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Fine structure of the retinal photoreceptors of the great horned owl *(Bubo virginianus)*

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Summary. The retinal photoreceptors of the great horned owl *(Bubo virginianus)* consist of rods, single cones and unequal double cones present in a ratio of about 30:1:2. In the light-adapted state the rods are stout cells which are not felt to undergo retinomotor movements. The rod outer segment consists of a stack of scalloped membranous discs enclosed by the cell membrane. The rod inner segment shows an ellipsoid of mitochondria and a wealth of rough endoplasmic reticulum (RER) and polysomes, Golgi zones and autophagic vacuoles but no hyperboloid of glycogen. Single cones show a slightly tapered outer segment, a heterogeneous oil droplet and an ellipsoid of mitochondria at the apex of the inner segment. Double cones consist of a larger chief member which also displays an oil droplet and a slightly smaller accessory member which does not. Both members of the double cone as well as the single cone show a prominent ellipsoid, plentiful polysomes and RER and Golgi zones in the inner segment. Neither single nor double cones possess a condensed paraboloid of glycogen but instead show plentiful scattered glycogen particles. Along the contiguous membranes between accessory and chief cones a few presumed junctional complexes are seen near the external limiting membrane. Judging by their morphology in light-adaptation the cones of this species do not undergo photomechanical movements. Rods and cones (both types) have both invaginated (ribbon) and numerous superficial (conventional) synaptic sites. Rods are more numerous in this nocturnally active bird than is usually noted in avian species.

Key words: Photoreceptors, Electron microscopy, Great horned owl, *Bubo virginianus*

Introduction

Retinal photoreceptors which are the first neuron in the visual pathway are extremely specialized and highly polarized cells. They have been extensively studied with a variety of techniques and comparative morphological studies have shown that all vertebrate photoreceptors are constructed on an essentially similar plan (Walls, 1942; Polyak, 1957; Cohen, 1972; Crescitelli, 1972; Young, 1974; Braekevelt, 1975, 1985, 1990, 1992a). This basic plan 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 an expanded synaptic ending (Cohen, 1972; Crescitelli, 1972; Rodieck, 1973). Phylogenetic specializations such as oil droplets or multiple receptors can often be superimposed on this basic plan (Cohen, 1972; Fineran and Nicol, 1974, 1976; Braekevelt, 1982, 1990).

Historically retinal photoreceptors have been classified as either rods or cones on the basis of their morphology at a light microscopic level (Walls, 1942; Polyak, 1957; Duke-Elder, 1958). With the enhanced resolution of electron microscopy some workers proposed a more elaborate method of classifying photoreceptors (Sjöstrand, 1958, 1959; Pedler, 1965, 1969) but for the majority of species investigated the traditional classification into rods or cones is still employed and both adequately and accurately differentiates these cells (Crescitelli, 1972; Rodieck, 1973; Braekevelt, 1983, 1984, 1985, 1989, 1990, 1992a).

Avian species typically display rods, single cones and double (unequal) cones in the retina with the cones often more plentiful than the rods (Morris, 1970; Meyer, 1977). As part of an ongoing comparative study of retinal photoreceptors this report describes the fine structure of the rods and cones (both single and double) in the duplex retina of the nocturnal great horned owl *(Bubo virginianus)*.

Materials and methods

For this study, both eyes from an adult light-adapted great horned owl *(Bubo virginianus)* were examined by light and electron microscopy. With the bird under deep anaesthesia, the eyeballs were quickly enucleated, sliced open at the equator and immersion fixed for 5 h at 4 °C

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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 7.3) and cut into pices 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 (pH 7.3) 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 nm) 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 EM 201 transmission electron microscope.

Results

As in other avian species, three morphologically distinct types of photoreceptors are found in the duplex retina of the great horned owl *(Bubo virginianus)*. There are rods, single cones and unequal double cones (Figs. 2, 3, 7, 8). These are present in a ratio of about 30:1:2 respectively with no obvious repeating pattern of arrangement or mosaic.

Rod photoreceptors show an outer segment about 10 μm in length and 4-5 μm in width (Figs. 7, 8, 10). The outer segment is composed of a stack of bimembranous discs enclosed in a limiting membrane (Figs. 8, 10). These discs display several shallow incisures at their periphery to give the outer segment a scalloped appearance in cross-section (Figs. 8-10, 12). In the light-adapted condition, rod (and cone) outer segments are surrounded by pigment-laden apical processes of the retinal epithelial (RPE) cells (Figs. 7, 8, 10, 12). These RPE apical processes also surround the rod and cone inner segments to some extent (Figs. 5, 6, 11) but do not reach to the external limiting membrane (ELM) (Fig. 1)

At the distal end of the inner segment the rods display a large accumulation of mitochondria (the ellipsoid) and below this the inner segment is rich in profiles of rough endoplasmic reticulum (RER), polysomes, Golgi zones and the occasional autophagic vacuole (Figs. 2, 3, 5, 6, 11). The inner segment of rods in this species does not contain an accumulation of glycogen (the hyperboloid seen in many birds). The inner segment of the rods measures about 5 μm in width along its entire length (about 25 μm) and does not show a narrowed myoid region in the light-adapted state (Figs. 2-6). In rod (and cone) photoreceptors the inner and outer segments are joined by an eccentrically located connecting cilium.

The nuclei of the rod photoreceptors display an electron dense and fairly condensed chromatin pattern and are found at all levels within the outer nuclear layer (ONL) (Figs. 1, 13, 14). The smaller synaptic spherules of rods are more electron dense than the 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 great horned owl are together outnumbered about 10:1 by the rod photoreceptors while double cones are about twice as numerous as the single cones (Figs. 1-3). Cones (both types) typically display a more electron lucent cytoplasm in all areas than do the rods (Figs. 2-4, 13, 14).

Single cones have an outer segment about 10 μm in length and which tapers from a proximal width of about 3 μm to about 1 μm at its tip (Figs. 7, 12). The cone outer segments are interspersed amongst the rod outer segments but are easily differentiated by their smaller diameter and lack of peripheral incisures (Fig. 12).

