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Development of the retinal tapetum lucidum of the walleye *(Stizostedion vitreum vitreum)*

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Summary. The development of the retinal tapetum lucidum within the cells of the retinal pigment epithelium (RPE) has been investigated by both light and electron microscopy in the walleye *(Stizostedion vitreum vitreum)* in specimens ranging in total length from 25-140 mm. In addition changes in the arrangement of the photoreceptors (both rods and cones) in both light and dark-adaptation have also been studied. At 25 mm no evidence of a tapetum is present. At about 30 mm it makes its initial appearance as granular bodies formed within the apical smooth endoplasmic reticulum (SER) cisternae of the RPE cells in the superior temporal fundus. The developing tapetum then spreads peripherally and continues to thicken in existing areas. By 90 mm it is well established throughout the fundus but always appears better developed in the superior fundus. By 125-140 mm it is essentially adult in appearance. At 60-70 mm the rods and cones begin to form bundles producing macroreceptors of 20-30 photoreceptors. In dark-adaptation the rod bundles are retracted and have one or more cone cells centrally located in each bundle, with the bundles separated from one another by melanosomes. Initially when no tapetal material is present, post-larval walleye are positively phototactic and feed on zooplankton. In the adult condition when a tapetum lucidum and large macroreceptors are present, the walleye is negatively phototactic and feeds almost exclusively on larger organisms such as other fish.

Key words: Tapetum lucidum, RPE, Development, Walleye

Introduction

The tapetum lucidum of the vertebrate eye is a reflective layer situated behind (scleral to) the photoreceptors of the retina which by reflecting light back on to the photoreceptors, provides these light-sensitive cells with a second opportunity for stimulation, thereby enhancing retinal sensitivity (Duke-Elder, 1958; Walls, 1967; Rodieck, 1973).

The tapetum lucidum is often located in the choroid immediately adjacent to the retina. In this location it consists of either a large collection of specialized cells containing a wide variety of reflective materials and referred to as a tapetum cellulosum or a large array of closely arranged extracellular collagen which is termed a tapetum fibrosum (Pedler, 1963; Hebel, 1969; Braekevelt, 1981, 1983; Lesiuk and Braekevelt, 1983).

The reflective material of a tapetum lucidum may also be located within the cells of the retinal epithelium in which case it is referred to as a retinal tapetum. This type of tapetum is most common amongst teleosts although it has been reported in other taxa as well (Pirie, 1966; Arnott et al., 1970; Braekevelt, 1976, 1977, 1984). The adult appearance of the retinal tapetum has been described in several species of fish including the walleye (Moore, 1944; Nicol et al., 1973; Zyznar and Ali, 1975; Ali and Anctil, 1976; Braekevelt, 1980a, 1980b, 1982b) but little is known concerning its development.

This study employs light and electron microscopy to describe the initial appearance and subsequent development of the retinal tapetum in the walleye *((Stizostedion vitreum vitreum)* and correlates these findings with changes in photoreceptor arrangement and with the size of the specimens studied.

Materials and methods

For this study the eyes of walleyes (*Stizostedion vitreum vitreum)* ranging in total length from 25 mm to 140 mm were examined by light and electron microscopy. At all stages a minimum of two light-adapted eyes were studied. In addition several specimens were dark-adapted to observe retinomotor changes.

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The fish were decapitated and the eyeballs enucleated. In the case of small specimens (25-40 mm) the eye was fixed intact while in larger specimens (50-140 mm) the globe was opened at the equator prior to fixation. The eyes were fixed for 5 hrs in 5% glutaraldehyde buffered to pH 7.3 with 0.1M Sorensen's phosphate buffer. The posterior half of the eyeball was then removed, washed in 5% sucrose in 0.1 M Sorensen's buffer (pH 7.3) and further divided into pieces less than 1 mm^2. In specimens over about 30 mm in length the retina was separated into superior and inferior portions and processed separately. The material was then post fixed for 2 hrs in 1% osmium tetroxide in the same phosphate buffer, dehydrated in graded ethanols to propylene oxide and embedded in Araldite.

