Electron Microscopy of the Tapetum Lucidum of the Cat*

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PLATES 7 TO 13

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ABSTRACT

The fine structure of the tapetum of the cat eye has been investigated by electron microscopy. The tapetum is made up of modified choroidal cells, seen as polygonal plates grouped around penetrating blood vessels which terminate in the anastomosing capillary network of the choriocapillaris. The tapetal cells are rectangular in cross-section, set in regular brick-like rows, and attain a depth of some thirty-five cell layers in the central region. This number is gradually reduced peripherally, and is replaced at the margin of the tapetum by normal choroidal tissue. The individual cells are packed with long slender rods 0.1 μ by 4 to 5 μ. The rods are packed in groups and with their long axes oriented roughly parallel to the plane of the retinal surface. Each cell contains several such groups. Cells at the periphery or in the outer layers of the tapetum are frequently seen to contain both tapetal rods and melanin granules, the latter typical of the choroidal melanocytes. Also melanocyte granules may have intermediate shapes. These observations plus the similar density of the two inclusions lead to the belief that the tapetal rods may be melanin derivatives.

A fibrous connective tissue layer lies between the tapetum and the retina. The subretinal capillary network, the choriocapillaris, rests on this layer and is covered by the basement membrane of the retinal epithelium. The cytoplasm of the retinal epithelium exhibits marked absorptive modifications where it comes in contact with the vessels of the choriocapillaris. This fibrous layer and the basement membrane of the retinal epithelium apparently comprise the structural elements of Bruch's membrane.

INTRODUCTION

The phenomenon of eye-shine is seen in a variety of animals, and is generally known to be related to the presence of a reflecting surface found in the eye, the tapetum. Three general types are known. The carnivores have a cellular tapetum, derived from modified choroidal cells. The ungulates have a collagenous, acellular layer between the retina and choroid. And finally, some fish and reptiles exhibit a retinal tapetum consisting of plates or clusters of guanine crystals in the pigment epithelium of the retina (4, 13, 16). The present report deals with the cellular tapetum of the cat.

The earliest formal description of a carnivore tapetum is attributed to von Haller in 1765, cited by Murr (7). In the latter part of the 19th century, a number of investigators concerned themselves with the microscopic structure of the tapetum in its various forms and manifestations in a variety of animals (2, 15). Birds are apparently the only large group of animals in which no tapetum is found. It was also during this period that guanine was identified as the crystalline material in the retinal tapetum and the argentea of fish (6).

Intermittent interest in the tapetum continued into the 20th century. Bruni and Murr (3, 7) made developmental studies, Murr detailing the development of the feline tapetum. He described the adult tapetum as a multilayered structure of flattened, plate-like cells filled with "Glanz-Stäbchen." These refractile rods appeared microscopically to

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be of a *quasi*-crystalline nature. This suggestion was strengthened by their function as part of a reflecting structure, as well as by implication from their relation to the guanine crystals found in the retinal tapetum of fish and reptiles. Actually, however, no identification has ever been made of the refractile (reflecting) material present in the tapetum cellulosum.

The present study, utilizing the resolving power of the electron microscope, gives a clearer picture of the high degree of order and complexity achieved by the tapetum cellulosum, and confirms and extends the earlier observations. The identity of the tapetal cells as modified choroidal cells is established. Evidence is presented that the units of refractile material in the tapetum are modified pigment granules. Some insight into the interrelations of chroid, tapetum, and retina also is provided.

Materials and Methods

All of the material to be described was obtained from adult cats.

Cats were placed under pentobarbital anesthesia, eyes were enucleated and immediately cut open just below the equator. The vitreous body was removed and the whole posterior half of the eye was immersed in cold 2 per cent osmium tetroxide, buffered with veronal to pH 7.4. The retinal surface was flooded repeatedly with fresh fixative. It was possible to separate the sclera and the choroid by peeling off the latter while submerged in the fixative. This produced a sheet of tissue including the tapetum, thin enough to permit adequate preservation. In some instances it was possible to retain adhesion between retina and choroid by working with fairly large areas of tissue. Retinal detachment invariably resulted from attempts to handle small pieces.

Tissues were fixed for at least 1 hour in the cold, then rapidly dehydrated in graded alcohols, and embedded in *n*-butyl methacrylate. Thin sections were cut, placed on bare grids, carbonized directly,[1] and examined in an RCA EMU-2E electron microscope.

OBSERVATIONS

The eye-shine of cats is typically a brilliant blue-green. The fresh tapetum is blue-white in color, with a dimpled appearance not unlike pigskin. After osmium tetroxide fixation it is a brilliant golden brown. The tapetum is a large triangular area, not centered on, but including the rear pole of the eye and the optic disc. The tapetum is not detectable in the gross in the new-born, but it is obvious and covers 50 per cent of the retinal surface in the 3 to 4 week old kitten. It is essentially full size at this time, so that subsequent enlargement of the eye reduces the relative extent of the tapetum. This rapid differentiation produces a tapetum that is at first pale blue in color.

Figs. 1 to 4 are phase contrast photomicrographs showing the histological organization of the tapetum and its relations to the retina and choroid. Fig. 1 shows a section cut perpendicular to the retina, tapetum, and the deeper choroid. In vertical sections the individual tapetal cells appear rectangular, set in even brick-like rows, and show an orderly arrangement in depth. The thicker central regions of the tapetum may approximate 35 cell layers in depth.

In a section oriented tangentially (Fig. 2) the tapetum is seen to be penetrated at regular intervals by blood vessels. As these vessels emerge on the subretinal surface "dimples" are created, the "stars of Wilson," visible with low magnification on the fresh surface of the tapetum.

In this tangential section the constituent cells appear roughly hexagonal in shape and are arrayed around the penetrating vessels. At higher magnifications (Figs. 3 and 4) the tapetal cells are seen to be packed with slender rod-like structures, oriented with their long axes parallel to the retinal surface. This orientation is not a rigidly fixed or exact one. It is sufficient, however, to give a distinct crystalline aspect to the tapetal cell inclusions.

In low power electron micrographs (Fig. 5) the palisading and the dense packing of the tapetal cells is strikingly evident. The ordered arrangement of the cells creates a solid wall of reflecting material which attains an impressive depth. At higher magnifications (Figs. 6 and 7) the uniformity of the cell inclusions can be seen. The rod-like structures are roughly circular in cross-section and possess a nearly uniform diameter of 0.1 μ. They are quite asymmetric and their length may be as much as 4 to 5 μ.

