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Ultrastructure of *Mugil brasiliensis* Teleost Retina I: Cones, Rods, Horizontal, Bipolar, Piriform Amacrines, Tubular Cells, Undulate Amacrine Cells, Outer and Inner Plexiform Layers

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Author's contribution

The sole author designed, analyzed and interpreted and prepared the manuscript.

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ABSTRACT

Aims: To analyze the ultrastructure of cones, rods, horizontal, bipolar and amacrines cells from *Mugil brasiliensis* teleost retina as well as all the connections found between the cells.
Methodology: The retina was fixed with glutaraldehyde and osmium tetroxide and radial and tangential sections stained with lead citrate and uranyl acetate to be analyzed in a Hitachi 11B electron microscope at 75 Kv.
Results: Horizontal cells had finger like process reaching the outer plexiform layer ending in cone and rod invaginations, and also lateral unions between plasma membranes, forming a net, with a functional contact between them. Bipolar cells were radially oriented with dendrites branching in the outer plexiform layer contacting cones and rods and lower terminals branching in the inner plexiform layer. Stellate amacrine cells send ascendant process to the outer plexiform layer and form a continuous net below horizontal cells. A new layer named tubular cells was described by the first time below internal horizontal cells forming a net. Undulate amacrine cells around bipolar cells were also described by the first time. Cones and rods terminals had ascendant expansions of

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horizontal and bipolar cells in a triad structure around the synaptic band. Piriform amacrine cells were described with dark cytoplasm due to numerous glycogen granules and with clear cytoplasm with scarce glycogen granules, both sending prolongations to the inner plexiform layer.

Conclusion: This paper is a comprehensive analysis of ultrastructure of seven retinal cells, finding two new cells in teleost retina, 1- tubular cells forming an extensive tangential net below internal horizontal cells, with characteristic structures not seen in the literature on retina before and, 2- undulate amacrine cells that surrounds many bipolar cells across the retina. Functional contacts structured by bilaminar membranes were found between digital terminals of horizontal cells and bipolar cells in rods and cones, between bipolar dendrites, tubular cells, stellate amacrine cells, piriform amacrine cells, as well as between lateral expansions of horizontal cells.

Keywords: Retina ultrastructure; horizontal cells; bipolar cells; cones and rods; stellate amacrine cells; piriform amacrine cells.

1. INTRODUCTION

The method of Golgi initiated knowledge on retina structure, used extensively by Cajal in vertebrates describing all layers, cells, and their connections creating a doctrine with physiological implications still alive today [1]. Retina ultrastructure in the guinea pig eye and in the albino rabbit described from outer plexiform layer finger like process penetrating rod and cone receptors named synaptic vacuoles or vesicles [2,3]. Bipolar, horizontal (Hc), amacrine, ganglion and Müller cells were described with the electron microscope from monkey (*Macaca rhesus, irus, and mulatta*), chicken (*Gallus domesticus var*.), turtle (*Pseudemys sp*.), toad (*Bufo marinus*), and fish (*Centropomidae*), without referring ascendant digital-like processes to photoreceptors in Hc cells [4]. Combining Ultrastructure and Golgi staining in fish retina it was determined that rod synaptic vacuoles were prolongations of Hc [5] and that the central structure in rod invaginations belonged to bipolar cells dendrites [6]. The structure of bipolar, amacrines, ganglion cells and the synaptic organization of outer and inner plexiform layers were also analyzed in the primate retina [7]. In retinas of carp, shark, rays, expansions of Hc to outer plexiform layer as well as fused membrane structures between lateral contacts in adjacent Hc cells were reported [8]. In vertebrate retina true amacrines without axons and association amacrines with a short axon were described [1], and in fish retinas a neuron type amacrine cell and a glial type amacrine cell similar to astrocytes were observed [9]. Synaptic bands with multiple synaptic contacts in pigeon and cat retinas were found in the inner plexiform layer [10]. Rod ultrastructure in guinea pig eye was analyzed in three-dimensional serial sections confirming the triad existence [11]. Hc send negative feedback to cones inhibiting brilliant light from the environment and form extensive nets with membrane gap junctions, reporting two morphologic Hc types in rabbit retina: Type A without axons and big dendrites contacting cones only and type B with axons contacting only rods and somatic dendrites contacting cones [12]. The rod cilium is a tubular structure that connects the inner cellular compartment, the major site of biosynthesis, to the outer segment responsible for photo transduction. Any mutation in primary cilium genes induced aberrant traffic and photoreceptors dead [13]. Visual pigments in cones photoreceptor cells are the molecules responsible for photopic vision, contains 11-cis retinal that isomerizes to trans retinal inducing conformational changes of the G protein to activate state. Rod visual pigment is rhodopsin responsible for scotopic vision. There are 3 visual pigments in cones with different absorption maxima base for the color discrimination [14].

The organization of the cone cells in the retinae of four teleosts (*Perca fluviatilis, Lucioperca lucioperca, Acerina cernua,* and *Coregonus albula*) [15] as well as Hc, bipolar and oligopolar cells in the Teleost retina [16] and calcium dynamics and regulation in Hc of the retina from teleosts [17] have been published increasing the knowledge about structure and function of the retina, confirming findings by other authors described above. This paper is a comprehensive analysis of ultrastructure of seven retinal cells, finding two new cells in teleost retina, 1- tubular cells forming an extensive tangential net below internal Hc, with characteristic structures not seen in the literature on retina before and, 2- undulate amacrine cells that surrounds many bipolar cells across the retina. New functional connections between retinal cells are also described.

2. MATERIALS AND METHODS

Teleost fish family Mugilidae, genera Mugil, specie brasiliensis, was used. Retinas were extracted after equatorial section of the eye to eliminate the anterior part and crystalline, cutting the choroid and sclerotic around the optic nerve which was preserved, taking out the vitreous humor. Retinas were fixed in 2% glutaraldehyde in 0.1 molar Na phosphate buffer pH 7.2 for 3 hrs at 4°C. [18]. Afterwards retinas were washed in 0.18 molar sucrose in 0.1 molar sodium phosphate buffer pH 7.2, with six changes one every 10 minutes. Subsequently retinas were cut in pieces 1 mm wide 1-3 mm long selecting the bests under inverted microscope and post fixed in equal parts of 2% osmium tetroxide and 0.18 molar sucrose in sodium phosphate buffer pH 7.2 at 4°C overnight [19]. After dehydration half the retinas were processed in Araldita and the other half in Maraglas. All sections were done from Araldite epoxy resin. Sections were around 20 nm and placed in Sjostrand grids. Radial and tangential sections were obtained in a Porter Blum MT2 ultramicrotome and stained with lead citrate and uranyl acetate to be analyzed in a Hitachi Hu-11B at 75 Kv.