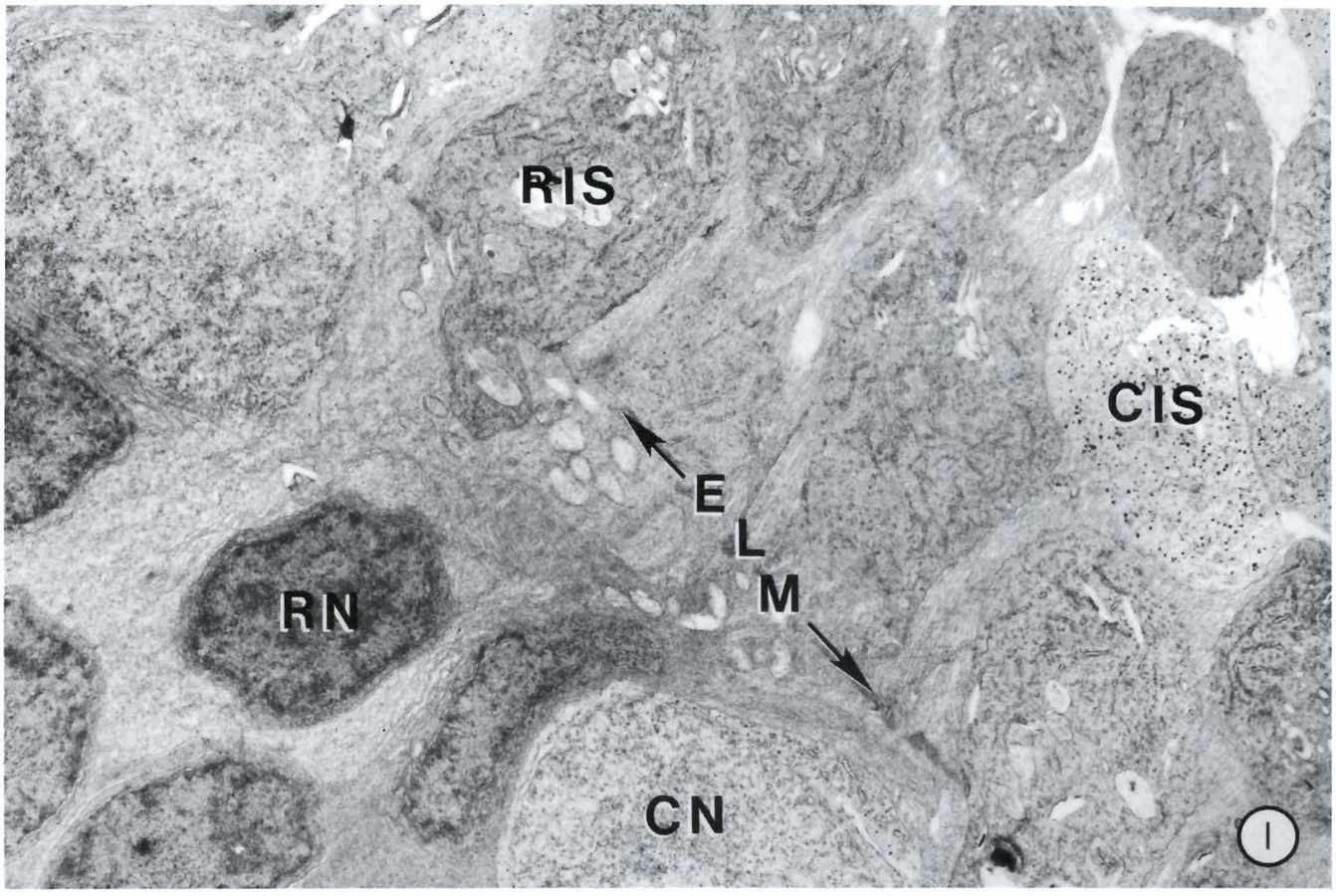
Below the connecting cilium, the single cones display a large (about 3.0 μm) relatively electron lucent and typically heterogeneous oil droplet (Figs. 7, 8). Proximal to this oil droplet is an ellipsoid of electron-lucent mitochondria (Fig. 7). The single cones are widest in the oil droplet/ellipsoid region where they measure 6-7 μm in width (Figs. 7, 8) while below this in the myoid region the cells measure only about 3.0 μm in width (Figs. 3, 4). In this so-called myoid region are found abundant profiles of RER, numerous polysomes and Golgi zones and often autophagic vacuoles (Figs. 2, 3). While the inner segment of single cones in this species does not contain a large condensed accumulation of glycogen (the paraboloid) it does have a dispersed array of glycogen-like particles that extends throughout the inner segment (Figs. 3, 4, 8). The nuclei of single cones are invariably located close to the ELM but do not normally protrude through it (Fig. 1).

Double cones which are about twice as numerous as single cones consist of two unequal cells. One member (the chief cone) is larger than the other and has an outer segment much like that in the single cone and also displays a heterogeneous oil droplet (about 3.0 μm in diameter) at the apex of the inner segment (Figs. 9, 10). This chief cone displays an ellipsoid of electron-lucent mitochondria and lacks a distinct paraboloid but like the single cone has a scattered array of glycogen within the

Fig. 1. Electron micrograph of the photoreceptors of the great horned owl taken near the external limiting membrane (ELM). Rod inner segments (RIS) and a single cone inner segment (CIS) are labelled as is a rod (RN) and cone (CN) nucleus. x 8,600

Fig. 2. Electron micrograph of several photoreceptors cut in transverse section near the external limiting membrane. Rods (R), the accessory (AC) and chief membrane (CC) of a double cone and Müller cell processes (MP) are indicated. x 14,400

