

Retinal Photoreceptor Fine Structure in some reptiles

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Abstract

The structure of the photoreceptors of four different reptiles: the homed viper *Cerastes cerastes* (diurnal and nocturnal), the European *Chameleo chameleo* (diurnal), the gold skink *Eumeces schneidrii* (diurnal) and the Egyptian gecko, *Tarentola annularis* (nocturnal) has been investigated by light and electron microscopy.

The photoreceptors of diurnal reptiles were mainly of the cone type and those of nocturnal were mainly rods. The ellipsoid region of both double rods in the nocturnals and large single cones in the species having both nocturnals and diurnal activity, consist of several mitochondria arranged in a remarkable radially gradient architecture which accommodates with the specific function of this region as a focusing device helping to condense light onto the outer segments. Moreover the principle cone of double cone and single cone of diurnal reptiles possessed a large oil droplet in the region between the inner segment and outer segment. This droplet is thought to play a role in filtering light and so doing enhanced contrast reduce glare and lessen chromatic aberration.

It is worth to mention that the outer segment of rods in nocturnal reptiles approaches a length of approximately four folds the length of the inner segments of the same photoreceptors cells. This character is of a particular interest, since the outer segment is the site of photopigments and the increase in its length magnifies its ability of light and consequently accommodate with the night vision.

Introduction

The structure of retinal photoreceptors has been investigated in a variety of vertebrate species (Cohen, 1963 a & b, Braekevelt, 1972, 1975, 1989, 1992, 1994). While some variation is noted between species, the typical photoreceptor consists of an outer segment, connecting cilium, inner segment nuclear region with synaptic process and paired or double cones occur widely in all groups below the placental mammals, including the mammalian marsupials (Braekevelt, 1972).

The outer segment of the photoreceptor lies close to and intimately associated with the pigment epithelium (Hogan, *et. al* , 1974).

The outer and inner segments were connected by an eccentrically positioned stalk (cilium) (Fawcett, 1966 ; Borwein & Hollenberg, 1973).

Coloured or colourless oil droplets are permanent inclusions of the adult visual cell in some non mammalian species ,They are

found in most scleral parts of the inner segment, mainly in cones, in amphibians, reptiles and birds (Hailman, 1976 & Mac Nichol *et. al* 1978). Synapses of rods and cones were first described by Dickson & Hollenberg, 1971, Borwein & Hollenberg, 1973).

Rods and cones are two distinct types of photoreceptors of the retina were first described by Schultze (1867 & 1873) , he studied both nocturnal and diurnal vertebrate species and formulated his duplicity theory.

Vertebrate retinae are duplex, containing both rods operating maximally at low light intensities and cones ,operating maximally at high insensitive and in colour vision (Borwein, 1981). Some retinae had been reported to contain rods only, e.g. in rats, but a few cones have been shown to be present by Hughes (1977).

Rods and cones appear together in primates. The cone inner segment is much

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bulky than the rod inner segment (Miller & Snyder, 1973). The difference in diameter between the cone and rod outer segments, however, is smaller in cones (Young, 1971 and Borwein *et.al*, 1980).

As part of a comparative morphological study of vertebrate photoreceptors, this report describes the fine structure of these rods and cones in the retinae of some reptiles and new observations are added to existing studies.

Materials And Methods

For this study the eyes of four healthy adult Egyptian reptiles, the homed viper (*Cerastes cerastes*), European Chameleon (*Chameleo chameleon*), gold skink (*Eumeces schneiderii*) and Egyptian gecko (*Tarentola annularis*) were used. All animals under investigation were collected from Abou-Rawash district, Giza Governorate in Egypt. Animals were sacrificed and the whole eye of each animal was quickly removed, opened at the equator and fixed for 5 hours in 5% gluteraldehyde buffered at pH 7.3 with 0.1 micron Sorensen's phosphate buffer at 4°C. The posterior half of the eye ball was then removed washed in 5% sucrose in 0.1 M phosphate buffer (pH 7.3) (Hayat, 1970) and cut into pieces less than 1mm². The tissue was then post-fixed for 2 hours in 1% osmium tetroxide in the same phosphate buffer they were washed twice for 15 minutes in a phosphate buffer pH 7.3. then dehydrated through graded ethanols to propylene oxide and embedded in araldite. Semithin sections of 0.7 μm thickness were cut with glass knives on the 6000 MT RMC ultratome. then stained with 0.25% toluidine blue (Davis, 1971) and examined by light microscopy. Thin sections (600-700Å) 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 JEOL 1200 EXIL transmission electron microscope.

Results

Light microscopic examination of the semi-thin sections of the retinae of all the

four studied reptiles were shown in first paper in figs. (1 a, b, c & d)

I. *Cerastes cerastes*

The retina of *Cerastes cerastes* is formed of two types of cones, large single cones and small single cones. The latter are in association with the rod type segments (Figs. 1a & 1b). The large and small single cones are composed of an outer and inner segments. The outer segments are closely associated with the pigment epithelial cells and their processes (Fig. 1). The inner segments have densely packed mitochondria in their ellipsoid region (Figs. 2 & 5). The outer segments of large single cones are short and wide (Figs. 2 & 3). They are occupied by double membrane disks, or flattened sacs (Figs. 3 & 4). The myoid region of the large single cones displays a barrel shape and is approximately close to the outer limiting membrane (Figs. 2 & 6) and also contains numerous Golgi cisternae with vacuoles (Fig. 6). Fine microvillar processes extend from the inner segment of the large single cones which are specifically found in this species (Fig. 6). The second type of cones are the small single cones which appear smaller than the large single cones (Figs. 1a, 1b & 2). The small single cones have short outer segment, which is not as wide as the corresponding segment of the large cone (Figs. 1b & 2). This region is filled with flattened double membrane disks (Fig. 7).

There is an accumulation of condensed mitochondria (ellipsoid) at the apex of the inner segment of small single cones (Figs. 8 & 9). The ellipsoid region of the small single cones differs from the ellipsoid region of the large single cones in the lack of association of mitochondria and microdroplet (Figs. 7 & 9). The myoid region of the small single cones contains numerous Golgi cisternae, with numerous vacuoles (Fig. 8). Each small single cone has a cytoplasmic process that extends from its inner segment and is called the claycal process (Fig. 7).

The rods have long cylindrical outer segments that reach to the pigments of the epithelial cells. The lamellar sacs or disks are more closely packed than the

corresponding compartment of the other photoreceptor (Figs.1,5 & 7). A prominent ellipsoid region is located at the apex of the inner segment of the rod, but no oil droplets or microdroplets are present (Figs.1 & 7). Unlike the cones ellipsoid the mitochondria of the rods ellipsoid are less packed and are mostly elongated to oval in shape (Figs.1& 7).

A structure similar to ellipsoid containing closely packed mitochondria is infrequently located underneath the outer limiting membrane(Fig.6).

The connecting cilium is the only connection between the outer segment and the inner segment of both large cone and small cone (Figs.3&10). This cilium is an eccentrically positioned stalk containing nine pairs of microtubules arranged circumferentially.

II. *Chameleo chameleo*

The photoreceptor layer of *Chameleo chameleo* contains only the cone-type of photoreceptors. It comprises single and double cone (Figs.1b & 11).