3. RESULTS

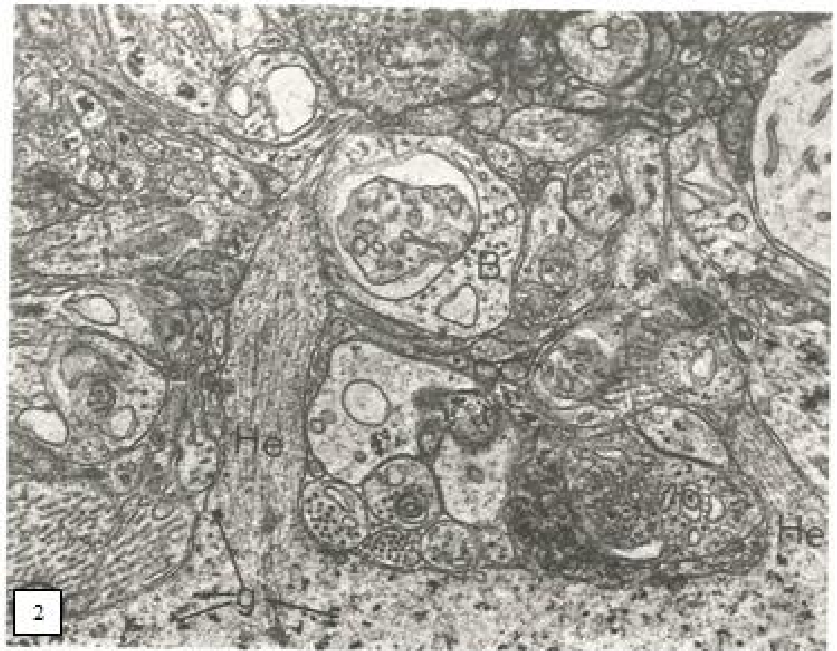
3.1 External Horizontal Cells

Cytoplasm shows abundant glycogen granules, mitochondria, few fibrils, dense bodies surrounded by membranes and prominent Golgi apparatus. Many finger like process originated from Hc external face ended in the outer plexiform layer as small invaginations at cones and rods (Figs. 1, 2, 3, 4). Lateral contacts exhibit functional contacts with dense undulated membranes between adjacent cells (Figs. 5, 6)

3.1.1 Medium and internal horizontal cells

Numerous parallel fibrils in packages penetrate the lateral expansions, its density decrease close to the cellular membrane a space with numerous elongated mitochondria and glycogen granules. The Nucleus is oval with big nucleolus and uniform chromatin surrounded by elongated mitochondria, Golgi apparatus and rough endoplasmic reticulum with dilated vesicles. Lateral contacts exhibit fused undulated dense membranes structuring a net in medium and internal horizontal cells with stellate configuration (Fig. 5). Numerous digital like expansions, from the outer face of both cells, cross the outer plexiform layer ending in cones and rods terminals (Figs. 1, 2, 3, 4, 6, 7).

Fig. 1. Retina mosaic (around 250 photos) from teleost *Mugil brasiliensis* radial section ***In horizontal planes the following cells and layers: cones [C], rods [R], outer plexiform layer [Op], external horizontal [He], medium horizontal [Hm]; internal horizontal [Hl], bipolar[B], undulated amacrine [Oa], tubular cells [T], Stellate amacrine [AmS], amacrine interstitial external [Amle], myelinated axons [Ax], Müller cell fiber [M], clear Piriform amacrine [Pc], dark Piriform amacrine [Po], amacrine interstitial internal [Amli]. Each photo X 3000***



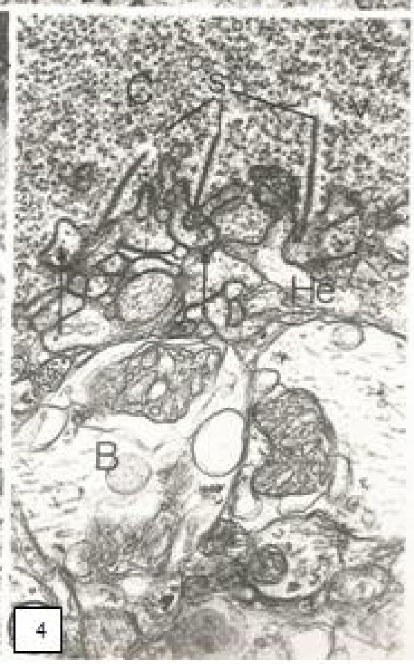


Fig. 2. Ascendant digital like process from external horizontal cell [He] branching under cone foot in the outer plexiform layer; bipolar cell dendrite [B], glycogen granules [g] in cytoplasm of external horizontal cell; Radial section, X 20400

Fig. 3. Cone foot [C] with invaginations from horizontal and bipolar cells, numerous synaptic vesicles [v] and horizontal cell process [He] penetrating invagination of cone foot (arrows). Radial section X 10800

Fig. 4. Cone foot with invaginations (arrows) from external horizontal and bipolar cell, synaptic lamina [s], expansion of external horizontal cell [He], penetrating cone invaginations, bipolar cell [B]. Radial section X 17500