Fig. 3. Electron micrograph to illustrate a single cone (SC) surrounded by several rod (R) photoreceptors. x 14,400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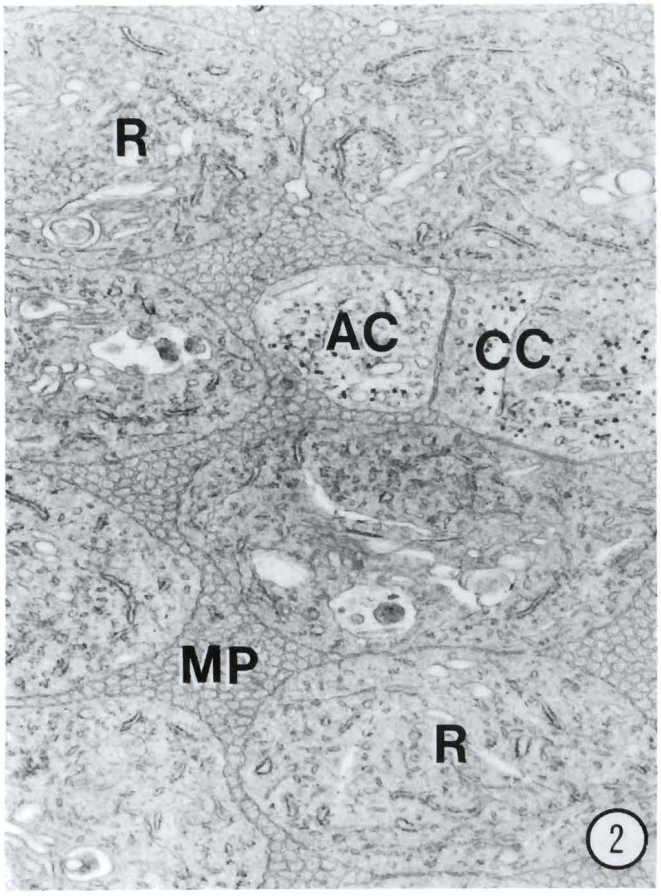
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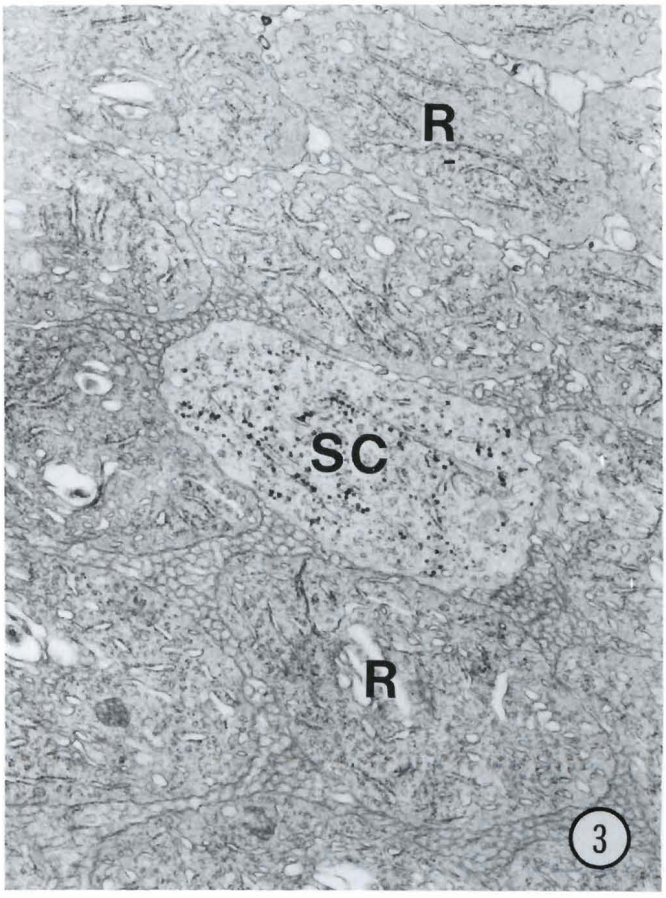
2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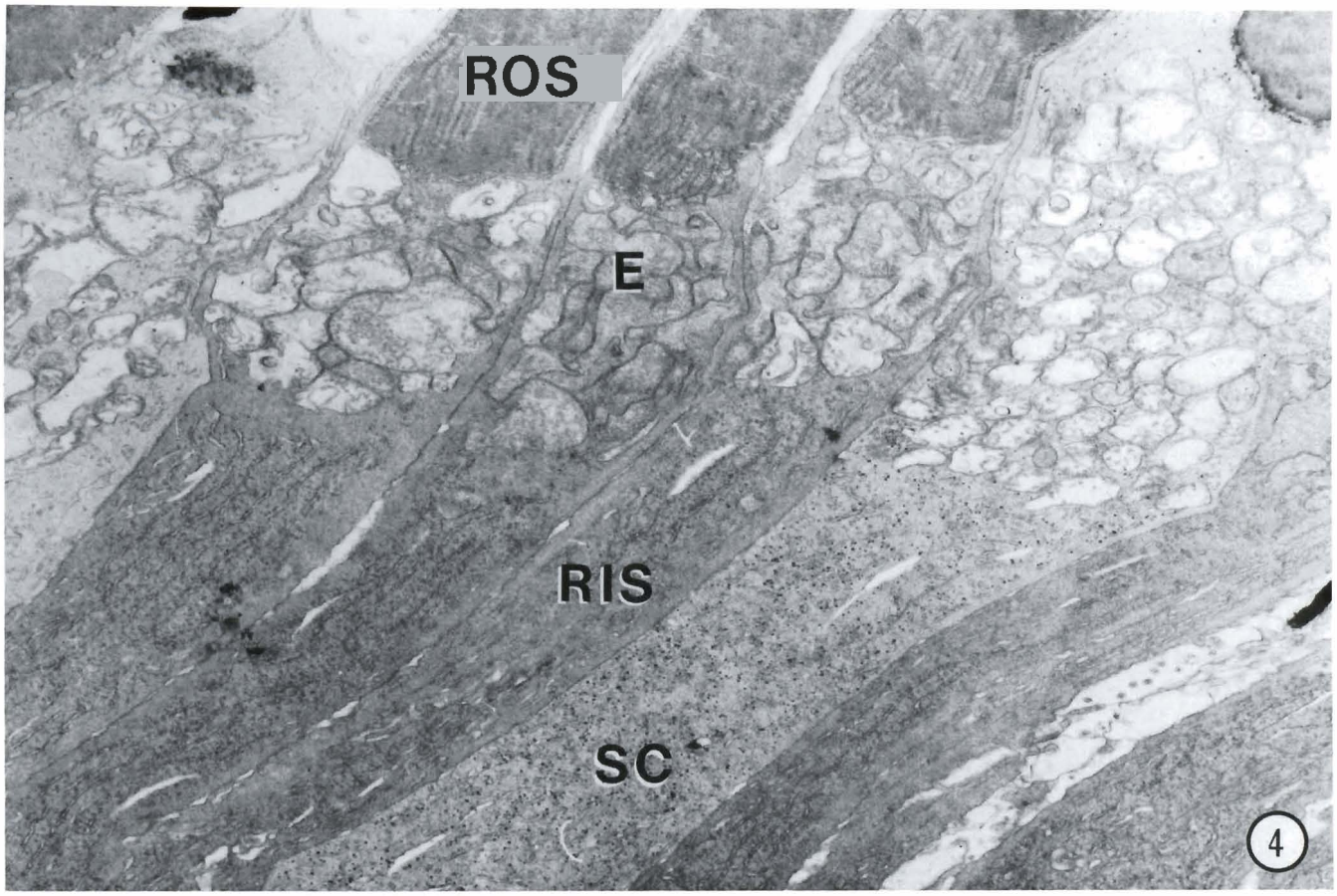
ROS
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RIS
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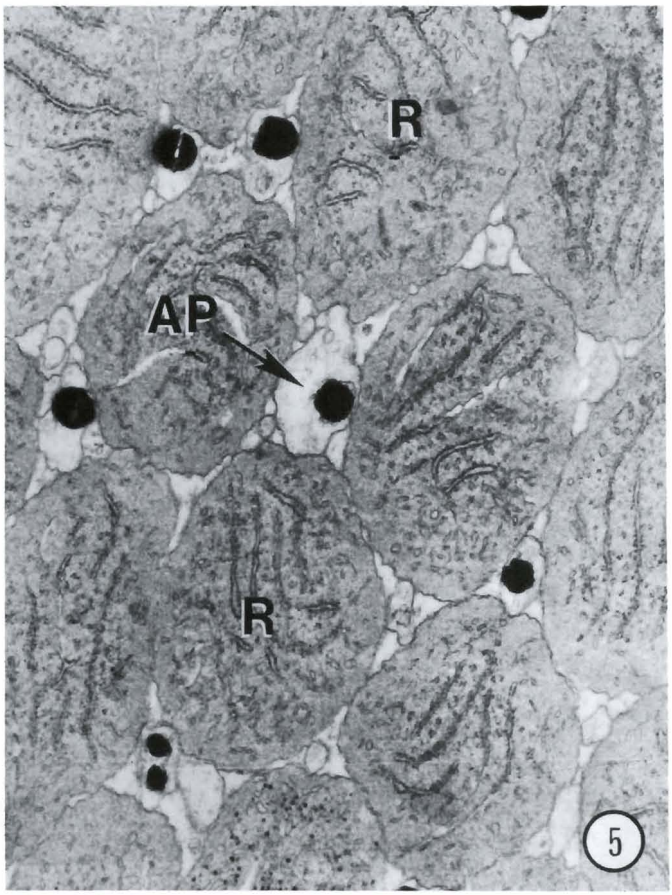
4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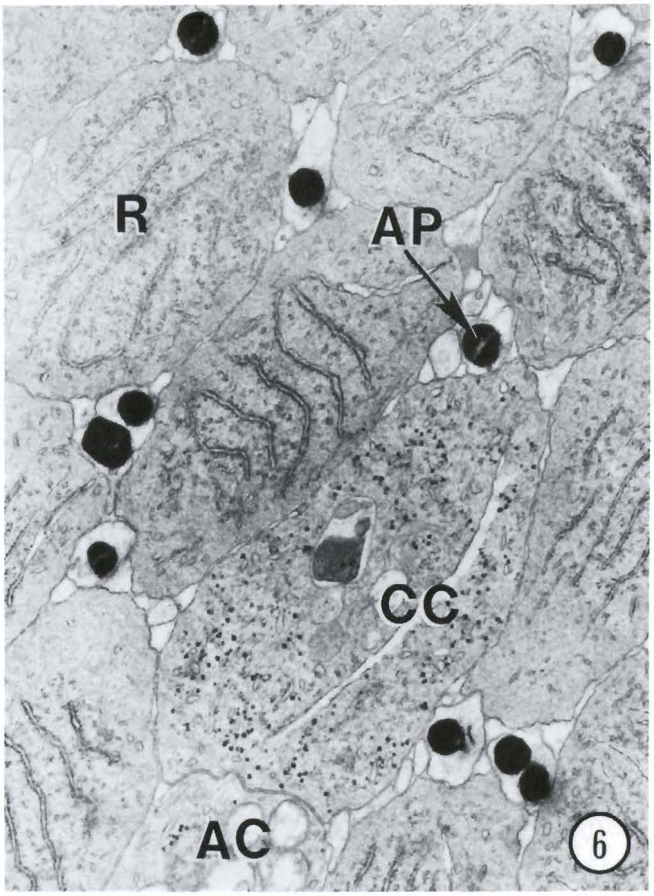
R
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6