Pieces of plastic-embedded tissue were reorientated to desired angles by means of a wax mount. Thick sections (0.5 μm) were cut, stained with toluidine blue and examined by light microscopy. Thin sections (60-70 nm) of selected areas were then cut on an LKB ultratome and collected on copper grids. The grids were stained in aqueous uranyl acetate and lead citrate and examined and photographed in a Philips EM 201 electron microscope.

Results

The retinal pigment epithelium (RPE) of the walleye consists of a single layer of cells which are initially roughly cuboidal in shape but which elongate to become columnar as the fish becomes larger. Basally the cells of the RPE abut on Bruch's membrane (complexus basalis) and show a few basal infoldings (Fig. 1). Apically the epithelial cells display numerous villous processes which enclose the photoreceptor outer segments (Figs. 1, 2, 7, 8). Wandering phagocytes which appear to be a fairly constant feature of the teleost retina are also noted in this species (Fig. 7).

Internally the RPE cells show plentiful smooth endoplasmic reticulum (SER), sparse rough endoplasmic reticulum (RER), numerous basally located mitochondria, several myeloid bodies and a pleomorphic vesicular nucleus (Fig. 1). Melanin pigment granules (melanosomes) occupy the tips of the apical processes and are scattered throughout the body of the RPE cells in light-adaptation (Figs. 1, 6). In dark-adaptation while the melanosomes in the body of the epithelial cells move to the basal region of the RPE cells, the melanosomes in the tips of the apical processes remain in place (Fig. 12).

In specimens 25 mm in length there is no indication of the presence of any reflective (tapetal) material in any location within the RPE cells (Figs. 1, 2). At about 30 mm of length in the superior temporal fundus, the first indication of tapetal development is seen. In the apical portion of the RPE cell body at the level of the photoreceptor outer segments, the SER begins to show small dilations which are initially filled with flocculent or granular material (Fig. 3). These granular sites become more numerous and gradually also become more electron dense. When they attain a size of approximately 0.2 μm in diameter, they usually display a square or rectangular electron-lucent center due to the loss or chipping out of the presumed crystalline center during sectioning of the material (Figs. 3-5). The granules of tapetal material while of much the same size as the melanosomes, never attain the very electron-dense appearance of melanin before the center is lost in sectioning (Figs. 3-5).

Once the beginning of the tapetum is established, the accumulation of tapetal material continues and the tapetum spreads laterally in all directions in the fundus as well as in an apical-basal fashion within the RPE cells (Fig. 4). By 40 mm the tapetum occupies a band about 20 mm wide in the superior temporal fundus (Fig. 5). The production of new tapetal material occurs both at the

Fig. 1. Electron micrograph of the retinal pigment epithelium (RPE) from a light-adapted 25 mm specimen. Bruch's membrane (B) an RPE nucleus (N) and rod outer segments (ROS) are indicated. No tapetal material is seen. × 6,600

Fig. 2. Electron micrograph of the retinal pigment epithelium (RPE) from a light-adapted 25 mm specimen. The rod (R) photoreceptors are cut in cross-section. A myeloid body (My) and melanosomes (M) are indicated. No tapetal material is present. × 9,900

Fig. 3. Electron micrograph of the RPE from the superior fundus of a 30 mm light-adapted specimen. Tapetal material (T) is beginning to form. Rod photoreceptors (R) and melanosomes (M) are also indicated. × 9,500

Fig. 4. Electron micrograph of the superior RPE from a light-adapted 35 mm specimen. Tapetal material (T) is more plentiful. Rod (R) and cone (C) photoreceptors are indicated. × 6,400

Fig. 5. Electron micrograph of the RPE from the superior fundus of a 40 mm specimen (light-adapted) to indicate a thickening of the tapetal region (T). A rod (R) is indicated. × 6,400

Fig. 6. Electron micrograph of the RPE from the inferior fundus of a light-adapted 50 mm specimen. No tapetal material is present. Melanosomes (M) are plentiful and a rod (R) is indicated. × 9,900

Fig. 7. Electron micrograph of the RPE from the superior fundus of a 50 mm specimen. The tapetal region (T) reaches almost to the rod (R) outer segments in this light-adapted specimen. A wandering phagocyte (WP) is also indicated. × 4,200

