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Retinal photoreceptor fine structure in the Australian Galah (*Eolophus roseicapillus*) (Aves)

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Summary. The retinal photoreceptors of the galah (*Eolophus roseicapillus*), an Australian cockatoo, consist of rods, single cones and double (unequal) cones present in a ratio of about 1:3:3 respectively. The rods are long slim cells which are believed to undergo retinomotor movements. The rod inner segment displays an ellipsoid of mitochondria, much rough endoplasmic reticulum (RER), numerous polysomes and some autophagic vacuoles. No hyperboloid of glycogen was noted. Single cones show a slightly tapered outer segment, no oil droplet but a prominent ellipsoid at the apex and glycogen scattered throughout the inner segment. Double cones consist of a chief member which displays a heterogeneous oil droplet but no paraboloid of glycogen and an accessory cone with no oil droplet but a prominent paraboloid. All cones show below the ellipsoid plentiful polysomes, RER, Golgi zones and autophagic vacuoles. Cones are not felt to undergo retinomotor movements. In the light-adapted state the pigment-laden apical processes of the retinal epithelium (RPE) cells surround all photoreceptor types down to the inner segments. Along the length of the contiguous membranes between the two members of the double cone are membrane densifications that are presumed to be junctions. All cone photoreceptors are relatively small in diameter and hence closely packed. Rods and cones (both types) display both invaginated (ribbon) and superficial (conventional) synaptic sites.

Key words: Photoreceptors, Fine structure, Aves, Galah, *Eolophus roseicapillus*

Introduction

Retinal photoreceptors are extremely specialized cells with the unique ability to transduce light into an action potential which is sent to the brain as a nervous impulse. They are highly polarized cells and as the prime receptor in the visual pathway they have been studied with a wide array of techniques in a variety of animals. Fine structural studies have shown that all vertebrate photoreceptors are constructed on an essentially similar plan with an outer segment (light-capture area) joined to an inner segment (synthetic area) by a non-motile connecting cilium; a nuclear region and a synaptic ending (Cohen, 1963, 1972; Crescitelli, 1972; Rodieck, 1973). Phylogenetic specializations such as glycogen deposits, oil droplets and even multiple receptors can often be superimposed on this basic plan (Cohen, 1972; Fineran and Nicol, 1974, 1976; Braekevelt, 1982, 1990a, 1992).

Traditionally vertebrate retinal photoreceptors have been classified as either rods or cones on the basis of light microscopic morphology (Walls, 1942; Cohen, 1972). With the advent of electron microscopy and the examination of more species, a more elaborate classification based on fine structural criteria was proposed (Sjöstrand, 1958, 1959; Pedler, 1965, 1969). While such a classification may indeed by more accurate and descriptive it is not in common usage and for most species the categories of rods and cones accurately and adequately differentiates these cells (Cohen, 1972; Crescitelli, 1972; Rodieck, 1973).

The avian retina typically shows rods, single cones and double (unequal) cones (Morris, 1970; Meyer, 1977). As part of an ongoing comparative fine structure study of vertebrate photoreceptors in general and avian photoreceptors in particular, this study describes the morphology of the photoreceptors in the duplex retina of the Australian galah (*Eolophus roseicapillus*) which is an extremely cone-dominant retina.

Materials and methods

For this study the eyes from two light-adapted galahs (*Eolophus roseicapillus*) were examined by light and electron microscopy. The adult birds were captured in mist nets under the Western Australian Department of Conservation and Land Management Licence # SF

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000503. With the animals under deep anaesthesia, the eyes were quickly enucleated, slit open at the equator and immersion fixed for 5 h 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 1 mm^2 taking care not to detach the retina. This tissue was then postfixed for 2 h in 1% OsO_4 in the same phosphate buffer, dehydrated through graded ethanols to methanol and then to propylene oxide and embedded in Araldite.

Pieces of plastic-embedded tissue were reoriented 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) were then cut of selected areas and collected on copper grids. These sections were stained with aqueous uranyl acetate and lead citrate and examined and photographed in a Philips EM201 transmission electron microscope.

Results

As in most avian species, three distinct types of photoreceptors are found in the duplex retina of the galah (*Eolophus roseicapillus*). These are rods, single cones and unequal double cones (Figs. 1, 2). These are present in a ratio of about 1:3:3 respectively in this species with no obviously apparent regular repeating pattern of arrangement (mosaic) noted.

Rod photoreceptors are slender and are usually more electron dense than the more plentiful cone photoreceptors (Figs. 1, 2). Their outer segments are difficult to locate but measure about 1 µm in diameter and at least 7 µm in length (Fig. 5). Rod outer segment discs in this species do not appear to have incisures at their periphery. In the light-adapted state the pigment-laden apical processes of the retinal epithelium (RPE) surround the rod outer segments and to some extend the rod inner segments as they reach to within about 10 µm of the external limiting membrane (ELM) (Fig. 1).

At the apex of the inner segment, rod photoreceptors measure 3-4 µm in diameter and have an accumulation of mitochondria (the ellipsoid) (Fig. 5). Below the ellipsoid, the myoid region constricts to 1-2 µm in diameter and remains narrow down to the external limiting membrane (Fig. 6). In the light-adapted state the inner segment of rods measure about 20 µm in length (Fig. 1). Within the inner segment below the ellipsoid rods show profiles of rough endoplasmic reticulum (RER) numerous polysomes, Golgi zones and autophagic vacuoles (Figs. 4-6). No hyperboloid of glycogen is present. Near the ELM rod photoreceptors display several longitudinally aligned fins of cytoplasm which project from the inner segment and interdigitate with Müller cell processes that project through the ELM (Fig. 2).

The nuclei of rod photoreceptors display an electron dense and fairly condensed heterochromatin pattern and are located at all levels within the outer nuclear layer (ONL) (Fig. 2). The synaptic spherule of rods are also difficult to locate but are smaller and more electron dense than the synaptic pedicles of cones. They display 2-4 invaginated (ribbon) synapses as well as several superficial (conventional) synaptic sites (Fig. 12). The single and double cones of the galah are about equal in number and together are 5 to 6 times more abundant than the rods (Figs. 1-4). Cones (both types) are typically more electron-lucent in all areas than are the rod photoreceptors (Figs. 1-4).