The rods are arranged in groups, with all of the rods in any one group showing the same orientation so that, as seen in thin sections, all the members of each group have similar profiles. Within

[1] We have been using this method of stabilizing methacrylate sections for over 2 years, and have described it in a previous publication (Schultz, Maynard, and Pease, *Am. J. Anat.*, 1957, **100,** 369). Subsequently E. de Harven has published a fuller description, indicating some of the special difficulties as well as advantages of the method (*J. Biophysic. and Biochem. Cytol.*, **4,** 133, 1958).

each cell, there may be several groups of rods, with each group having its own characteristic and independent orientation. This arrangement is particularly evident in Fig. 7. Note also that small cytoplasmic remnants, possibly of the endoplasmic reticulum, are present in the spaces between groups of rods. Otherwise the rod-like inclusions fill the tapetal cells to such an extent that the cytoplasmic organelles are limited to the extreme cell periphery, and to the immediate perinuclear regions. Although moderate numbers of small mitochondria are present, other organelles are inconspicuous.

Occasionally each rod appears enclosed in a "halo" of protoplasmic substance. Neighboring rods are then often cross-connected to form a 2- or 3-dimensional grid. When this is observed, however, other protoplasmic structures seem poorly preserved, and it seems likely that this is a fixation artifact. Probably the rods normally are suspended in an amorphous gel.

There is some reason to think that in life the tapetal rods may be highly ordered in 3-dimensions. In limited areas sharply defined hexagonal arrays can be found with center to center spacings of as little as 1,400 A.U. More commonly the spacings are larger than this, and the arrangement of rods is more 2-dimensional than 3-dimensional. However, if the cells were swollen as they were fixed, this would be an expected derivative pattern.

In Figs. 6 and 7 the presumptive sites of formation of these rod-like inclusions may be seen. For example, in the perinuclear area and at the cell periphery, rods of smaller-than-average diameter are seen occasionally. These are in small clear packets or vacuoles, surrounded by a layer of cytoplasm, and are interpreted to be newly forming rods. In some cases small groups of these encapsulated rods are found immediately adjacent to an existing group of rods. If these "juvenile" rods have the same spatial orientation as the neighboring group, then they are also in proper position to be added to the group at some later time.

It is particularly evident in Fig. 7 that there can be an enormous variety in the specific orientations of the various groups of rods. There is, nonetheless, a prevalent tendency for the rods to have their long axes roughly parallel to the surface of the retina. This is, however, a general orientation, readily visible in the light microscope (Figs. 2 and 4), but not sufficiently rigid to be obvious at the level of resolution of the electron microscope.

Towards the margin of the tapetum the number of cell layers gradually is reduced until finally they disappear altogether, leaving the retina in direct contact with a typical mammalian choroid. Fig. 9 is a low power micrograph of a transitional area with a single tapetal layer. Note that the melanocytes of the choroid form distinct layers comparable to those of the tapetum. An extensive connective tissue infiltration separates the layers so that the over-all pigment pattern is diffuse.

At a cytological level the melanocytes are as thoroughly dominated by a single type of cytoplasmic component (melanin granules) as are the tapetal cells. That is, the melanocytes are filled with melanin granules with only minimal quantities of other organelles, and to an extent comparable to the packing of the tapetal cells. (Figs. 8 and 9). The principal difference is in the high degree of order of the tapetal rods as compared to the random packing of the melanin granules. Nonetheless, the characteristic similarities of choroidal and tapetal cells persist. This is not surprising since both tissues apparently have a common origin from the cells of the endomeninx which invests the primitive optic cup.

The initial impression obtained is that the rods which fill the tapetal cells are quite unusual and unrelated to more familiar cell inclusions. The uniformity in size, asymmetry of form, and density of packing, as observed in the light microscope, suggested the possibility of a crystalline character for these rods. It seems clear, however, from the electron microscopic analysis, that these rods are not truly crystalline. The individual rods are not sufficiently homogeneous and lack sharp angles. The groups do not exhibit the degree of ordered close-packing to be expected of crystalline inclusions. Moreover, it is important to point out that tapetal cells adjacent to the choroid are frequently seen to contain both the rods characteristic of the tapetum and the pigment granules common to the choroidal melanocytes. (Figs. 8 and 9, encircled areas). Figs. 8 and 9 also demonstrate occasional elongate melanin granules which sporadically approach the proportions of tapetal rods. The similarities in osmiophilia and/or density also are strikingly evident. The probability that these two inclusions consist of the same material will be discussed below.

As seen in Figs. 2 and 4 the cells of the tapetum are organized around penetrating blood vessels. These vessels run from the vascular layer of the choroid through the tapetum (Fig. 11) to terminate

in the extensive, anastomosing, capillary network lying between the tapetum and the retinal epithelium. These capillaries (Fig. 10) which underlie all parts of the retina are separated from the tapetum or pigment cells of the choroid by a narrow layer of connective tissue, which also extends over the whole retinal surface. When no capillary is interposed this fibrous layer may be in direct contact with the retinal epithelium.

These capillaries exhibit two specializations that perhaps are interrelated. The nuclei of the endothelial cells regularly are found to be in contact with the fibrous layer (Fig. 10). The endothelial sheet adjacent to the retinal layer is greatly attenuated, and possesses pores (Figs. 10 and 12) quite like those first described in the glomerular and peritubular capillaries of the kidney (5 and 8), and which have since been reported in other capillaries (1).

Associated with the fenestrated endothelium is a specialization of the basal surface of the overlying pigment layer of the retina. In the immediate vicinity of capillaries the plasma membranes are elaborately infolded in a manner to increase greatly their surface area, and to create large numbers of irregularly shaped feet (Fig. 12). Deep folding of the basal cell surface was first observed in the tubules of the kidney by Sjöstrand and Rhodin (14), Rhodin (12), and Pease (9). Similar specialization has since been observed in other tissues (1). There is at least some correlation with water transport mechanisms and secretory activity (10).

Electron microscopic examination has uniformly indicated the presence of a thin basement membrane associated with the capillary endothelium. Also, underlying the pigment layer of the retina there is a basement membrane. This is notably thin in the tapetal region, but massive in other parts of the retina. Fig. 10 shows the combined membranes in the region of the tapetum; Fig. 12 shows the thickened membrane in a non-tapetal area.

The subretinal basement membrane corresponds to an integral structural part of Bruch's membrane. Bruch's membrane is a two component layer, 1 to 4 μ thick, lying between the choroid and the retina. The inner (retinal) component is described as a homogeneous lamella apparently derived from the pigment epithelium, while the outer component is a dense reticular layer. No "membrane" recognizable as such has been observed in this work. However, it seems clear (Figs. 9 and 10) that the described elements are present in the form of the basement membrane of the retinal epithelium, interpreted as the homogeneous band, and the fibrous layer interposed between the retina and the tapetum, and continuous over the choroid, interpreted as the dense reticular component.

The polarization of the endothelial cells comprising the subretinal capillaries, the increased surface of the retinal epithelium, and the thinning of the basement membrane appear to be interrelated modifications. These specializations presumably influence the transport of metabolites to the retina.

