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Fine structure of the retina of black bass, *Micropterus salmoides* (Centrarchidae, Teleostei)

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Summary. The structure of light- and dark-adapted retina of the black bass, *Micropterus salmoides* has been studied by light and electron microscopy. This retina lacks blood vessels at all levels. The optic fiber layer is divided into fascicles by the processes of Müller cells and the ganglion cell layer is represented by a single row of voluminous cells. The inner nuclear layer consists of two layers of horizontal cells and bipolar, amacrine and interplexiform cells. In the outer plexiform layer we observed the synaptic terminals of photoreceptor cells, rod spherules and cone pedicles and terminal processes of bipolar and horizontal cells. The spherules have a single synaptic ribbon and the pedicles possess multiple synaptic ribbons. Morphologically, we have identified three types of photoreceptors: rods, single cones and equal double cones which undergo retinomotor movements in response to changes in light conditions. The cones are arranged in a square mosaic whereas the rods are dispersed between the cones.

Key words: Ultrastructure, Retina, Fish, Electron microscopy, Photoreceptor

Introduction

The visual system of fish presents various adaptations in response to habitat and behavioral pattern. Although the retinal structure is basically the same as in the rest of the vertebrates, the retina of fish presents unique properties as a consequence of their adaptation to the environment (Wagner, 1990). This is reflected in many aspects of retinal structure such as 1) the presence of retinomotor movements in response to changes in light conditions (Ali, 1971, 1975; Burnside and Nagle, 1983; Burnside and Dearry, 1986), 2) the presence of large outer segments and prominent ellipsoids to improve absorption of light (Wagner, 1990), 3) the existence of double cones which increase the area available for the absorption of light (Ali and Anctil, 1968), 4) regular cone mosaics (Wagner, 1978), 5) the existence of a well developed retinal tapetum in nocturnal and bottom-living species (Wagner and Ali, 1978), 6) presence of foveae or areas with an increase in photoreceptors and other neurons (Wagner, 1990), and 7) a marked synaptic plasticity as is demonstrated by the formation of spinules (Wagner, 1980) during light adaptation and their disappearance during dark-adaptation, and others. In summary, these features demonstrate the importance of vision in the mode of life and survival of the species.

Micropterus salmoides, known as black bass, is a member of the family Centrarchidae (Order Perciformes) which has been introduced into freshwaters in Spain and is a native of North America. It occurs largely in ponds, lagoons, and calm fresh water, especially in backwaters with vegetation. It is a fish typically crepuscular and a good predator, piscivorous, although they may also feed on crustaceans and insects. Their ethology suggests that, as in all predatory fish, vision is an important sense for their survival, and this is reflected in the morphology of the retina by: the presence of many cones, the exhibition of retinomotor movements in response to changes in light, the existence of prominent ellipsoids in double cones which are arranged in regular cone mosaics, the presence of a marked synaptic plasticity in the outer plexiform layer which is reflected in the presence of spinules, nematosomes, synaptic ribbons and a thick inner plexiform layer which implies a high degree of complexity of the neural interactions.

This study describes the fine structure of the black bass retina to provide more data of the vision of a predatory fish in order to increase our understanding of the morphology of the retina and its relation with the ecology and ethology of the species.

Materials and methods

Experimental animals and tissue preservation

Experiments were carried out with black bass, *Micropterus salmoides*, with a body length of 12-15 cm. Fish were maintained in an aquarium for 12-h light/12h dark cycle for at least 1 month prior to use. All

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experiments were carried out at noon in order to equalize circadian effects on retinomotor positions.

We have examined the effects of light and dark-adaptation on the cone retinomotor movements. For light-experiments, 2 animals were dark-adapted for at least 2 h and then the light was switched on for 1 h to elicit the retinomotor responses to light. Inversely, for the dark-experiments, 2 fish were adapted to light for at least 2 h and then, the light was switched off for 1 h. Previously, we have verified that periods longer than 1 h of light- and dark-adaptation do not produce more pronounced cone retinomotor movements. The sacrifice and surgery of dark-adapted fish were performed under dim red light.

After decapitation, the fishes eyes were enucleated and hemisected, and the retinas removed and immersed in the fixative (1% paraformaldehyde, 1.6% glutaraldehyde, 0.15 mM $CaCl_2$ in 0.1M phosphate buffer, pH 7.4) for 2 h and then at 4 °C overnight. The fragments were then postfixed in 2% OsO_4 in 0.1M phosphate buffer for 1 h, pH 7.4, and then dehydrated in ascending concentrations of ethanol, cleared in propylene oxide and flat-embedded in Epon 812. Blocks were oriented to obtain longitudinal sections through the photoreceptors and 1.0 μm-thick sections were cut on a Reichert ultramicrotome, mounted on glass slides, and stained with 0.5% toluidine blue for light-microscopical examination. Favourable areas in the specimens were selected by light microscopy for thin sections. Vertical ultrathin sections were obtained and double-contrasted with uranyl acetate and lead citrate and examined using a Zeiss EM10.

Measurement of retinomotor position

Semi-thin sections were examined using a light microscope equipped with an ocular micrometer and the changes in the cone myoid length were determined. Cone myoid length was defined as the distance in micrometers between the outer limiting membrane to the base of ellipsoid. At least 30 cones were measured in each retina and 4 retinas were analyzed for each series. Statistical differences were checked by one-tailed Student's t-tests. All quantitative data are expressed as means ± SEM.

Results

The retina of black bass, *Micropterus salmoides*, as in all vertebrate retinas, is organized into ten well defined layers that can be identified with the light microscope (Fig. 1). These layers are: 1) retinal pigment epithelium (RPE), 2) photoreceptor cell layer, cone (C) and rod (R), 3) outer limiting membrane (OLM), 4) outer nuclear layer (ONL), 5) outer plexiform layer (OPL), 6) inner nuclear layer (INL), 7) inner plexiform layer (IPL), 8) ganglion cell layer (GCL), 9) optic nerve fiber layer (OFL), and 10) inner limiting membrane (ILM). This retina is approximately 250 μm thick with a relative thickness of the photoreceptor cell layer compared to the neural retina of 1:1 approximately, and lacks blood vessels.

The *Micropterus salmoides* retina contained the two types of photoreceptors that are found in the majority of vertebrates: rods and cones, with a rod-to-cone ratio of about 40 rods : 4 double cones : 1 single cone. The double cones, in close contact, were comprised of two morphologically identical cells and were bigger than the single cone. In tangential section through the ellipsoid region we observed a precise organization into square mosaic. This organization consisted of four double cones forming the sides of a square and a single cone in the centre (Fig. 2). The rods were interspersed within the