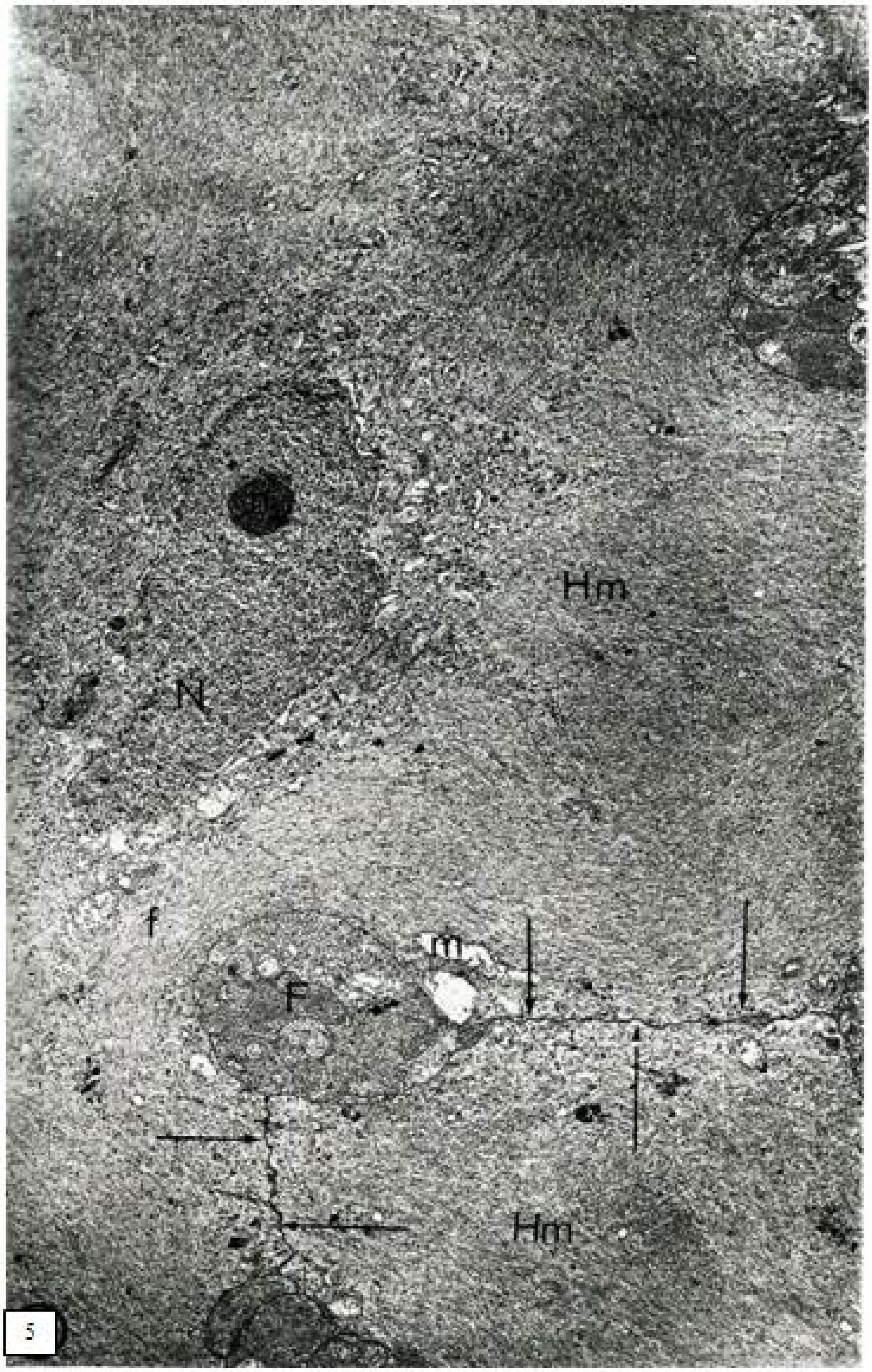


Fig. 5. Medium horizontal cell [Hm] with nucleus [N], nucleolus [n], cytoplasmic fibrils[f]. Note fused membranes in lateral contacts between cells of same layer (arrows) elongated mitochondria [m], fenestration or hole formed by horizontal cells to allow passage of prolongations from cells of lower layers [F]. Tangential section X 6000

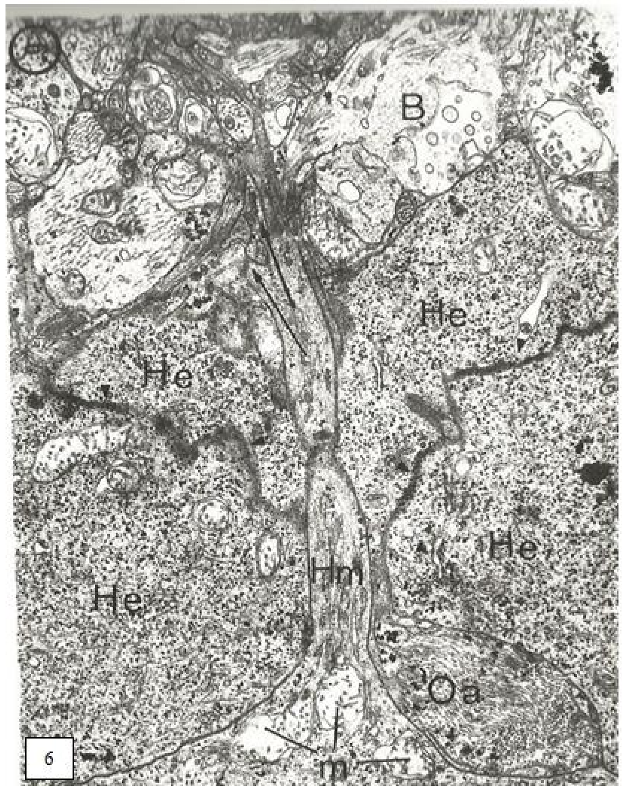
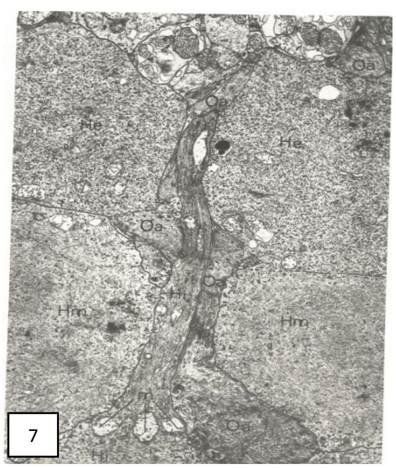


Fig. 6. External horizontal cell [He] with fused dense membranes in lateral contacts and abundant glycogen granules, bipolar cell [B], undulated amacrine cell [Oa], digital expansion of medium horizontal cell [Hm] to the outer plexiform layer going to a cone foot. (arrows), mitochondria [m]. Tangential section X 8400



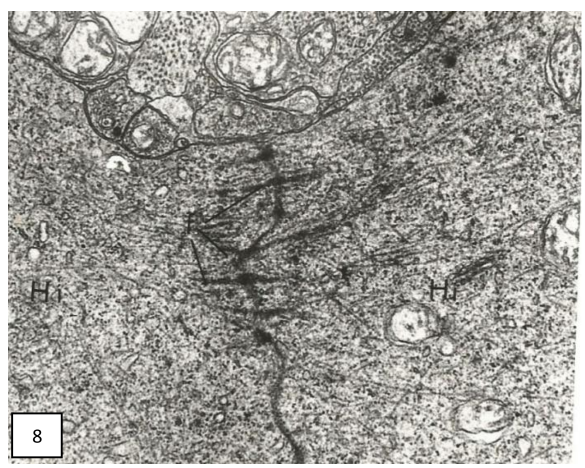
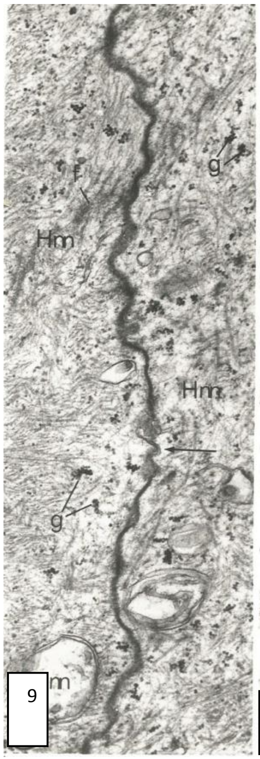
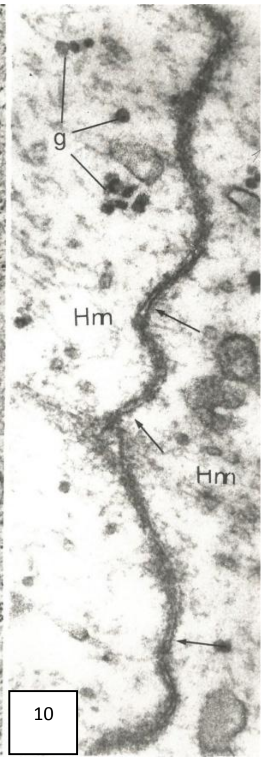


