972). As only light-adapted specimens were studied however it is uncertain if the myoid of either the rods or cones in the mallard will change in size and shape in response to variations in environmental lighting. Meyer (1977) reports that with the exception of accessory cones, photomechanical changes are quite rapid and extensive in birds. While the elongated morphology of the rods in the mallard are indicative of retinomotor movements, the cones are not obviously shortened.

In the myoid region, interrecepter junctions are often reported between the two members of the double cones. In teleosts this junctional specialization is often quite elaborate, involving submembranous cisternae (Berger, 1967; Braekevelt, 1982) while in avian species it usually takes the form of gap and intermediate junctions between the two members (Nishimura et al., 1981; Smith et al., 1985). A slight thickening of the apposing membranes of the accessory and chief cones are noted in the mallard near the ELM.

As is the case in most other vertebrates, the external limiting membrane (ELM) in the mallard is composed of a series of zonulae adherentes between Müller cells and photoreceptors (Uga and Smelser, 1973). Also as in

many other species, particularly those with an avascular retina (as the mallard) the Müller cells form a series of villous processes which project through the ELM and surround the inner segments of the photoreceptors. These processes coupled with the presence of vertical, lateral fins of the inner segments of the photoreceptors are felt to aid in transport between the glial Müller cells and the photoreceptors.

Within the outer plexiform layer, the synaptic pedicle of the cone cell is typically larger and displays more synaptic sites than the rod spherule (Cohen, 1972; Crescitelli, 1972). Synaptic sites on retinal photoreceptors are either invaginated and associated with a synaptic ribbon (Missotten, 1965) or are the more conventional superficial type involving only membrane densifications (Dowling, 1968; Cohen, 1972). While bipolar and horizontal cells are both involved at invaginated synapses (Kolb, 1970), superficial synapses may be between photoreceptors and bipolar cells or between photoreceptors themselves (Cohen, 1964; Missotten, 1965; Kolb, 1970). In a few lower vertebrates, only superficial synapses are reported (Dowling and Werblin, 1969). The mallard duck displays both typical invaginated (ribbon) and superficial (conventional) synaptic sites on rods, single cones and both members of the double cones.

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