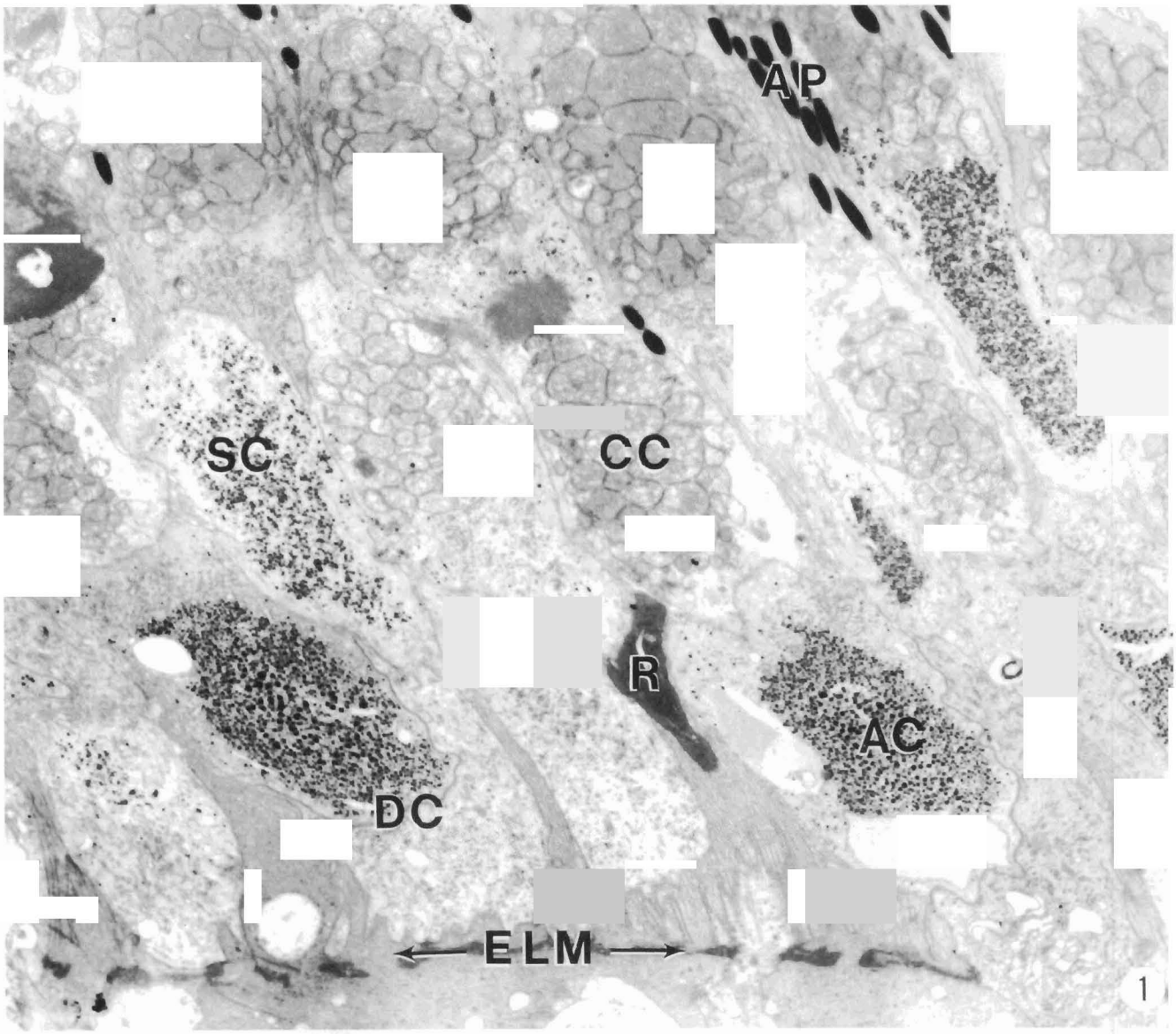
Single cones have an outer segment that is about 3 µm in width basally, about 8 µm in length and tapers only slightly (Fig. 1). In the light-adapted state the outer segments of all photoreceptors are on much the same level and all are surrounded by the pigment-laden apical processes of the RPE (Figs. 1, 5).

Below the connecting cilium which joins the inner and outer segments of all photoreceptor types, the single cone displays a large ellipsoid of mitochondria (Figs. 1, 3, 8). The single cones are widest in the ellipsoid region, where they measure about 5 µm in diameter (Fig. 8) while below the ellipsoid in the myoid region they average 3 µm in diameter (Figs. 2, 3, 8). In the light adapted state the inner segments of cones (all types) measures 20-25 µm in length (Figs. 1, 3). In the myoid region of single cones are found abundant profiles of RER and numerous polysomes as well as Golgi zones and autophagic vacuoles (Figs. 1-4). The glycogen within the inner segments of single cones is not usually in a compact accumulation (the paraboloid) but is dispersed throughout the inner segment and not associated with membranes (Figs. 1, 3, 8). Near the ELM the single cone does not display the vertically oriented fins of cytoplasm that are noted on rods (and the chief member of double cones) but instead shows a fairly smooth profile (Figs. 2, 4). The nuclei of single cones (indeed of all cones) are large and vesicular and are found at all levels of the ONL but do not usually project through the ELM (Fig. 2).

Double cones are about as numerous as single cones and consist of two unequal members. One member (the chief cone) is normally slightly longer than the other (accessory cone) and displays a heterogeneous oil droplet at the apex of the inner segment (Figs. 1, 3, 5, 9).

