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# Fine structure of the retinal photoreceptors of the barred owl (*Strix varia*)

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**Summary.** The photoreceptors of the barred owl (*Strix varia*) consist of rods, single cones and unequal double cones present in a ratio of about 35:1:3. In the light-adapted condition the rods are of uniform diameter along their entire length and are therefore not felt to undergo photomechanical changes. The rod outer segment consists of a stack of scalloped bimembranous discs enclosed in a limiting membrane. The rod inner segment displays an ellipsoid of mitochondria, much rough endoplasmic reticulum (RER), numerous polysomes, Golgi zones and autophagic vacuoles, but no hyperboloid of glycogen. Single cones show a slightly tapered outer segment and a heterogeneous oil droplet along with an ellipsoid of mitochondria at the apex of the inner segment. Double cones consist of a larger chief member which also displays a heterogeneous oil droplet and a slightly smaller accesory member which does not. Both members of the double cone as well as the single cones show plentiful polysomes and RER as well as Golgi zones in the inner segment, but none of the cones possessed a condensed paraboloid of glycogen. The contiguous membranes of the chief and accessory cones displayed a few presumed junctional complexes. Judging by their elongated shape in the light-adapted state, cones in this species do not undergo retinomotor movements. Rods and both types of cones have both invaginated (ribbon) and superficial (conventional) synaptic sites.

**Key words:** Retina, Photoreceptors, Electron microscopy, Barred owl, *Strix varia*

## Introduction

Retinal photoreceptors are extremely specialized and highly polarized cells. Comparative morphological studies have shown that all vertebrate photoreceptors are constructed on the same basic plan (Walls, 1942; Polyak, 1957; Cohen, 1972; Crescitelli, 1972; Young, 1976; Braekevelt, 1985, 1990, 1993a,b, 1994a,b). The typical photoreceptor consists of an outer segment (light-sensitive area) joined to an inner segment (synthetic area) by a non-motile connecting cilium, a nuclear region and a synaptic ending (Cohen, 1972; Crescitelli, 1972; Rodieck, 1973). Phylogenetic specializations such as oil droplets and/or multiple receptors can often be superimposed on this basic design (Cohen, 1972; Fineran and Nicol, 1974; Braekevelt, 1982, 1990, 1992).

Historically, retinal photoreceptors have been classified as either rods or cones based on their morphological appearance at a light microscopic level (Walls, 1942; Polyak, 1957; Duke-Elder, 1958). With the enhanced resolution of electron microscopy, some workers proposed more elaborate and probably more precise methods of classifying photoreceptors (Sjöstrand, 1958, 1959; Pedler, 1965, 1969), but these never became popular and the old terms of rods and cones are still widely used (Crescitelli, 1972; Rodieck, 1973; Braekevelt, 1983, 1984, 1985, 1989, 1990, 1992, 1993a, 1994b).

Avian species typically display rods, single cones and double (unequal) cones with the cones often in the majority (Morris, 1970; Meyer, 1977). As part of an ongoing comparative study of vertebrate photoreceptors in general, and avian species in particular, the fine structure of the rods and cones (both single and double) in the duplex rod-dominant retina of the barred owl (*Strix varia*) are described in this report.

## Materials and methods

For this study the eyes from two adult and one juvenile light-adapted barred owls (*Strix varia*) were examined by light and electron microscopy. With the specimens under deep anesthesia the eyes were quickly enucleated, sliced 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 and washed in 5% sucrose in 0.1M Sorensen's buffer (pH

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7.3) and cut into pieces less than 1 $mm^2$, taking care not to detach the retina. The tissue was then postfixed for 2 h in 1% osmium tetroxide in the same phosphate buffer, dehydrated up through graded ethanols to methanol and then propylene oxide and embedded in Araldite.

Pieces of plastic-embedded tissue were subsequently reoriented to desired angles using a wax mount, and both thick (0.5 µm) and thin (50-60 µm) sections were cut on an LKB ultramicrotome. Thick sections were stained with toluidine blue and examined by light microscopy. Thin sections of selected areas were collected on copper grids, stained in aqueous uranyl acetate and lead citrate, and examined and photographed in a Philips EM201 transmission electron microscope.

## Results

The retinal photoreceptors of the barred owl (*Strix varia*) consist of rods, single cones and double (unequal) cones present in a ratio of about 35:1:3, respectively. No obvious repeating or mosaic pattern was noted in the arrangement of these photoreceptor types (Figs. 1, 2).

Rod photoreceptors have an outer segment about 15 µm in length and 2.0 µm in width (Figs. 2, 10-12). The outer segment is composed of a stack of bimembranous discs enclosed in a limiting membrane (Fig. 10). These discs display several shallow incisures at their periphery, giving the outer segment a scalloped appearance in cross-section (Figs. 11, 12). In the light-adapted condition, rod (and cone) outer segments are surrounded by the apical processes of the retinal epithelial (RPE) cells (Fig. 1). The RPE in this owl is not heavily pigmented, however, and it is doubtful if the amount of pigment present is effective in isolating photoreceptor outer segments from one another (Fig. 1).

An accumulation of mitochondria referred to as the ellipsoid is present at the distal end of the rod inner segment (Figs. 7, 8, 10). Below the ellipsoid the inner segment is rich in profiles of rough endoplasmic reticulum (RER), polysomes, Golgi zones and autophagic vacuoles (Figs. 3, 5, 7, 8). The inner segment of rods in this owl does not contain an accumulation of glycogen, the so-called hyperboloid seen in many birds. The inner segment of rods measured about 2.5 µm in width along its entire length (about 18 µm) and does not show a narrowed myoid region in the light-adapted state (Figs. 5-8). In rod (and cone) photoreceptors the inner and outer segments are joined by an eccentrically located connecting cilium (Figs. 7, 9, 10).

The nuclei of rod photoreceptors are located at all levels of the outer nuclear layer (ONL), and display an electron dense and fairly condensed chromatin pattern (Figs. 2, 13, 14). The smaller synaptic spherules of rods are more electron dense than the larger synaptic pedicles of cones and display 3-5 invaginated (ribbon) synapses as well as several superficial (conventional) synaptic sites (Figs. 13, 14).