Fig. 4. Electron micrograph of rod photoreceptors to illustrate the outer segment (ROS), ellipsoid (E) and inner segment (RIS). A single cone (SC) is also indicated. x 8,600

Fig. 5. Electron micrograph of several rod photoreceptors (R) cut transversely near the retinal pigment epithelial layer. The apical processes (AP) of the RPE cells are also indicated. x 14,400

Fig. 6. Electron micrograph of several rod (R) photoreceptors and the accessory (AC) and chief members (CC) of a double cone cut near the RPE layer. The apical processes (AP) of the RPE cells are labelled. x 13,800

inner segment (Figs. 2, 6, 10). The chief cone is about 5.0 μm in width in most locations and widens only slightly in the oil droplet/ellipsoid region (Figs. 6, 9, 10). Below the ellipsoid in the myoid region are again located plentiful profiles of RER, numerous polysomes and autophagic vacuoles (Figs. 2, 6).

The other member of a double cone (the accessory cone) is normally shorter and thinner (at about 3.0 μm) than the chief cone (Figs. 2, 6). It shows no oil droplet and is usually somewhat flattened against the chief cone (Figs. 2, 6, 10). The accessory cone outer segment is shorter and thinner than that of the chief or single cones (Fig. 9). Also like the single and chief cones the accessory cone has an ellipsoid of mitochondria (Fig. 10). It lacks a distinct paraboloid but does have a scattered array of glycogen within the myoid region with the profiles of RER, numerous polysomes and autophagic vacuoles (Figs. 2, 6).

Along the length of the contiguous membranes of the chief and accessory cones, membrane densifications which are present in most avian species and which are presumed to indicate interreceptor junctions are quite rare in this species even close to the ELM. Also none of the photoreceptors (rods or cones) in this species display the vertically oriented fins of cytoplasm that are often noted in birds. Within the outer nuclear layer (ONL) the nuclei of both members of the double cone are large and vesicular and located near the ELM (Fig. 1).

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 rods (Figs. 13, 14). Like the rods the synaptic pedicles of all cone types are rich in synaptic vesicles (Figs. 13, 14). The synaptic pedicle of a single cone is indistinguishable from that of either the 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 densification (Figs. 13, 14).

The external limiting membrane of the great horned owl is composed of a series of zonulae adherentes between rods, single and double cones and Müller cells (Fig. 1). Fine processes of the Müller cells (about 10 μm in length) project through the ELM to surround the base of all photoreceptor cells (Fig. 1). In this species these Müller cell processes do not reach to the apical cell processes of the RPE cells (Fig. 1).

Discussion

Most avian species are highly active diurnal animals with good vision and their retinas typically contain numerous cone photoreceptors that in many cases actually outnumber the rods (Walls, 1942; Crescitelli, 1972; Meyer and May, 1973; Braekevelt, 1990, 1992a,b). The great horned owl *(Bubo virginianus)* while showing the three types of photoreceptors normally found in the avian retina namely rods, single cones and double unequal cones has a preponderance of rods in the ratio of about 30:1:2 respectively.

The ratio of rods: cones normally shows a preponderance of cones over rods in most diurnal avian species (Braekevelt, 1990, 1992a,b). This would reflect the importance of cone vision to these active diurnal birds. Although small differences in the ratio of rods to cones are noted between avian species these probably indicate differences in feeding habits that are reflected in their visual requirements (Walls, 1942). The preponderance of rods over cones in this species is almost certainly due to the crepuscular and nocturnal habits of this owl and reflects its reliance on rods.