Fig. 1. Low power electron micrograph to illustrate the photoreceptor types. A rod (R), double cone (DC), the chief (CC) and the accessory member (AC) of another double cone and a single cone (SC) are observed. For orientation the external limiting membrane (ELM) and RPE apical processes (AP) are also indicated. x 7,000

Fig. 2. Electron micrograph to indicate a single cone (SC), and the chief (CC) and accessory members (AC) of a double cone. A rod nucleus (RN) and a cone nucleus (CN) are also indicated. x 9,000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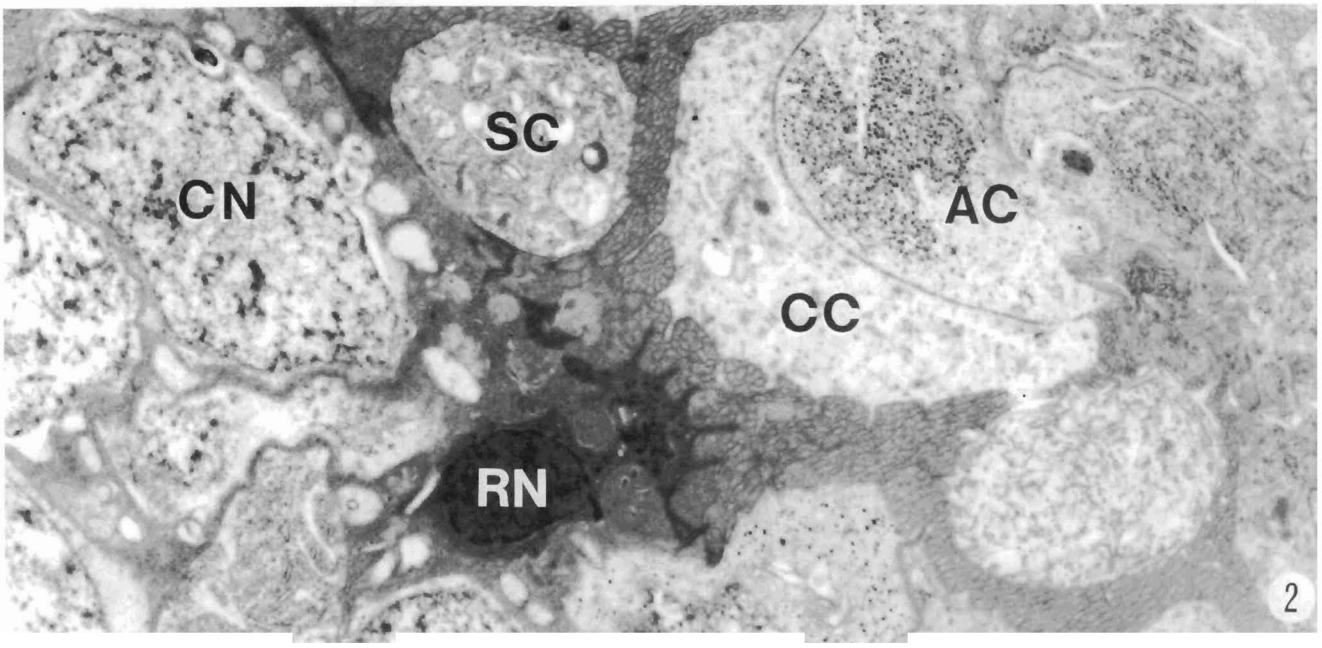
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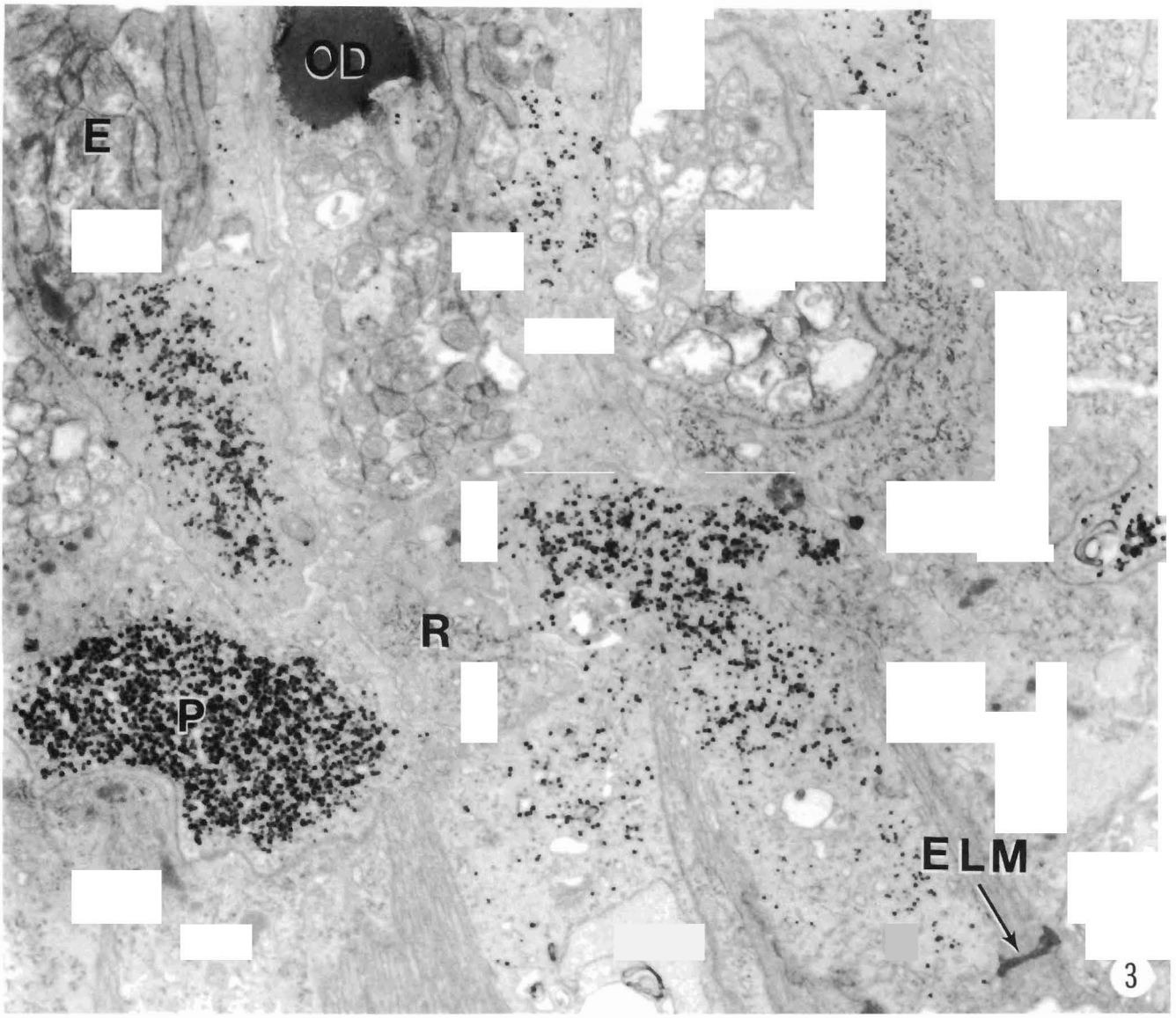
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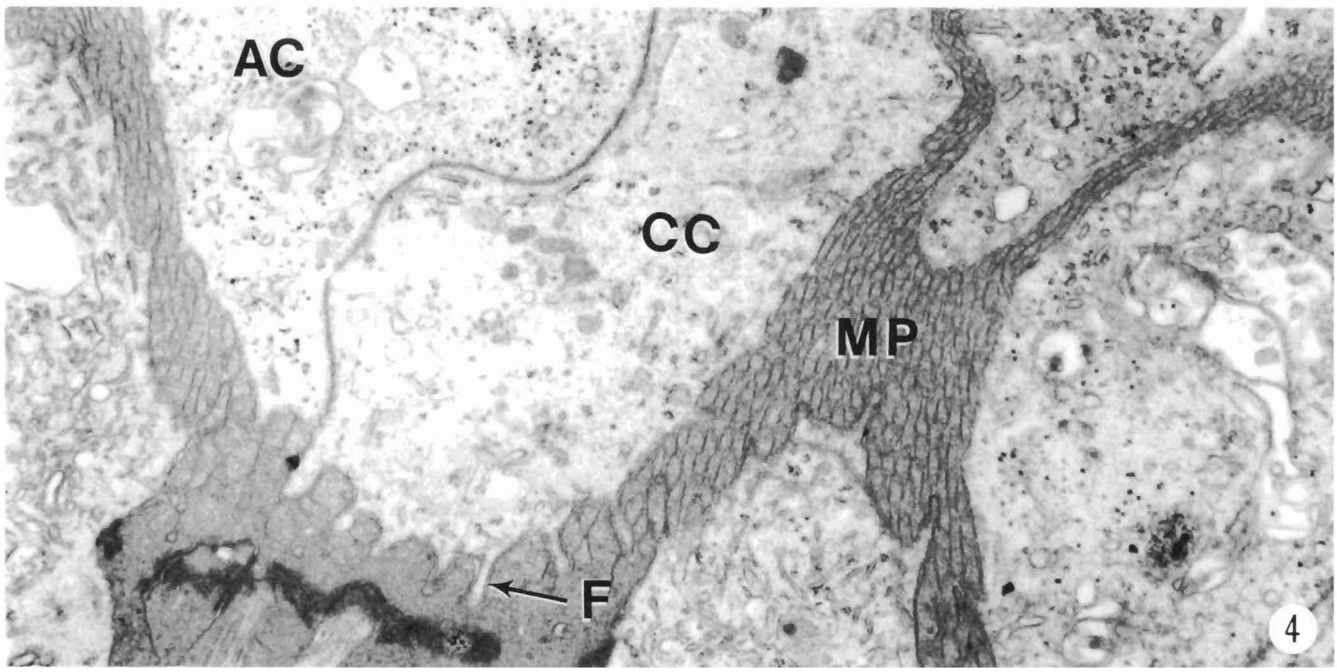
AC
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Below the oil droplet the chief cone has the normal ellipsoid of mitochondria while below this is an array of RER, polysomes, Golgi zones and autophagic vacuoles (Figs. 3, 7, 10, 11).