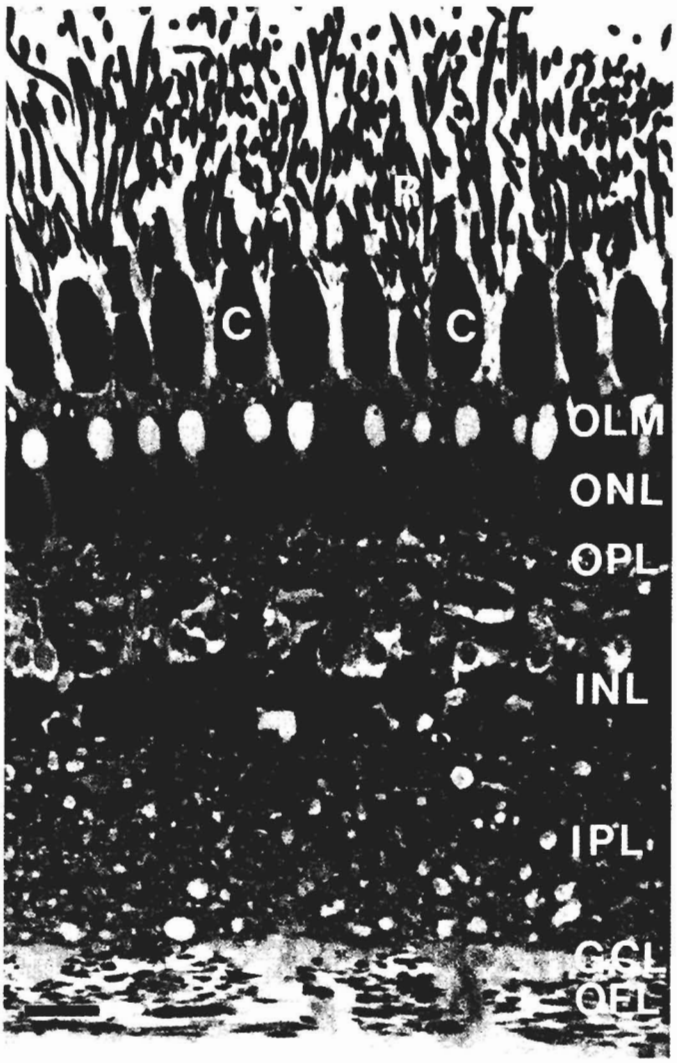


Fig. 1. Light micrograph of a 1-μm retinal section stained with toluidine blue from a light-adapted retina showing the following layers: photoreceptor cell layer, cone (C) and rod (R), outer limiting membrane (OLM), outer nuclear layer (ONL), outer plexiform layer (OPL), inner nuclear layer (INL), inner plexiform layer (IPL), ganglion cell layer (GCL) and optic nerve fiber layer (OFL). The process of Müller cells (arrowheads) divides the OFL into fascicles. Bar: 20 μm.

cones without a regular pattern.

Photoreceptors and RPE underwent rearrangements named retinomotor movements (MRM) in response to changes in light conditions. When exposed to light, the cone contractions moved their outer segments toward the incoming light and the rods buried their outer segments in the dispersing pigment of the RPE. In the dark, these movements were reversed (Fig. 3). In this study we have analyzed the changes that occur in the cones during light- and dark-adaptation. Both types of cones, single and double cones, contracted from 46.5±1 μm to 5.0±0.4 μm after 1 h exposed to light.

The rod outer segment was long and cylindrical, about 50 μm in length and approximately 2.2 μm in width. This region consisted of stacks of membranous discs forming isolated cisternae surrounded by a membrane (Fig. 4a). The discs displayed several incisures of various lengths. By contrast, the cone outer segment was shorter than the rods (about 18 μm in length in both types of cones) and displayed a conical morphology (their diameter ranged from about 4.5 μm in the base to 1 μm in the scleral tip). The discs maintained their continuity with the plasma membrane so that the discs were filled with the extracellular matrix. On the other hand, the cone outer segments lacked incisures in their discs.

The photoreceptor inner segment consisted of two regions: the ellipsoid that joined the outer segment and the myoid, which was continuous with the cell body. The ellipsoid lacked paraboloid and oil droplets. The rod ellipsoid (Fig. 4b) was small and short whereas the cone ellipsoid was a bulky region of the cell. The ellipsoid was rich in mitochondria which were morphologically different in rods and cones. In effect, in rods, the mitochondria had an electron lucent matrix which presented electrondense granules (Fig. 4b). In contrast, the mitochondria of cones were electrondense and lacked granules. In the equal double cones (Fig. 5b), the ellipsoids were semicircular in tangential section and their apposed surfaces had no membrane specializations. The ellipsoids of whole double cone were 20 μm in diameter at their widest and about 40 μm in length. Single cone ellipsoids (Fig. 5a) were 20 μm in length and 10 μm in diameter, whereas rod ellipsoids were 3.6 μm in diameter and 9 μm in length.

The myoid was rich in the organelles associated with the protein synthesis: free ribosomes, rough and smooth endoplasmic reticulum and Golgi apparatus. This region was also rich in microtubules and microfilaments which were responsible for the MRM observed (Burnside and Nagle, 1983).

The next region in the cell was the nucleus located in the ONL below the OLM, which was a region of tight junctions between photoreceptors and Müller cells. In the ONL, which measured about 30 μm, the rod nuclei were arranged in 4 rows. They were round or slightly oval with a diameter of approximately 3.5 μm and their chromatin was condensed. The cone nuclei were located near the OLM, at the distal border of the ONL. They were also slightly oval in shape and larger than those of the rods, and measured approximately 6.5 μm in diameter in both types of cones. They were vesicular and the nucleolus was frequently observed.

A narrow axon lay between the nucleus and the synaptic terminal. The synaptic terminals were located in the OPL, of about 10 μm. The OPL was a region free of cell bodies in which synapses were made between photoreceptors, horizontal and bipolar cells. In the OPL

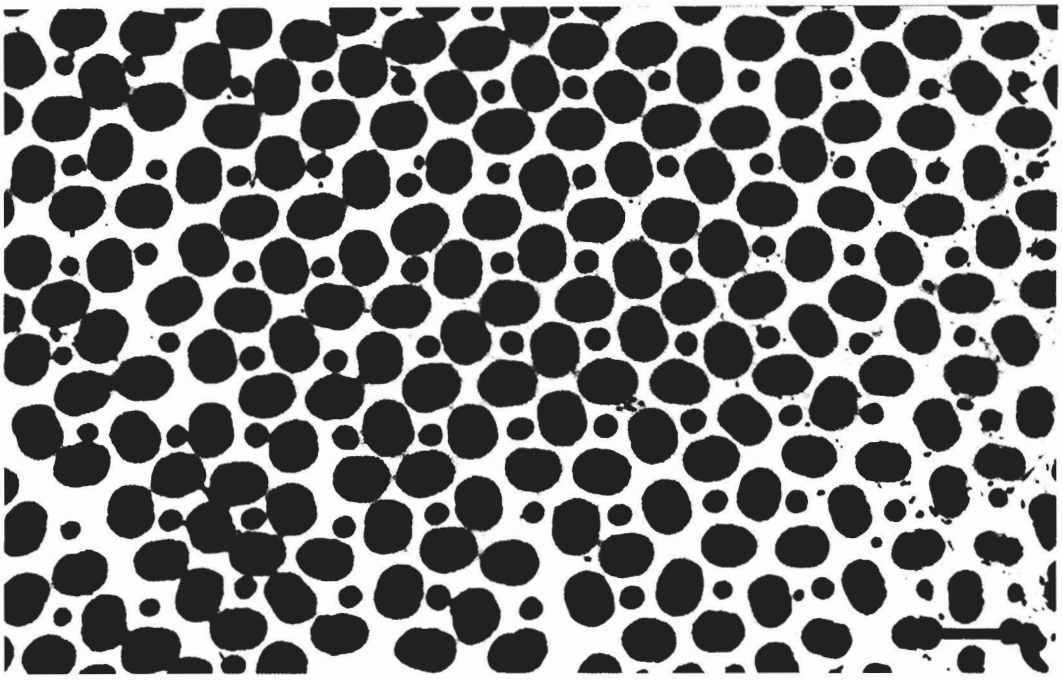


Fig. 2. Mosaic pattern of cones in 1-μm tangential section through the cone ellipsoid from light-adapted retina. Note the square pattern of double cones with a single cone in the centre. Bar: 15 μm.

two distinct zones could be distinguished: the outer zone contained the rod spherules and cone pedicles; the inner zone was composed of the processes of the horizontal and bipolar cells. Rod synaptic terminals, named spherules, were round or oval and they lay external to the cone endings. In cross section they measured about 2 μm and contained only a single deep invagination with a single synaptic ribbon of approximately 0.8 μm in length into which the dendrites of bipolar and horizontal cells were inserted (Fig. 6a). Cone terminals, named pedicles, had a pyramidal shape in vertical section, with a base of about 8 μm (Fig. 6b). This base showed invaginations with 2 to 5 synaptic ribbons, which were approximately the same length (0.5 μm in length) in light-adapted retinas as ones which had been dark-adapted for 1 h. Usually, the synaptic ribbons were surrounded by two processes, probably of horizontal cells and a bipolar process as the central element. This is called a "triad" (Boycott and Dowling, 1969).