A few remarks about the pigment epithelium of the retina are of interest. First of all, the pigment is almost totally absent in the area of the tapetum (Fig. 10). This is reasonable in that the pigment would defeat the purpose of the tapetum, and it is, in fact, generally observed (4) that the pigment is absent over the area of the tapetum. In the same sense, there is no fovea in the tapetalized eye (4, 16) since the function of visual acuity is usurped by the tapetum. It can be seen in Fig. 9 that the pigment epithelium contains three unusual cytoplasmic elements. The first of these is obviously the pigment granules for which these cells are named. There is also a large "spherical granule" which probably is secretory. Finally, there are membrane-enclosed, lamellar structures very similar in appearance to the lamellae seen in the outer segments of the retinal receptor cells (Figs. 9 and 12). It seems possible that these structures are analogous to the myeloid bodies described by Porter (11) although his material showed no enclosing membrane, and the lamellae could be shown to be continuous with the tubular structures of the endoplasmic reticulum. These are possibly abortive or incomplete efforts on the part of these ectodermal cells to manufacture rod processes.

The question of color vision in cats is apparently still unsettled (16). It may be remarked that in the fairly extensive series of retinal sections examined in this study, the observed receptor cells were invariably rods.

DISCUSSION

The tapetum represents a remarkable case of cell specialization and adaptation. For the specific purpose of providing an effective reflecting surface

with a minimum of scattered light (and consequent image blurring), the close-packed array of long slender rods, oriented to present their long axis to the incident light, would be difficult to improve. This arrangement of the rod-like tapetal cell inclusions also acts as an effective diffraction grating, thus accounting for the iridescent quality of the eye-shine seen in cats. The dominance of the short wave lengths in the reflected light is in keeping with the Rayleigh scattering by objects small with regard to the wave length of light (tapetal rods, 1000 A.U. or less).

Thus far, one paramount question remains unanswered. Namely, what is the material of the tapetal rods? The ungulate tapetum fibrosum is known as noted above to be a glistening white sheet of collagen, and obviously quite different from what we have been considering. The retinal tapetum of fish and reptiles is made up of crystalline aggregates of guanine. This is perhaps a reasonable possibility for the carnivore tapetum, and several workers have (apparently by extrapolation) assumed that this was the case. Several factors argue against this possibility, however, for the tapetal rods have neither the silvery aspect seen in the argentea or the scales of fish, nor do they exhibit the uniform close-packing expected of crystalline structures.

While a definitive identification of the material of the tapetal cell inclusions has not been made, it seems reasonable to suggest that the tapetal rods are melanin products. Figs. 8 and 9 provide the basic visualizations for this hypothesis, namely, the presence of typical choroidal melanin granules in tapetal cells, as well as granules of intermediate shape in melanocytes. By electron microscopy, the rods and the melanin granules have similar densities. Both inclusions commonly are seen together in the external layers of the tapetum and in the peripheral areas where the tapetum is reduced to one or two cell layers.[2]

[2] After this manuscript had been submitted for publication, the work of Weitzel and his collaborators (Weitzel, G., *et al.*, Hoppe-Seyler's *Z. physiol. chem.*, 1955, **299**, 193) was brought to our attention. These investigators have shown the choroid of the dog, fox, and other carnivores to have the highest zinc content of any animal tissues, approximating 16 per cent of the dry matter in some cases. The zinc is present almost exclusively in the form of zinc-cysteinate, and this material is located in the tapetal region of the choroid.

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Explanation of Plates

Plate 7

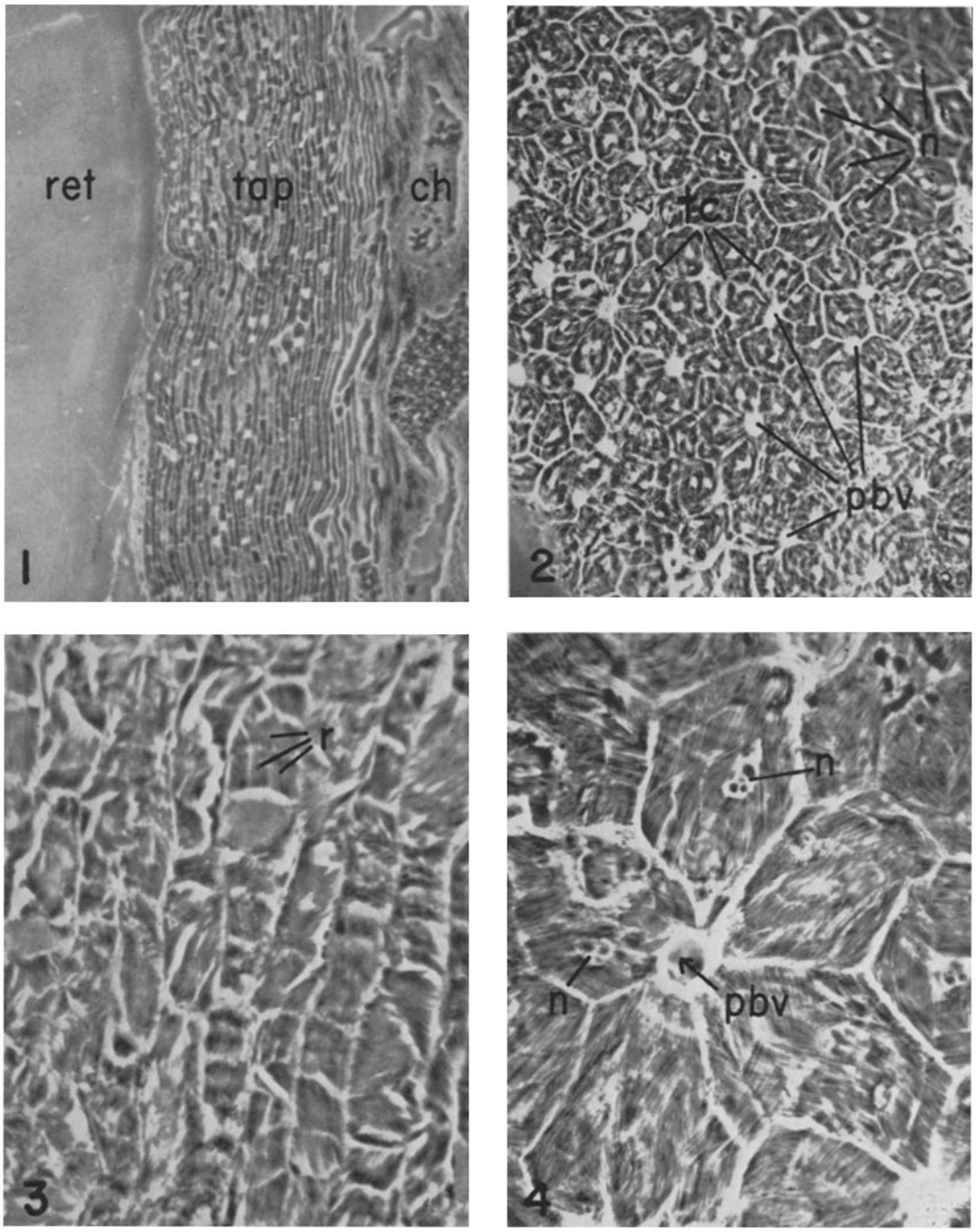
Figs. 1 to 4. Phase contrast photomicrographs of relatively thick methacrylate sections of osmium-fixed tissue. The spatial relations of the tapetum, sandwiched between retina and choroid, can be seen (Fig. 1). The tapetal cells are rectangular in cross-section, set in even, brick-like rows (Figs. 1 and 3). Viewed in tangential section, the tapetal cells appear as roughly hexagonal plates grouped around penetrating blood vessels which run through the mass of the tapetum at regular intervals (Figs. 2 and 4). The individual cells are almost completely filled with masses of slender rod-like inclusions.