Fig. 7. Internal horizontal cell [Hi] with digital expansion to the outer plexiform layer thru fenestrations between medium and external horizontal cells, undulate amacrine cell [Oa] around internal horizontal cell digital process, mitochondria [m], external horizontal cell [He], medium horizontal cell [Hm]. It should be noted the highest concentration of glycogen granules in He. Radial section X 6400

Fig. 8. Internal horizontal cells with functional contacts between them (arrows) also encircling a hole for digital expansions of amacrine stellate cells [AmS], bipolar cells [B] and Muller fiber [M]. Tangential section X 6250





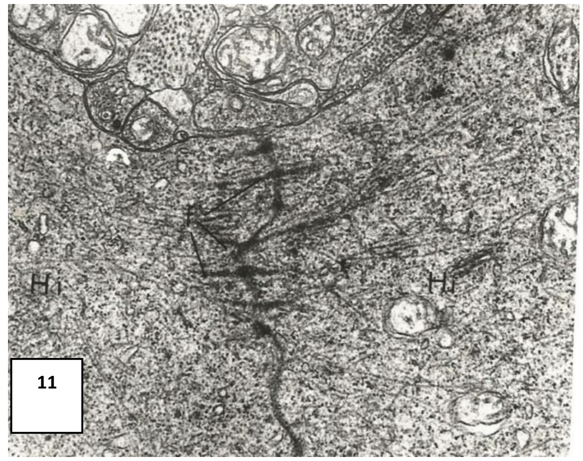


Fig. 9. Functional contacts between medium horizontal cells [Hm] with fused dense membranes alternating with non-fused spaces (arrows). mitochondria [m], glycogen [g]. Tangential section, X 27200

Fig. 10. Equal to Fig. 9 with clear spaces between membranes (arrows) at higher magnification. X 108000

Fig. 11. Dense fibrils perpendicular to functional contacts, at high density spots on the membrane. Tangential section X 20000

Presence of glycogen granules distinguished bipolar cells with very few glycogen, from horizontal cells with abundant granules. Noteworthy the undulated membrane structure in fused dense membranes, between horizontal cells, to increase functional contact between them (Fig. 8). Functional contacts between horizontal cells at high magnification showed that fusion is not continuous, alternating fused membranes with clear spaces between them (Figs. 9,10). Perpendicular dense filaments are seen contacting fused membranes at dense circular spots (Fig. 11).

3.1.2 Bipolar cells

Radially oriented, are found in the same plane of medium and internal horizontal cells (Fig. 1). Exhibit a clear cytoplasm, with many fibrils, elongated mitochondria of dense matrix with vesicular and lamellar cristae, numerous ribosomes and rough endoplasmic reticulum, more abundant at the origin of the dendrite. The nucleus is oval with homogenously distributed chromatin (Fig. 12). The upper terminal of the bipolar cells is seen branching at the outer plexiform layer below cones and rods with packed parallel microtubules and ribosomes in the cytoplasm (Fig. 13).

3.1.3 Stellate amacrines cells

Located in a continuous net below internal horizontal and tubular cells, have stellate appearance, long lateral expansions and numerous cytoplasmic fibrils, glycogen granules mitochondria and Golgi apparatus. The nucleus appears elongated with homogeneous dense

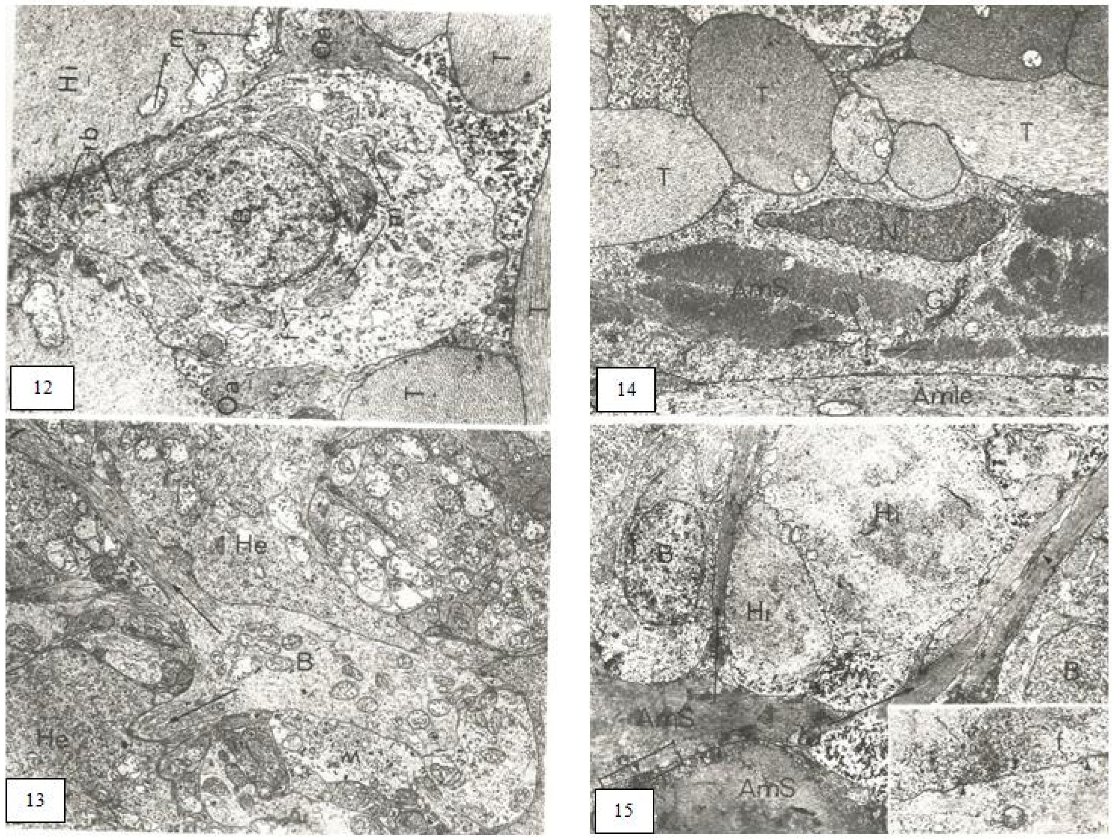


Fig. 12. Bipolar cell with numerous ribosomes [rb] mitochondria [m] and fibrils [f]. Undulate amacrine cell [Oa]. Tubular cells [T], internal horizontal cell [Hi], Müller cell fiber [M]. Radial section X 9200