The double cone consists of a principal cone and an accessory cone. Both the single and double cones are composed of an outer and an inner segments. The inner segment posses a large oil droplet ,an ellipsoid, paraboloid and myoid .

However, the accessory cone lacks the oil droplet, ellipsoid , paraboloid and myoid. (Figs. 1b & 11)

The double cone consist of a principal cone, which posses an oil droplet in the scleral portion of its inner segment and an accessory cone which never has an oil droplet (Figs.11& 12). The outer segment of both types of cones, is filled with double membrane disks, or flattened disks and slightly tapers (Fig.13).

The claycal processes are thin cytoplasmic extensions from the distal end of the inner segment and they form a palisade around the proximal outer segment of both single and double cones (Figs.12&13). Regardless of the type of cone to which they belong ,the oil droplets are oval shape and the lipid matrix is of a very homogenous electron density (Figs.11&12).

The membrane surrounding the oil droplets has an irregular outline with several reinforcements, or dense foci at definitive points of adhesion with the external membranes of the mitochondria that surround the oil droplet (Fig.13). These mitochondria encircle the entire perimeter of the oil droplet. In the internal portion of the cone inner segments, the mitochondria are spherical, while in the external region of the inner segments they are oval, or elongated in shape (Fig.12). As the mitochondria approach the scleral portions of the ellipsoid, they acquire a transverse disposition, with the cristae parallel to the major axis of the mitochondria (Figs 12 & 15). At this level ,adhesions between the mitochondrial membranes are frequently observed. A greater electron density of the mitochondrial matrix is also noticeable in the scleral portions of the inner segments (Figs.12&13)

The outer and inner segments are connected by a well developed connecting cilium (Fig.14).

In the inner segments, glycogen granules are usually accumulated in a compact area,(the paraboloid). In this region, the glycogen granules are associated with several profiles of both types of endoplasmic reticulum (Fig.16). The principal cone does not have a paraboloid region(Fig.11). The paraboloid of the accessory cone is different from that of the single cone by its remarkable circumferential limiting membrane(Fig.11). The myoid region of single cones contains cytoplasmic vacuoles and Golgi apparatus (Fig.17). The myoid region of the double cones displayed a similar fine structural features of the corresponding area of the single cone.

III. *Eumeces schendrii*:

The retina of the *Eumeces schendrii* is extremely of cone dominant with very few rod. All cones are single cones and multiple photoreceptors are not present(Figs.1c & 18). The cones are large cells with project through out the outer limiting membrane (Fig.19). All cones outer segments display a single membrane-bound oil droplet (Figs.19&21). Below the oil droplet a very

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large accumulation of mitochondria (the ellipsoid), with an aggregation of glycogen (parabloid) (Figs.19,21&22).

The parabloid is followed by the inner segment (myoid) which is rich in Golgi complexes and cytoplasmic vacuoles (Figs.22&23).

The cone outer segments are relatively short and taper distally (Figs.19&20). Rod photoreceptors are much narrower than cones and their inner segments are smaller than cone inner segments (Fig.20).

A prominent ellipsoid is located at the tip of the inner segment, but no oil droplet are recognized (Fig.20). Rods outer segment are longer than those of cones outer segment and are not taper distally (Fig.20).

IV-Tarentola annularis

The photoreceptor layer of *Tarentola annularis* contain only the rod-type of photoreceptors. It comprises single and double rods (Figs.1d & 24). The double rod consist of a principal rod and an accessory rod (Figs.1d & 24). Both rods are composed of long outer segment, ellipsoid and a myoid. However, the principal rod has characteristic parabloid body (Figs.24 & 26). In addition, it posses a long outer segment. The inner segment of the principal rod contains in its upper region, condensed aggregation of mitochondria (ellipsoid).

The mitochondria occupying the peripheral region of the ellipsoid are elongated and contain well defined cristae. The central mitochondria are highly electron dense. Below this area is an aggregation of glycogen particles, the parabloid region (Figs.24&27). After the parabloid, the myoid region contains numerous Golgi zones (Fig.24), the accessory rod consists of a long outer segment (Fig.1d). The ellipsoid region of the accessory rod contains few aggregation of rounded mitochondria (Fig.25). Below the ellipsoid, the long myoid region contains Golgi zones (Fig.29).

The single rod contains a large outer segments (Figs.1d & 24), the ellipsoid region with an aggregated rounded mitochondria (Figs.25 & 26), and the myoid which contains several cytoplasmic

vacuoles, accumulation of rough endoplasmic reticulum and the Golgi apparatus (Figs.24 & 27). The outer segment of both types of rods composed of bimembranous disks (Figs. 24,26 & 29).

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Fig.1: Electron micrograph of the *Cerastes cerastes* retina photoreceptor layer showing the interdigitation of the melanosomes (Me) containing cytoplasmic process of retinal pigment of epithelial layer (RPE) are closely associated with the outer segment (os) of photoreceptors layer. The photoreceptors are formed of large single cones (Lsc), small single cones (ssc) and rods (R).

X 4500

Fig.2: Electron micrograph showing photoreceptors layer of *Cerastes cerastes* retina layer, with small single cones (ssc) and large single cones (Lsc) consists of a lamellated outer segment (os) and a large dense inner segment which contains dense ellipsoid region (e) and a myoid region (my). The outer limiting membrane is also indicated (olm).

X 6000

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X 90000

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X15000

Fig.6: Electron micrograph of photoreceptor layer in *Cerastes cerastes* retina showing a large single cone (Lsc.) with their round nucleus (N) and small single cones (ssc) with their ellipsoid region (e) lying above the outer limiting

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Fig.12:Electron micrograph in *Chameleo chameleo* photoreceptor layer

showing the presence of oil droplet (od) only in the single cone (SC) and in the principal cone (pc) of the double cone (DC) ,and its absence from the accessory cone (AC). Clayal process (CP) surrounds the outer segment (os).

X 12.000

Fig.13:High magnification in *Chameleo chameleo* photoreceptor layer showing a part of the principal cone, several mitochondria (mi), enclose a position to a large oil droplet (od), lamellated outer segment (os) and a clayal process (Cp).

X 60.000

Fig.14:High magnification in *Chameleo chameleo* photoreceptor layer of an accessory cone showing a connecting cilium (cc) between its inner segment (IS) and outer segment(os). X 75.000

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X 30.000

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X 30.000

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X 12000

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of the principal rod contain a well developed Golgi zone (Ga).The single rod (Sr) consists of an outer segment (ros),ellipsoid (e) and myoid (m).fine processes of Muller cells (F) and outer limiting membrane (olm) are also located. X 6000