Fig. 1. A cross-section through the retina (*ret*), tapetum (*tap*), and choroid (*ch*), showing the palisade of tapetal cells to good advantage. In this picture, 32 to 35 layers of tapetal cells are discernible. × 300.

Fig. 2. In tangential section, the ordered arrangement of the polygonal tapetal cells (*tc*) around the penetrating blood vessels (*pbv*) is apparent. The nuclei (*n*) of the tapetal cells appear as small clear holes within the cells. × 200.

Fig. 3. At high magnification a cross-section through the tapetum shows the wall-like facade, the dense packing and the groupings of the rod-like (*r*) cell inclusions. × 2370.

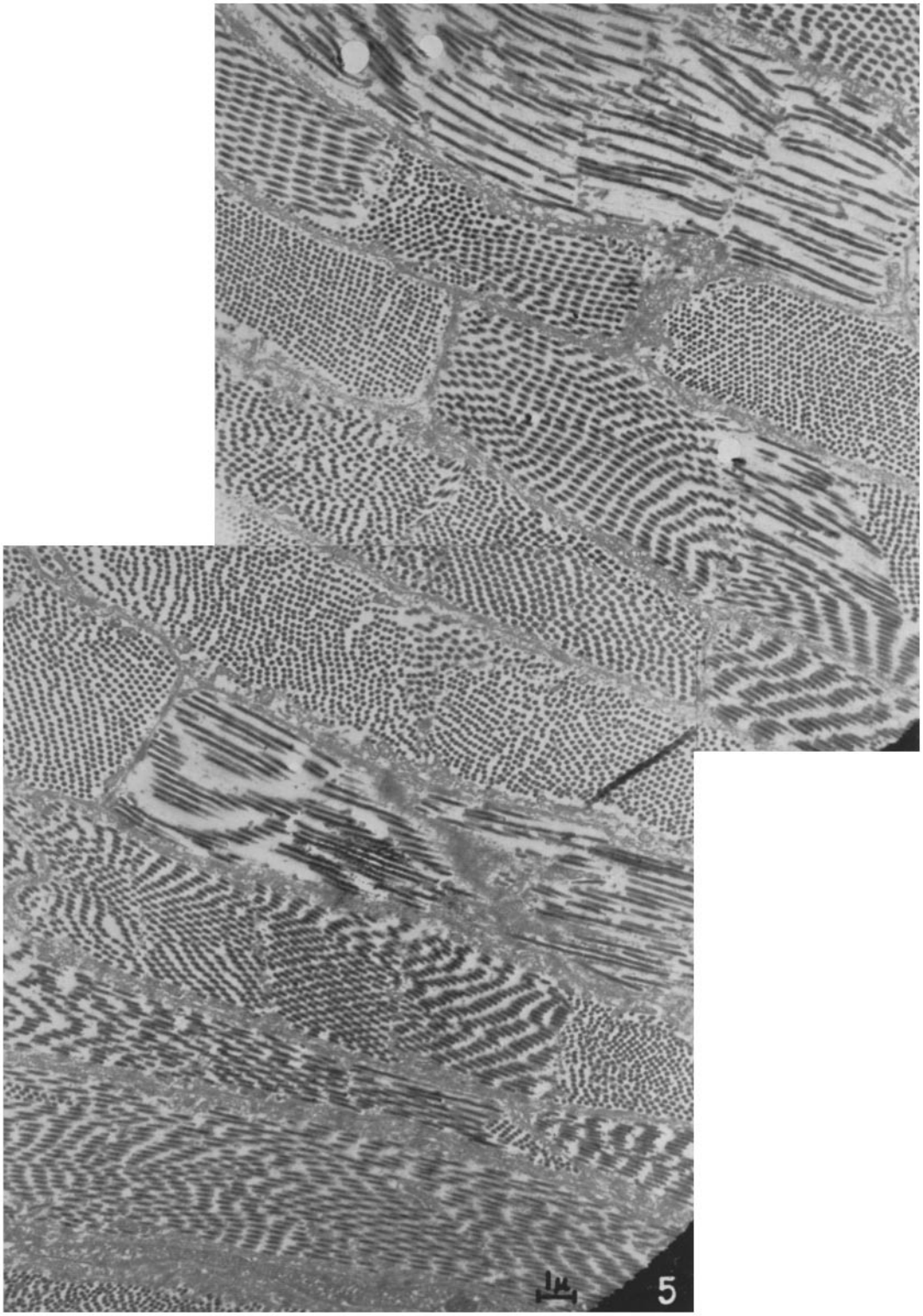
Fig. 4. A single group of cells around a penetrating blood vessel (*pbv*), indicated in Fig. 2 is seen at higher magnification. The slender rod-like nature of the cell inclusions and their arrangement in groups is evident. Nuclei (*n*) also are visible. × 700.