Rows of pedicles occurred in the same plane, whereas the spherules were located in-between the pedicles. Both spherules and pedicles contained mitochondria and a large number of presynaptic vesicles. These vesicles were scattered throughout the synaptic terminal but they were more dense close to the presynaptic membrane. In the light-adapted retinas, the terminal dendrites of horizontal cells formed finger-like protrusions named spinules (Wagner, 1980) invaginanting into the central cavity of the cone pedicle (10±0.4 spinules per pedicle) (Fig. 7b), whereas in dark-adapted retinas, cone pedicles showed an almost total lack of them (0.3±0.05 spinules per pedicle) (Fig. 7a). The spinules were typically 0.5 μm in length and about 0.1 μm in width and they were characterized by

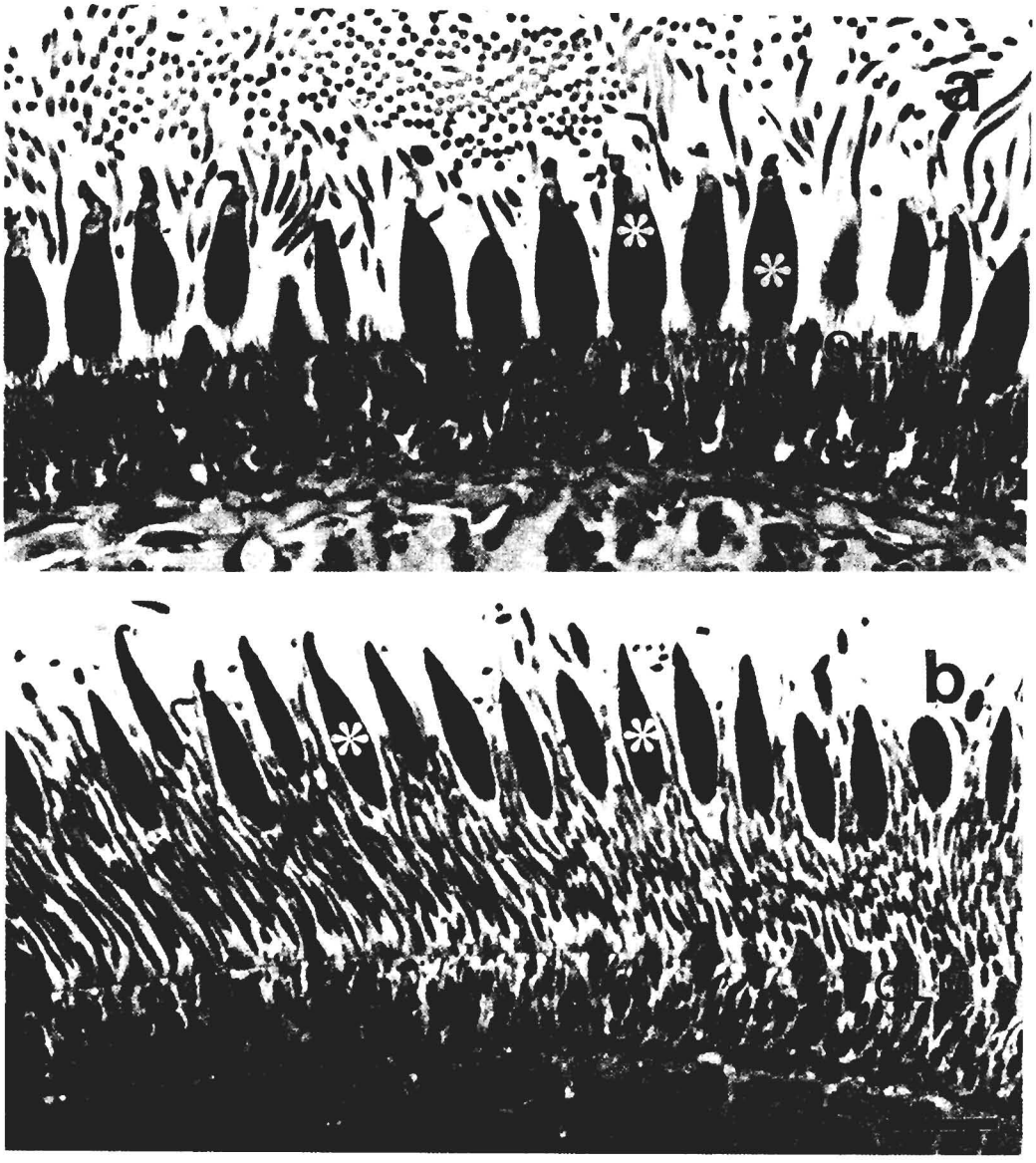


Fig. 3. Light micrographs of 1-μm semithin section of a light-adapted (**a**) and a dark-adapted (**b**) retina exposed for 60 min. Cone ellipsoids (*) are close to the OLM in the light-adapted retina and lie more scleral to the OLM in the dark-adapted retina. Bar: 30 μm.

prominent densities beneath the membrane (Fig. 7b).

The INL, of about 38 μm in thickness, consisted of horizontal, bipolar, amacrine, and Müller cells. The horizontal cells, of about 7 μm in diameter, were located in the outermost layer near to the OPL. They were arranged in two rows; probably the most distal corresponded to cone horizontal cells and the most vitreal were the rod horizontal cells. In both types, the nucleus presented a cuboidal morphology with a fine granular chromatin and a prominent nucleolus. Their cytoplasm showed numerous mitochondria, free ribosomes and glycogen particles. In addition, the cytoplasm presented some profiles of smooth endoplasmic reticulum. However, the most characteristic feature was the presence of cytoplasmic inclusions called nematosomes in the external horizontal cells (De Juan et al., 1991) (Fig. 8a). These inclusions, spherical or ovoid in shape, were composed of a filamentous material embedded in a matrix of low electron density (Fig. 8b,c). They lacked a limiting membrane and they were often situated near the mitochondria or the cell membrane. The nematosomes were larger and more numerous in dark-adapted (0.419±0.015) (Fig. 8c) than light-adapted retinae (0.257±0.012) (Fig. 8b) and the inner horizontal cells lacked nematosomes.

The bipolar cells (of about 4-6 μm) presented a rounded nucleus with granular chromatin. The perikarya formed a narrow rim around the nucleus although there were some bipolar cells with a large pyriform cytoplasm (Fig. 9). Although the existence of various cell subtypes has been reported (Dowling, 1987), we could not distinguish them without histological markers. They contained numerous mitochondria, free ribosomes, granular and agranular endoplasmic reticulum and small Golgi fields. Their dendrites contained neurofilaments, microtubules and cisternae of smooth endoplasmic reticulum. The axon terminals were characterized by many clear vesicles with a homogenous distribution, and by the presence of various synaptic ribbons, shorter than those observed in the photoreceptor synaptic terminals.

The amacrine were situated in the inner border of the INL. At light microscopy level, the amacrine cells were observed as rounded cells with an abundant cytoplasm, larger than those of the bipolar cells, and a lightly stained nucleus. The perikaryon contained cytoplasmic organelles typical for neurons.