The single and double cones in the barred owl are together outnumbered about 10:1 by the rod photoreceptors, while double cones are 2-3 times as numerous as the single cones (Figs. 1, 2). Cones (both types) typically display a more electron lucent cytoplasm in all areas than do the rod photoreceptors (Figs. 2, 4, 8, 13).

Single cones have an outer segment 8-10 µm in length which tapers from a proximal width of about 3:0 µm to about 1.0 µm at its distal end (Figs. 10, 12). The outer segments of cones are scattered amongst the more numerous rod outer segments, where they are easily differentiated by their smaller size and lack of peripheral incisures (Figs. 2, 12).

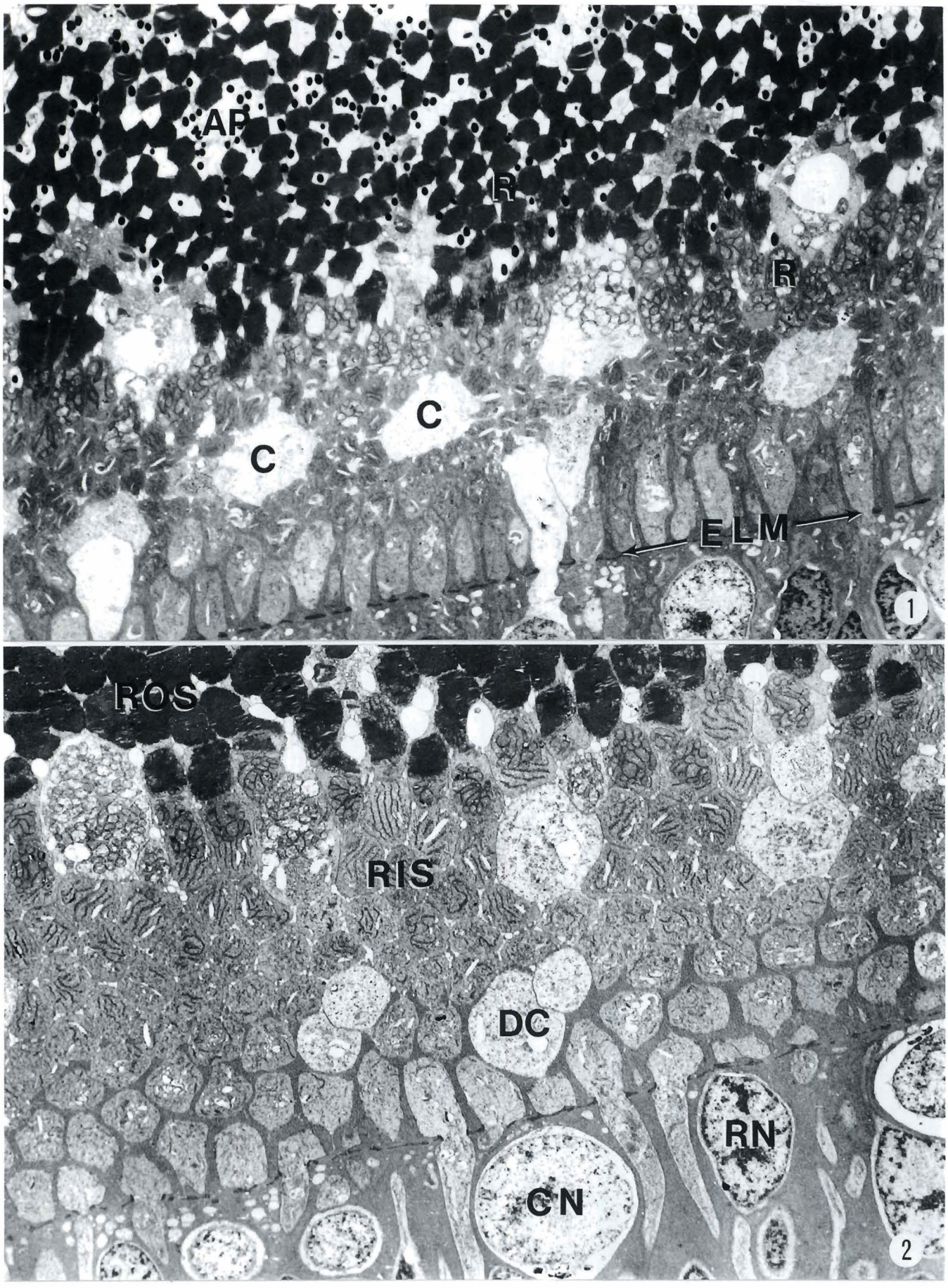
Below the non-motile connecting cilium (Fig. 9) the single cone displays a large (about 4.0 µm) relatively electron lucent and heterogeneous oil droplet (Figs. 10, 11). Proximal to the oil droplet is an ellipsoid of mitochondria (Fig. 10). The single cones are widest in the oil droplet/ellipsoid region, where they measure 5-6 µm in width (Figs. 10, 11). Below the ellipsoid in the myoid region the cones measure about 3.0 µm in width (Fig. 8). In this myoid region are found profiles of RER, numerous polysomes, Golgi zones and often autophagic vacuoles (Figs. 4, 6, 8). In this species the myoid region of the single cones does not contain a large condensed accumulation of glycogen (the paraboloid), but a much dispersed array of glycogen-like particles extends throughout the inner segment (Figs. 4, 8). The nuclei of single cones are invariably located close to, but do not normally protrude through, the external limiting membrane (ELM) (Figs. 2, 6, 13).

The double cones are 2-3 times as numerous as the single cones and consist of two unequal members. One member (the chief cone) is essentially similar to the single cone as described above. The outer segment, oil droplet, ellipsoid and lack of a discrete paraboloid are all as described for the single cone (Fig. 9). Below the ellipsoid in the myoid region are again located profiles of RER, numerous polysomes, Golgi zones and autophagic vacuoles (Figs. 3, 5).