(Bernstein and Pease: Fine structure of tapetum)

PLATE 8

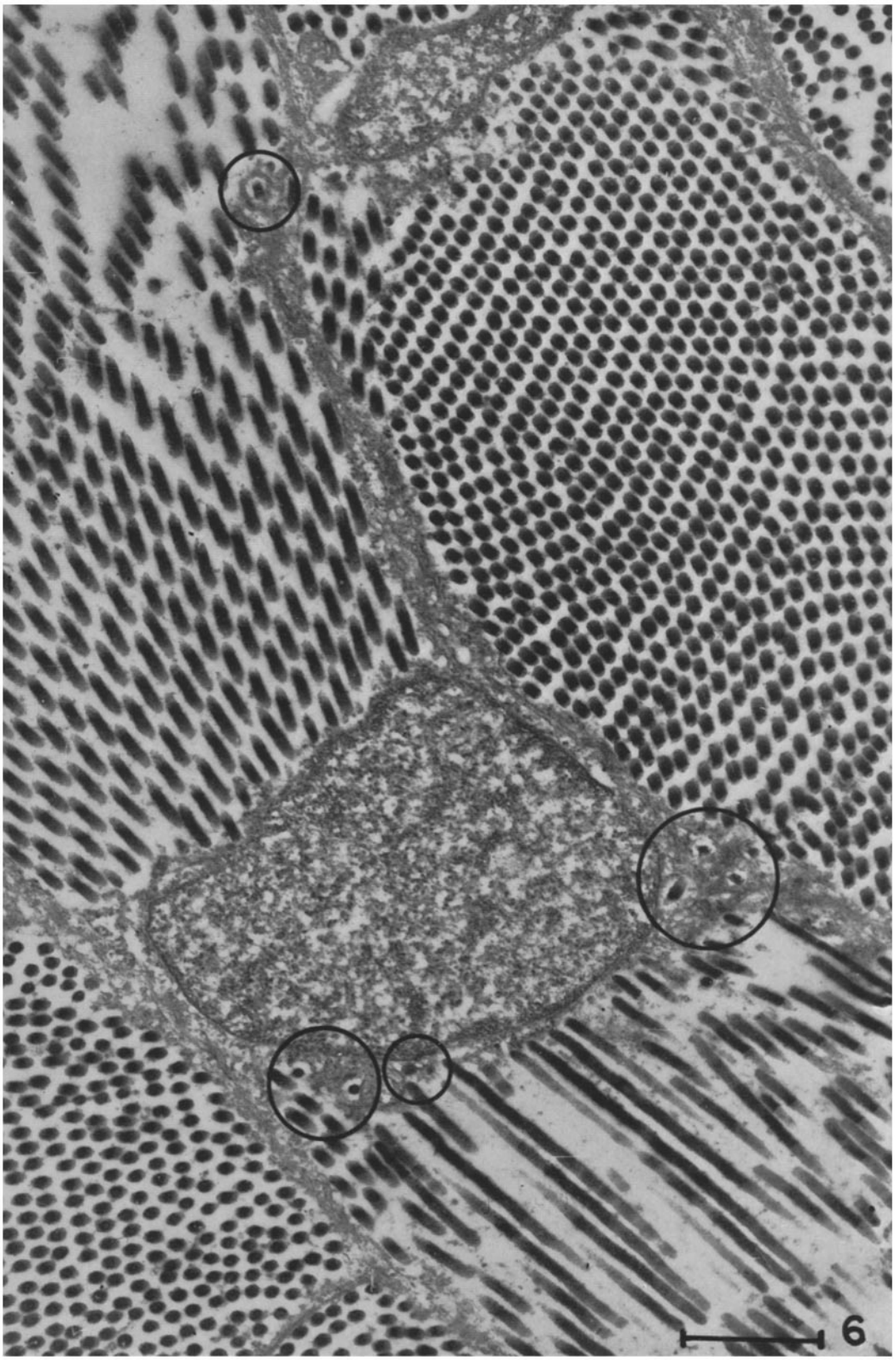
FIG. 5. This montage of electron micrographs shows the palisading of the cells of the tapetum, as seen in vertical section. The cells are arranged in orderly rows, with each cell set squarely against another. The rows are offset sufficiently so that the intercellular joints are not aligned in depth. The general tendency for the tapetal rods to be oriented parallel to the plane of the retina is apparent. The rods are arranged in groups with several groups present in each cell. In the upper right portion of the figure the length of the rods (approximately 5 μ) is strikingly evident in contrast to their diameter (0.1 μ). In this and subsequent figures, micron marks indicate scale.



(Bernstein and Pease: Fine structure of tapetum)

PLATE 9

FIG. 6. This view shows a section through the nuclear region of a tapetal cell. Note the absence of normal cytoplasmic organelles except in the immediate perinuclear region and in the extreme cell periphery. The marginated chromatin and the absence of any distinct nucleolus is typical of these cells. Note also the smaller than average rods (encircled) enclosed in small clear vacuoles. Presumably, (see text) these are immature rods.