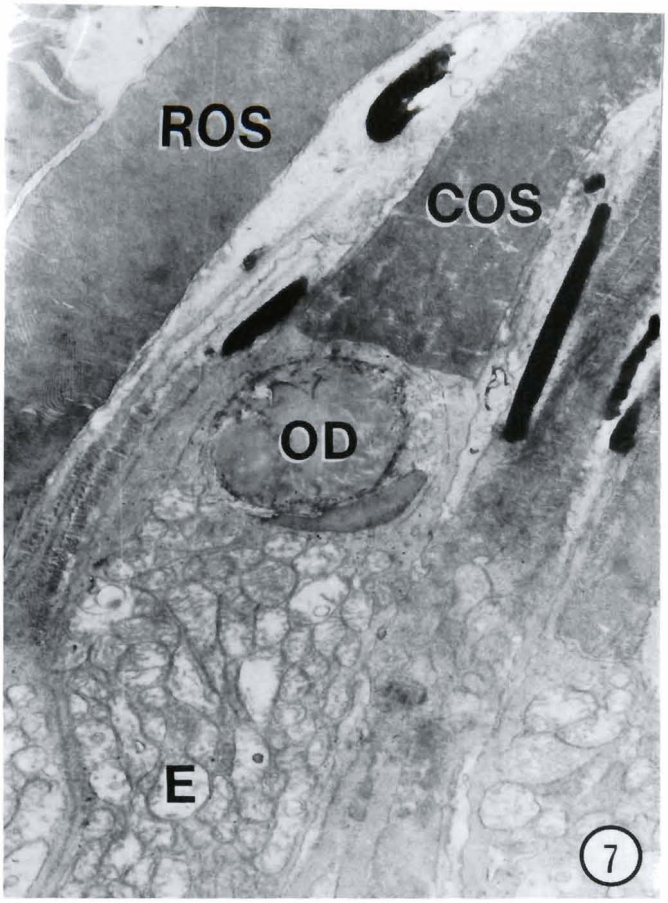
The rods of the great horned owl are large and relatively stout cells which in the light-adapted state do not show a markedly narrowed myoid region which would indicate that these cells elongated during light-adaptation. Instead the rod inner segments in this species are fairly uniform in width along their entire length. This

Fig. 7. Electron micrograph of a single cone to illustrate the outer segment (COS), oil droplet (OD) and ellipsoid (E). A neighbouring rod outer segment (ROS) is also labelled. x 9,500

Fig. 8. Electron micrograph of transversely sectioned photoreceptors to indicate rod outer segments (ROS) and the oil droplet (OD) of a single cone. RPE apical processes (AP) are also indicated. x 6,400

Fig. 9. Electron micrograph of a double cone to illustrate the outer segment (ROS), oil droplet (OD) and ellipsoid (E) of the chief member. The outer segment (OS) of the accessory cone and of a rod (ROS) are also indicated. x 13,800