The most important glial cells of the retina: the Müller cells, were located from the intermediate portion of the INL to the inner border of the INL. They were characterized by a big perikarya of irregular morphology

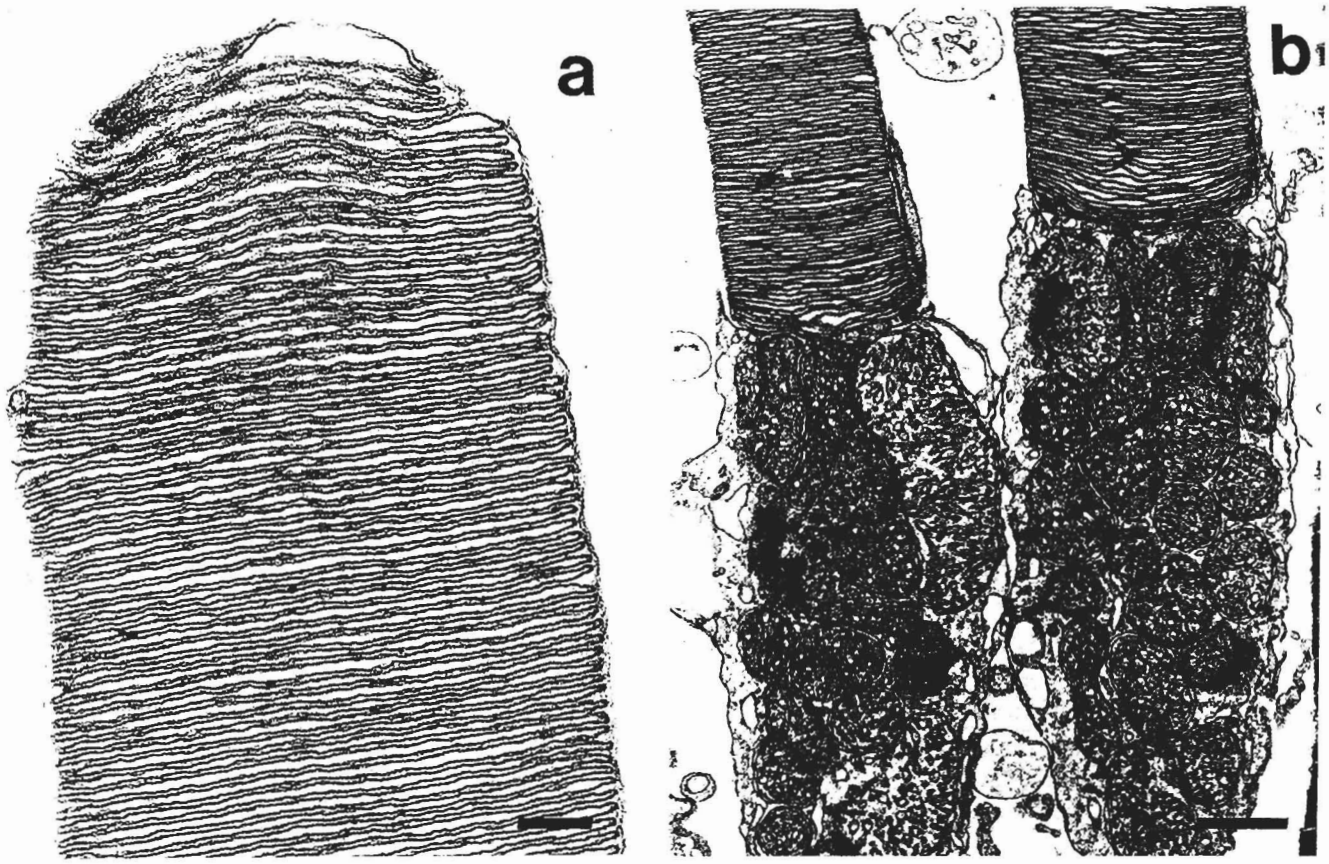
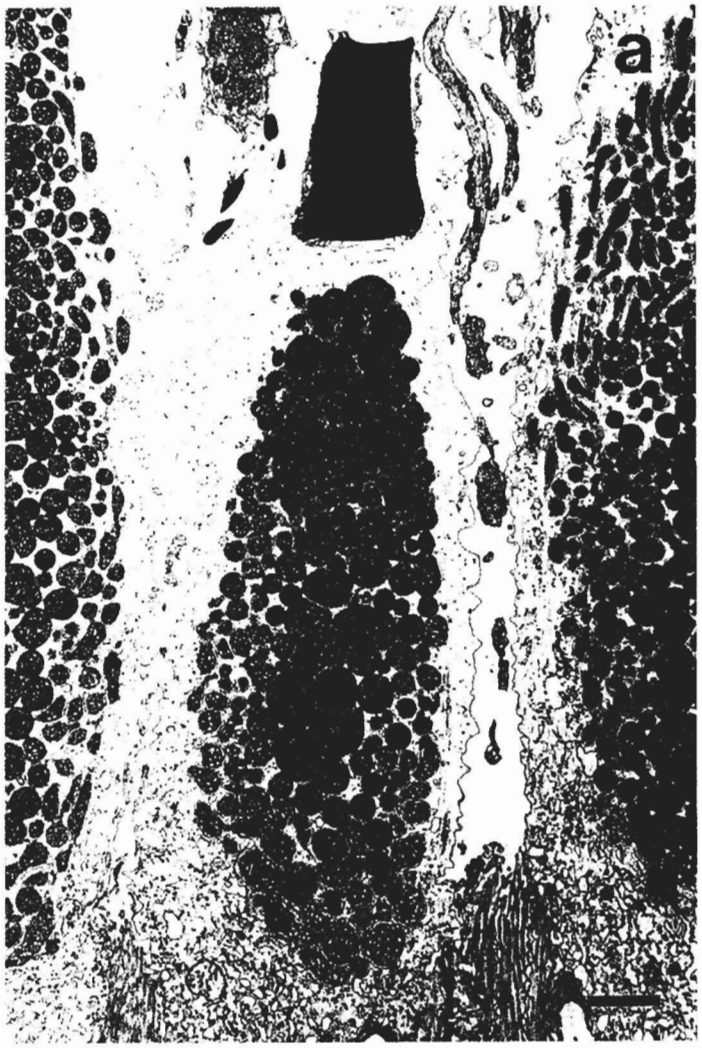
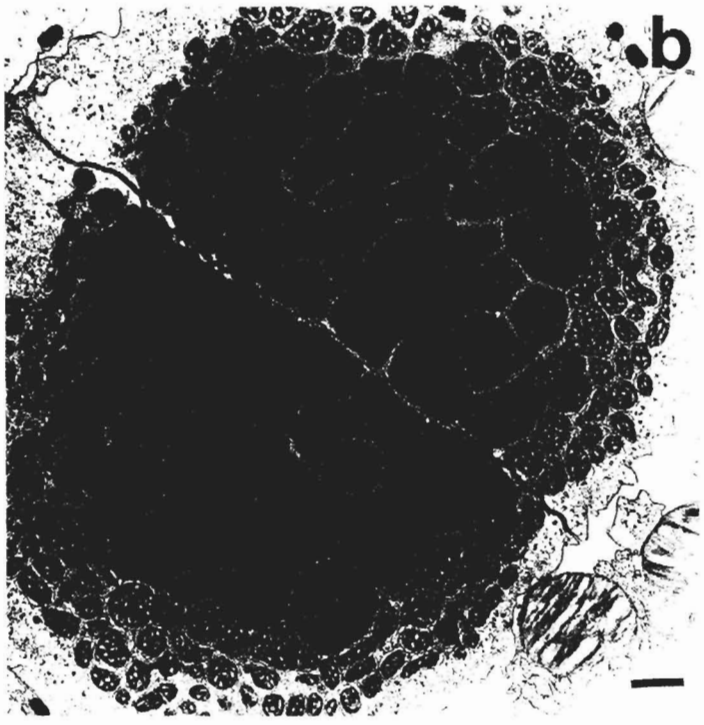


Fig. 4. Electron- micrographs of rod photoreceptors in transverse sections **a.** Outer segment showing stacks of discs surrounded by a membrane. Bar: 0.2 μm. **b.** Ellipsoid of a rod showing mitochondria with electron dense granules. Note the incisures in the outer segments (arrowheads). Bar: 1 μm.





with an angular nucleus which had a dense chromatin (Fig. 10). Their stem processes radially crossed all the retina forming the internal and external limiting membranes. Their fine processes enclosed most of the neurons. In the outer plexiform layer various layers of Müller cell microvilli surrounded the photoreceptor terminals.