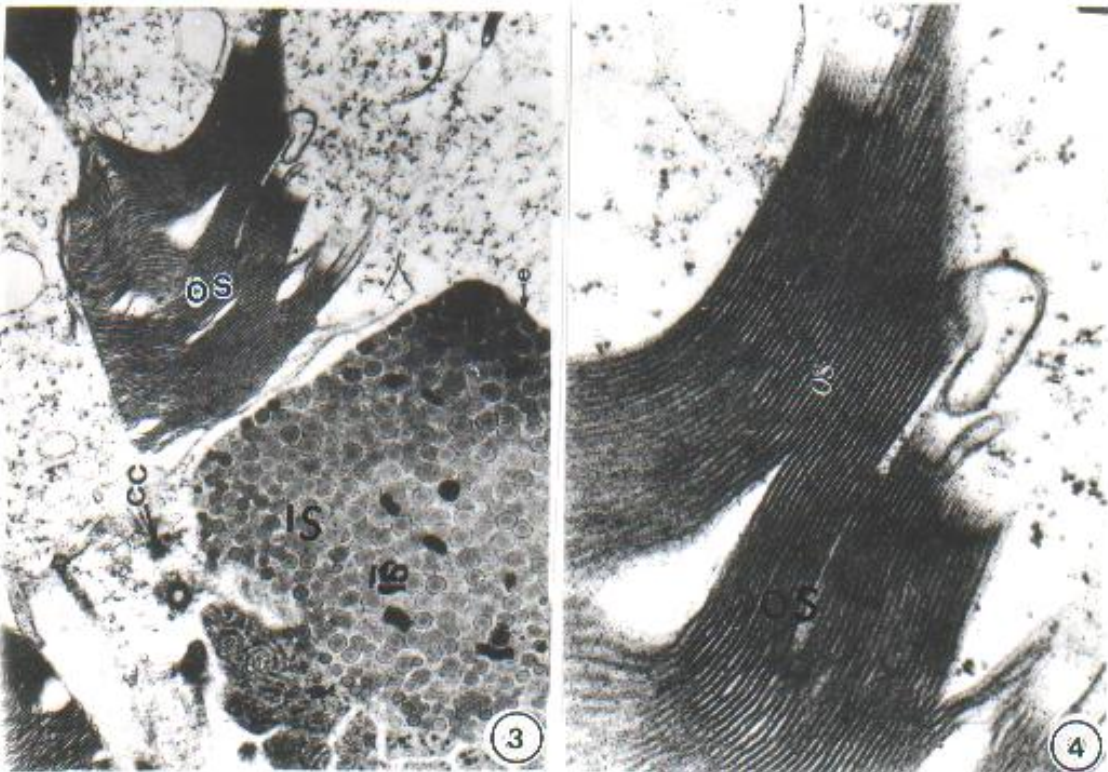
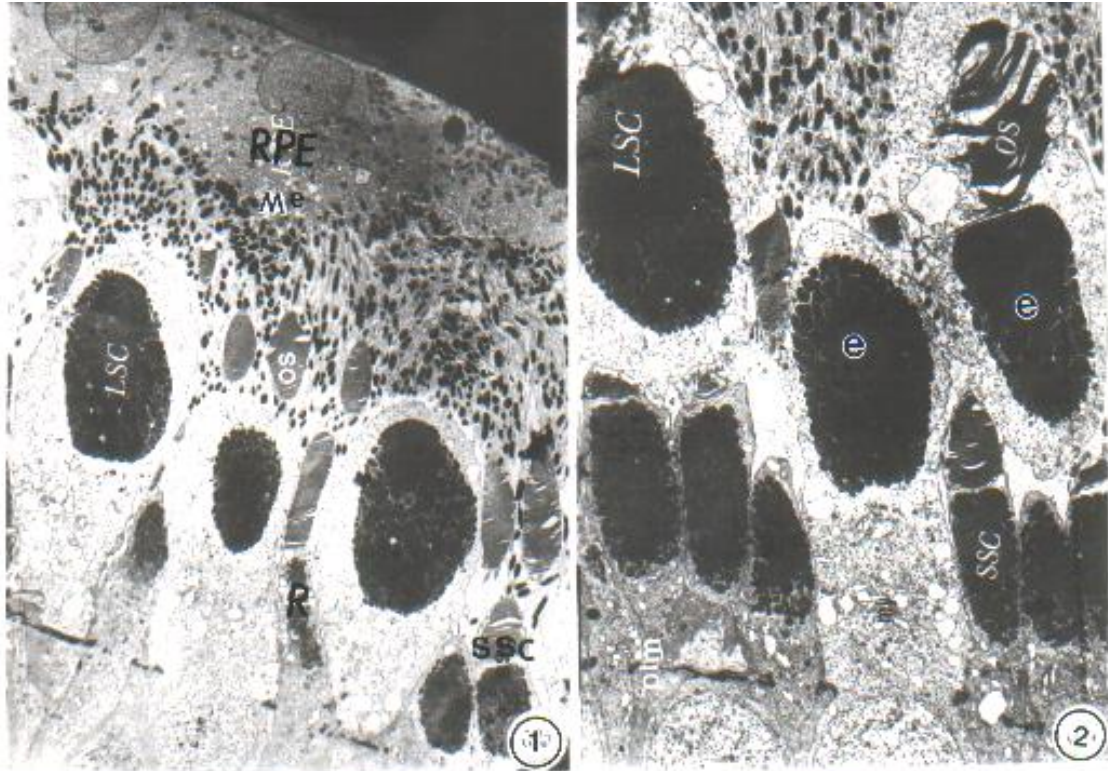
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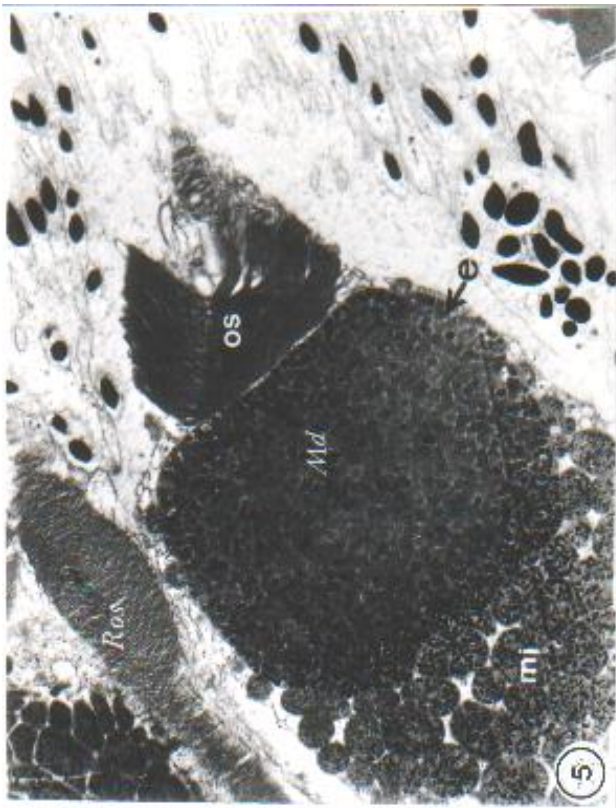
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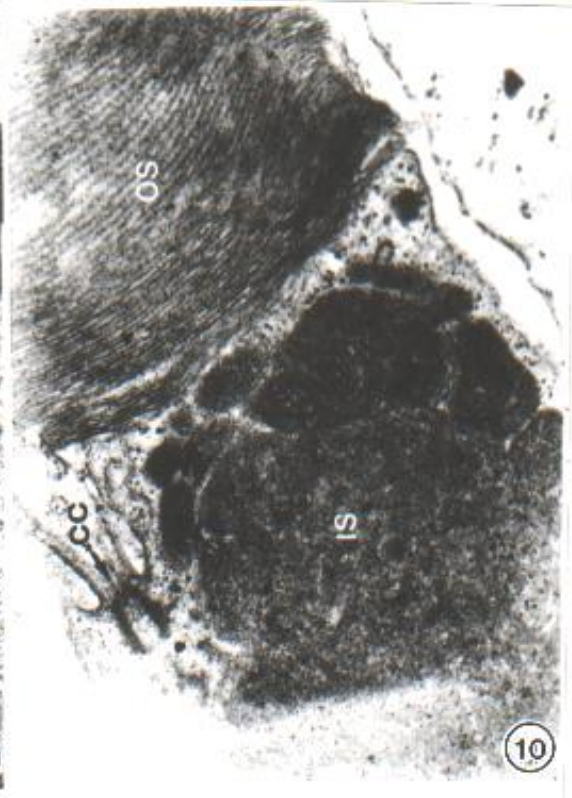
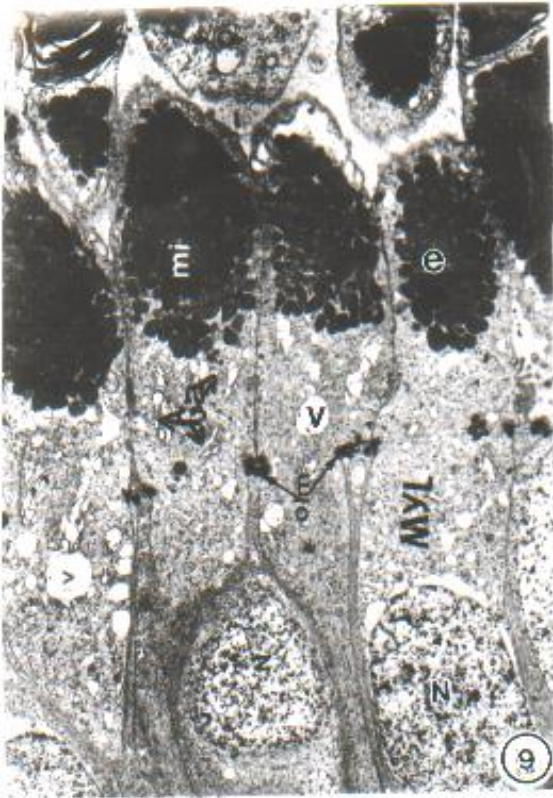
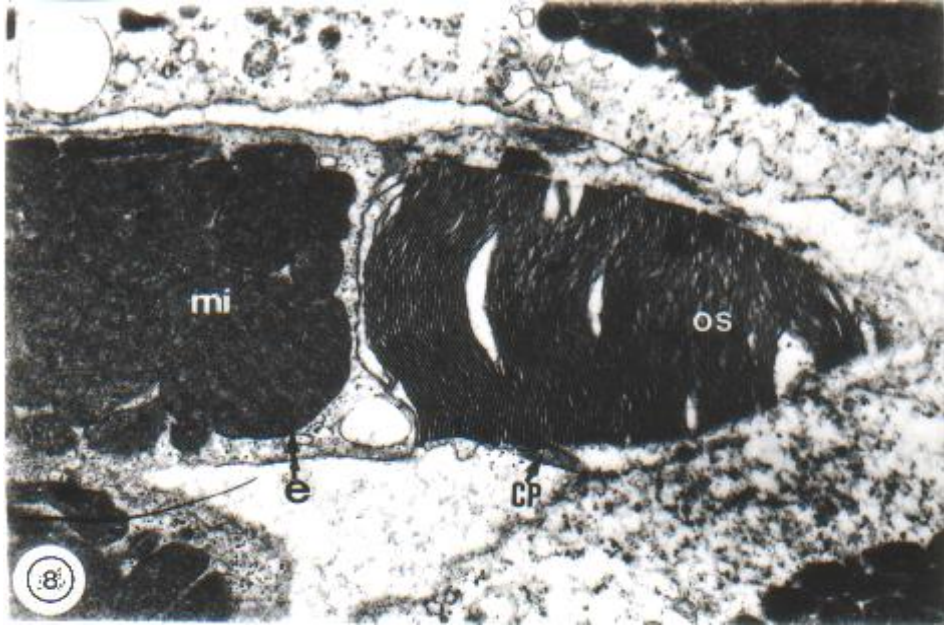
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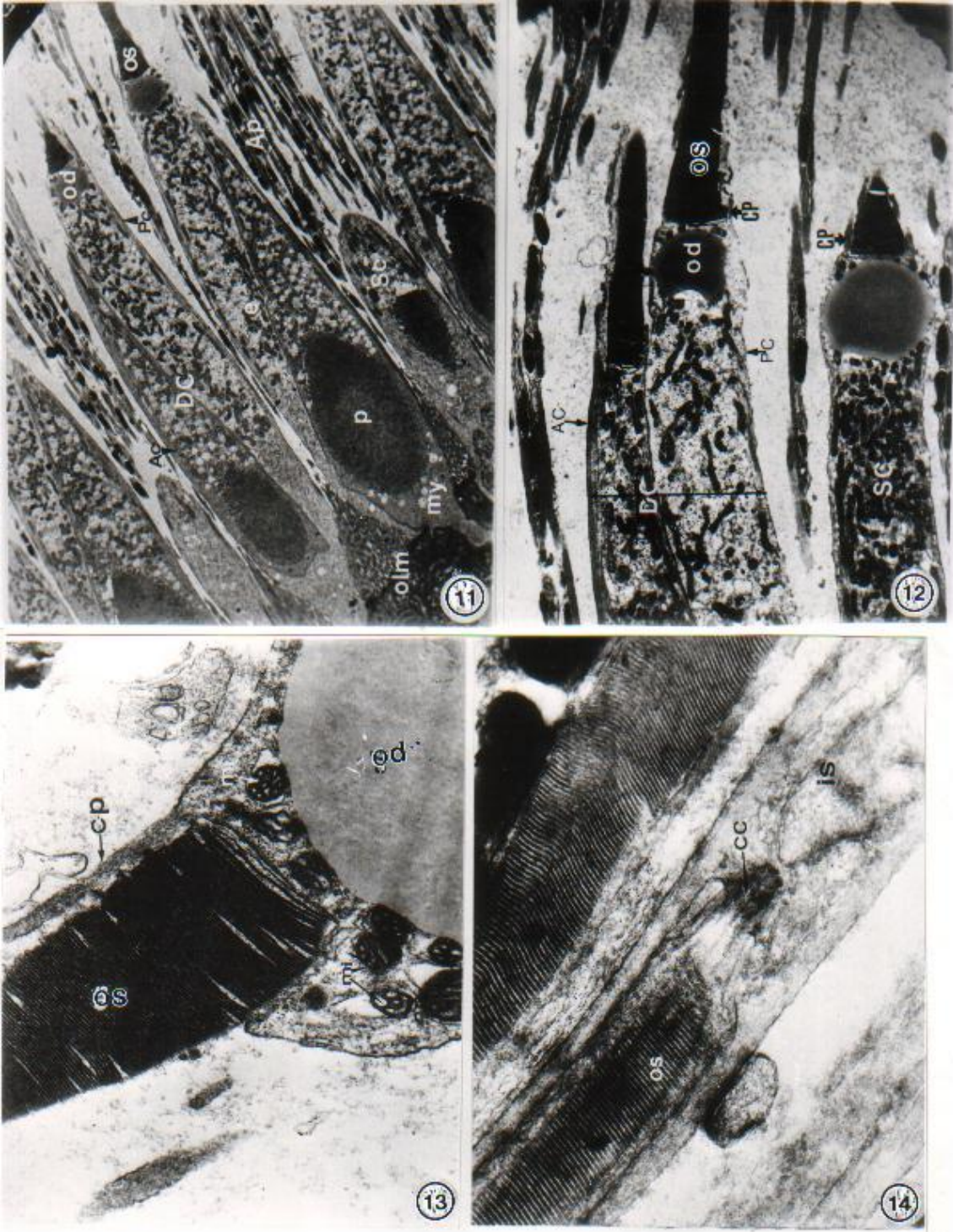