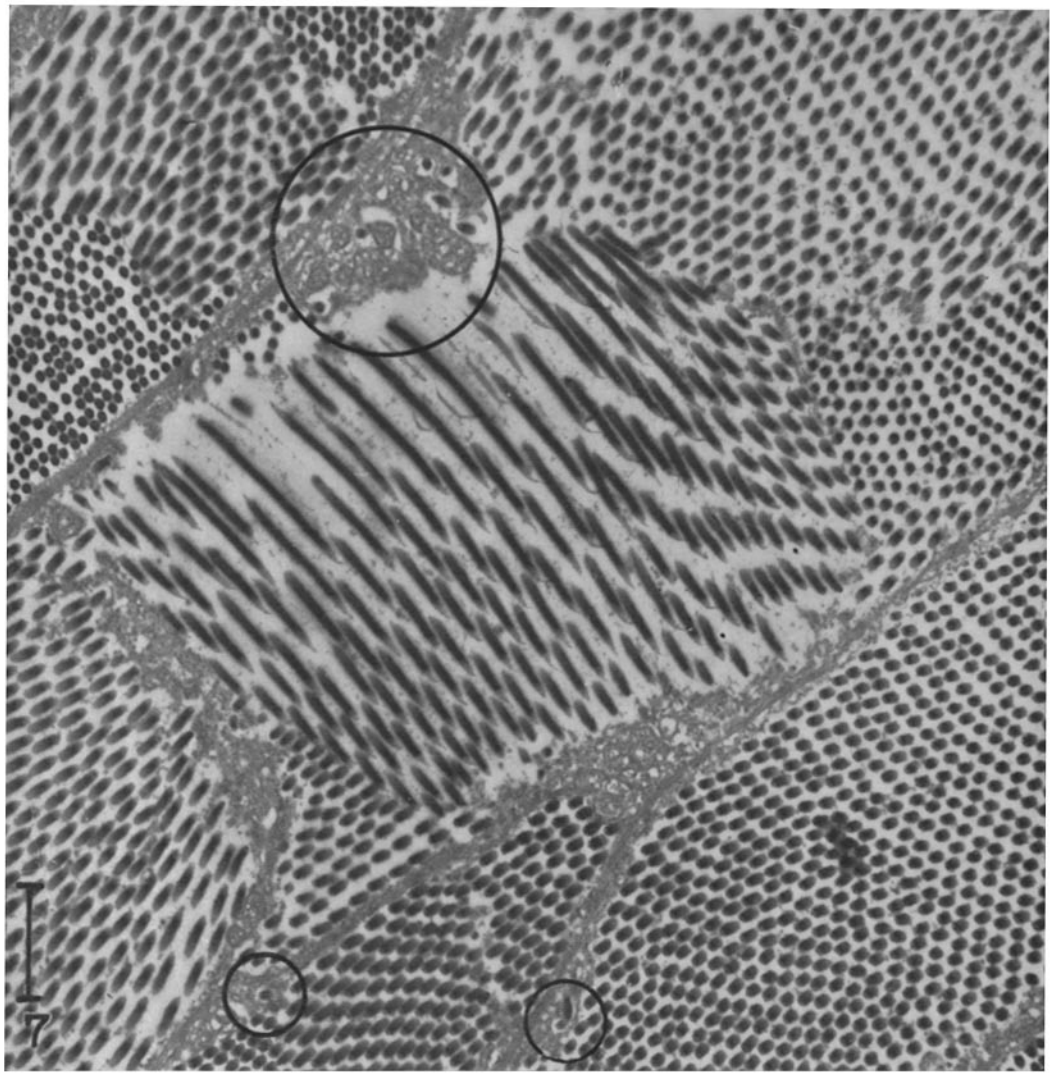


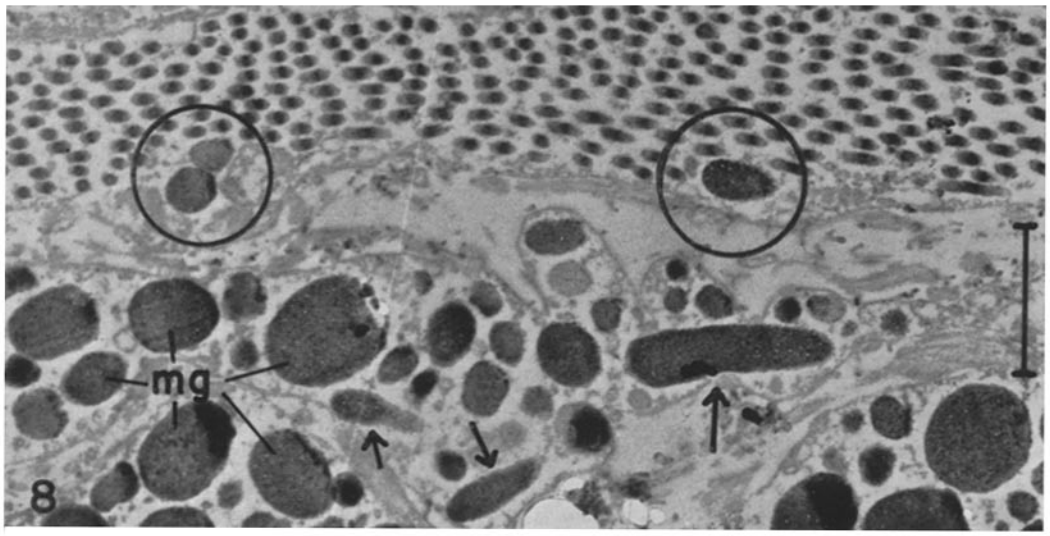
(Bernstein and Pease: Fine structure of tapetum)

PLATE 10

FIG. 7. In this cross-section, the peripheral distribution of the immature rods is again seen (encircled). The apparently infinite variety of specific orientations available to the tapetal rods is quite striking. Within each group of rods the positioning is sufficiently rigid that each rod presents the same profile. While each group appears to be set at a different angle, the general orientation with respect to the retinal surface is retained.

FIG. 8. In the peripheral regions of the tapetum, cells of mixed character frequently are encountered. Here the tapetum is reduced to a single layer, and both melanin granules (*mg*) and tapetal rods may be found in the same cell (encircled areas). In addition, some of the melanin granules in otherwise typical choroidal melanocytes may be decidedly elongated, approaching the asymmetry of tapetal rods (arrows). Note also the similar electron densities of both types of inclusion.





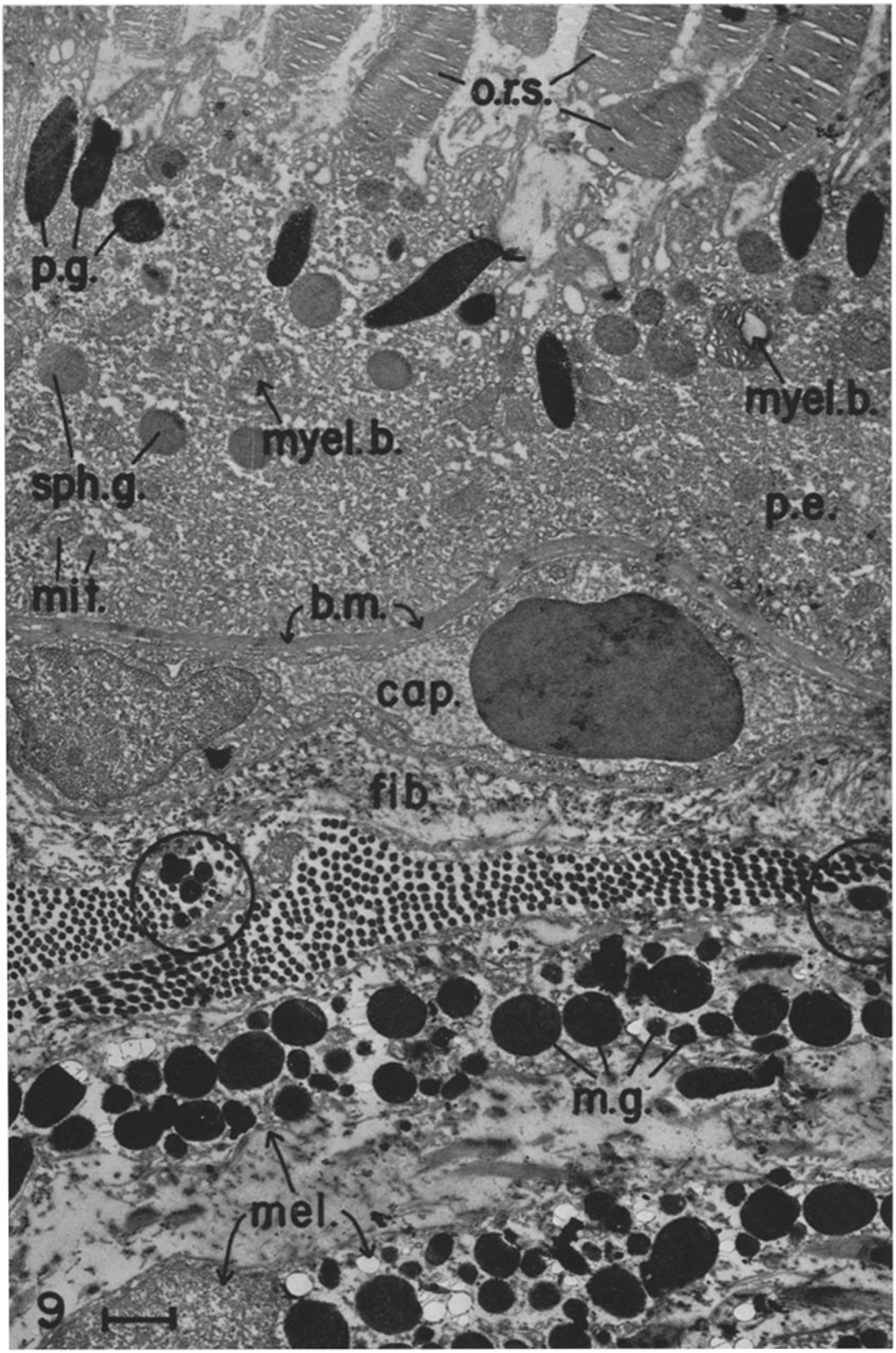
(Bernstein and Pease: Fine structure of tapetum)