Fig. 10. Electron micrograph of a transversely sectioned double cone to illustrate the ellipsoid (E) of the accessory cone and the oil droplet (OD) of the chief cone. Rod outer segments (ROS) are also indicated. x 9,500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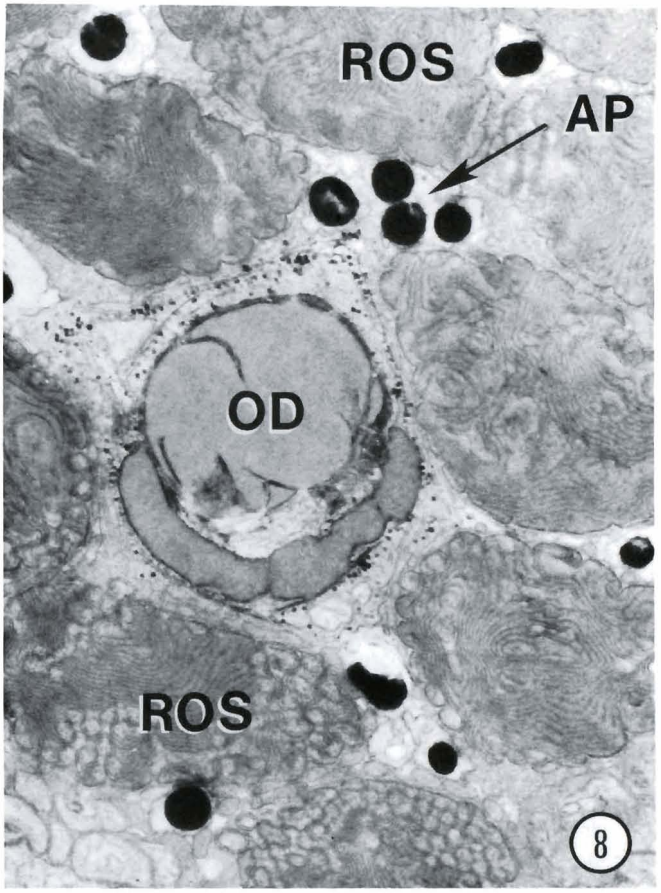
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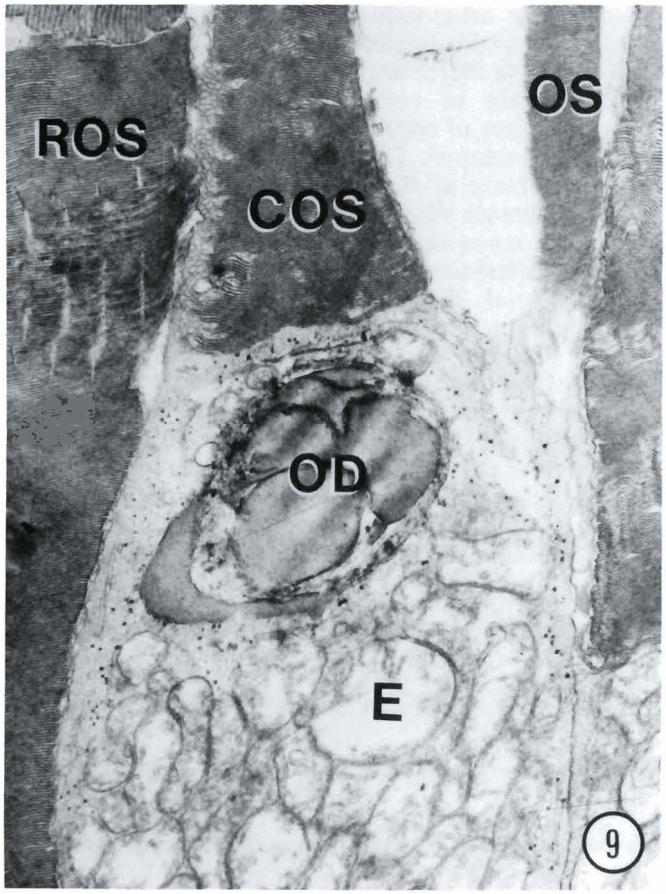
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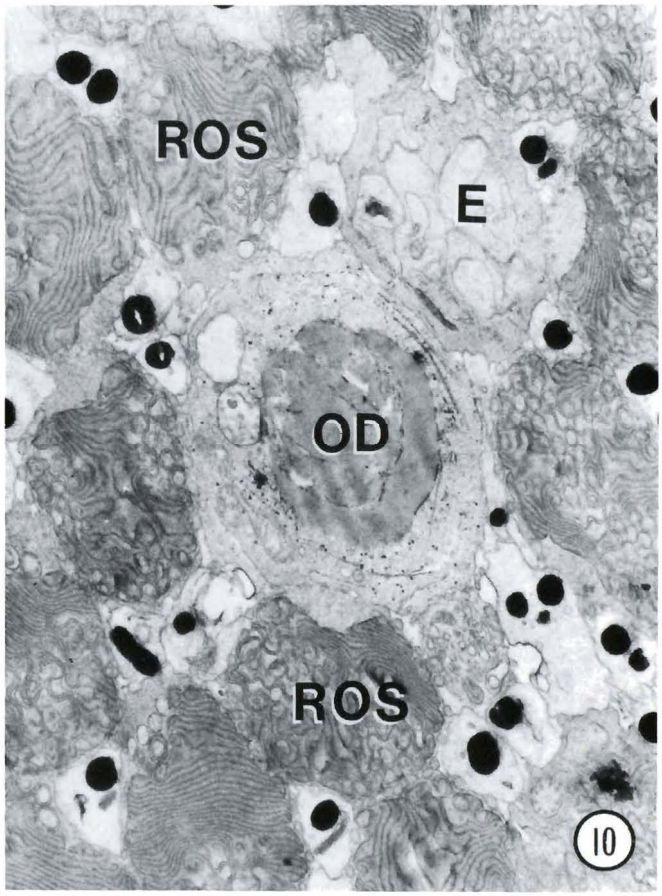
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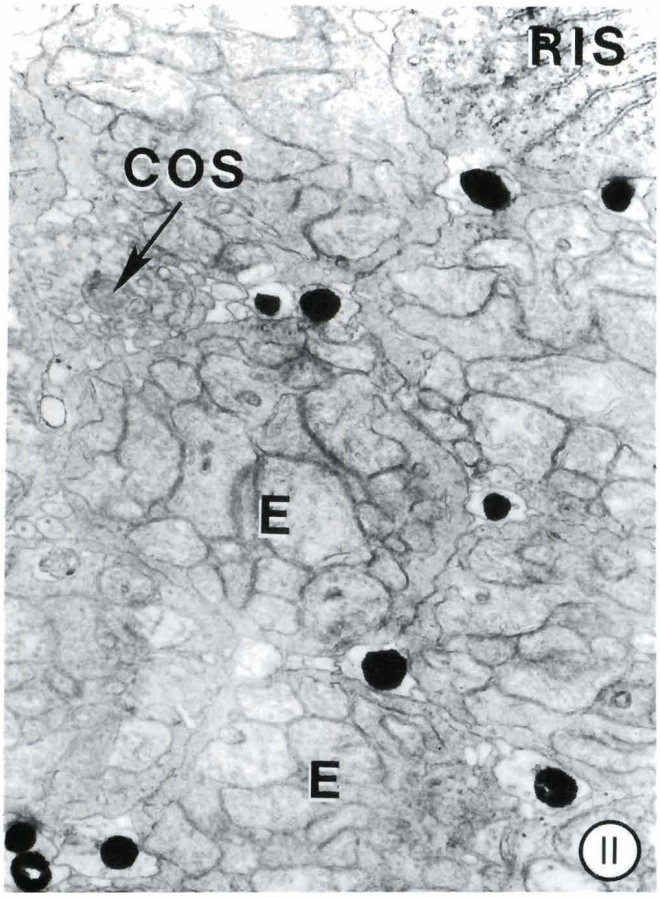
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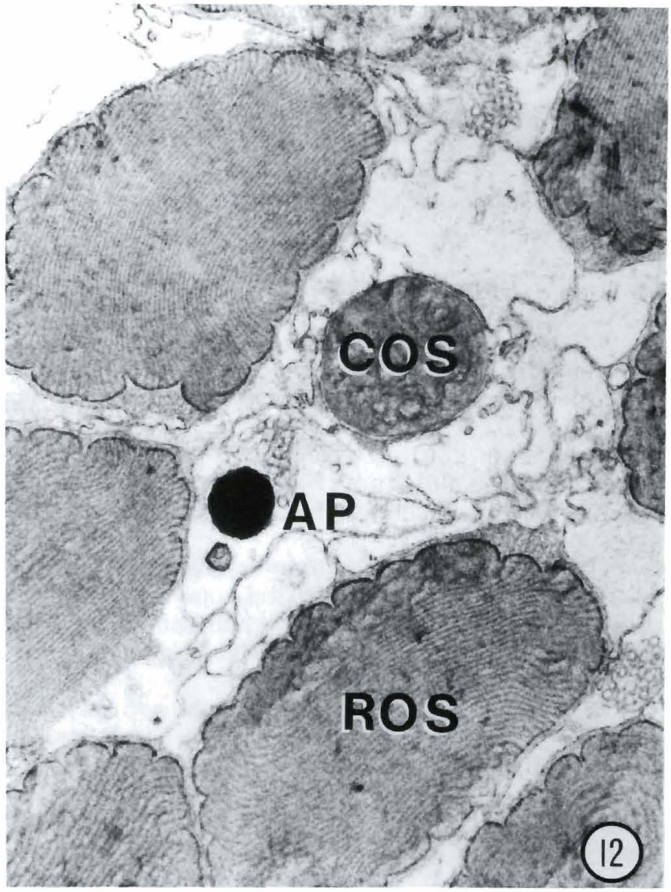
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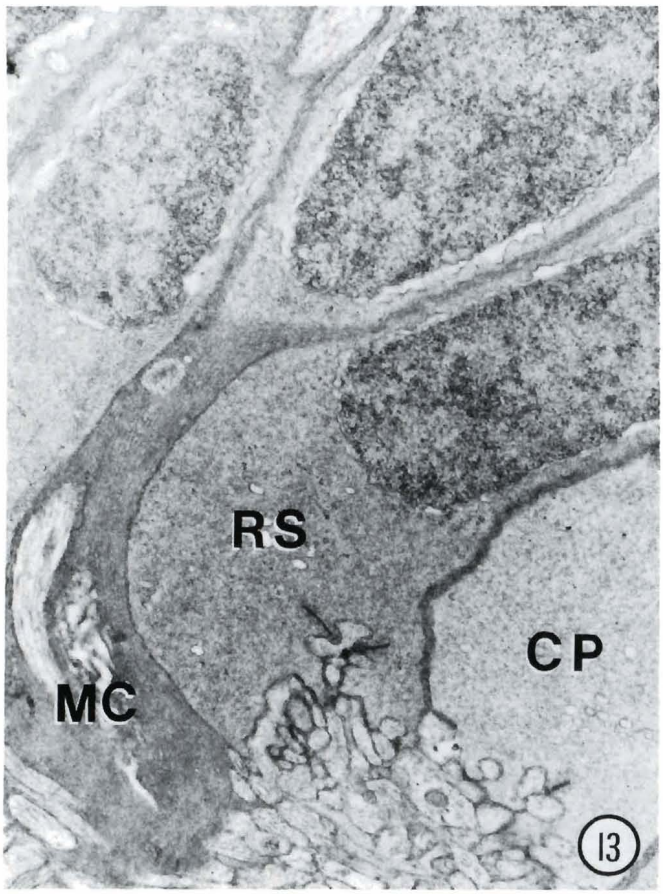
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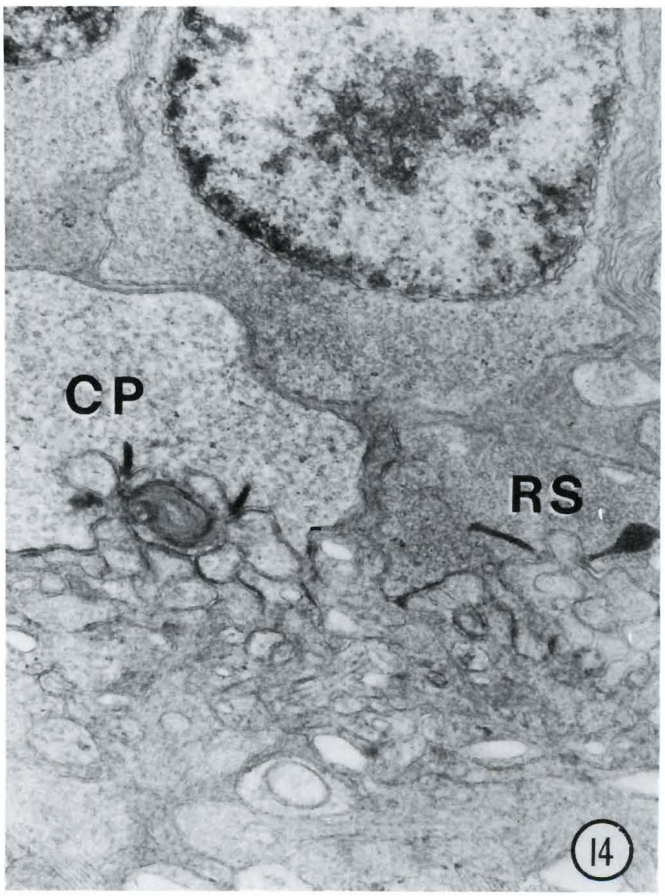
CP
RS
14