The IPL measured 45 μm and consisted of an intricate network of processes of the cells of the inner nuclear (bipolar cells, amacrine and Müller cells) and the ganglion cell layers. Occasionally, some nuclei were observed which probably corresponded to amacrine or displaced ganglion cells. It was possible to observe some myelinated axons too.

The GCL contained the ganglion cells forming a single row. These cells were voluminous, with a round or oval nucleus which possessed a disperse chromatin and a prominent nucleolus (Fig. 11). There were also smaller cells that corresponded to subtypes which could not be distinguished without histological markers. Their cytoplasm showed organelles typical of a neuron: mitochondria, Golgi apparatus, and Nissl substance, etc. Their axons, unmyelinated, ran internally and parallel to the inner surface of the retina and they formed the optic nerve fiber layer. These fibers were surrounded by Müller cell processes, which divided this layer into portions. The optic nerve fiber layer was thickest around the optic disc (around 30 μm) and it thinned peripherally.

Discusion

The overall thickness of the *Micropterus salmoides* retina (250 μm) was in the common range of the majority of teleosts (between 200 to 300 μm). The relative proportion between the thickness of the photoreceptor cell layer compared to the neural retina (a 1:1 ratio) was the reported relation in species with good vision (Wagner, 1990). Among the cyprinid species which show an extensive system of vitreal blood vessels overlying the inner limiting membrane (Hanyu, 1962; Kohbara et al., 1987; Collin, 1989; Collin et al., 1996a,b), *Micropterus salmoides* lacked the vascular system. Therefore, in this retina the oxygen and nutritive substances are supplied by the choroidal blood system.

The GCL consisted of a single row of voluminous cells. This is a common feature of many vertebrate retinas. Their axons, which formed the optic nerve fiber layer, were grouped in fascicles dividing this layer into sections. This fasciculation, produced by the processes of Müller cells, has been described in many vertebrates: fish (Collin, 1988; Collin and Collin, 1993;

Fig. 5. Electron-micrographs of cone photoreceptors in transverse sections. **a.** Ellipsoid of a single cone showing mitochondria with an electrondense matrix which lacks electrondense granules. Bar: 2 μm. **b.** Tangential section showing each component of the cone doublet lies in close contact. Bar: 1 μm.

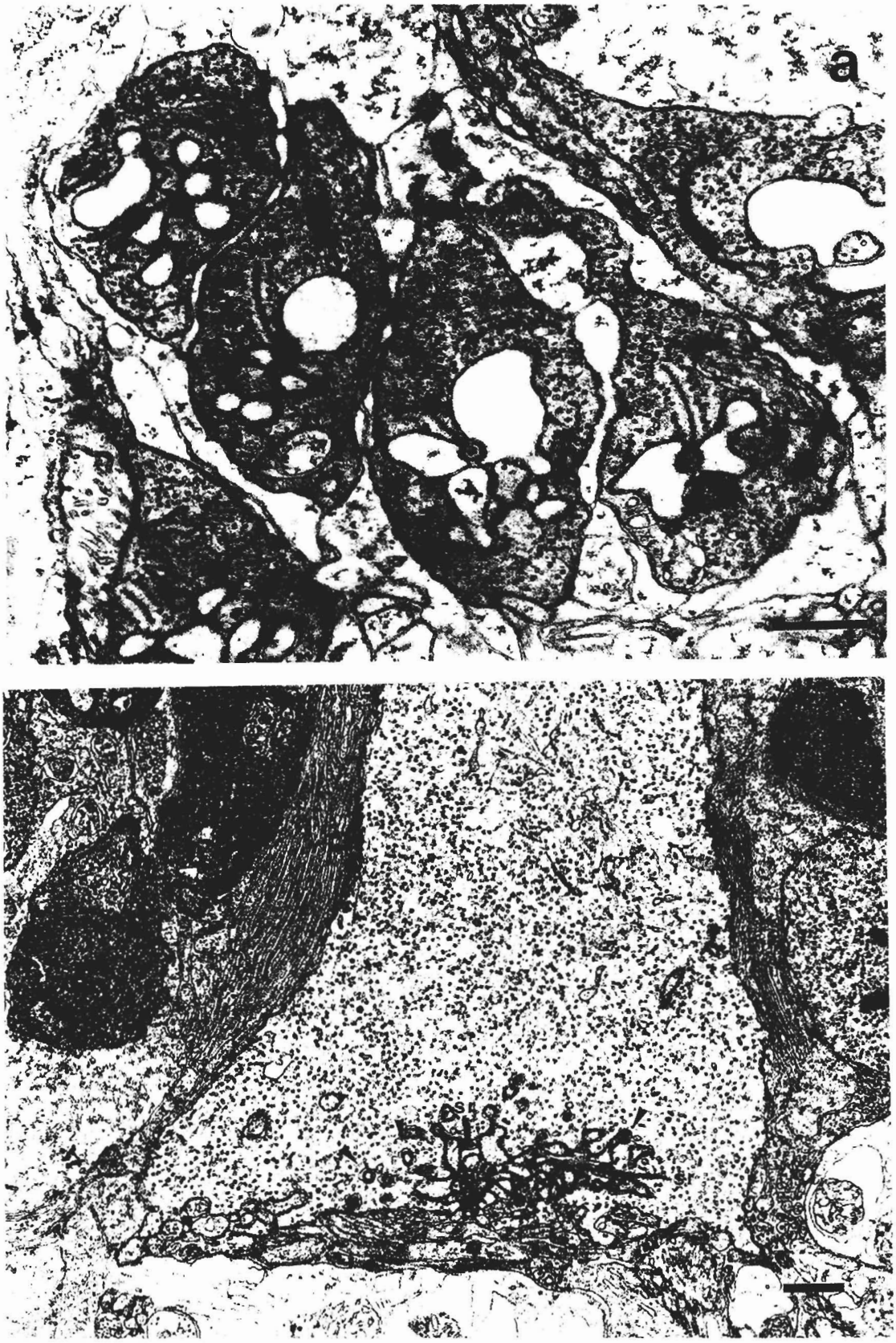


Fig. 6. Electron-micrographs from transverse sections of the retina showing the ultrastructure of the photoreceptor terminals. **a.** Rod spherules with a single synaptic ribbon (sr) in a light-adapted retina. **b.** Cone pedicle with two synaptic ribbons and several spinules (arrowheads) of a light-adapted retina. Bar: 1 μm.

Collin et al., 1996a), amphibians (Graydon and Giorgi, 1984) and mammals (Stone and Johnstone, 1981). The function of this fasciculation is unknown, but as has been proposed by Collin et al. (1996a) it is probable that it provides adequate retinal nutrition.

The IPL and INL morphology is difficult to interpret functionally and they present many differences between species (Wagner, 1990). In the *Micropterus salmoides* retina, these layers were similar in width which reflected a high degree of integration of visual information in the retina. Although in cyprinids and other members of the Centrarchidae, four types of horizontal cells have been described, in *Micropterus salmoides* we have observed just 2 rows. The most vitreal horizontal cells are probably the rod horizontal cells and the most distal cells are the cone horizontal cells. However, it is not possible to determine this without the use of specific staining.