PLATE 11

FIG. 9. This micrograph shows again relations between choroid, tapetum, and retina. The melanocytes (*mel.*) of the choroid are filled with melanin granules (*m.g.*), and arrayed in a wall-like facade similar to the tapetum. The extensive connective tissue component gives the choroid an appearance of lesser pigment density than the tapetum.

This is an area at the edge of the tapetum, where it is reduced to a single cell layer. Here, again, melanin granules are seen in the tapetal cells (encircled), as well as occasional elongated melanin granules in the melanocytes. A layer of fibrous connective tissue (*fib.*) separates the tapetum and the retina. The pigment layer of the retina (*p.e.*) overlies this fibrous layer and a thickened basement membrane (*b.m.*) is present. The fibrous layer and the basement membrane of the retinal epithelium constitute Bruch's membrane (see text). The vessels of the choriocapillaries (*cap.*) are inserted between the fibroblast layer and the retinal epithelium.

Here at the edge of the tapetum, pigment granules (*p.g.*) are again present in the retinal epithelium. These are not seen over the more central regions of the tapetum. Large spherical granules (*sph. g.*) possibly secretory, are seen in the cytoplasm of the retinal epithelium, along with numerous mitochondria (*mit*). Lamellated structures, possibly myeloid bodies (*myel. b.*) are also present. At the extreme right, the tips of the outer rod segments (*o.r.s.*) of the retinal photoreceptors may be seen.