The accessory cone does not possesses an oil droplet but below the ellipsoid does have a large array of glycogen (the paraboloid) (Figs. 3, 7-9). The glycogen of the paraboloid of the accessory cone is normally in a compact region that appears to be infiltrated with membranes that separate the glycogen particles (Figs. 7, 8, 11). While the accessory member does not shown an oil droplet it often has small bodies of presumed lipid material scattered throughout the ellipsoid (Figs. 6-8).

The outer segments of both members of a double cone are essentially the same as that described for the single cone. It is normally impossible to differentiate them with certainty. The inner segment of both members of the double cone show an ellipsoid, much RER and polysomes as is noted for the single cones.

Within the ONL the two members of the double cone are normally separated by Müller cell cytoplasm and their nuclei can be found at all levels within the ONL (Figs. 2, 11). Cone synaptic pedicles are larger than the spherules of rods but the synaptic endings of single, chief and accessory cones are indistinguishable. All cone pedicles contain numerous synaptic vesicles and display several invaginated (ribbon) synapses as well as many of the more conventional (superficial) synapses involving only membrane densifications (Fig. 12).

The ELM of the galah is composed of a series of zonulae adherentes between rods, single cones, double cones and Müller cells (Figs. 2-4, 11). Fine microvillar processes of these Muller cells project through the ELM for about 10 µm to interdigitate with the inner segments of the photoreceptors (Figs. 2-4).

Discussion

Most diurnal avian species are highly active animals with good vision. Their retinas typically display many cones that in many instances substantially outnumber the rod photoreceptors (Walls, 1942; Crescitelli, 1972; Meyer and May, 1973; Braekevelt, 1990a, 1993b). The duplex avian retina characteristically shows three types of photoreceptor, namely rods, single cones and double (unequal) cones (Meyer, 1977) with some investigators further subdividing the single cones into two or three subtypes (Morris, 1970; Mariani and Leure du Pree, 1978; Mariani, 1987). The Australian galah (*Eolophus roseicapillus*) shows rods, double (unequal) cones and one type of single cone.

Rods are outnumbered by cone (all type) photoreceptors about five to one but all photoreceptor types appear to be distributed equally throughout the retina with no mosaic pattern of arrangement as is normally presented in teleost retinas (Braekevelt, 1990b, 1992). While the ratio of 1:3:3 noted for the galah for rods: single cones: double cones differs somewhat from that reported in the mallard duck (1:2:1; Braekevelt, 1990a), red-tailed hawk (2:1:5; Braekevelt, 1993a) great blue heron (2:1:1; Braekevelt, 1994a) and American crow (4:3:3 Braekevelt, 1994b), the small differences in the observed ratios of photoreceptor types may reflect differences in feeding habits which are mirrored by their visual requirements (Walls, 1942). In all cases however the preponderance of cones would indicate the importance of cone vision in these diurnal species. The galah is the most cone-dominant bird studied by this author to date and this may prove to be characteristic of the parrots and cockatoos.