The other member of a double cone (the accessory cone) is normally shorter and thinner (at about 3.0 µm) than the chief cone (Fig. 9). It possesses no oil droplet and is usually somewhat flattened against the chief cone (Figs. 3, 9). Like the single and chief cones it lacks a paraboloid but does have a scattered array of glycogen within the myoid region amongst the profiles of RER, numerous polysomes, Golgi zones and autophagic vacuoles (Figs. 3, 5, 9).

**Fig. 1.** Low power electron micrograph illustrating the preponderance of rod (R) to cone (C) photoreceptors. For orientation, the retinal epithelial apical processes (AP) and external limiting membrane (ELM) are indicated. x 3,200

**Fig. 2.** Electron micrograph to indicate rod inner (RIS) and outer segments (ROS). A double cone (DC) is indicated as are a cone nucleus (CN) and a rod nucleus (RN). x 3,900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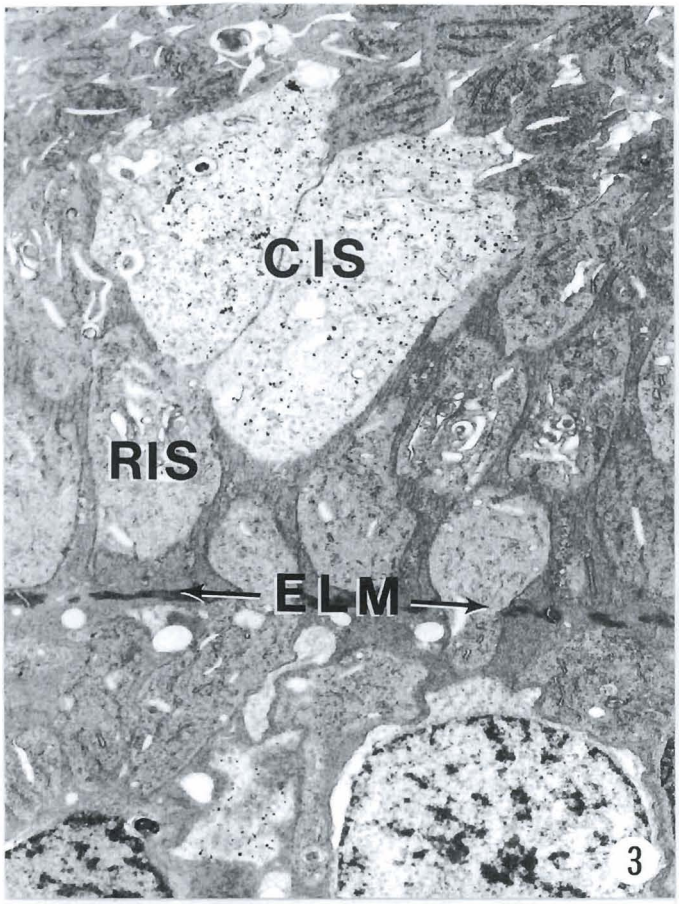
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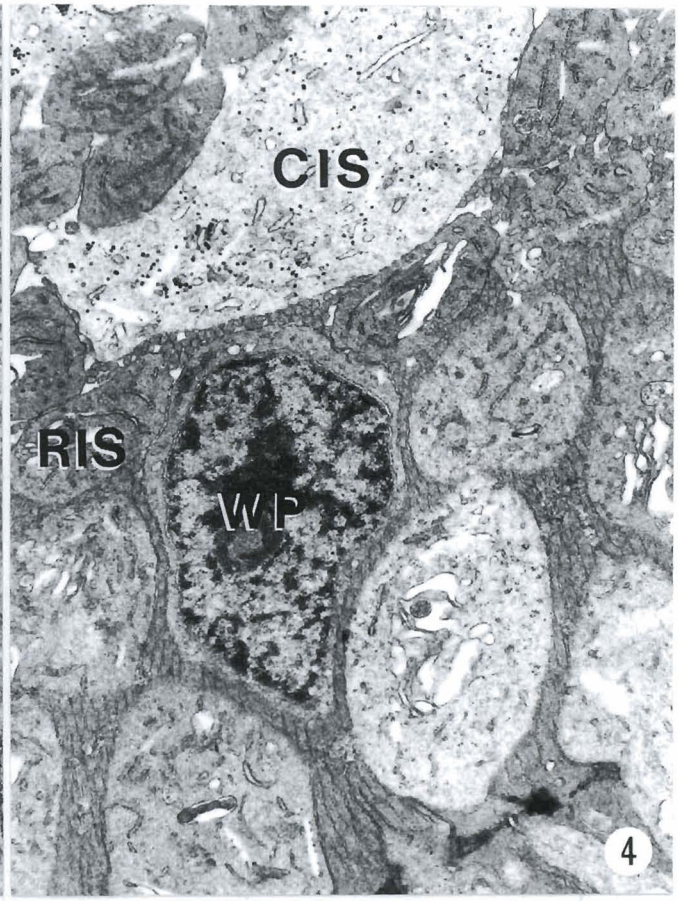
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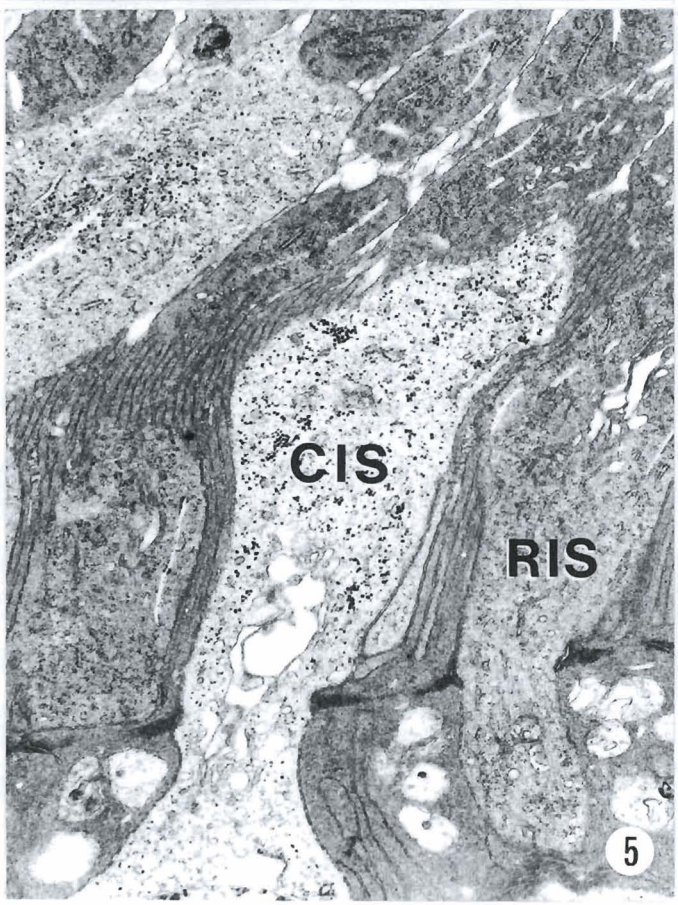
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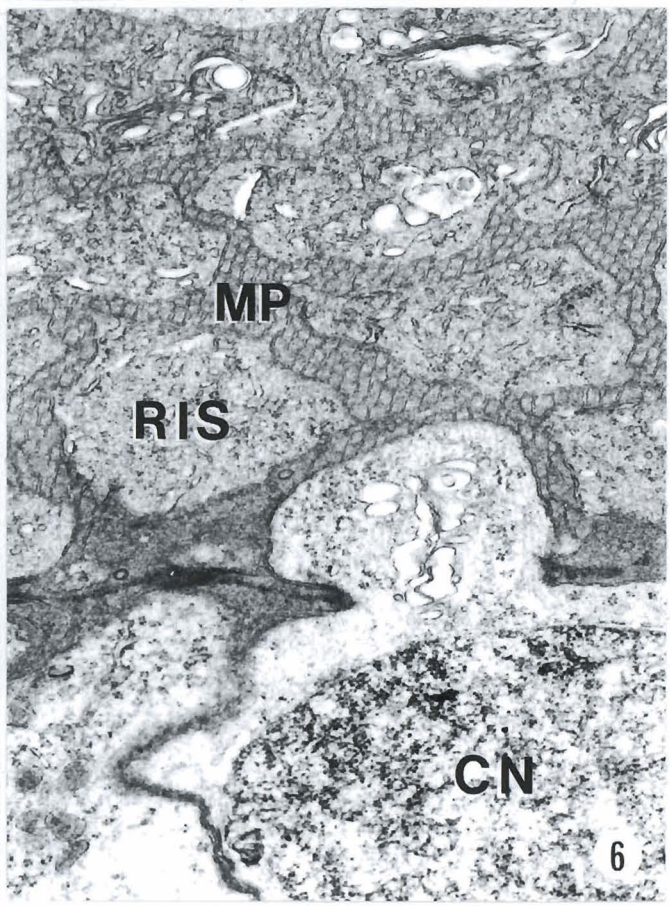
MP
RIS
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6