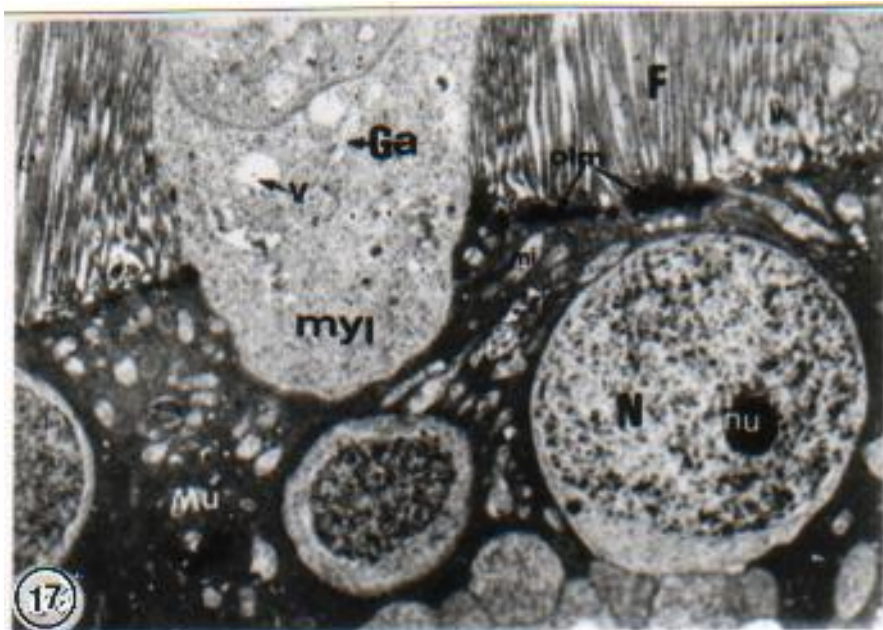
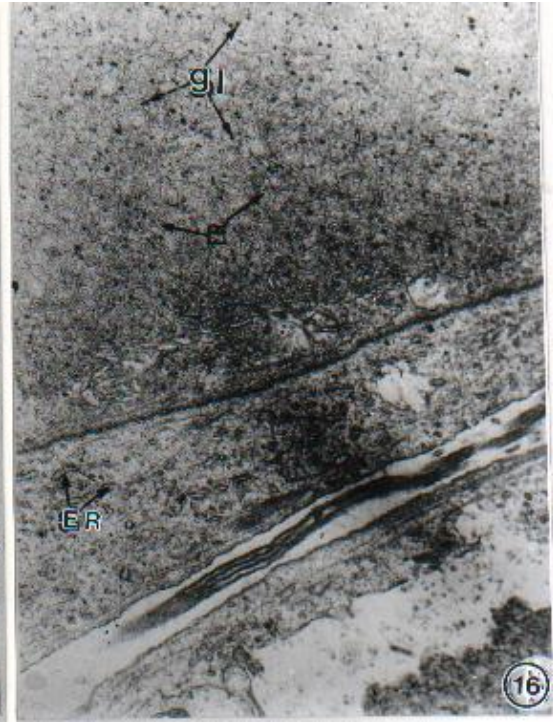
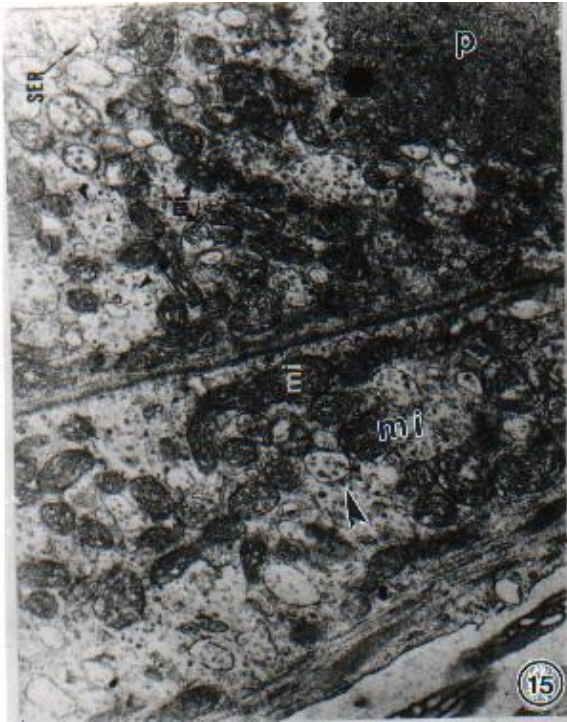
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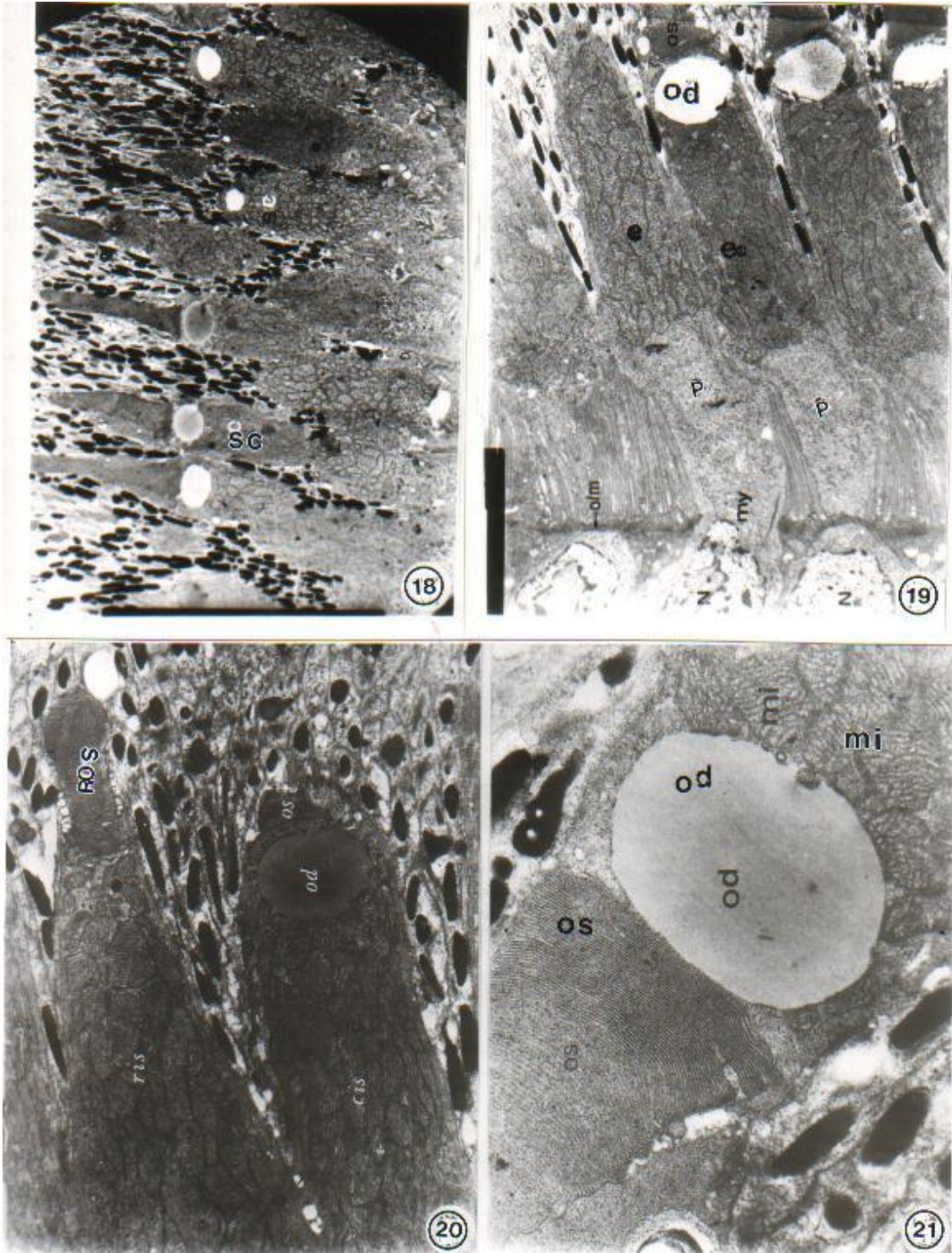