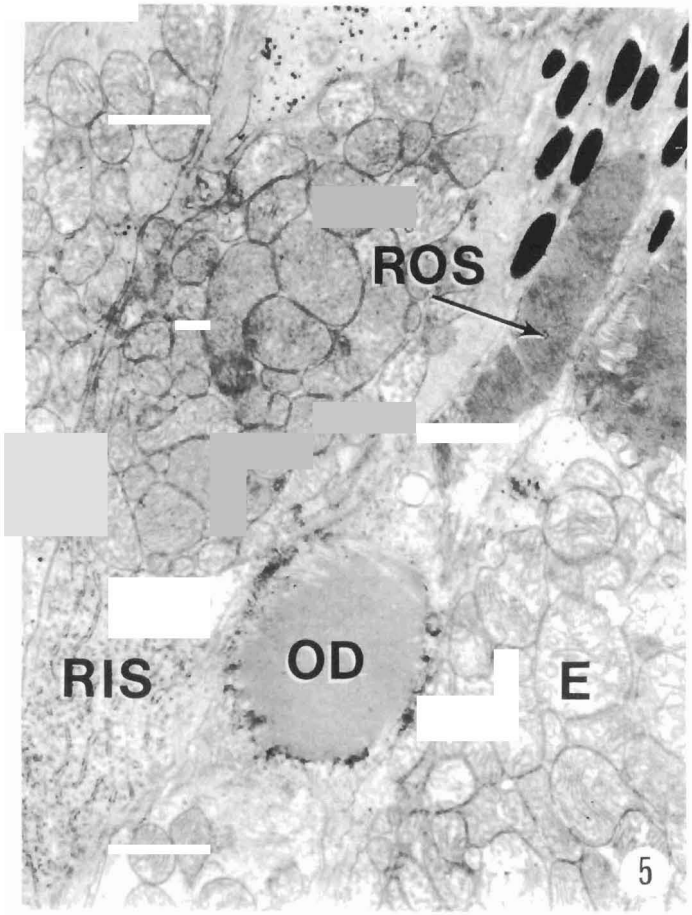
The rods in this species are long and relatively slim cells which in the light-adapted state show a very narrow myoid region. This would seem to indicate that rod photoreceptors do undergo retinomotor or photomechanical movements in response to environmental lighting. Rod outer segments reach to the RPE cell bodies and the apical processes of these cells reach down to the inner segment region of all photoreceptors. It is felt that the pigment in these apical processes also undergoes retinomotor movements (Braekevelt and Richardon, 1996).

Cones in the galah (both types) are also elongated cells which reach to the cell bodies of the RPE cells in the light-adapted state. Cones do not show a markedly thickened myoid region that would indicate that they have shortened in light-adaptation. This would seem to indicate that cones do not move (i.e. shorten) in light-adaptation. This observation is contrary to reports that indicate that except for the accessory member of double cones, all avian photoreceptors show rapid and extensive retinomotor movements (Meyer, 1977) however, observations on fully dark-adapted photoreceptors of the galah would be required to properly address this discrepancy.

The outer segments of both rods and cones consist of a stack of bimembranous discs (Cohen, 1972). These discs contain the photopigments and represent the light-capture area of photoreceptors. In rods the outer segment discs are normally all of the same diameter while in cones those closer to the inner segment are wider than those at the apex and this gives cone outer segments a tapered or conical shape (Cohen, 1963, 1972). Rod outer segments in the galah are smaller in diameter but of much the same length as cone outer segments. While in many species rod outer segments are much longer and often wider than cone outer segments, their relatively

Fig. 3. Electron micrograph to illustrate the ellipsoid (E) of a single cone, the oil droplet (OD) of the chief member of a double cone and the paraboloid (P) of the accessory member of a double cone. A rod (R) is also indicated as is the external limiting membrane (ELM). x 10,600

Fig. 4. Electron micrograph to indicate the chief (CC) and accessory members (AC) of a double cone. Note the lateral fins (F) on the chief cone. Müller cell processes (MP) are indicated. x 15,800



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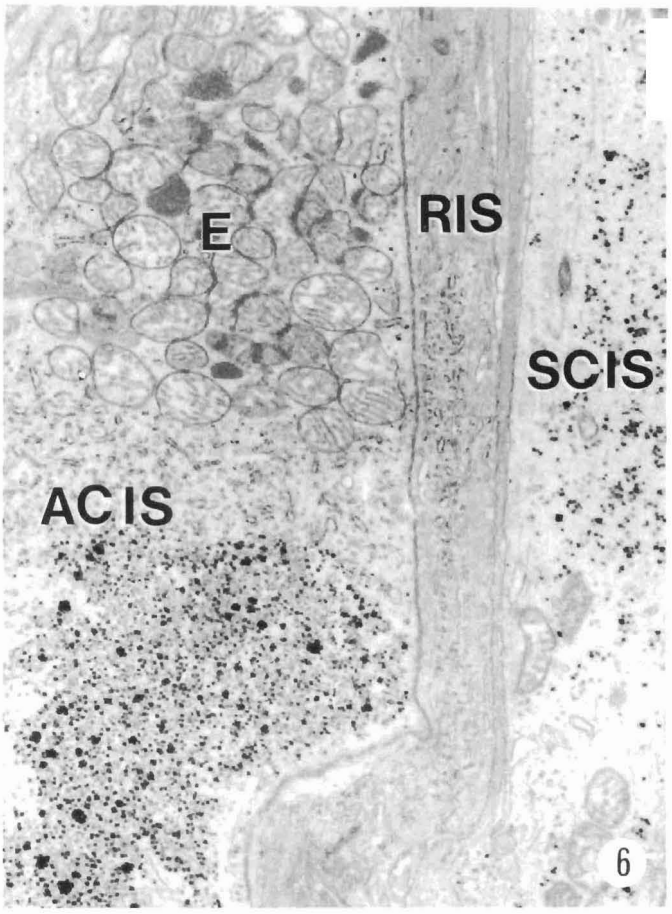