Fig. 13. Bipolar cell dendrite [B] branching in outer plexiform layer (arrows), Müller cell fiber [M], external horizontal cell [He]. Tangential section X 7500

Fig. 14. Stellate amacrine cell [AmS], External interstitial amacrine cell [Amle], Tubular cell [T], nucleus [N], fibrils [f] in packages, Golgi apparatus [G]. Radial section X 6250

Fig. 15. Stellate amacrine cell [AmS] with ascendant expansions (arrows), bipolar cell [B]. Internal Horizontal cell [Hi]. Radial section X 4800. In rectangle functional contact between two amacrine cells at higher magnification at lower right X 10200

chromatin in tangential and radial sections. Functional contacts between adjacent cells with dense undulated membranes were seen similar to contacts in horizontal cells (Figs. 1, 14, 15).

3.1.4 Tubular cells

This cell layer is described by the first time in the retina, it is formed by tubular structures as a net between internal horizontal and stellate amacrine cells layers (Figs. 1, 14, 16).

The tubular cell body shows a clear matrix, with numerous glycogen granules, abundant parallel cytoplasmic microtubules, elongated mitochondria and dense bodies surrounded by membranes, among myelinated axons and Müller cell fibers (Figs. 17, 18).Tubular cells showed a particular cytoplasmic structure of circular very dense lines around packages of microtubules (Fig. 19). The surface of tubular cells also exhibits a spherical protrusion with inner curve microtubules penetrating in the Müller cell fiber (Fig. 20). Some sections showed a nucleus and fused dense membranes contacts between tubular cells which are similar to functional contacts between horizontal cells (Fig. 21).

3.1.5 Undulate amacrines cells

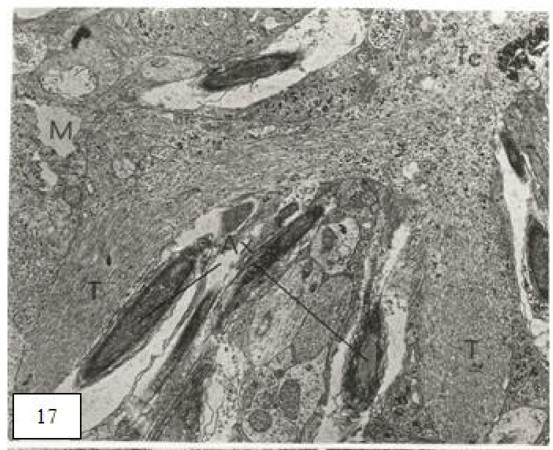
The cytoplasm is structured with parallel undulated fibrils with abundant dense granules and cell expansions that are observed surrounding bipolar and internal horizontal cells, and sometimes as a net below and paralleled to internal horizontal cells which had dense membranes in functional contact between cells. (Figs. 1, 22, 23).

3.1.6 Outer plexiform layer

Many expansions from cells located below in the retina were found. Bipolar cell dendrites are abundant with many fussed dense plasma membranes among them around cones with synaptic laminas and triads (Fig. 24).

3.1.7 Cones foot and rod spherules

Terminal of Hc were observed besides synaptic lamina forming triads with bipolar cells terminals at the center. Hc membranes in contacts with rod spherules were dense with no synaptic vesicles in their terminals nor in terminals dendrites of bipolar cells (Figs. 25, 26, 27, 28). Serial sections revealed bipolar cells digital like terminals entering rod (Fig. 29).



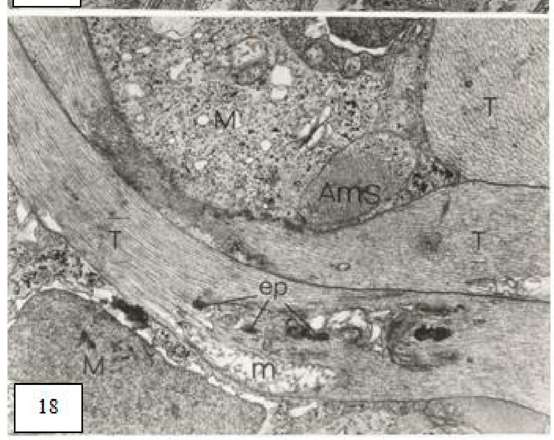


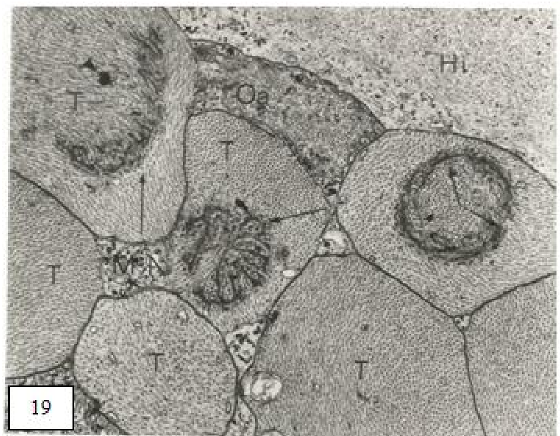
Fig. 16. Mosaic (around 150 photos) of tubular cells [T], bipolar cell [B], internal horizontal cell [Hi], stellate amacrines cell [AmS], undulated amacrines cell [Oa], Müller cell fiber [M]. Tangential section. Each photo X 1800