**Fig. 3.** Electron micrograph to illustrate a double cone inner segment region (CIS) as well as rod inner segments (RIS). The external limiting membrane (ELM) is also indicated. x 7,700

**Fig. 4.** Electron micrograph of a single cone inner segment (CIS) as well as rod inner segment (RIS). A presumed wandering phagocyte (WP) is also labelled. x 11,400

**Fig. 5.** Electron micrograph of a double cone inner segment (CIS) and a rod inner segment (RIS) at the level of the external limiting membrane. Note the scattered glycogen-like particles in the cone. x 11,400

**Fig. 6.** Electron micrograph to illustrate the numerous Müller microvilli (MP) surrounding rod inner segments (RIS). A cone nucleus (CN) is also indicated. x 16,700

Along the length of the contiguous membranes of the chief and accessory cones, membrane densifications which are presumed to be interreceptor junctions are scarce even close to the ELM (Figs. 3, 9). Also in this owl, none of the photoreceptors (rods or cones) display the vertically-oriented fins of cytoplasm that are often reported projecting from the inner segments of the photoreceptors of birds. Within the outer nuclear layer the nuclei of both members of the double cone are large and vesicular and located near the ELM (Figs. 2, 6).

The synaptic pedicles of all cones (single, chief and accessory) are typically larger, more electron lucent and display more synaptic sites than those of the rod photoreceptors (Figs. 13, 14). Like the rods the synaptic pedicles of cones (all types) are rich in synaptic vesicles (Fig. 14). The synaptic pedicles of single cones are indistinguishable from those of either chief or accessory cones in that they are all separated by intervening Müller cell processes and display several invaginated (ribbon) synapses as well as several of the more conventional (superficial) synaptic sites involving only membrane densifications (Figs. 13, 14).

The ELM of the barred owl is composed of a series of zonulae adherentes between rods, single and double cones and Müller cells (Figs. 1-6). Fine processes of the Müller cells (about 5.0 µm in length and 0.1 µm in width) project through the ELM to surround the base of all photoreceptor cells (Figs. 3-6). In this species the Müller cell processes do not reach to the apical processes of the RPE cells (Fig. 1). Nucleated cells were occasionally noted amongst the photoreceptor cells near the ELM, and were presumed to be wandering phagocytic cells that are noted in the subretinal space of many species (Fig. 4).