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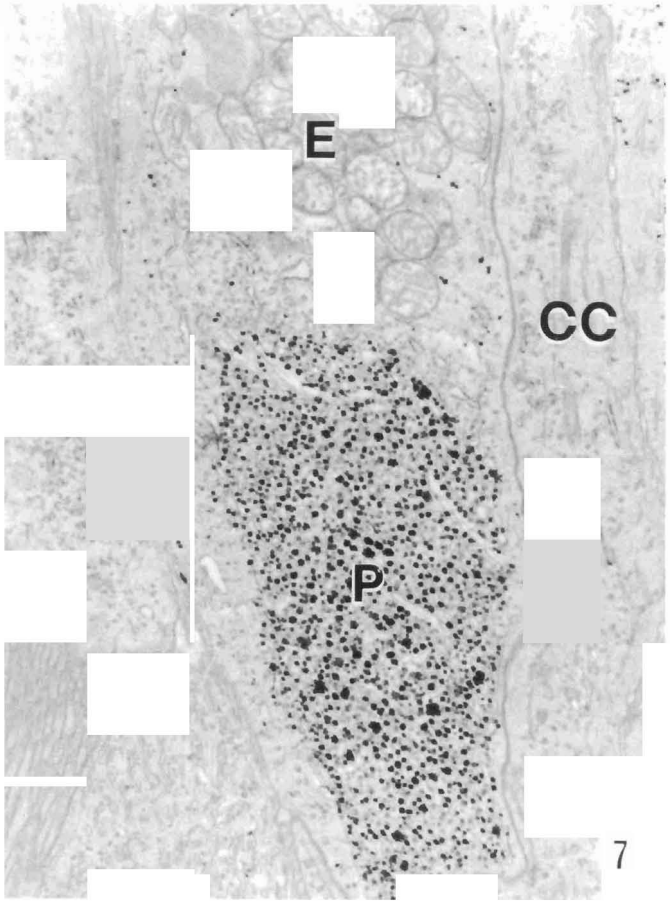

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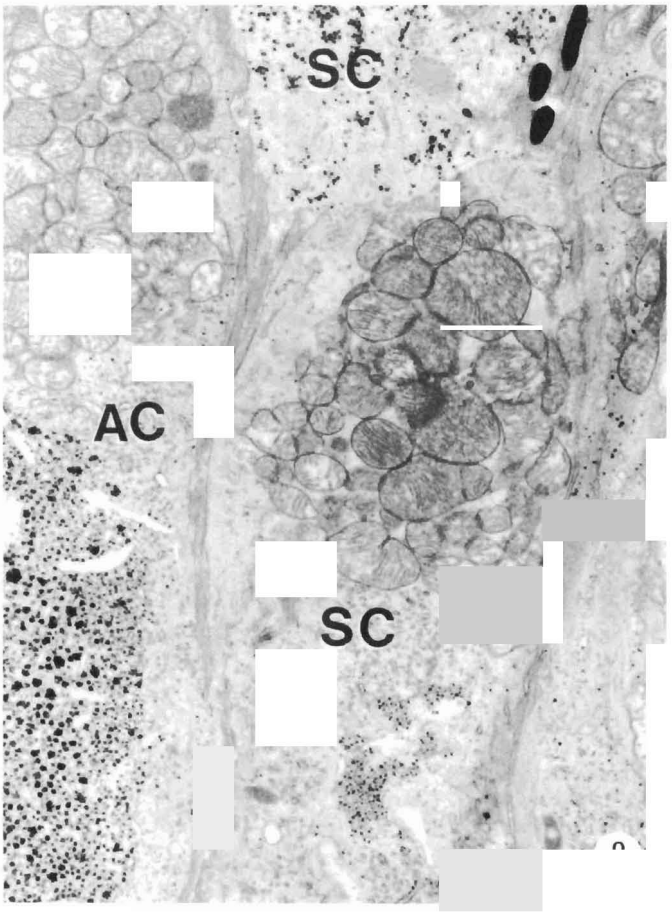


small size (and number) in the galah presumably emphasizes the minor role of rods and relative importance of cone vision in this species.

Rod outer segment discs in many species display one or more peripheral incisures which are felt to be present to increase surface area and hence the light-capture area of these discs (Cohen, 1963; Nilsson, 1965; Braekevelt, 1983, 1987). In diurnal avian species with high visual acuity, rod discs show only very shallow incisures or lack incisures completely as in this species (Braekevelt, 1993a). This would again indicate the importance of cone vision in the galah. Finally the widest diameter of cones in this species is reported at 3-5 µm, comparable to that of the red-tailed hawk (Braekevelt, 1993a), great blue heron (1994a) and American crow (1994b). The relatively small diameter of cones in these visually active species allows for an increased density of cones and hence a greater reliance on cone vision.

The inner segment region of photoreceptor cells is known to be synthetic center of these cells and it is here that the materials for new outer segment discs and other metabolic requirements are produced and that most of the cell organelles are located (Young, 1976, 1978).

In the galah, a single large oil droplet is located at the apex of the inner segment of the chief member of the double cone but not in rods, single cones or accessory cones. Such oil droplets have been reported in the cones of amphibians, birds, reptiles and non-placental mammals (Braekevelt, 1973, 1989; Rodieck, 1973; 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). Oil droplets come in a range of colours with diurnal species having orange to red droplets while nocturnal species show colourless droplets (Meyer, 1977). The colour of the oil droplets in the galah was not determined but they are presumably brightly coloured.

In many avian species, oil droplets are reported within the single cones also (Braekevelt, 1993a, 1994a) with other reports also finding them in the accessory cones (Meyer, 1977). In the galah as in some other birds the accessory cone does not show a single large oil droplet but instead displays several small droplets of presumed lipid material scattered amongst the mitochondria of the ellipsoid that may constitute an accessory cone oil droplet. The variation seen amongst avian species as to which cones do or do not possess an oil droplet is difficult to explain.

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, the accumulation of glycogen found in the cone inner segments of some birds, fish, amphibians and reptiles (Cohen, 1972) is noted in the galah in only the accessory cones. This differs from the crow where only the chief member shows a paraboloid (Braekevelt, 1994b) and the mallard where single cones and both members of the double cone display a paraboloid (Braekevelt, 1990a) but is similar to the condition in the red-tailed hawk and great blue heron where accessory cones alone show a paraboloid (Braekevelt, 1993a, 1994a). The single cones in the galah do not show a prominent paraboloid but instead display much glycogen scattered throughout the inner segment. Unlike many avian species, the galah does not show a prominent accumulation of glycogen within the rod inner segment (Meyer, 1977; Braekevelt, 1939b, 1994a). The significance, of the presence or absence of a paraboloid or hyperboloid within the various photoreceptor types is uncertain. While early workers felt that these glycogen bodies were refractile structures, it is now felt that these glycogen concentrations are energy sources for visual cell metabolism (Meyer, 1977) and are most prominent in retinas lacking intraretinal vascularization. The presence of large numbers of mitochondria (the ellipsoid), large amounts of glycogen (the paraboloid or hyperboloid), numerous polysomes and profiles of RER, Golgi zones and autophagic vacuoles within the inner segment of photoreceptor cells are all indicative of the high metabolic activity of these cells (Cohen, 1972; Remé and Sulser, 1977).