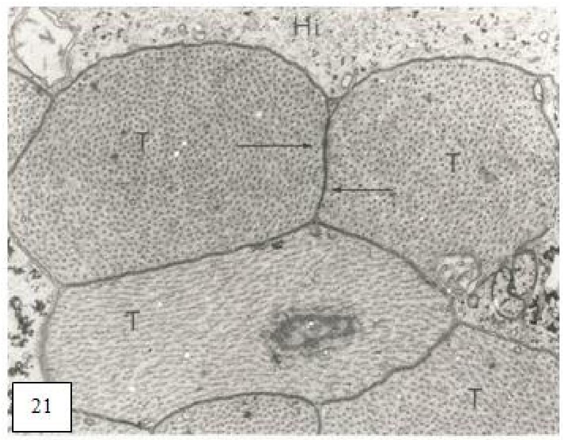
Fig. 17. Tubular cell body [Tc] with two expansions [T], mielinated axons [Ax]. Müller cell fiber [M]. Tangential section X 10000

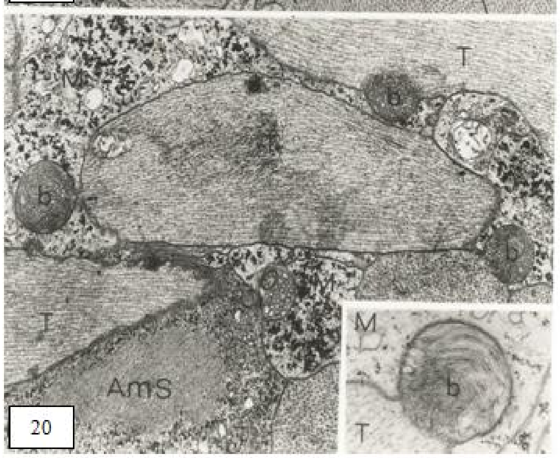
Fig. 18. Tubular cell [T] with elongated mitochondria [m], numerous parallel fibers and dense particles in cytoplasm [ep], Expansion of stellate amacrine cell [AmS], Müller cell fiber [M]. Tangential section X 12500

3.1.8 Piriform amacrine cells

There are two types: I-Dark cytoplasm due to abundant glycogen granules, numerous mitochondria and rough endoplasmic reticulum, with prominent Golgi apparatus and very dense bodies surrounded by membrane, oval or spherical nucleus with dense homogeneous distributed chromatin. The plasma membranes are undulated in contact with Müller cell plasma membrane which separated amacrine pairs of dark piriform cells in contact from the rest of cellular elements in the retina (Fig. 30). II- Clear cytoplasm with less glycogen granules abundant ribosomes, dense bodies surrounded by membranes and abundant vesicles of rough endoplasmic reticulum, also observed in pairs with functional contacts between them (Figs. 31, 32) and sending descendant prolongations to the inner plexiform layer (Fig. 33).The Müller cell fiber has a segmented nucleus with dense chromatin homogenously distributed (Fig. 34). Also pairs of clear and dark piriform cells were observed (Figs. 1, 30)







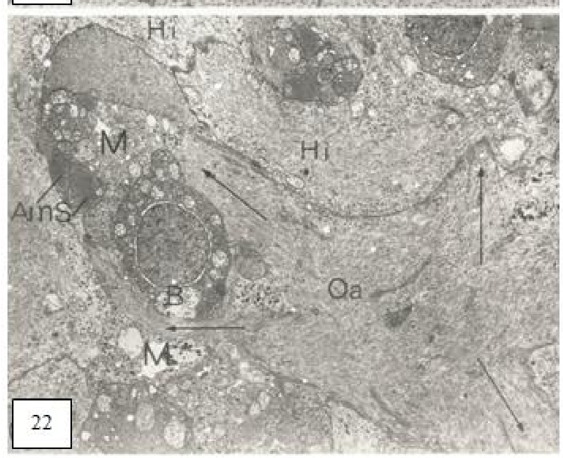
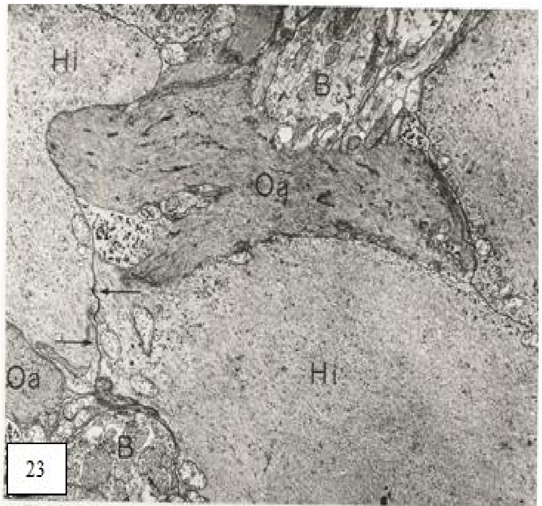


Fig. 19. Tubular cells [T] with particular structure (arrows). Undulate amacrine cell [Oa], Internal horizontal cell [Hi], Müller cell fiber [M]. Radial section, X 12500

Fig. 20. Tubular cells [T] with protrusion bubble like [b] on cell surface in contact with Müller cell fiber [M], Stellate amacrine cell [AmS]. Radial section X 10000. At lower right protrusion of tubular cells in Müller cell fiber cytoplasm [M] X 25000

Fig. 21. Functional contacts with fused membranes in tubular cells (arrows) with abundant cytoplasmic microtubules and a nucleus. Internal horizontal cell [Hi]. Radial section X 20.000

Fig. 22. Undulate amacrine cell [Oa] with expansions around bipolar cell [B], Internal horizontal cell [Hi], Ascendant expansions of stellate amacrine cells [AmS] , Müller cell fiber[M] Tangential section X 7000



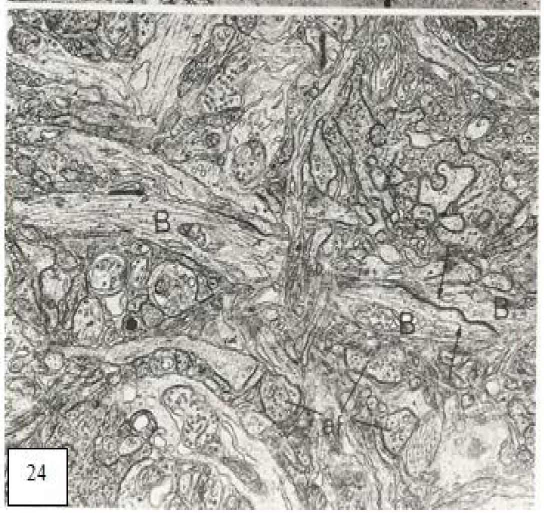


Fig. 23. Undulated amacrine cell [Oa] surrounding inner horizontal cells [Hi] showing functional contacts with fussed dense membranes (arrows) at cells from the same layer, bipolar cell [B]. Radial section X 5600

Fig. 24. Outer plexiform layer with dendritic branching of bipolar cells [B] with fusion of plasma membranes (arrows). Adrenergic vesicles [af], Cone foot [C] with synaptic lamina and triad invaginations. Tangential section X 12750

Clear Piriform cells send descendants prolongations to the inner plexiform layer (Fig. 31) with functional contacts with dense membranes between them (Fig. 32), branching in opposite directions in the inner plexiform layer (Fig. 33). There were also functional contacts between stellate amacrine cells with external interstitial amacrine cell (Fig. 34).