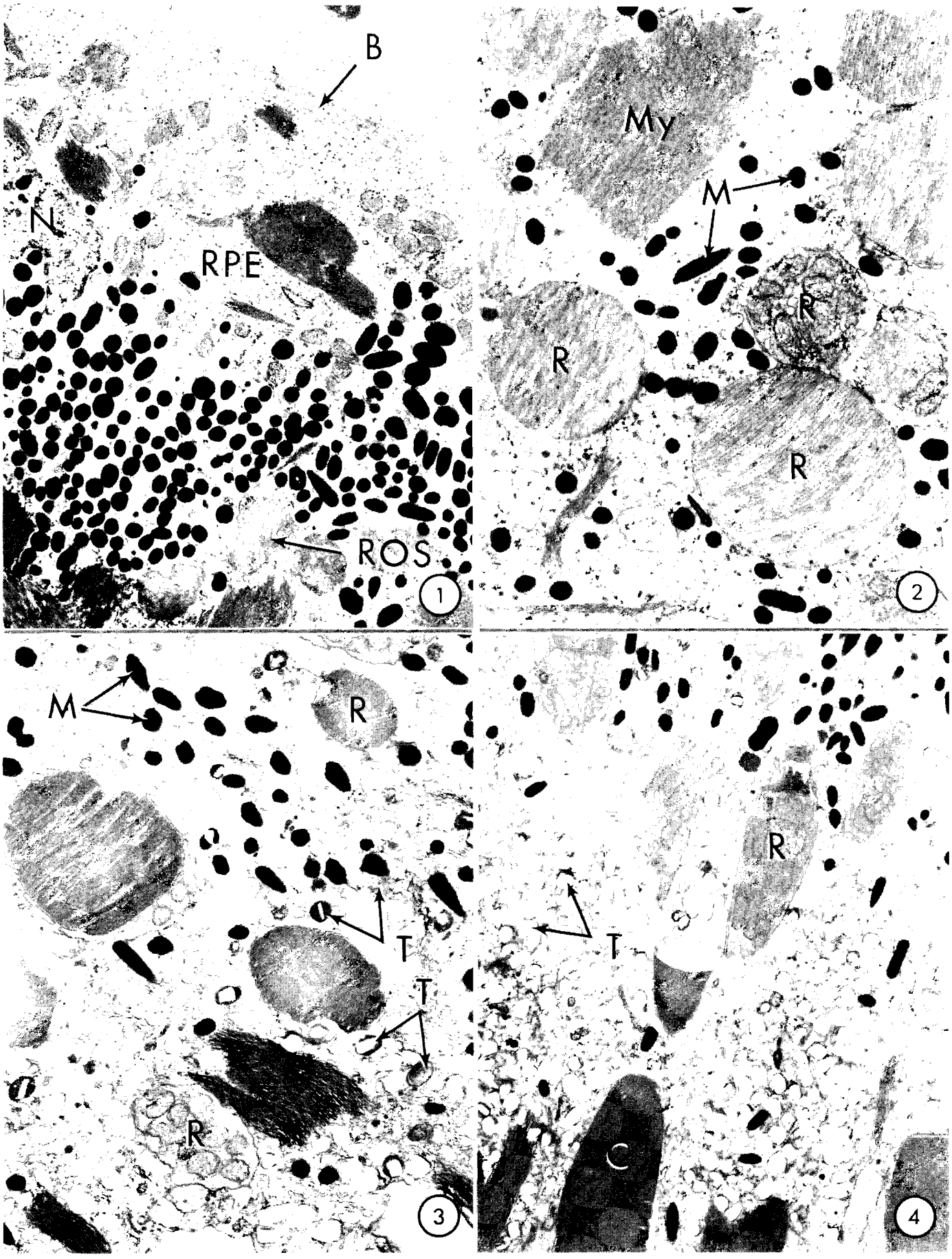
Fig. 8. Electron micrograph of the RPE from the superior fundus of a 60 mm light-adapted specimen. The rods (R) are beginning to form bundles and the tapetal material has spread around the rod outer segments. × 3,900

Fig. 9. Electron micrograph of the tapetal region in the inferior fundus of a 90 mm light-adapted specimen. Melanosomes (M) are not plentiful within the tapetum (T). Both rods (R) and cones (C) are indicated. × 2,700