In the myoid region of the inner segment, interreceptor junctions are typically reported between the contiguous membranes of the two members of a double cone. In teleosts these junctional specializations are often quite elaborate involving large submembranous cisternae (Berger, 1967; Braekevelt, 1982). In avian species these interreceptor junctions usually take the form of gap and intermediate junctions between the chief and accessory cones and presumably allow the two members of a double cone to function as a single unit (Nishimura et al., 1981; Smith et al., 1985; Braekevelt, 1990a, 1993a, 1994a).

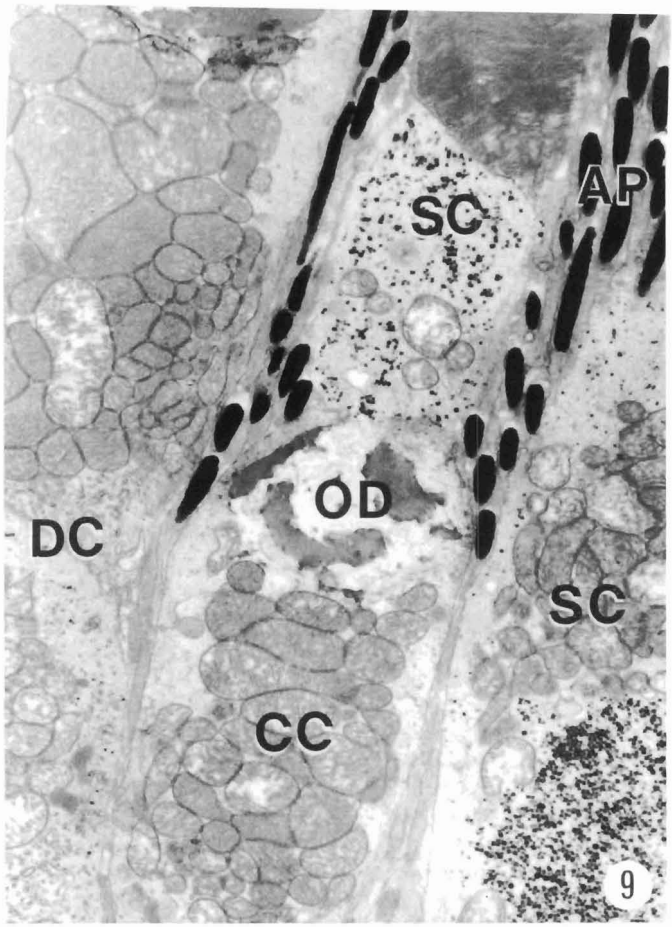
As is the case in all vertebrates described to date, the ELM in the galah is composed of a series of zonulae

Fig. 5. Electron micrograph to illustrate a rod inner segment (RIS) and rod outer segment (ROS), the oil droplet (OD) of a chief cone and the ellipsoid (E) of a single cone. x 10,500

Fig. 6. Electron micrograph to illustrate a rod inner segment (RIS), a single cone inner segment (SCIS) and the inner segment of an accessory cone (ACIS). Note the presumed oil droplets within the ellipsoid (E) of the accessory cone. x 10,700

Fig. 7. Electron micrograph to illustrate the paraboloid (P) and the ellipsoid (E) of an accessory cone. The chief member (CC) of the double cone is indicated. x 10,700