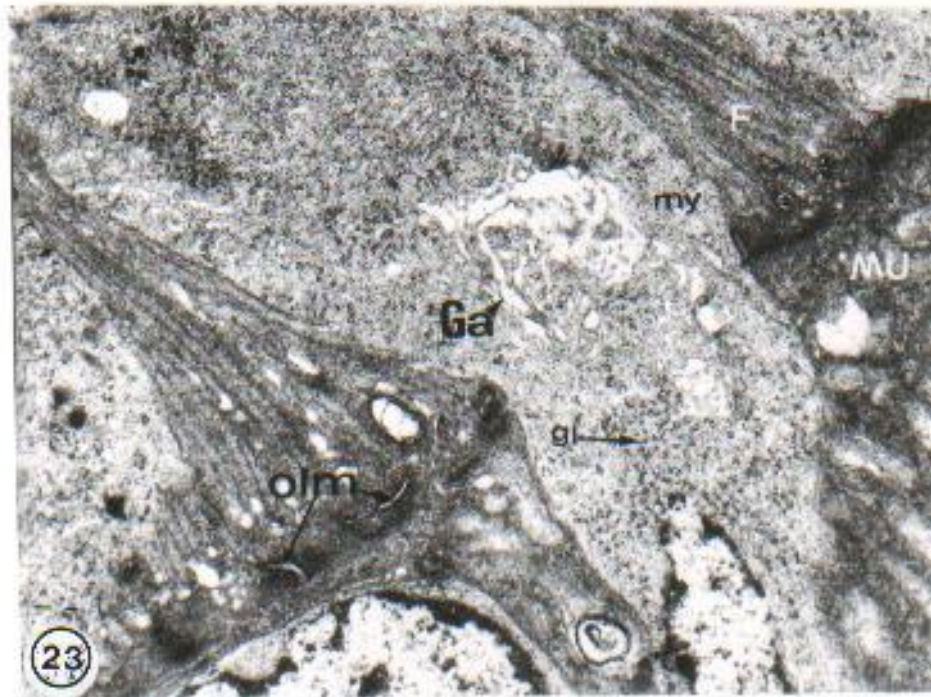
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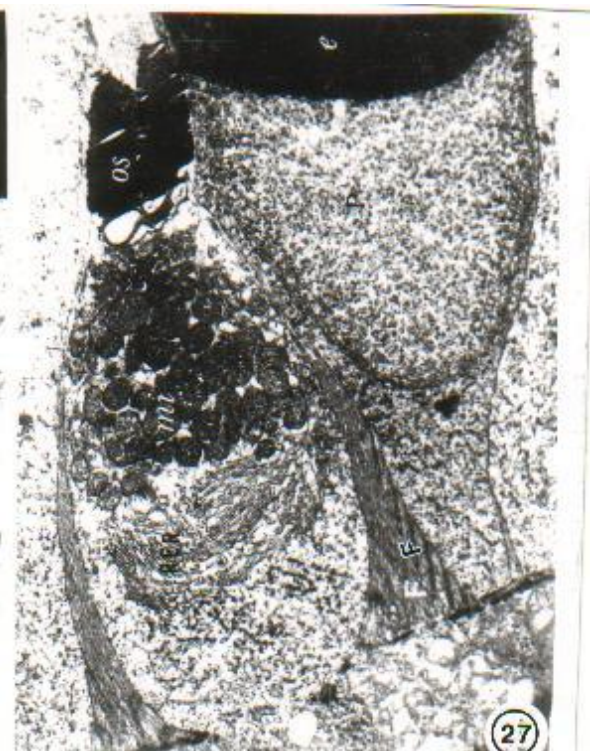
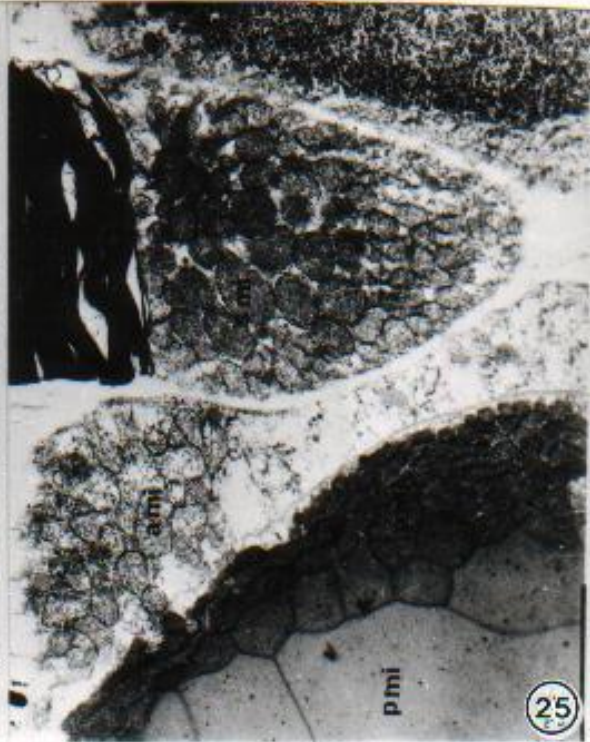