Usually clear Piriform cells are in contact by membranes with dark Piriform cells, both surrounded by Müller cell fiber except at the fusion area between both cells (Fig. 35).

4. DISCUSSION

Cajal described in Teleost retina external or ascendant expansions of Hc called dendrites and a long expansion named axons [1]. We found in all Hc numerous ascendant digital like expansions connecting with rods and cones without the appearance of dendrites or axons. It has been published the ultrastructure, of ascendant expansions in Hc but no mention to axons [5,6]. In this work we found a functional contact between Hc membranes lateral expansions, different to dendrites or axons, with no synaptic vesicles, contact that explained the S potentials found in Hc [20,21,22,23]. Trilaminar complexes forming electrotonic junctions but not chemical synapses with neurotransmitter have been found in fish in some adjacent neurons [24] different to our bilaminar membrane structures in horizontal cells and other cells found in the teleost retina. Electrical connexions between horizontal cells in the dogfish retina were published reporting also close membrane apposition between neighboring external horizontal cells [25] as found in our work. We have found ATPase activity at the functional contacts between retinal cells which produce S-potential [26]. Unusual type of S-potential in a cyprinid fish retina revealed blue/green-sensitive hyperpolarizing responses with a red-sensitive depolarizing component found in horizontal cells with H2-like morphologies different to the classic S-potential [27]. Horizontal cells are electrically coupled in the teleost retina. This coupling is modulated by dopamine, which is in turn liberated from amacrine cells and both H+ and cAMP are second messengers involved in dopamine's modulation of intercellular coupling, which is produced by changes in the resistance of intercellular unions, while Ca^{2+} would act as a modulator through its effect on the cell membrane resistance [28]. In our work we found bilaminar functional contacts between Hc, and some other cells structured by undulated membrane fusion with filaments perpendicularly oriented to them. Stellate amacrine cells with ascendant, horizontal and descendent expansions [16,22] have been described. In this work we found dark and clear piriform amacrines distinguished by their glycogen granules density appearing as pairs in close contact by their membranes, not seen in the literature before.

The modulation of electrical coupling of horizontal cells of the retina has been published [29].