Fig. 8. Electron micrograph of two single cones (SC) and accessory member (AC) of a double cone. x 9,500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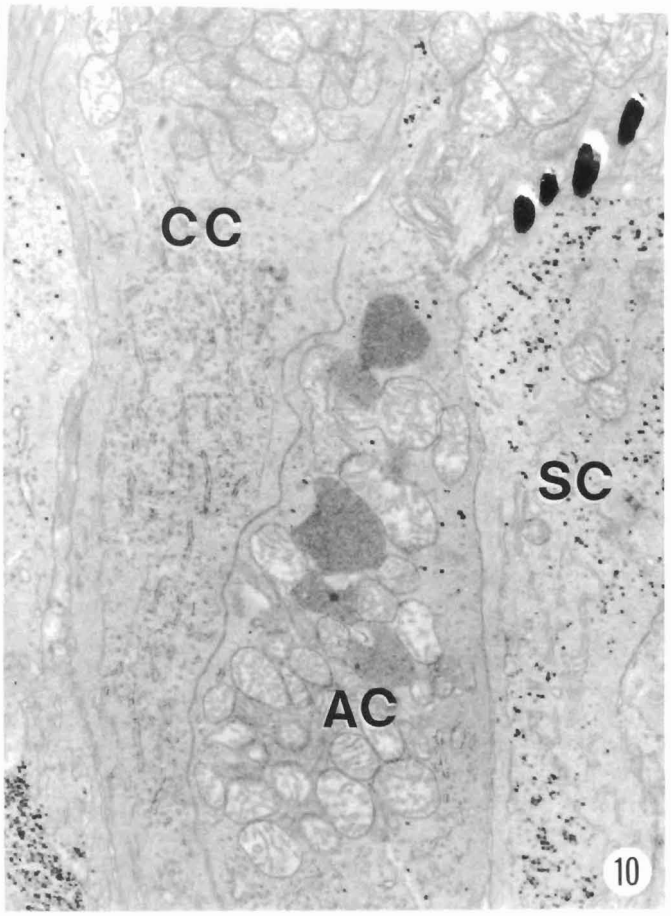
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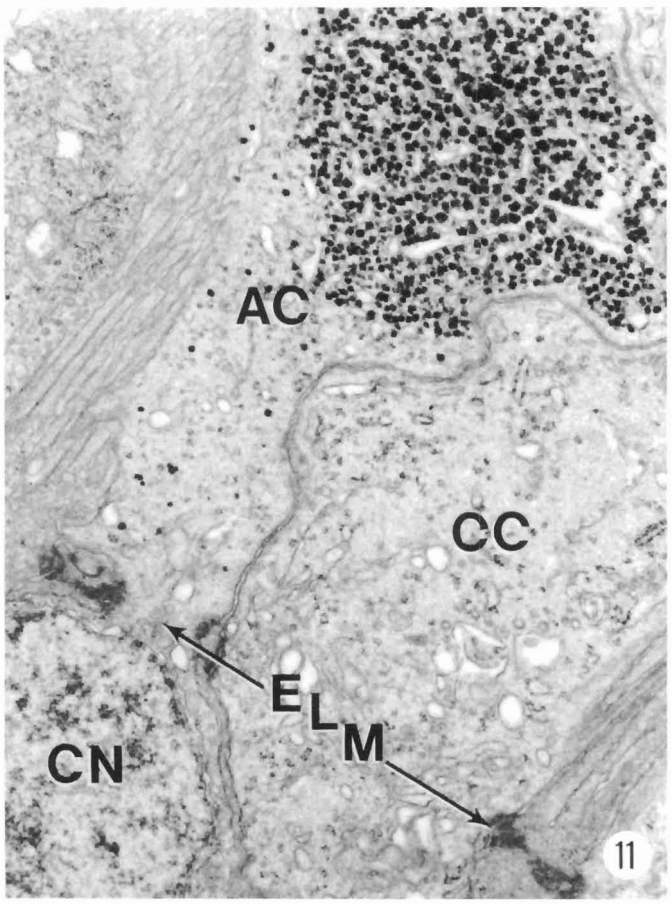
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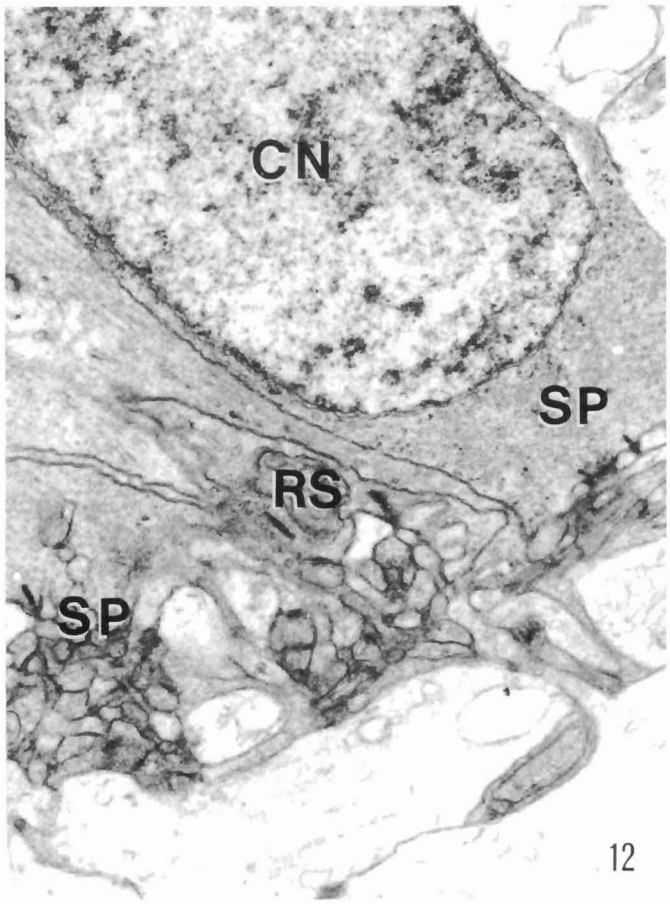
CN
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RS
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12

Fig. 9. Electron micrograph to illustrate two single cones (SC), a chief cone (CC) and another double cone (DC). The oil droplet (OD) of a chief cone and apical processes (AP) of the retinal epithelium are indicated. x 9,500

Fig. 10. Electron micrograph to illustrate the chief (CC) and accessory members (AC) of a double cone. Note the presumed lipid droplets in the ellipsoid of the accessory cone. A single cone (SC) is also indicated. x 10,700

Fig. 11. Electron micrograph of a double cone near the external limiting membrane (ELM). The accessory (AC) and chief members (CC) of the double cone are labelled as is the nucleus (CN) of the accessory cone. x 15,500

Fig. 12. Electron micrograph of the outer plexiform layer. A cone nucleus (CN) and cone synaptic pedicles (SP) as well as presumed rod synaptic spherule (RS) are indicated. x 15,500

adherentes between Müller cells and the three types of photoreceptor present (Uga and Smelser, 1973). Also as is noted in many other species, the Müller cells form a series of villous processes which project through the ELM and surround the base of the photoreceptors (Braekevelt, 1990a, 1993a). In this region the photoreceptors may display a number of vertically oriented lateral fins which interdigitate with the Müller cell processes and are presumably important in increasing surface area for exchange in this area (Crescitelli, 1972; Braekevelt, 1990a). Such lateral fins were present on rods and the chief member of the double cones of the galah but were absent from the accessory cones and single cones. In the great blue heron these lateral fins appear on the accessory cones and rods (Braekevelt, 1994a) but were absent from all photoreceptor types in the red-tailed hawk (Braekevelt, 1993a). Again the significance, if any, of the presence or absence of these lateral fins on the various photoreceptors in avian species is unknown.

Within the outer plexiform layer (OPL) the synaptic pedicles of cones are normally larger, more electron lucent and display more synaptic sites than the spherules of rods (Cohen, 1972; Crescitelli, 1972). Synaptic sites on vertebrate retinal photoreceptors are either invaginated and associated with a synaptic ribbon (Missotten, 1965) or are of the more conventional type which involves superficial membrane densifications (Dowling, 1968; Cohen, 1972). While bipolar and horizontal cells are both involved at invaginated synaptic sites (Kolb, 1970), superficial synapses may be between photoreceptors and bipolar cells or between photoreceptors themselves (Cohen, 1964; Missotten, 1965; Kolb, 1970). The Australian galah shows both typical invaginated (ribbon) and superficial (conventional) synaptic sites on the rods, single cones and both members of the double cones.

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