Since the morphology of the outer retina shows many features determined by ecological and ethological factors, we centre our discussion in this area.

As in most teleosts, cones and rods were present in the *Micropterus salmoides* retina and it was possible to distinguish two different types of cones: single cones and twin cones. It has been reported that twin cones are more common than unequal double cones (Wagner, 1978). Double cones are coupled and it has been speculated that they may function as a single cone (Walls, 1942). They have a greater area available for the absorption of light as an adaptation to vision at low light intensities (Wagner, 1990). This explains the existence of double cones in the *Micropterus salmoides* retina because this fish is crepuscular and inhabits calm waters with higher levels of suspended particles which impede light penetration. Triple and quadruple cones have not been observed.

The ratio of rods: cones (8:1) was similar to other species of teleosts such as members of the Cyprinidae family (5:1 in *Semotilus atromaculatus*, 7:1 in *Exoglossum maxillingua*) (Collin et al., 1996a,b). The different cone types were arranged in a square mosaic, which is a striking feature of many teleost retinae (Bowmaker, 1990). As in the majority of retinas which present mosaics (Wagner, 1978), in *Micropterus salmoides*, the principal elements of mosaics were the cones; rods did not conform to the regular pattern but they filled the spaces between the cones. It has been suggested that a regular mosaic is an efficient packing method of increasing the number of photoreceptors in the retina and it is associated with high acuity vision (Fernald, 1982). On the other hand, it has been suggested that regular cone mosaics are present in fish with superior visual capabilities and that square mosaics appear to be common in predatory fishes (Wagner, 1990).

All types of photoreceptors in *Micropterus salmoides* retina underwent dramatic MRM in response to changes in ambient light. The cones contracted in the light and elongated in the dark, whereas rods underwent the opposite movements. Thus, the photoreceptors arrange their outer segments for optimal function in

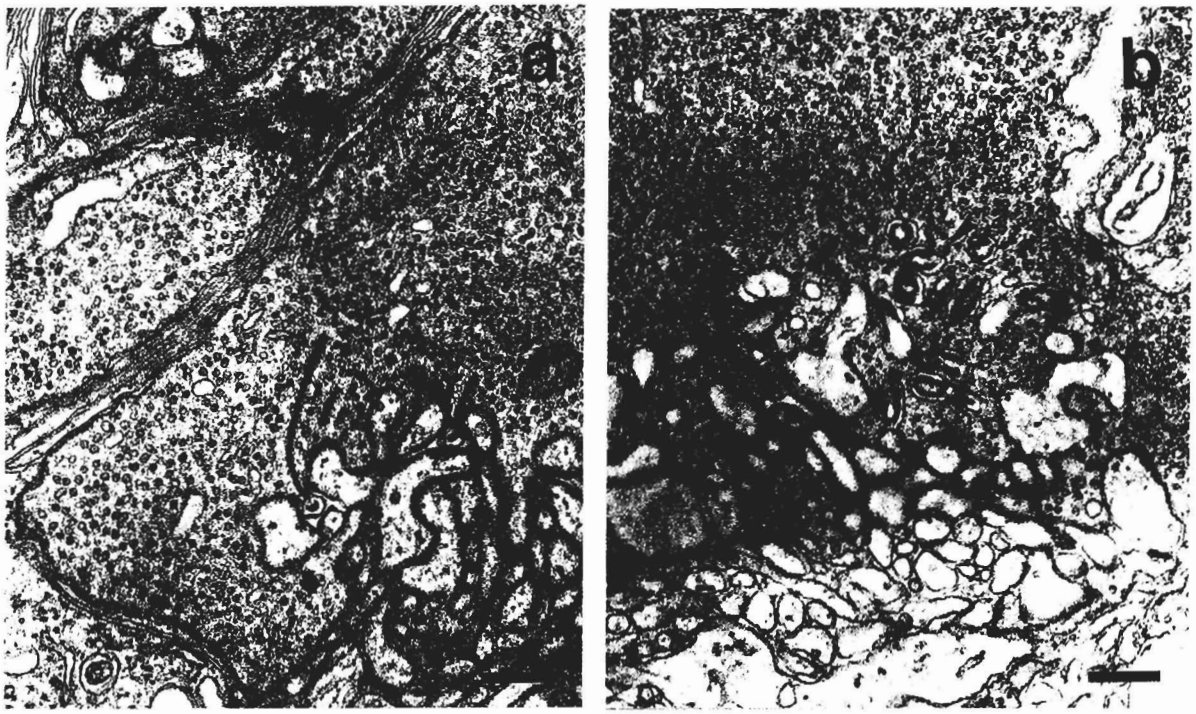


Fig. 7. Electron-micrographs of pedicles from vertical sections of light-adapted and dark-adapted retina. **a.** Dark-adapted retina without spinules. **b.** Light-adapted retina showing many spinules (arrowheads). Bar: 0.5 μm.

bright and dim light. In teleost fish a great species variation in MRM is observed with respect to affected cells; moreover, the extent of the migrations differs. In this sense, cones of *Micropterus salmoides* underwent elongation in the dark of approximately 46 μm whereas in *Lepomis cyanellus* (Centrarchidae) it is 86 μm (Dearry and Burnside, 1986), in *Roccus americana* (Centrarchidae) it is about 60 μm (our data, not reported). In cyprinids the variations are more prominent. In *Exoglossum maxillingua*, all photoreceptors display retinomotor responses (Collin et al. 1996b), in *Semotilus atromaculatus* (Collin et al. 1996a), *Leuciscus rutilus* (Engström and Rosstorp, 1963) and *Ericymba buccata* (Moore et al., 1950), the short single cones do not display any retinomotor responses. Other members of the Cyprinidae such as *Tinca tinca* do not exhibit cone retinomotor response (Douglas and Wagner, 1982). These differences may be explained in relation to