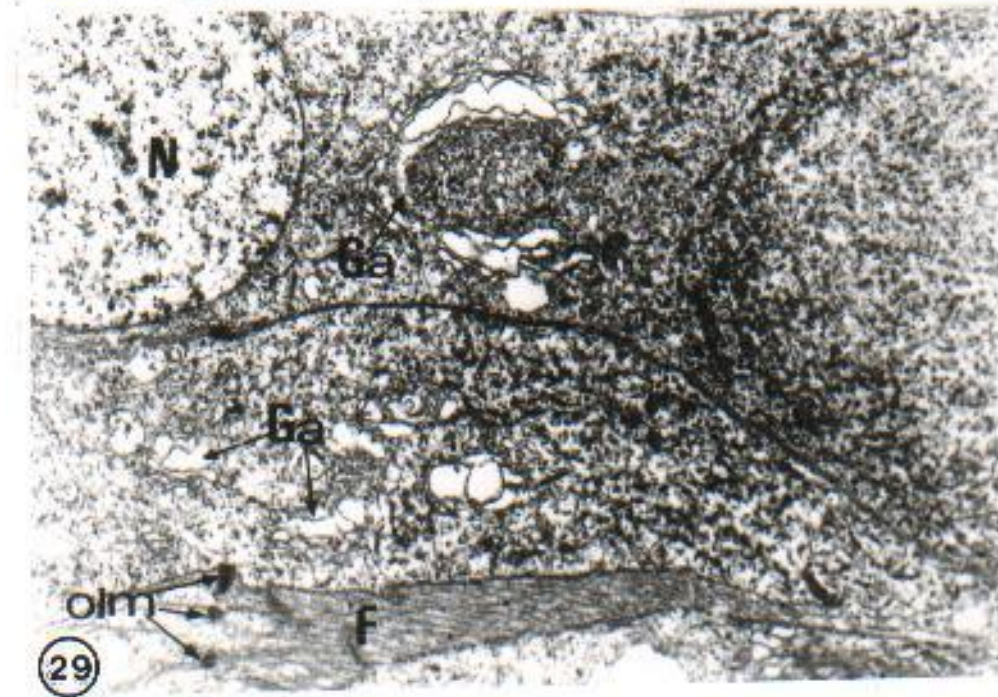
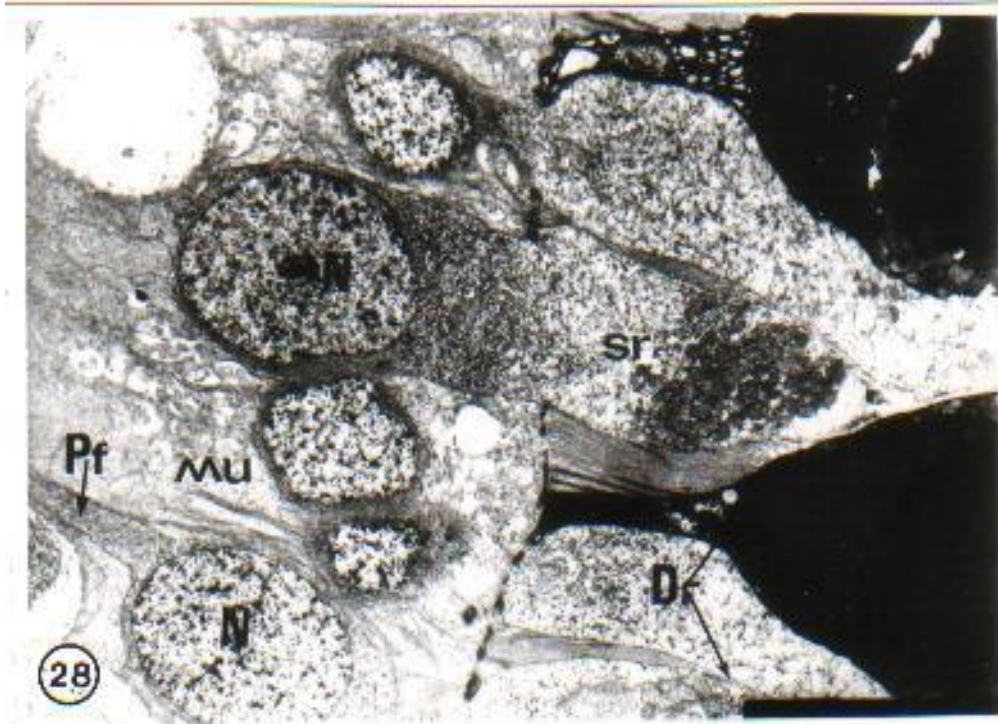
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Discussion