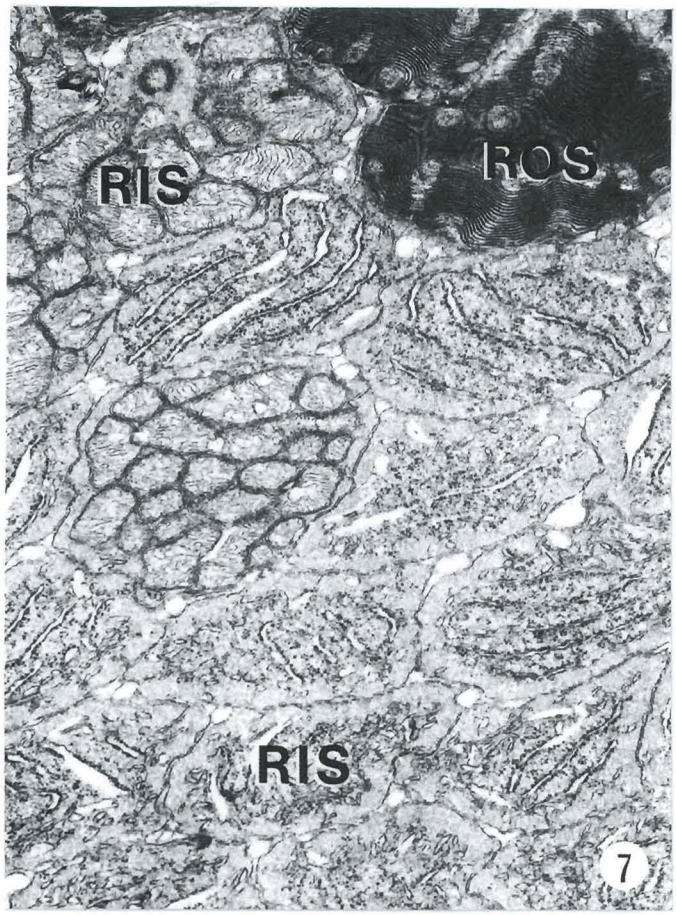
## Discussion

Many avian species are highly active diurnal animals with good vision. The retinas of these species contain numerous cone photoreceptors that in many cases actually outnumber the rods (Walls, 1942; Crescitelli, 1972; Meyer and May, 1973; Braekevelt, 1990, 1993a, 1994a,b). The barred owl (*Strix varia*) shows the three rods types of photoreceptor normally found in the avian retina, namely rods, single cones and double unequal cones, but has a preponderance of rods in the ratio of about 35:1:3 respectively. The ratio of rods:single cones:double cones normally shows a preponderance of cones over rods in diurnal avian species (Walls, 1942; Braekevelt, 1993a, 1994a,b). This would reflect the importance of cone (colour) vision in diurnal birds. The differences in the ratio of rods and cones that are reported within avian species probably reflects differences in feeding habits that are reflected in their visual requirements (Walls, 1942). The preponderance of rods over cones in this species and the great horned owl (Braekevelt, 1993b) is almost certainly due to the crepuscular and nocturnal habits of these birds and indicates their reliance on rod photoreceptors, which have a lower threshold of stimulation.

The rods of the barred owl are numerous and relatively thin cells with an outer segment that measures only about 2.0 µm in diameter. This is compared to the width of rod outer segments in most other avian species, including those species with a cone dominant retina (range of rod outer segments from 1.5-4 µm) (Braekevelt, 1990, 1993a, 1994a,b). However, the 2.0 µm wide rods reported in this owl are thinner than those noted for the great horned owl at 4-5 µm in width (Braekevelt, 1993b). The preponderance of rods coupled with their thin diameter would allow for a large light-capture area and make this an extremely sensitive retina.

The inner segments of rods in the light-adapted condition do not show a markedly constricted myoid region which would indicate that these cells have elongated during light-adaptation. Instead the rod inner segments in the barred owl remain fairly uniform in width along their entire length. This would indicate that rod photoreceptors in this species do not undergo photomechanical or retinomotor movements in response to environmental lighting.