Fig. 10. Electron micrograph of a bundle of rods (R) from a 125 mm light-adapted specimen taken from the superior fundus. While rod bundles are mainly isolated by tapetum (T) scattered melanosomes (M) are also present. × 7,300

Fig. 11. Electron micrograph of rod bundles (R) from a dark-adapted 140 mm specimen taken from the inferior fundus. No melanosomes are noted amongst the tapetal material (T). × 4,100

Fig. 12. Electron micrograph of a rod bundle (R), from the superior fundus of a dark-adapted 140 mm specimen. A cone (C) photoreceptor is indicated as are melanosomes (M) located in the apical process of the RPE cells and which separate the photoreceptor bundles. Tapetal material (T) is also indicated. × 9,900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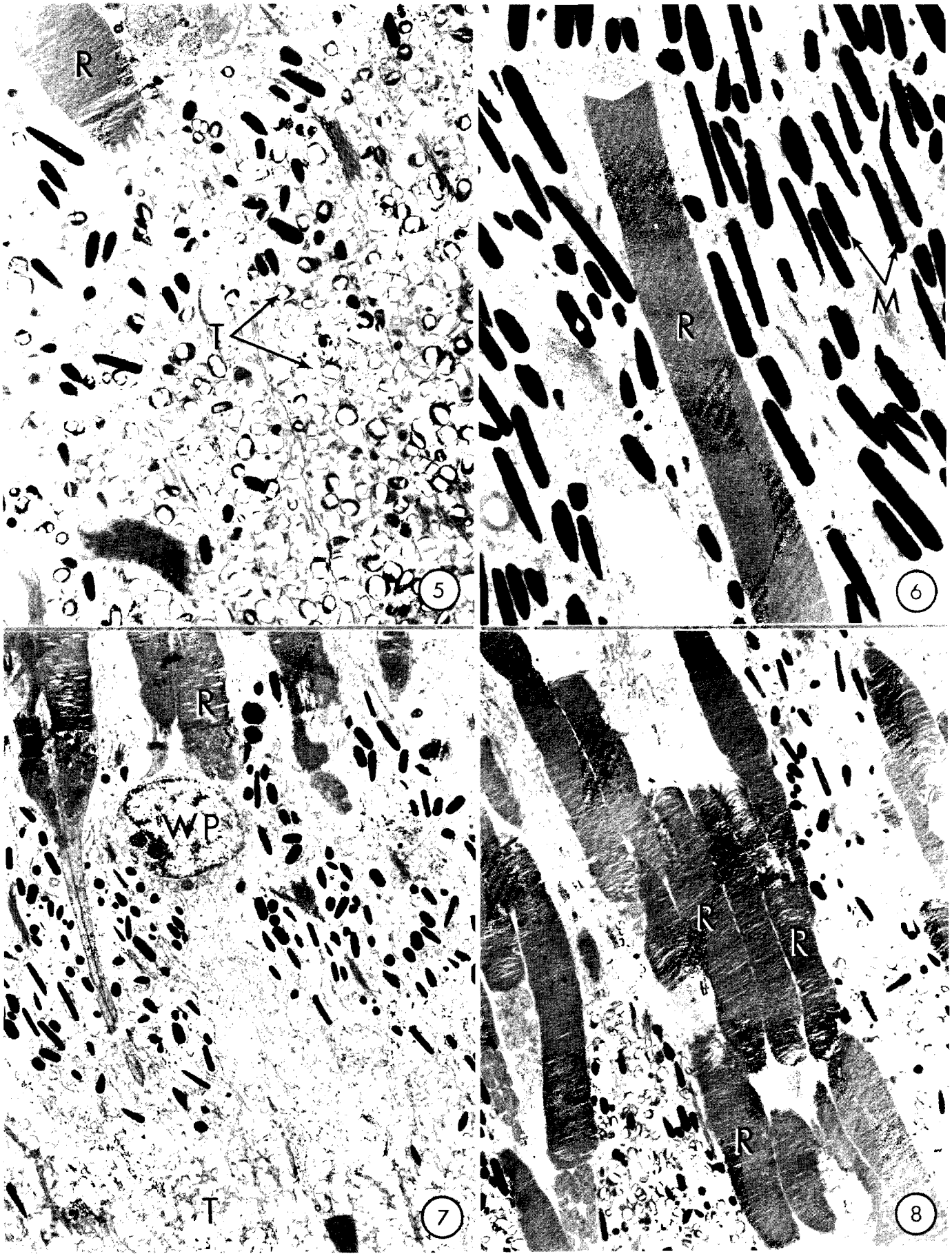
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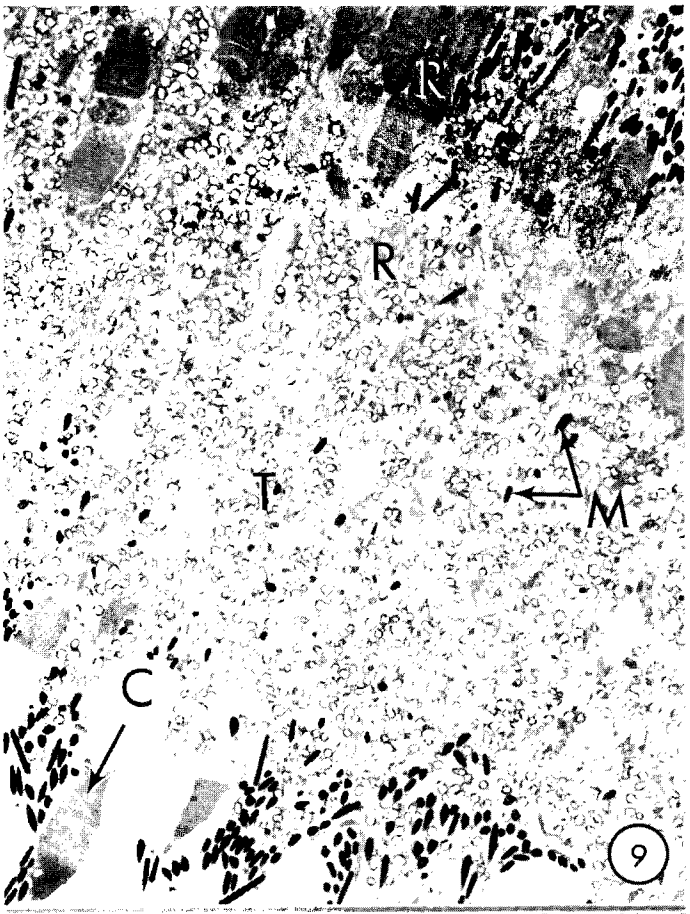