Fig. 11. Electron micrograph of several rod photoreceptors to indicate the inner segment (RIS) and ellipsoid (E) regions. A cone outer segment (COS) is also indicated. x 13,800

Fig. 12. Electron micrograph to illustrate scalloped rod outer segments (ROS) and a smooth cone outer segment (COS). RPE apical processes (AP) are also labelled. x 20,300

Fig. 13. Electron micrograph to indicate a rod spherule (RS) and a cone pedicle (CP). A Müller cell (MC) is also indicated. x 13,800

Fig. 14. Electron micrograph to illustrate a cone pedicle (CP) and a rod spherule (RS). Note both invaginated (ribbon) and conventional synaptic sites on both photoreceptor types as well as the abundance of synaptic vesicles. x 19,500

would indicate that rod photoreceptors in the great horned owl do not undergo photomechanical or retinomotor movements in response to environmental lighting.

Despite the apparent lack of movement on the part of the rod photoreceptors however, rod outer segments are surrounded by and isolated from one another by the pigment-laden apical processes of the retinal epithelial cells (Braekevelt and Thorlakson, 1993).

Cones (both types) in the great horned owl are also elongated cells in the light-adapted state which would seem to indicate that the cones also do not move (i.e. shorten) in light adaptation. This is contrary to observations that indicate 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 specimen of the great horned owl are required to adequately settle this question.

The outer segments of both rods and cones consist of a stack of bimembranous discs that represent the light-capture area of photoreceptors (Cohen, 1972; Crescitelli, 1972). In rods the outer segment discs are normally all of the same diameter and usually show one or more peripheral incisures presumably to increase their surface area (Nilsson, 1965; Braekevelt, 1983). In cones the outer segment discs closest 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 seldom show peripheral incisures (Braekevelt, 1983). Rod outer segments in the great horned owl are only a bit longer and larger in overall size than the cone outer segments but because of their relative abundance the rod photoreceptors will collectively present a larger light-capture area emphasizing the importance of rod vision in this species. The presence of several peripheral incisors in rod outer segment discs in this species would also support this position.

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

In the great horned owl a single large oil droplet is located at the apex of the inner segment of single cones and 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 (Rodieck, 1973; Braekevelt, 1973, 1989, 1990, 1992a; 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). No attempt was made to determine the colour of the oil droplets in the great horned owl but they are presumed to be colourless as is reported for 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 an accumulation of glycogen found in the cone inner segment of some birds, fish, amphibians and reptiles (Cohen, 1972; Braekevelt, 1989) is not present in the great horned owl. The inner segment of all the cones in this species however is rich in glycogen that is widely dispersed 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 entirely absent from the rods of the great horned owl (Meyer and Cooper, 1966; Meyer, 1977; Braekevelt, 1992a,b). Early workers felt that these glycogen bodies (paraboloids in cones, hyperboloid in rods) were refractile structures but it is now believed that these glycogen concentrations are energy sources for visual cell metabolism (Meyer, 1977). The significance of the variations noted within various species as to what photoreceptors do or do not show a paraboloid or hyperboloid is unknown (Meyer, 1977; Braekevelt, 1990, 1992a,b).

In the myoid region of the inner segment, interreceptor junctions are typically reported between the two members of a double cone. In teleosts these junctional specializations are often quite extensive and involve prominent submembranous cisternae (Berger, 1967; Braekevelt, 1982). In avian species these interreceptor junctions usually take the form of gap or intermediate junctions between the chief and accessory cones and can often be quite extensive (Nishimura et al., 1981; Smith et al. 1985; Braekevelt, 1990, 1992a,b).

While interreceptor junctions are noted between the two members of the double cones in the great horned owl they were not widespread.

As is the case in all vertebrates described to date, the external limiting membrane in the great horned owl is composed of a series of zonulae 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 inner segments of the photoreceptors (Braekevelt, 1989, 1990, 1992a,b). In this same region the photoreceptors of many birds show a number of vertically oriented lateral fins which interdigitate with these Müller cell processes (Crescitelli, 1972; Braekevelt, 1990, 1991a,b). These lateral fins were entirely absent from any of the photoreceptor types in the great horned owl. As these lateral fins are presumed to be involved in transport functions, their absence may indicate a lower metabolic activity for the photoreceptors of this nocturnal bird.

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 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 only a superficial membrane densification (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 be between photoreceptors themselves (Cohen, 1964; Missotten, 1965; Kolb, 1970). The great horned owl shows both typical invaginated (ribbon) and superficial (conventional) synaptic sites on the rods, single cones and both the chief and accessory members of the double cones.