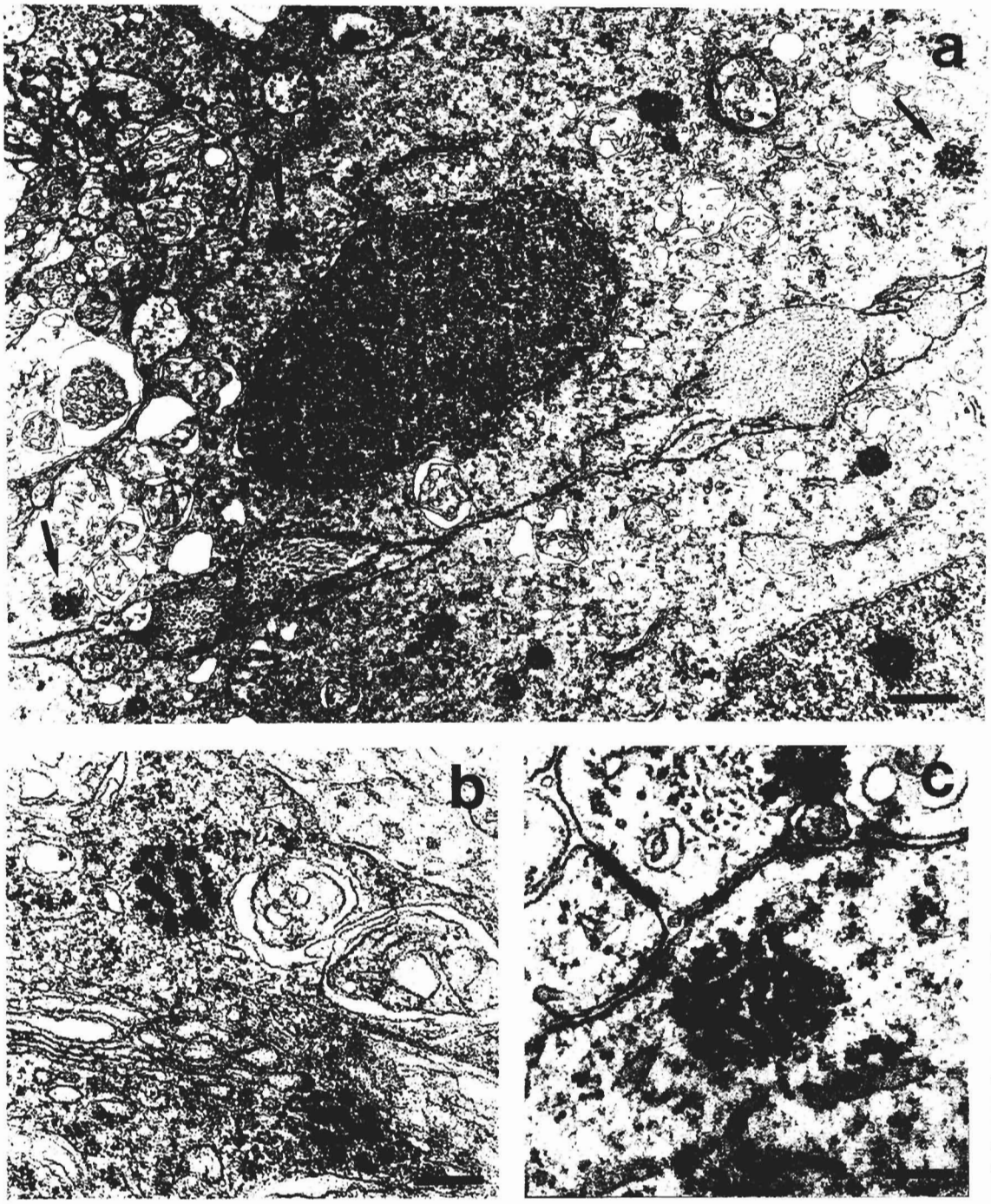


Fig. 8. a. Fine structure of a distal horizontal cell showing nematosomes (arrows) Bar: 1 μm. **b and c.** Electron micrographs of nematosomes. Note the difference in size between the nematosomes observed in light- (b) and dark-adaptation (c). Bar: 0.2 μm.

ecological adaptation (Ali, 1975; Ali and Wagner, 1975; Douglas and Wagner, 1982). *Tinca tinca* does not exhibit cone MRM because it is a nocturnal fish. However, *Lepomys cyanellus*, *Roccus americana* and *Micropterus salmoides* with a crepuscular activity pattern present marked changes which enable good adaptation to photopic and scotopic states. The fact that in many cyprinids the single cones do not present MRM, may provide other advantages for their vision.

Rod and cone outer segments were formed by a stack of membranous discs where the photopigments were located. In rods, the disks remained separate from the cell membrane. In contrast, the disks of cones maintained their attachment to the membrane (Cohen, 1972). As in other species studied, the rod outer segments presented several incisures (Braekevelt, 1983, 1994; Braekevelt et al., 1996). These structures have been interpreted as a means of increasing the surface area of the light-sensitive outer segments (Braekevelt, 1994) or a mechanism to aid in the diffusion of substances to and from the disc membranes (Collin et al., 1996a,b). Although they may be found in cones (Braekevelt, 1983, 1992) we could not observe their existence in *Micropterus salmoides* retina.

Another characteristic feature present in *Micropterus salmoides* retinas, which also occurs in many teleosts, was the presence of a bulky ellipsoid replete with mitochondria. It was more prominent in cones than rods. Their existence has been interpreted as an adaptation of photoreceptors to optimize sensitivity by amplifying the signal (Wagner, 1990), so that the mitochondria are the organelles responsible for the supply of metabolic energy. We have observed some differences between the cone and rod mitochondria with regard to size, the appearance of the matrix and the presence of glycogen granules. However, we have no explanation for this.

The arrangement of the cone nuclei close to the outer limiting membrane and rod nuclei forming rows in the outer nuclear layer is a constant in all duplex retinas and it reflects the order of appearance and differentiation

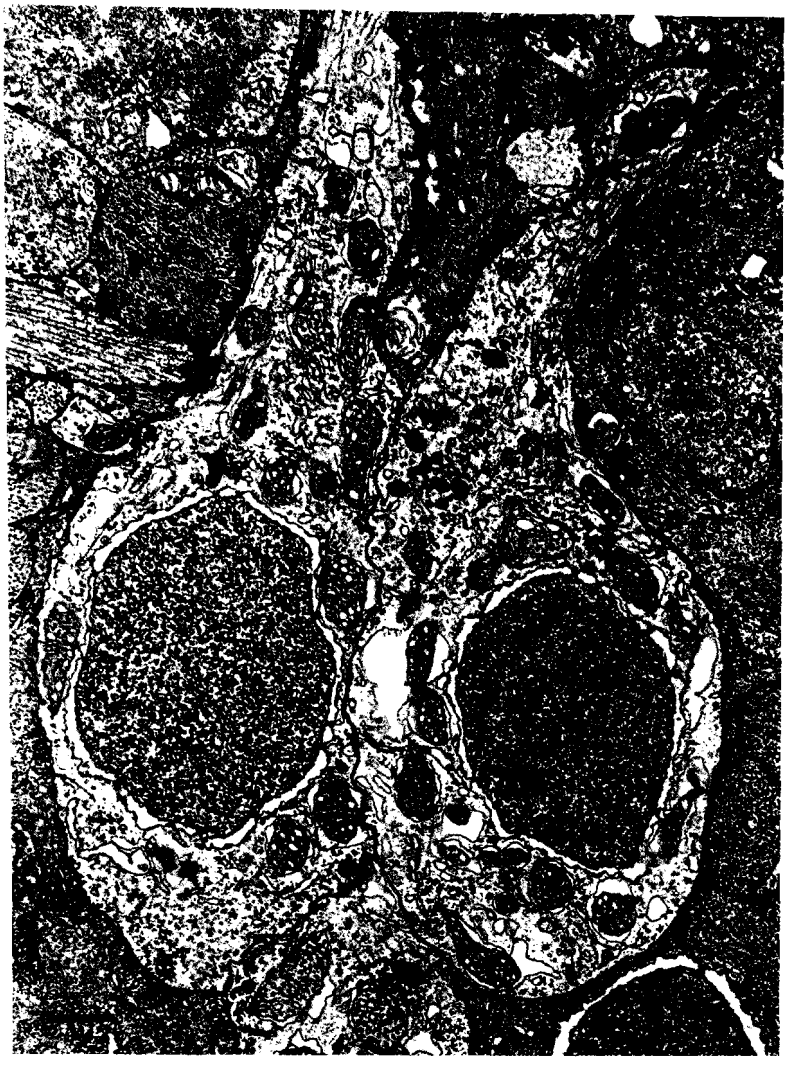


Fig. 9. Fine structure of the bipolar cells with a large pyriform cytoplasm. They have numerous mitochondria, free ribosomes, granular and agranular endoplasmic, lysosomes and cytoskeleton elements in their dendrites. Bar: 1 μm.

of photoreceptors (Walls, 1942). We have observed some differences in the nuclear chromatin pattern of cones and rods in *Micropterus salmoides* retina. In cones, the chromatin was vesicular whereas in rods it was more condensed.