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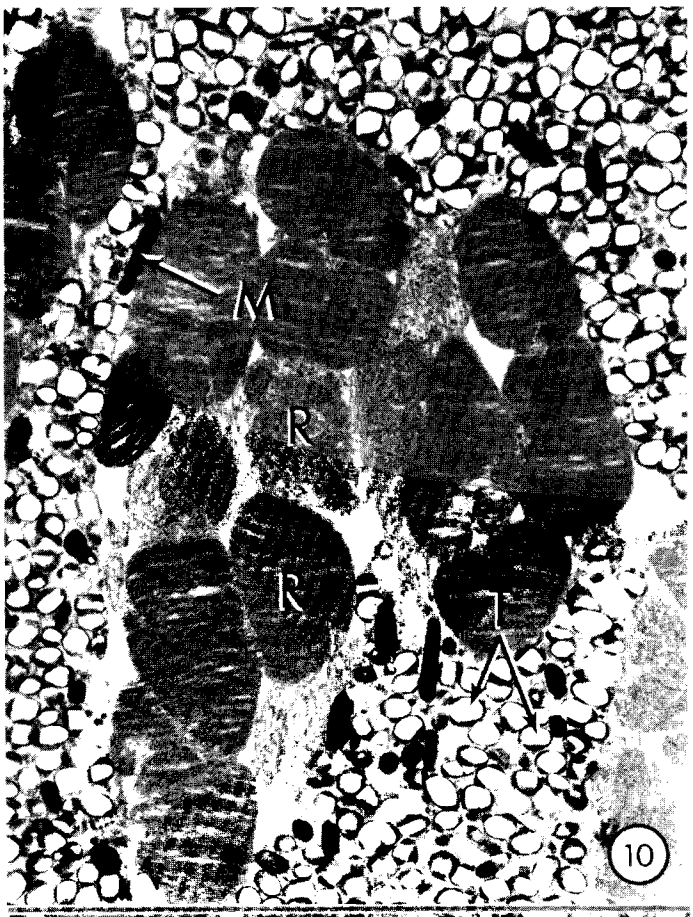