Both types of cone in the barred owl are also elongated cells in the light-adapted state with a fairly uniform inner segment (width about 6 µm below the ellipsoid region). This would also seem to indicate that cones do not move (i.e shorten) in light-adaptation. These observations for rods agree with Walls (1942), who noted little or no movement of these cells in response to the photoperiod, but are contrary to other fundings indicating that except for the accessory member of double cones, all avian photoreceptors show rapid and extensive retinomotor movements (Meyer, 1977). Observations on a fully dark-adapted barred owl would be required to adequately settle this question, but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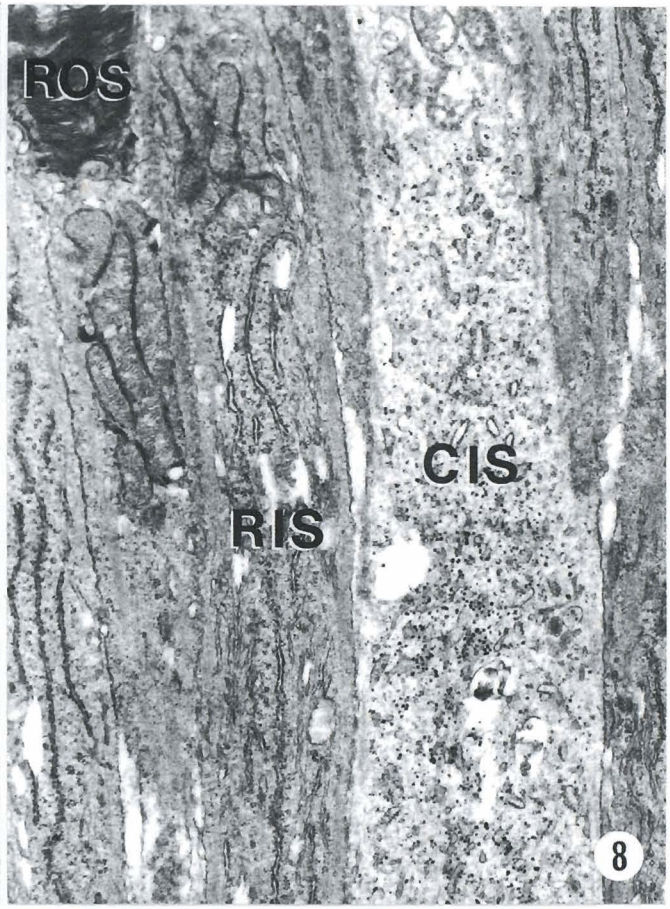
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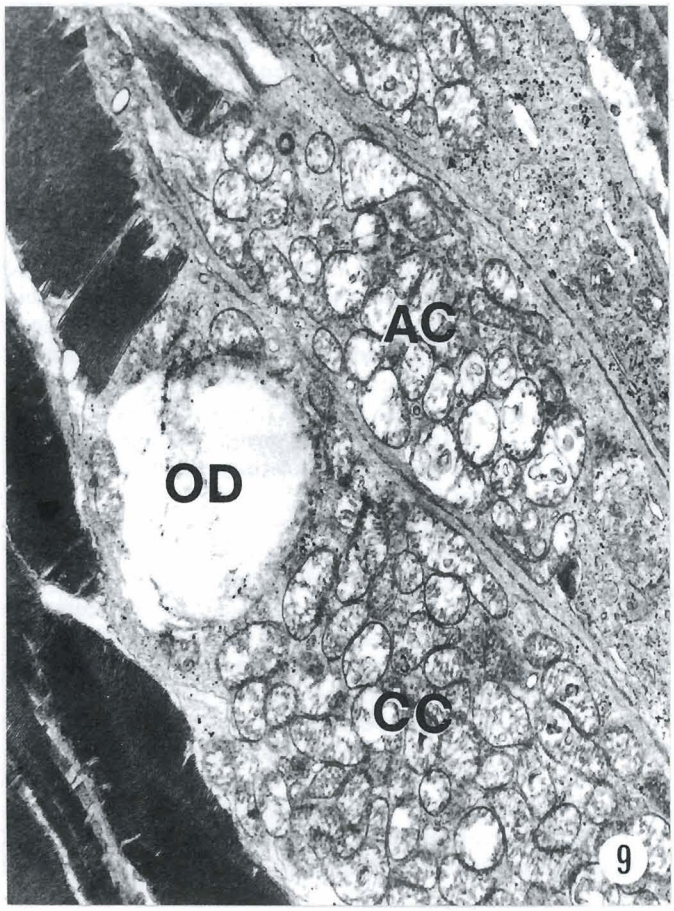
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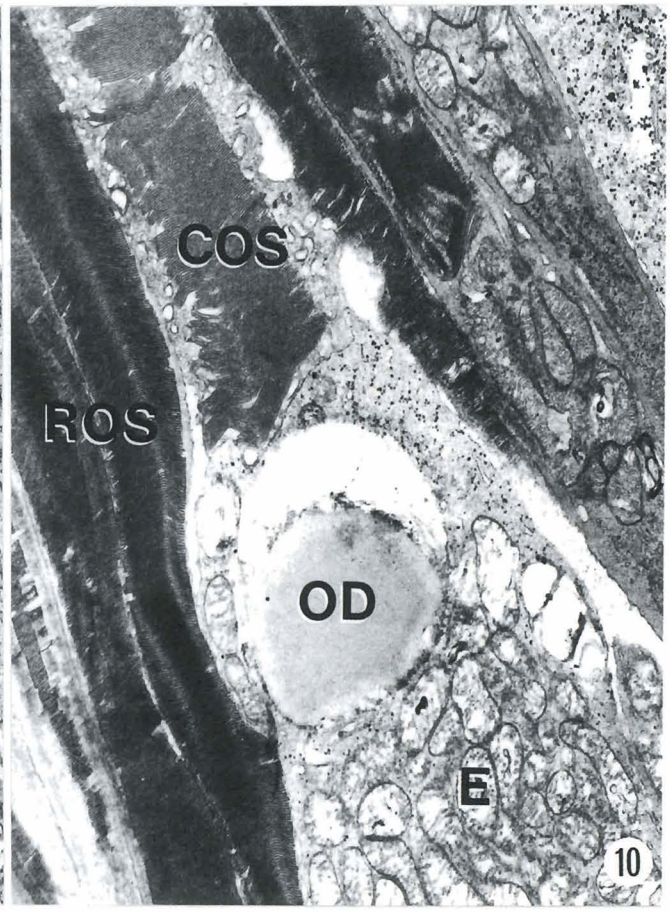
COS
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**Fig. 7.** Electron micrograph illustrating rod outer segments (ROS) and inner segments (RIS) at several levels. x 16,700

**Fig. 8.** Electron micrograph to illustrate the size and electron density differences between rod (RIS) and cone inner segments (CIS). A rod outer segment (ROS) is also indicated. x 11,400

**Fig. 9.** Electron micrograph of a double cone to indicate the chief member (CC) and accessory member (AC). The chief cone has an oil droplet (OD) while the accessory member does not. x 10,700

**Fig. 10.** Electron micrograph of a single cone to illustrate its outer segment (COS), oil droplet (OD) and ellipsoid (E). Rod outer segments (ROS) are also labelled. x 10,700

it may be that nocturnal species like the barred owl and great horned owl (Braekevelt, 1993b) lack photochemical movements of their photoreceptors entirely.

In the barred owl, the RPE is but lightly pigmented. While it is felt that this pigment undergoes photomechanical movements, it is unlikely that even in the fully lightly-adapted state this pigment could adequately mask the rod outer segments. The pupillary response in birds is however reported to be extensive and this may compensate for the apparent lack of photoreceptor movement in response to environmental lighting (Walls, 1942).