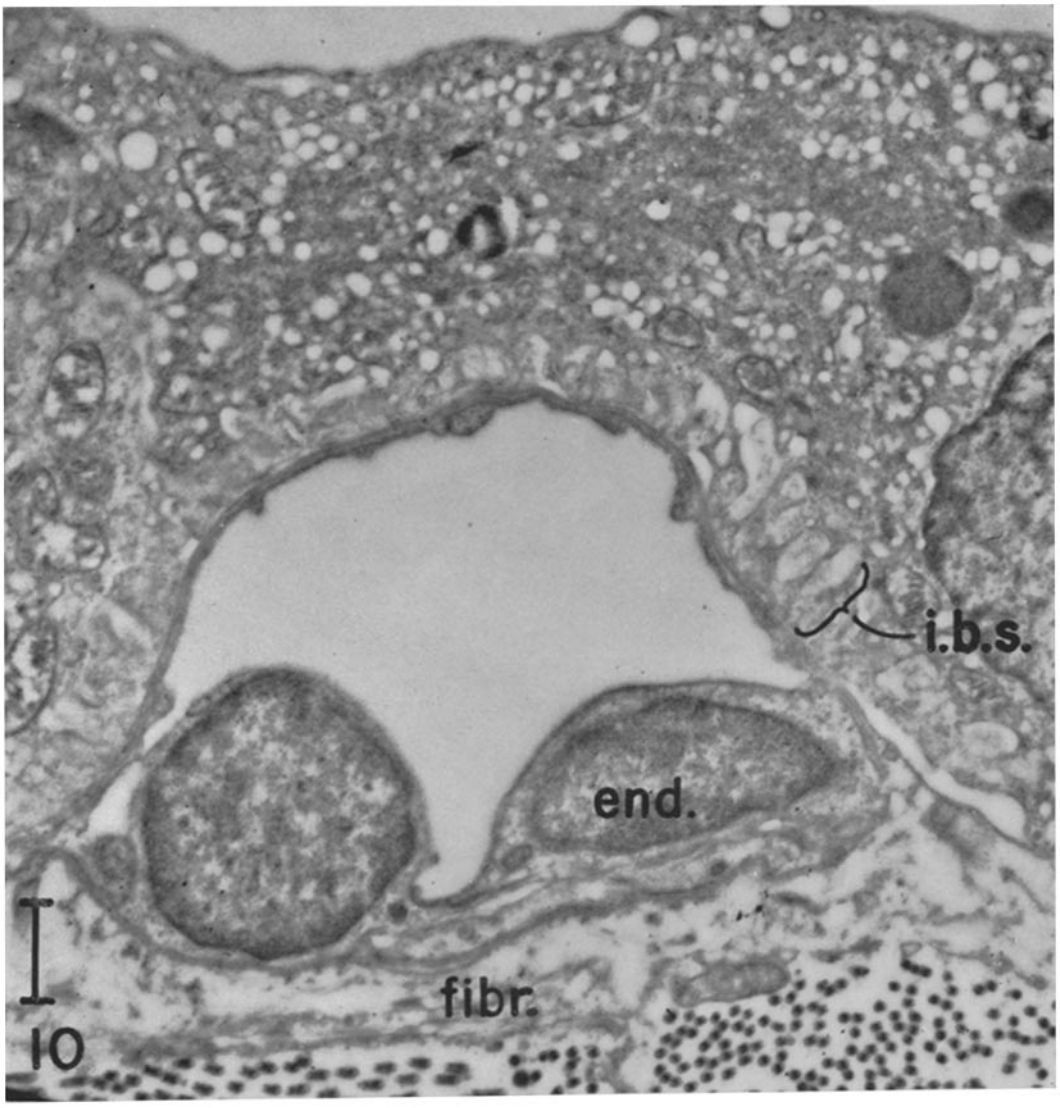


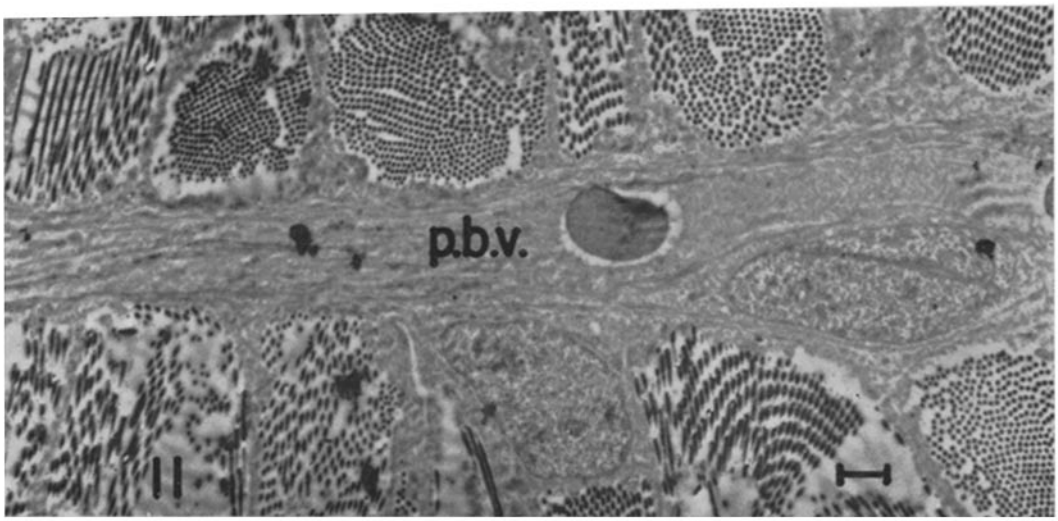
(Bernstein and Pease: Fine structure of tapetum)

PLATE 12

FIG. 10. This is a vertical section through the surface layer of the tapetum to show the junctional region of the tapetum and the retinal epithelium. Note that the tapetum is covered by a fibrous layer (*fibr.*), and that the endothelial nuclei (*end.*) of the choriocapillaris typically lie upon this. On the opposite surface, the attenuated endothelial sheet with its characteristic fenestrations is in contact with the infolded basal surface (*i.b.s.*) of the retinal epithelium. Here, in the central region of the tapetum, the basement membrane of the epithelial surface is thinned greatly. At the lower right of the capillary, the separation of the epithelial and endothelial components of the basement membrane can be seen. Note the absence of pigment granules, and the presence of but a single "spherical granule" in this part of the retinal epithelium overlying tapetum.

FIG. 11. A penetrating blood vessel (*p.b.v.*) seen in logitudinal section as it passes through successive layers of tapetum.

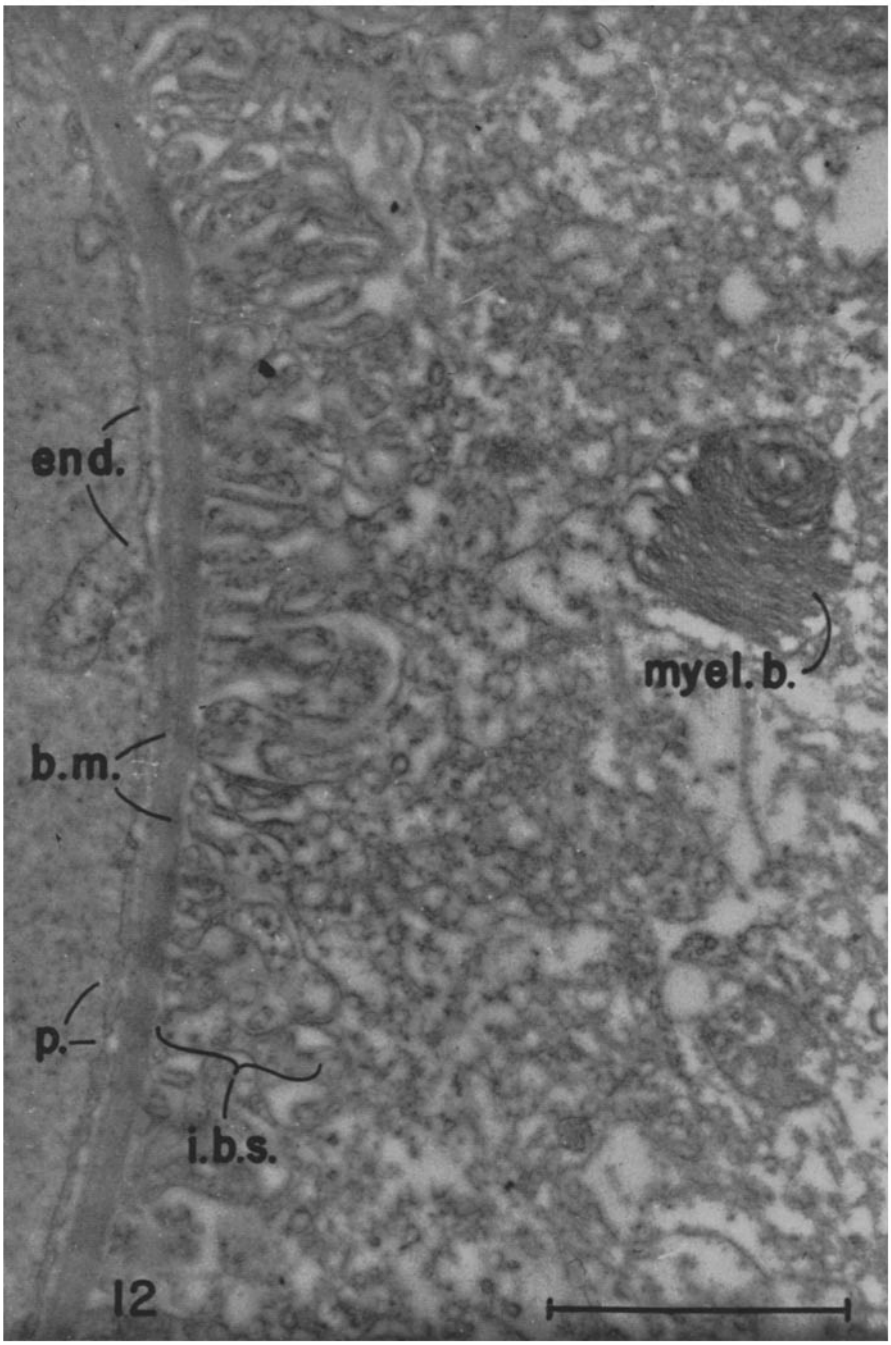




(Bernstein and Pease: Fine structure of tapetum)

PLATE 13

FIG. 12. At the edge of the tapetum the basement membrane (*b.m.*) of the retinal epithelium becomes considerably thickened. The relations of the attenuated endothelial sheet (*end.*) to the basement membrane and the infolded basal surface (*i.b.s.*) of the retinal epithelium are seen here at higher magnification. The pores (*p.*) in the endothelial sheet are also visible. What is possibly a "myeloid body" (*myel. b.*) as discussed in the text is conspicuously present.



(Bernstein and Pease: Fine structure of tapetum)