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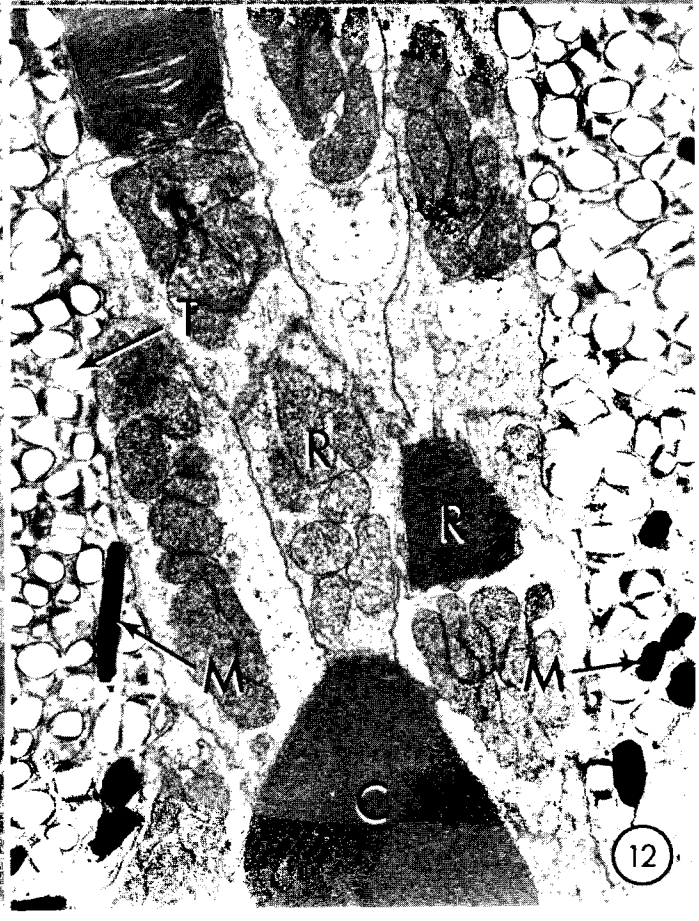

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advancing front of the tapetum as well as within the thickness of the established tapetum to give a very dense accumulation of tapetal material that soon outweighs the melanosomes in both numbers and volume (Fig. 5). As more tapetal material is formed and the tapetum widens within the RPE cells, it comes to surround the photoreceptor inner and outer segments with the apical melanin granules being displaced into a thin layer between cone photoreceptors. During this time the RPE cells gradually become taller (more columnar) to accommodate the increase of tapetal material.

By 50 mm of length, while the tapetum is well established in the superior fundus (Fig. 7) it has not yet spread to the inferior fundus which still shows only an abundance of melanosomes (Fig. 6). At about 60 mm the tapetum in the superior fundus has increased in thickness such that the inner and outer segments of the light-adapted rods are now separated by both tapetal material and melanosomes, the latter of which have been almost excluded from the main tapetal mass (Fig. 8). Also at approximately 60-70 mm the first indications of the grouping of rod photoreceptors into bundles of 20-30 cells, which will be the condition in the adult retina, are first noted (Fig. 8).

By 90 mm the tapetum has spread further peripherally and is now also well established in the inferior fundus as well (Fig. 9). While a good deal of variability is noted within specimens of similar length, at all intervals sampled, the tapetum in the superior fundus is always thicker and more prominent than in the inferior fundus, and thus we cannot confirm the observation made by Ali and Anctil (1977) that the tapetum is more highly developed in the ventral region of the walleye's retina.

By 125 to 140 mm the superior fundal region is essentially adult in appearance with a large tapetum lucidum and the rods being arranged in definite bundles of 25-30 cells with these bundles being separated from one another by tapetal material (Fig. 10). In the light-adapted state when the rod bundles are most fully extended into the RPE cells, melanosomes are noted between the rod bundles (Fig. 10) whereas in the dark-adapted state when the rod bundles retract they are completely surrounded by tapetal material with no melanosomes present in the body of the tapetum (Fig. 11).