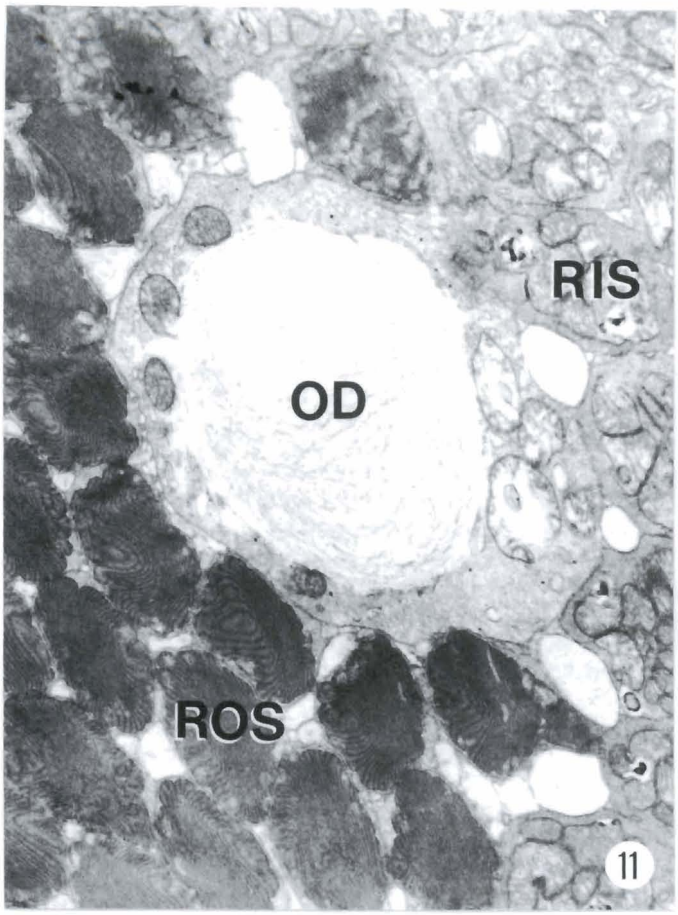
The outer segments of both rods and cones consist of a stack of bimembranous discs that represent the light-capture area of the photoreceptors (Cohen, 1972; Crescitelli, 1972). In rods the outer segment discs are normally all of the same diameter and totally enclosed within a limiting membrane. They also usually show one or more peripheral incisures, presumably to increase their surface area (Nilsson, 1965; Braekevelt, 1983). In cones the outer segment discs close to the inner segment are normally wider than those at the apex, and hence the outer segment has a tapered or conical shape (Cohen, 1963, 1972). In addition, cone outer segment discs in the basal region are often continuous with the limiting membrane and seldom show any peripheral incisures (Braekevelt, 1982). Rod and cone outer segments are of much the same diameter in the barred owl. However, because of the longer length of rod outer segments and their numerical preponderance, rod photoreceptors would present a much larger light-capture area again emphasizing the importance of rod (non-colour) vision in this nocturnal owl. The inner segment region of all photoreceptors is known to be the 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).

In the barred owl, a single large oil droplet is located at the apex of the inner segment of single cones as well as the chief member of the double cone, but not in rods or accessory cones. These oil droplets have been reported in the cones of amphibians, reptiles, birds and non-placental mammals (Braekevelt, 1973, 1989, 1990; Rodieck, 1973; Meyer, 1977; Kolb and Jones, 1982). Oil droplets are felt to selectively filter the incoming light and in so doing probably enhance contrast, reduce glare and lessen chromatic aberration (Meyer, 1977). Oil droplets are reported in a range of colours with highly diurnal species having orange to red droplets and nocturnal species showing colourless droplets (Meyer, 1977). The colour of the droplets in this species was not determined by they are presumed to be colourless as reported in other owls (Yew et al., 1977).

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 a compact accumulation of glycogen found in the cone inner segment of many birds, fish, amphibians and reptiles (Cohen, 1972; Braekevelt, 1989), is not present in the cones of the barred owl. However, the inner segment of all cones in this species is rich in glycogen that is widely scattered throughout the inner segment, and this may represent a diffuse type of paraboloid. A number of avian species also show a glycogen mass in rods (the hyperboloid), but this was not observed in either the barred owl or great horned owl and it may be that nocturnal species characteristically lack this hyperboloid (Meyer and Coper, 1966; Meyer, 1977; Braekevelt, 1990, 1993a,b, 1994a). These glycogen bodies (paraboloids in cones, hyperboloids in rods) were once thought to be refractile structures, but are now believed to be energy sources for visual cell metabolism (Meyer, 1977). The significance of the variations noted among species as to what photoreceptor types do or do not show a paraboloid or hyperboloid is unknown, but may correlate with nocturnal and diurnal requirements (Meyer, 1977; Braekevelt, 1990, 1993a,b).

In the myoid region of the inner segment, interreceptor junctions are typically reported between the two members of a double cone. In teleost fish these junctional specializations are often quite extensive and involve prominent submembranous cisternae (Berger, 1967; Braekevelt 1982). In avian species these interreceptors junctions usually take the form of gap and intermediate junctions between the chief and accesory cones (Nishimura et al., 1981; Smith et al., 1985; Braekevelt, 1990, 1993a,b). While interreceptor junctions were noted between the two members of the double cones in the barred owl, they were not widespread.