The photoreceptor layer varied greatly in its histological and fine structural details among the four different reptilian species. This variation is mainly contributed to the number, distribution and existence of the principal cell type of this layer, the rods and the cones. These cells represent the actual receptors of the retina and are highly sensitive to light stimuli (El-dawi & Swelim, 1995). In principle, the rods mediate dim-light vision, whereas cones function in bright light (Blanks, 1994). In addition rods provide great sensitivity, especially to blue-green light (scotopic vision), whereas cones provide visual acuity for pattern detection as well as colour vision (Blanks, 1994).

In the present work, the photoreceptors layer of the viper *Cerastes cerastes* appeared in both the light and electron microscopes consisting of both types of photoreceptors, rods and cones. The cones were of two types, small single cones and large single cones. This morphological architecture of the photoreceptors layer may accommodate with the living habitat of this viper which has both nocturnal and diurnal activity. In comparison with other vipers, Underwood (1970) reported the presence of both types of the photoreceptors in the retina of *Heterodon platyhinos* which has both nocturnal and diurnal activity.

On the other hand Wong (1989) described three morphological types of cones (large single cone, small single cone and double cones) in the retina of the American garden snake *Thamnophis sirtalis*, which is active only during the day light (diurnal snake).

In the present study, the photoreceptor layer of the diurnal lizard, *Eumeces scheindrii* consist mainly of single cones, in association with a very few number of rods. No multiple photoreceptors were present nor a photoreceptor mosaic was observed, although it is common feature in diurnal lizards (Dunn, 1966).

The fine structure of the retinal photoreceptors has been studied by electron

microscopy in the bobtail goanna (*Tiliqua rugosa*), an Australian diurnal lizard (Braekevelt, 1989). He reported that the photoreceptors in this species were readily divisible into rods or cones based on morphological criteria. Single cones were dominant cell type with a cone, rod ratio of about 80: 1.

In the present work, the photoreceptor layer of the retina of the diurnal lizard, *Chameleo chameleon* contains only pure cones differentiated into single and double cones. Each double cone comprises a principal cone and an accessory cone. Both the principal and single cone possess a characteristic large oil droplet, between their outer and inner segments. Early investigations of photoreceptor organization suggest that strictly the diurnal vertebrates, including lizards, snakes, some birds and majority of squirrel family have pure cone retinae (Walls, 1967). Williams' and Fisher (1986) found that the diurnal lizards *sceloporus occidentalis* has only cone photoreceptors. Recently, some authors recorded that the pure-cone American *Chameleon* retina all visual opsins including rod opsin are expressed (Kawamura & Yokoyama 1997).

In the present work, the photoreceptor layer of *Tarentola annularis*, a nocturnal lizard consist of pure rods. These rods are of two types, single rods and double rods. The later comprise principal rods and accessory rods. This histological finding accommodates with either studies on the retina of *Gecko* sp. and *Hemidactylus* sp. (Pedler & Tilly, 1964) and *Tarentola* sp. and *Phyllodactylus* sp. (Underwood, 1970). In other related species, *Gecko gecko*, the photoreceptor layer contains both single and double rods (Crescitelli, 1977).

In the present work, the electron microscopic studies revealed certain common fine structural features the outer segments of both rods and cones in the four different reptilian species. Each segment consists of a stack of bimembranous discs, which revealed by other investigators as the site of photopigments and represent the

light capture area of the photoreceptors (Braekevelt & Richardson,1996).