While the rods of the walleye undergo extensive retinomotor or photomechanical movements, the cones (both single and twin) appear to move but little in response to environmental lighting. In light-adaptation when rods and cones are most completely separated, no spatial relationships are noted between the two photoreceptor types (Fig. 9). However, in dark-adaptation when the rod bundles are retracted and are in close proximity to the cones it can be appreciated that each rod bundle has in its central region one or more large cone photoreceptors (Fig. 12).

In dark-adaptation, while the vast majority of melanosomes within the RPE migrate to the basal region of these cells, those melanosomes located in the apical processes remain in place and serve to isolate the bundles of rods or «macroreceptors» from one another (Fig. 12). In the dark therefore the tapetum is devoid of melanosomes and light passing to the rod outer segments would best gain acess to the photoreceptors by passing along the macroreceptors. Also as the mass of tapetal material is very large in proportion to the melanosomes present, it is unlikely that these melanosomes can completely occlude or mask the tapetum during light-adaptation in this species.

Discussion

The basic morphology of the retinal epithelium (RPE) of the walleye (*Stizostedion vitreum vitreum*) is essentially similar to that described for other vertebrates (Nguyen-Legros, 1978; Braekevelt, 1980a, 1982a). Although the retinal epithelial cells in teleosts are usually columnar (Braekevelt, 1974, 1980d), in those species such as the walleye and goldeye (*Hiodon alosides*) with a retinal tapetum, the RPE cells become extremely tall (Zyznar and Ali, 1975; Braekevelt, 1982b). This is perhaps due to the very large accumulation of reflective material within these cells and also the necessity for these cells to accommodate the movement of the photoreceptors and internal structures during retinomotor movements.

The wandering phagocytes at the photoreceptor-retinal epithelial interface noted in the walleye have been reported in most other teleost species examined (Braekevelt, 1980c, 1985). As these phagocytes are present in apparently non-pathological retinas, they are felt to be a normal constituent of the teleost retina. Fish often have long photoreceptor outer segments and it may be that there is an accelerated rate or volume of outer segment shedding necessitating the presence of a second group of phagocytic cells in addition to the retinal epithelium itself.

A tapetum lucidum is often present in the eye of species whose habitat is ordinarily poorly illuminated. The design of a tapetum is basically quite simple, consisting of a reflecting layer located scleral to the photoreceptor cells. This reflecting layer is most usually located in the choroid immediately external to the retinal epithelium (choroidal tapetum). The retinal epithelium overlying such a tapetum is unpigmented to allow light to reach to and be reflected back from the tapetal area (Walls, 1967; Rodieck, 1973; Braekevelt, 1982a, 1983). In comparatively fewer species the tapetal material is located within the retinal epithelial cells themselves (retinal tapetum). Amongst the vertebrates reported with retinal tapeta lucida are a number of teleosts (Nicol et al., 1973; Braekevelt, 1980a,b, 1982b) the *Crocodrilians* (Laurens and Detwiler, 1921; Braekevelt, 1977), the fruit bat *Pteropus cynopterus* (Walls, 1967) the opossum *Didelphis virginiana* (Walls, 1967; Braekevelt, 1976) and the nighthawk *Chordeiles minor* (Braekevelt, 1984).

The reflecting material within a tapetum lucidum can vary widely in chemical composition from species to species. Amongst the compounds reported are guanine, cholesterol, zinc cysterne, riboflavin, pteridine and various lipids (Pirie, 1966; Arnott et al., 1970; Nicol et al., 1973). The reflective bodies in the walleye are reported to be 7, 8-dihydroxanthopterin, a reduced

pteridine (Zyznar and Ali, 1975).

In most species with crystalline reflecting material (eg guanine) in the tapetum, the crystals are very precisely arranged so as to reflect light almost straight back along the incoming path (Nicol, 1969; Locket, 1974). Such a tapetum is normally choroidally located and probably reflects light most effectively. In species such as the walleye with a retinal tapetum however the reflecting material is usually more haphazardly scattered within the RPE cells (Braekevelt, 1976, 1977, 1980a,b). Perhaps the closer proximity of the reflecting material to the photoreceptors compensates for the more diffuse reflectance that would be produced by a retinal tapetum.