As in the case in all vertebrates described to date, the external limiting membrane in the barred owl is composed of a series of zonulae adherentes between Müller cells and the three types of photoreceptor present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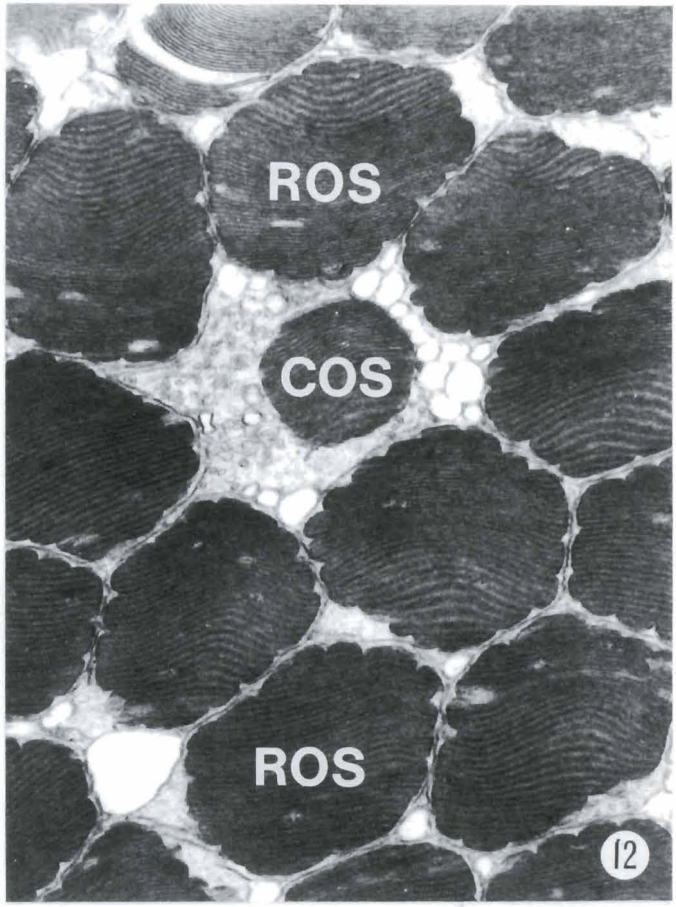
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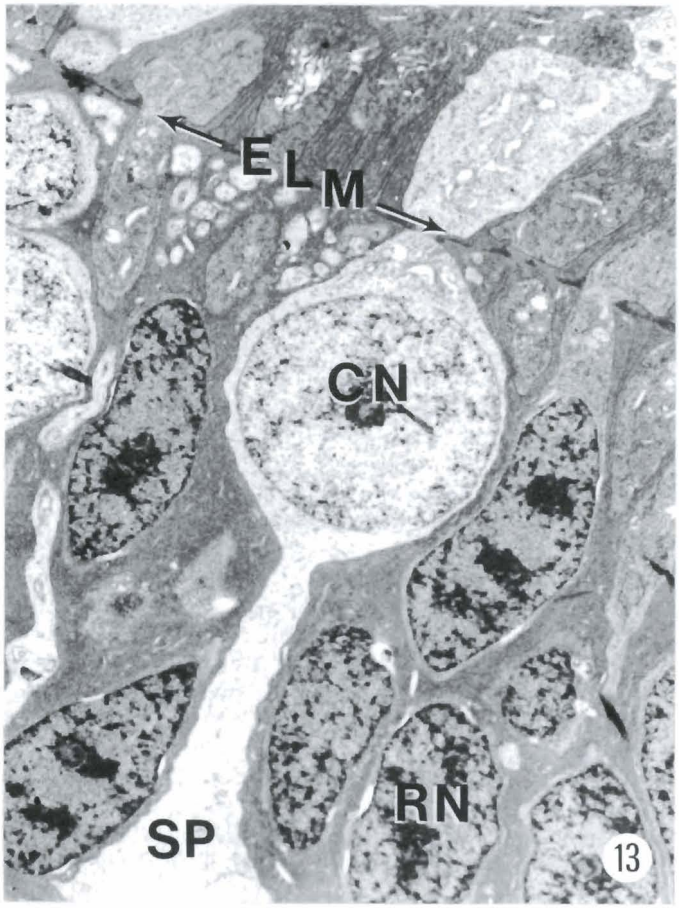
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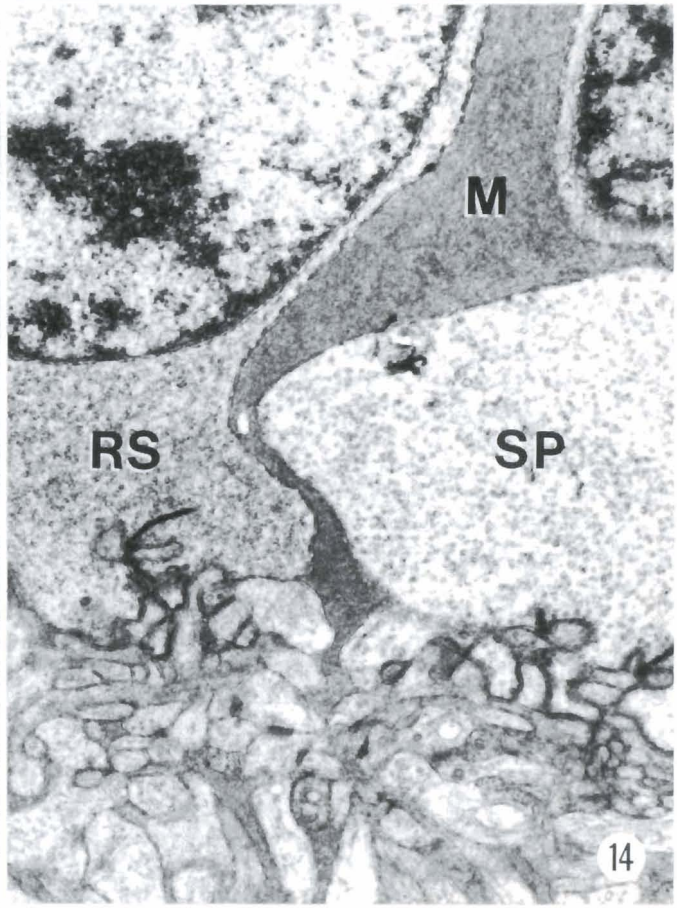
M
RS
SP
14

**Fig. 11.** Electron micrograph of a single cone illustrating the oil droplet (OD). Rod inner (RIS) and outer segments (ROS) are also labelled. x 11,500

**Fig. 12.** Electron micrograph to illustrate the difference between rod (ROS) and cone (COS) outer segments in cross section. x 11,500

**Fig. 13.** Electron micrograph of a cone photoreceptor from the external limiting membrane (ELM) to its synaptic pedicle (SP). Rod (RN) and cone nuclei (CN) are indicated. x 5,000

**Fig. 14.** Electron micrograph of the synaptic spherule of a rod (RS) and the synaptic pedicle (SP) of a cone. A Müller cell (M) intervenes between the two photoreceptors. x 11,500

(Uga and Smelser, 1973). Also as is noted in many other species, the Müller cells form a series of microvillar processes which project through the ELM and surround the base of the inner segments (Braekevelt, 1989, 1990, 1993a,b). In this region, the photoreceptors of many birds also show a number of vertically oriented lateral fins which interdigitate with these Müller cell processes (Crescitelli, 1972; Braekevelt, 1990, 1993a,b). These lateral fins were not present on any of the photoreceptor types in the barred owl. The significance (if any) of the presence or absence of these lateral fins on the various photoreceptor types is unknown.

Within the outer plexiform layer (OPL) the synaptic pedicle of cone photoreceptors is typically larger, more electron-lucent and displays more synaptic sites than the smaller spherule or 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 only a superficial membrane densification (Dowling, 1968; Cohen, 1972). While bipolar and horizontal cells are both involved at invaginated synapses (Kolb, 1970), superficial synapses may occur between photoreceptors and bipolar cells or between photoreceptors themselves (Cohen, 1964; Missotten, 1965; Kolb, 1970). The barred owl 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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