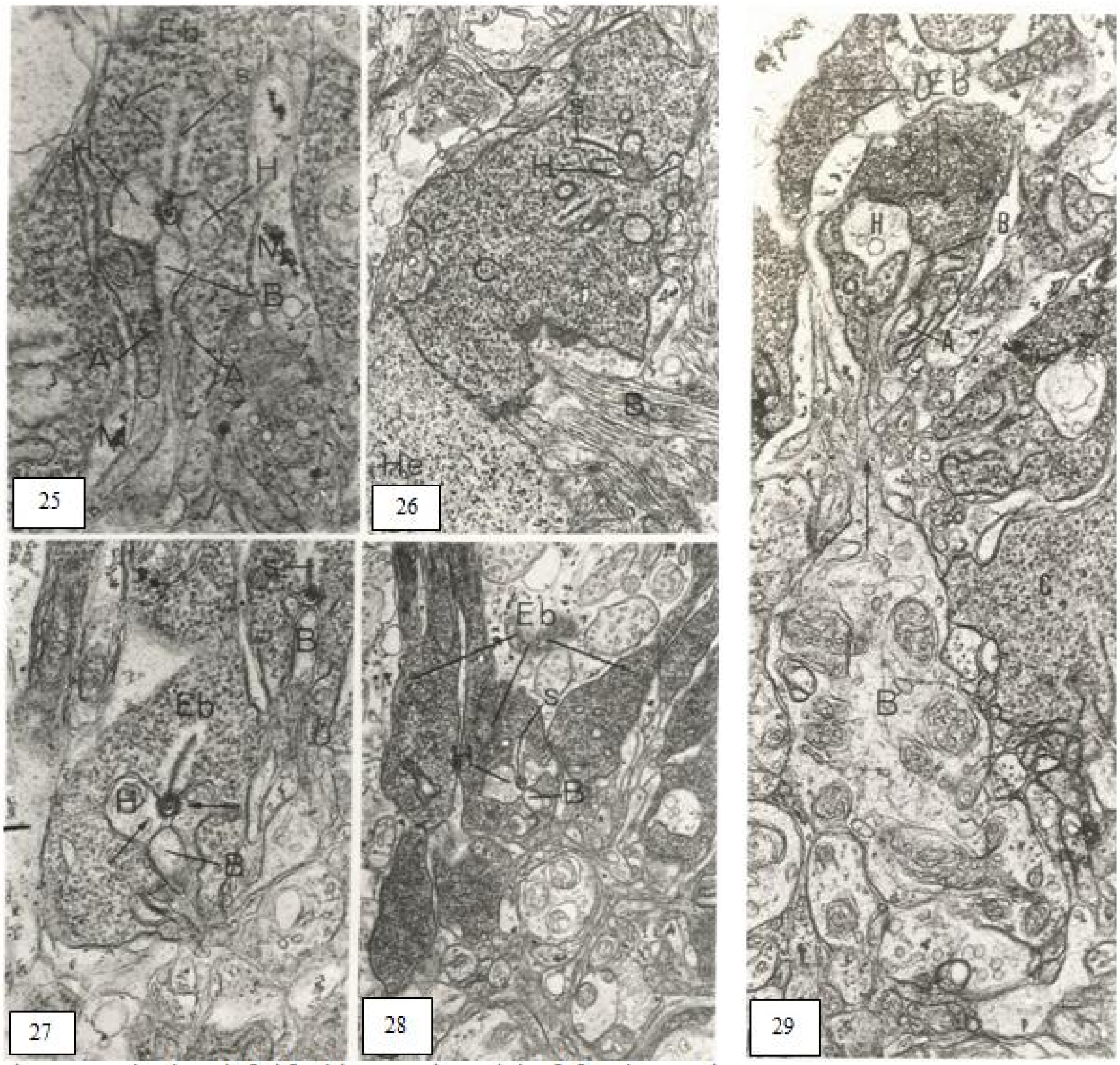


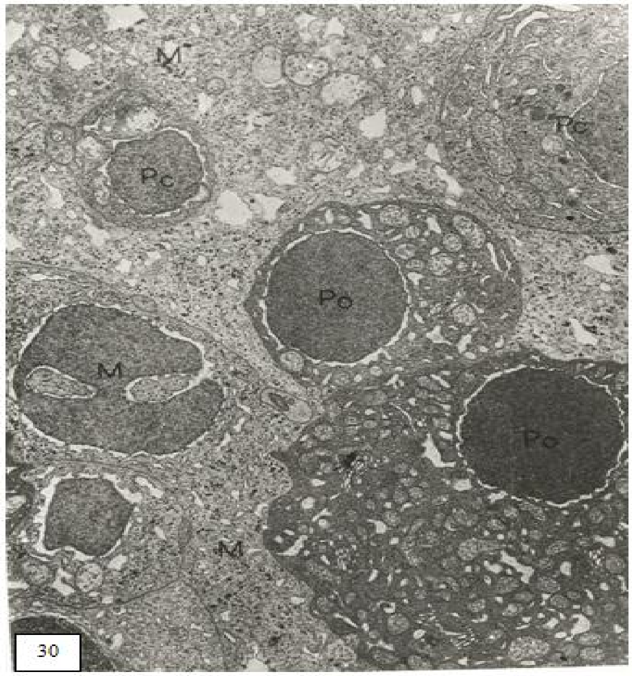
Fig. 25. Rod spherule [Eb] with synaptic vesicles [v] and synaptic lamina [s] forming a triad with lateral terminals of horizontal cells [H], and bipolar cell dendrite [B] at the center, Müller cell fiber [M] around rod. X 25200

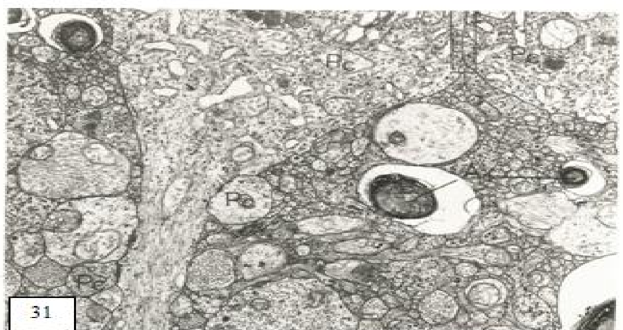
Fig. 26. Cone [C] foot with synaptic laminas [s] and horizontal cell terminals [H] in a triad, External horizontal cell [He], bipolar cell [B]. Tangential section X 15750

Fig. 27. Rod spherule [Eb] with horizontal [H] and bipolar [B] cells terminals in a triad with fussed horizontal cells membranes to the synaptic lamina [arrows]. Radial section X 20500

Fig. 28. Rod spherules [Eb] with very dense vesicles some of higher size around terminal endings of horizontal [H] and bipolar cells [B] in a triad. synaptic lamina [S]. Radial section X 13000

Fig. 29. Horizontal cells terminals [H], Bipolar cell dendrites [A, B] with branching terminals [arrows] to end in rod spherule [Eb] contacting horizontal cell terminal [H]. cone [C] foot with abundant dense vesicles. Radial section X 25000





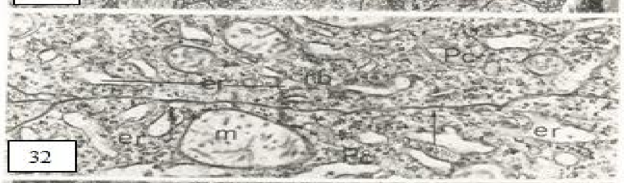


Fig. 30. Clear [Pc] and dark [Po] Piriform amacrine cells, Müller cell fiber [M] with segmented nucleus Tangential section X 7750

Fig. 31. Cell body and descendant expansion of clear Piriform cell [Pc]. myelinated axons [Ax]. Radial section X 6500

Fig. 32. Rectangle from fig 35 with fused membranes from two clear Piriform cells (arrows). Mitochondria [m], rough endoplasmic reticulum[er], ribosomes[rb]. Radial section X 20400

Fig. 33. Clear Piriform cells [Pc] with descendant terminal branching in inner plexiform layer (arrows) with glycogen (g) granules inside dilated vesicles and ribosomes. Radial section X 4250

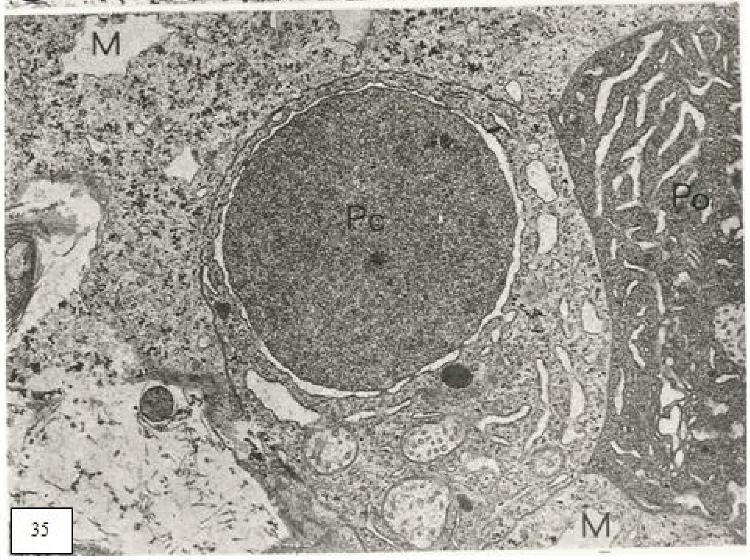


Fig. 34. Stellate amacrine cell [AmS] with membrane fusion with amacrine interstitial external [Amli] cell. Radial section X 20500

Fig. 35. Clear Piriform amacrine cell [Pc] with fused membranes with dark piriform amacrine cell [Po] surrounded by Müller [M] cell fiber which did not separated the contact area between both cells. Tangential section X 12500

5. CONCLUSIONS

External, medium and internal horizontal cells form three layers in the teleost retina exhibited ascendant and lateral expansions. Functional contacts structured by bilaminar membranes were found between digital terminals of horizontal cells and bipolar cells in rods and cones, between bipolar dendrites, tubular cells, stellate amacrine cells, piriform amacrine cells, as well as lateral expansions of horizontal cells. Tubular cells are described by the first time forming a net below internal horizontal cells, as well as undulated amacrine cells forming an spiral expansion around bipolar cells. Piriform amacrines dark and clear cells are distinguished by their glycogen content.

CONSENT

It is not applicable.

ETHICAL APPROVAL

It is not applicable.

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COMPETING INTERESTS

Author has declared that no competing interests exist.

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