The first indication of the presence of a retinal tapetum in the walleye is noted in the superior fundus of specimens about 30 mm in length where it appears to be formed as isolated granules within the smooth endoplasmic reticulum. It would not appear to be functional at this time as walleye at this stage are positively phototactic and feed exclusively on zooplankton (Houde and Forney, 1970; Bulkowski and Meade, 1983). As the tapetum continues to thicken up and spread peripherally in the fundus the young walleye becomes increasingly negatively phototactic (Ryder, 1977). As subadults and adults they are active after sunset when they often return to surface waters to feed (Kelso and Ward, 1977), while in turbid waters walleye are often active during the day (Ryder, 1977).

Concomitant with the formation of a functional tapetum lucidum and beginning about 60-70 mm in length is the arrangement of the rod photoreceptors into bundles of 25-30 to form «macroreceptors».

Grouped or bundled photoreceptors have been reported in several teleost species but to date in no other animal groups (Moore, 1944; Locket, 1970; Meyer-Rochow, 1972; Ali and Anctil, 1976; Munk, 1977). All teleost species which display grouped photoreceptors inhabit either turbid or deep-sea waters where the level of illumination is low. Some of these species also show a prominent retinal tapetum lucidum (Ali and Anctil, 1976; Braekevelt, 1982b). The bundling of photoreceptors results in the close apposition of the inner and outer segments of numerous photoreceptors. Since each photoreceptor bundle is isolated and closely invested by a reflective layer (retinal tapetum) it is likely that each bundle has a great deal of internal reflectance and probably functions as a wave-guide structure to funnel light to the closely packed and extremely long outer segments of the rods. The melanosomes which remain in the apical processes of the RPE cells in dark-adaptation in the walleye and goldeye (Braekevelt, 1982b) would further serve to isolate each bundle of photoreceptors or macroreceptor and enhance its wave-guide function. Zyznar and Ali (1975) have shown that transmitted light passes most effectively through the macroreceptors of the walleye retina.

Retinomotor responses or photomechanical movements which refer both to the movement of melanosomes within RPE cells and the lengthening or shortening of photoreceptor cells in response to environmental illumination are a common feature in teleosts, amphibians and some birds (Walls, 1967; Ali 1971, 1975; Rodieck, 1973; Burnside and Laties, 1979). It is believed that retinomotor responses occur to adapt the eye for day or night vision by shielding or unmasking photoreceptor outer segments to incident light (Walls, 1967). With a few exceptions photomechanical movements appear to replace active pupillary responses (Burnside and Laties, 1979).

All teleost species in which photomechanical movements have been reported showed marked movements of the rod photoreceptors (Engstrom, 1963; Braekevelt, 1975). In most species, cones also change length to some extent in response to environmental illumination, although some species including the goldeye and walleye appear to have no cone movement (Zyznar and Ali, 1977; Braekevelt, 1982b). As both the goldeye and walleye have prominent bundled photoreceptors, perhaps the non-movement of the cones in some way is connected with the maintenance of the bundles during dark-adaptation.

While the majority of the melanosomes of the RPE cells move basally in dark-adaptation, the melanosomes of the apical region always remain in position. In light-adaptation when the melanosomes in the body of the RPE cells become more widely dispersed, they probably cannot effectively mask the tapetal material and hence even during the day the tapetum would be functional to some extent as light would continue to reach the rod outer segments via the large cone photoreceptor cell bodies which would remain as pathways through the apically located melanosomes of the RPE cells. The negative phototaxis of the adult walleye would tend to support this view.

The development of a functional tapetum lucidum and the subsequent formation of macroreceptors during the first summer of life is consistent with changes in response to environmental illumination and changes in feeding behavior. Walleye larvae are positively phototactic prior to the development of a functional tapetum lucidum, but become increasingly negatively phototactic at lengths greater than 30 mm (Ryder, 1977; Bulkowski and Meade, 1983). Initially walleye feed on small organisms, principally zooplankton, (Houde, 1967) but a transition to selecting larger organisms such as minnows takes place at a walleye length of about 60-70 mm (Smith and Noyle, 1945). This transition occurs when photoreceptors are bundling to form macroreceptors. Bundling may enhance perception or larger objects such as forage fish in dim light in clear water or in turbid water.

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