In the OPL, the arrangement of processes of

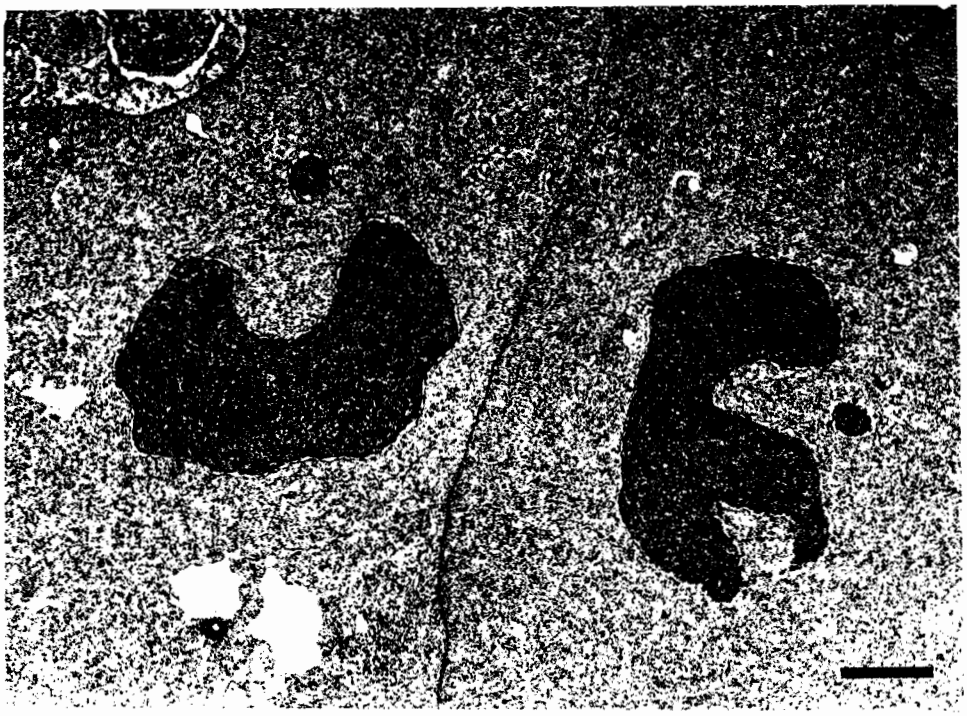


Fig. 10. Ultrastructure of the Müller cells. Note the angular nucleus which has a dense chromatin. Bar: 2 μm.

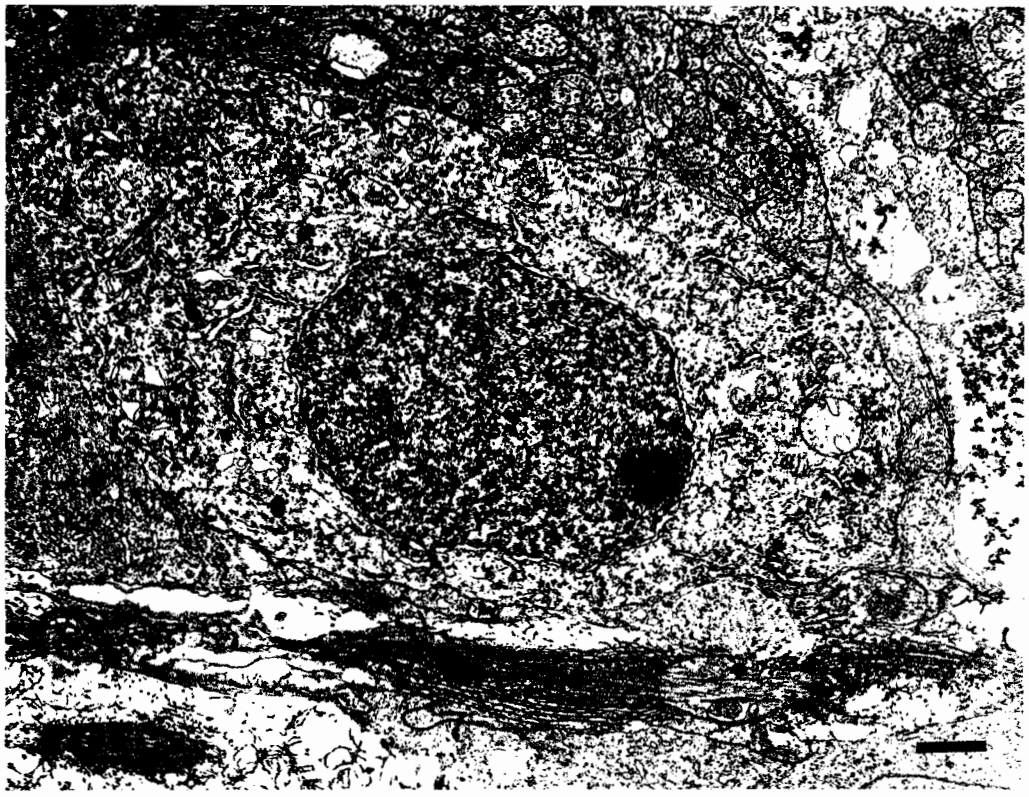


Fig. 11. Fine structure of the ganglion cells with a round nucleus, a disperse chromatin and a prominent nucleolus. Bar: 1 μm.

horizontal cells and bipolar cells forming a "triad" in the photoreceptor terminals is a common feature of fish, amphibians, birds and mammals (Boycott and Dowling, 1969). Stell and Lightfoot (1975) observed that in goldfish, the central process may be of a horizontal cell. In this report we have no stains of horizontal and bipolar cells and we cannot affirm what the central process is. The number of synaptic ribbons in the pedicles in *Micropterus salmoides* retina varies between 2 and 5. In this sense, it has been reported that the number of synaptic ribbons of double cones is higher than in single cones (Wagner, 1978). An interesting feature in some teleosts is that synaptic ribbons disappear from cone pedicles in dark-adapted retinas (Wagner 1973; Wagner and Ali, 1977). This effect is prominent in the cichlids but in salmonids and cyprinids it is less prominent and more difficult to register (Raynauld and Wagner, 1978). In *Micropterus salmoides*, the number of synaptic ribbons did not change after 1 h regardless of light conditions

A striking feature in *Micropterus salmoides* retinas, as in many teleosts, was the presence of protrusions of horizontal cells, termed spinules. They are dynamic structures which form during light adaptation and disappear during dark adaptation (Wagner, 1980; Wagner and Djamgoz, 1993) and are influenced by the central nervous system (De Juan et al., 1996; De Juan and García, 1998). Although the significance of spinules is unknown, the combination of intracellular recording and quantitative ultrastructural analysis has suggested that spinules may be the sites of feedback transmission from cone horizontal cells (HCs) to pedicles of cones (Raynauld et al., 1979; Djamgoz et al., 1988; Kirsch et al., 1990; Wagner and Djamgoz, 1993). Various pharmacological experiments suggest that spinule formation involves the neuromodulator dopamine (Weiler et al., 1988; Kholer and Weiler , 1990) and their degradation is controlled by glutamate and melatonin (Weiler et al., 1988; Weiler and Schultz, 1993; Behrens et al., 1998).

Nematosomes, located in the external HCs, might contribute to the formation of the spinules as previously (De Juan et al., 1991, 1996; De Juan and García, 1998). These structures were described in retinas for the first time in white perch, *Roccus americana* (De Juan et al., 1991). Nematosomes are larger and more numerous in dark-adapted retinas than in light-adapted ones. We found that there existed an inverse relationship between number and size of nematosomes, and spinule number, suggesting that electron-dense material observed in spinules may originate in the nematosomes (De Juan et al., 1991, 1996; De Juan and García, 1998).

In conclusion, *Micropterus salmoides* possesses well-developed vision as is demonstrated by various features of the morphology of its retina: 1) single and double cones with prominent ellipsoids arranged in regular mosaics, 2) exhibition of retinomotor movements in response to changes in light, 3) a marked synaptic plasticity in the outer plexiform layer in response to changes in light as is the presence of spinules, nematosomes, and synaptic ribbons, and 4) a thick inner plexiform layer which implies a high degree of complexity of the neural interactions.

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