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References

Braekevelt C.R. (1973). Fine structure of the retinal pigment epithelium and photoreceptor cells of an Australian marsupial *Setonix brachyrus*. Can. J. Zool. 51, 1093-1100.

Braekevelt C.R. (1975). Photoreceptor fine structure in the northern pike *(Esox lucius)* . J. Fish. Res. Bd. Can. 32, 1711-1721.

Braekevelt C.R. (1982). Photoreceptor fine structure in the goldeye *(Hiodon alosoides)* Teleost. Anat. Embryol. 165, 177-192.

Braekevelt C.R. (1983). Photoreceptor fine structure in the domestic ferret. Anat. Anz. 153, 33-44.

Braekevelt C.R. (1984). Retinal fine structure in the European eel *Anguilla anguilla* II. Photoreceptors of the glass eel stage. Anat. Anz. 157, 233-243.

Braekevelt C.R. (1985). Photoreceptor fine structure in the archerfish *(Toxotes jaculatrix)*. Am. J. Anat. 173, 89-98.

Braekevelt C.R. (1989). Photoreceptor fine structure in the bobtail goanna *(Tiliqua rugosa)*. Histol. Histopath. 4, 281-286.

Braekevelt C.R. (1990). Retinal photoreceptor fine structure in the mallard duck *(Anas platyrhynchos)*. Histol. Histopath. 5, 123-131.

Braekevelt C.R. (1992a). Retinal photoreceptor fine structure in the red-tailed hawk *(Buteo jamaicensis)*. Anat. Histol. Embryol. (in press).

Braekevelt C.R. (1992b). Retinal photoreceptor fine structure in the great blue heron *(Ardea herodias)*. Anat. Histol. Embryol. (in press).

Braekevelt C.R. and Thorlakson I.J. (1993). Fine structure of the retinal pigment epithelium of the great horned owl *(Bubo virginianus)*. Histol. Histopath. 8, 17-23.

Berger E.R. (1967). Subsurface membranes in paired cone photoreceptor inner segments of adult and neonatal *Lebistes retinae*. J. Ultrastruct. Res. 17, 220-232.

Cohen A.I. (1963). Vertebrate retinal cells and their organization. Biol. Rev. 38, 427-459.

Cohen A.I. (1964). Some observations on the fine structure of the retinal receptors of the American gray squirrel. Invest. Opthalmol. 3, 198-216.

Cohen A.I. (1972). Rods and cones. In: Handbook of sensory physiology. Vol. VII/2 Physiology of photoreceptor organs. Fuortes M. (ed). Springer-Verlag. Berlin. pp 63-110.

Crescitelli F. (1972). The visual cells and visual pigments of the vertebrate eye. In: Handbook of sensory physiology. Vol. VII/1. Photochemistry of vision. Dartnell H.S.A. (ed). Springer-Verlag. Berlin. pp 245-363.

Dowling J.E. (1968). Synaptic organization of the frog retina: an electron microscopic analysis comparing the retinas of frogs and primates. Proc. R. Soc. London (Biol.)170, 205-228.

Duke-Elder Sir, S. (1958). System of ophthalmology. Vol. 1. The eye in evolution. Henry Kimpton. London.

Fineran B.A. and Nicol J.A.C. (1974). Studies on the eye of New Zealand parrot-fishes *(Labridae)*. Proc. R. Soc. London (Biol.) 186, 217-247.

Fineran B.A. and Nicol J.A.C. (1976). Novel cones in the retina of the anchovy *(Archoa)*. J. Ultrastruct. Res. 54, 296-306.

Kolb H. (1970). Organization of the outer plexiform layer of the primate retina: electron microscopy of Golgi-impregnated cells. Philos. Trans. R. Soc. London (Biol.) 258, 261-283.

Kolb H. and Jones J. (1982). Light and electron microscopy of the photoreceptors in the retina of the red-eared slider, *Pseudemys scripta elegans*. J. Comp. Neurol. 209, 331-338.

Meyer D.B. (1977). The avian eye and its adaptations. In: Handbook of sensory physiology. Vol. VII/5. The visual system in vertebrates. Crescitelli F. (ed). Springer-Verlag. Berlin. pp 549-612.

Meyer D.B. and Cooper T.G. (1966). The visual cells of the chicken as revealed by phase contrast microscopy. Am. J. Anat. 118, 723-734.

Meyer D.B. and May H.C. Jr. (1973). The topographical distribution of rods and cones in the adult chicken retina. Exp. Eye Res. 17, 347-355.

Missotten L. (1965). The ultrastructure of the human retina. Arsica, S.A. Brussels.

Morris V.B. (1970). Symmetry in a receptor mosaic demonstrated in the

chick from the frequencies, spacing and arrangement of the types of retinal receptor. J. Comp. Neurol. 140, 359-398.

Nilsson S.E.G. (1965). Ultrastructure of the receptor outer segments in the retina of the leopard frog *(Rana pipiens)*. J. Ultrastruct. Res. 12, 207-231.

Nishimura Y., Smith R.L. and Shimai K. (1981). Junction-like structures appearing at apposing membranes in the double cone of chick retina. Cell Tissue Res. 218, 113-116.

Pedler C. (1965). Rods and cones - fresh approach. In: Biochemistry of the retina. Graymore C.N. (ed). Academic Press. New York. pp 1-4.

Pedler C. (1969). Rods and cones - a new approach. Int. Rev. Gen. Exp. Zool. 4, 219-274.

Polyak S.L. (1957). The vertebrate visual system. Univ. Chicago Press. Chicago.

Rodieck R.W. (1973). The vertebrate retina. Principles of structure and function. Freeman W.H. San Francisco.

Sjöstrand F.S. (1958). Ultrastructure of retinal rod synapses of the guinea pig eye as revealed by three-dimensional reconstructions from serial sections. J. Ultrastruct. Res. 2, 122-170.

Sjöstrand F.S. (1959). The ultrastructure of the retinal receptors of the vertebrate eye. Ergeb. Biol. 2, 128-160.

Smith R.L., Nishimura Y. and Raviola G. (1985). Interreceptor junctions in the double cone of the chicken retina. J. Submicrosc. Cytol. 17, 183-186.

Uga S. and Smelser G.K. (1973). Comparative study of the fine structure of retinal Müller cells in various vertebrates. Invest. Ophthalmol. 12, 434-448.

Walls G.L. (1942). The vertebrate eye and its adaptive radiation. Cranbrook Press. Blomfield Hills.

Yew D.T., Woo H.H. and Meyer D.B. (1977). Further studies on the morphology of the owl's retina. Acta Anat. 99, 166-168.

Young R.W. (1974). Biogenesis and renewal of visual cell outer segment membranes. Exp. Eye Res. 18, 215-223.

Young R.W. (1976). Visual cells and the concept of renewal. Invest. Opthalmol. 15, 700-725.

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