As a matter of fact, rod cells are sensitive to light because they contain a visual pigment called rhodopsin which is capable of trapping photons (Blanks,1994). The outer segment of rods of *Tarentola annularis* are typically elongated cylinders. The outer segment of cones are much more variable in shape than those of rods; they tend to be small and conical as in *Chameleo chameleon* and small single cones in *Cerastes cerastes* and single cones of *Eumeces scheindrii*.

The morphological architecture of the photoreceptor layer *Chameleo chameleon* reflects a diurnal adapted activity of these animal due to the presence of pure cones, similar studies, Kawamura and Yokoyama (1998) revealed the ability of similar species of *Chameleon* for night vision.

In addition, the photoreceptor layer of the Egyptian Gecko, *Tarentola annularis* accommodates with the nocturnal activity due to presence of pure rods, Kojima *et al.* (1992) reported that the retina of *Gecko gecko* has two kinds of visual pigments.

Taniguchi *et al.*(1999) found that despite the large morphological difference between the diurnal and nocturnal gecko photoreceptor types.

In the present work ,light and electron microscopic studies of the inner segment of photoreceptor layer revealed the presence of three different highly specialized areas which varied greatly not only in the two major types of photoreceptors(rods and cones) but also in each types of cells in the four different reptilian species. These areas are ; the ellipsoid, paraboloid and myoid.

The ellipsoid areas is an aggregation of different sized mitochondria ,whose distribution and orientation varied greatly among the four different reptilian species. In the *Cerastes cerastes* and *Tarentola annularis*, the mitochondria have a radial gradient with the smallest ones are at periphery of the ellipsoid. This radial gradient of mitochondria reflects a functional significant in the ability of these animals for the night vision, since the ellipsoid area acts as a focusing device,

helping to condense light onto the outer segment(Borwein,1981).

The ellipsoid may act as a convex lens to enhance the vision ability in these nocturnal animals.

On the other hand the mitochondria in the ellipsoid area of *Eumeces schenrdii* and *Chameleo chameleon* have another linear orientation at the long axis of this area. This linear organization of the mitochondria reflects an unnecessary requirement of the ellipsoid area in these diurnal animals for light condensation onto the outer segment.

The paraboloid area was absent from the rods and cones of *Cerastes cerastes*.This subcellular structure consists of smooth surface membranes of endoplasmic reticulum, and an abundance of glycogen granules, which accumulate later though development (Borwein,1981). This organelle may affect optical function in these animals (Amemiya & Ueno,1977).

Pedler (1969) found that in the nocturnal *gecko* the paraboloid merged with the surrounding cytoplasm, but that it was definitively demarkated in diurnal geckos. The glycogen of the paraboloid does not seem to be depleted in frogs even after long starvation (Gourevitch,1954) or by light and dark stimulation (Yamada,1960).

In the inner segment of certain types of photoreceptor in *Chameleo chameleon*, *Eumeces schenrdii* and *Tarentola annularis*, a multiple profiles of rough endoplasmic reticulum and Golgi zones occupied a vitreal position in respect to the associated paraboloid, this area is defined as the myoid. In *Cerastes cerastes* this subcellular structures was located directly vitreal to the ellipsoid. Bok, (1970) revealed that RNA synthesized in the nucleus travels to myoid, which is rich in ribosomes which are the site of protein synthesis.

During photo mechanical movements the myoid can shorten up to 90% of its length within two minutes to one hour in fish, amphibians and birds depending on species (Ali,1971 and Reme & Sulser1977).

In *Chameleo chameleon* a large single oil droplet was found in the apex of the inner segment of the principal cones and single cones.

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But in *Eumeces schendrii* the large oil droplet was found in the apex of the inner segment of single cones.

In *Cerastes cerastes* a large number of dense micro droplet occupied an approximately central position in the apex of the large cones inner segments. No oil droplet or micro droplets were found in *Tarentola annularis*. The morphological structure of the droplets varied from large single as in amphibians, fish, turtle and birds (Hailman,1976, Kunz & Wise,1978, Kolb & Jones,1987, Braekevelt 1989, Braekevelt & Richardson,1996) to a less observed smaller droplets as in geckos and snakes (Ishikawa & Yamada, 1969,&Wong 1989).

Oil droplets apparently selectively filter light and is so doing probably enhance contrast, reduce glare and lessen chromatic aberration(Meyer,1977).The most striking feature of the retinas of diurnal form is the presence of brightly coloured oil droplets.

The synaptic terminal is the photoreceptor site where information is exchanged or transmitted and its structure is so consistent that Pedler (1969) who studied 71 vertebrate species, regarded it as the most reliable indicator of whether the photoreceptor is cone like or rod like.

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دراسات بالميكروسكوب الضوئي و الميكروسكوب الالكتروني علي طبقة مستقبلات الضوء في شبكة العين في بعض الزواحف.

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تتضمن هذه الدراسة مقارنة التركيب النسيجي و الدقيق لطبقة مستقبلات الضوء لشبكية العين بين أنواع مختلفة من الزواحف منها النهاري كالحرباء الأوروبية و أم الحيات و الليلي مثل البرص رباعي النقط و زواحف لها نشاط ليلي و نهاري مثل الحية المقرنة. و قد إختلفت طبقة مستقبلات الضوء إختلافا كبيرا بين الزواحف الأربعة و كان هذا الإختلاف واضح في الأشكال الرئيسية لهذه الخلايا كالأشكال المخروطية و الأشكال العضوية فقد إحتوت شبكة العين المقرنة علي مخاريط أحادية صغيرة و مخاريط أحادية كبيرة مع وجود عصبي , كما إحتوت مستقبلات الضوء في شبكية أم الحيات علي مخاريط أحادية صغيرة و قليل من العصبي, بينما إحتوت هذه الطبقة في الحرباء الأوروبية علي مخاريط فقط بعضها أحادي التركيب و البعض الآخر ثنائي التركيب. إشتملت المخاريط ثنائية التركيب علي وحدة أساسية و أخرى مساعدة.

و قد ظهرت هذه الطبقة في البرص رباعي النقط و بها مستقبلات الضوء من النوع العضوي فقط و كان بعضها أحادي التركيب و الآخر ثنائي التركيب. و قد إشتملت أيضا العصبي ثنائية التركيب علي وحدة أساسية و أخرى مساعدة. و قد تميزت مستقبلات الضوء من النوع العضوي في البرص رباعي النقط فقط بطول قطاعها الخارجية مقارنة بالقطع الداخلية لنفس الخلايا.

إحتوت المنطقة الداخلية لمستقبلات الضوء في كل من البرص رباعي النقط و الحية المقرنة علي أعداد كبيرة متراسة من الميتوكوندريا شديدة الكثافة بينما إنتشرت الميتوكوندريا في هذه المنطقة في النوعين الآخرين (الحرباء الأوروبية و أم الحيات) بشكل متباعد و تميزت بالتركيب الواضح لأعرافها الداخلية. و قد إحتوت أيضا القطع الداخلية في ثلاثة أنواع فقط من الزواحف علي منطقة واضحة من البارابلويد (تجمع كثيف من الجليكوجين) بينما إختفت هذه المنطقة في الحية المقرنة.