Albrecht v. Graefes Arch. klin. exp. Ophthal. 190, 27—45 (1974)

The Fine Structure of the Pig's Retina*

Marie Louise Beauchemin

University Eye Clinic (Dir.: Prof. J. Babel), Geneva

Received December 27, 1973

Summary. Retinas from 3 groups of pigs were examined; three farm pigs of 2 months, nine miniature pigs of 4 to 5 months and nine slaughter house pigs of about 12 months. No ultrastructural differences were observed between these 3 groups. With the major exception that the pig's retina does not have a fovea, it was found to closely resemble that of man. The inner layers of the pig's retina tended to thicken somewhat towards the peripapillary region. The more distinctive points of the pig's retina are the following:

1. The relatively even distribution of cones throughout the retina with their large, polymorphous ellipsoidal mitochondria showing transversally oriented cristae.
2. The presence of a microtubular structure in the rod from retinas fixed with glutaraldehyde.
3. The impressive size of the horizontal cells with their large cytoplasmic processes.
4. The prominant RER and mitochondria with a granular content and scarce cristae present in the Müller cells at the inner nuclear layer level.
5. The presence of numerous astrocytes in the more inner layers.
6. The presence of capillaries in the thicker nerve fiber layer in the peripapillary region.

The pig's retina, and most notably that of the conveniantly small miniature pig, was concluded to be a suitable model for future retinal studies.

Introduction

The ultrastructure of the retina in many higher vertebrates has been extensively studied (Missotten, 1965; Dowling and Boycott, 1966; Dowling, 1970; Sjöstrand, 1961a; Cohen, 1963; Hogan *et al.*, 1971). The pig's retina has been thought to be quite similar to man's (Prince *et al.*, 1960), however a study of the pig's retinal ultrastructure, to our knowledge, has not yet been carried out, with the exception of the study of its vasculature (Bloodworth *et al.*, 1960) and a pathological ultrastructural study of the inner layers of the pig's retina (Shakib and Ashton, 1966). As such we undertook this study with considerable interest, realising that a better knowledge of its ultrastructure could be beneficial to other research workers, serving as a model for future experiments and studies on the retina.

* Supported by SNSF grant No 3.1150.73.

Material and Methods

Eyes used for this study were obtained from 3 different groups of pigs: 3 farm pigs of about 2 months old and weighing up to 25 kilos, 9 miniature pigs of about 4 months old and weighing about 12 kilos and 9 pigs obtained from the slaughter house, of about 12 months old and weighing about 80 kilos. The miniature pigs were a Göttingen breed being an extra small genetical variation of the normal pig. They were obtained from the Tierzucht Institut of the University of Zürich. Of these animals, 13 had been under prolonged anaesthesia and 8 not. The anaesthesia used was the same as that carried out by Tsacopoulos *et al.* (1973).

Twelve eyes were fixed by direct immersion in a 3% glutaraldehyde-phosphate solution, pH 7.3 at 4° C where they were left for 3 to 4 days. They were then washed over night at 4° C in a Phosphate buffer and post fixed for 2 hours in OsO_4 at room temperature. Four eyes were fixed for only one hour in the 3% glutaradehyde-phosphate fixative at room temperature and washed for 2 hours in the phosphate buffer. Three eyes were perfused with 2.5% glutaraldehyde in the external carotid. This technique, however, was not continued since its results were not superior to those obtained by direct immersion. Two eyes were fixed only in 2% OsO_4, followed by an overnight washing in a phosphate buffer. All eyes were dehydrated in alcohol and embedded in Epon. Thin sections were cut at 500–700 Å thick on a Porter Blum microtome and stained 5 minutes with uranyl acetate and 2 minutes with lead citrate. They were then examined with a Philips 300 E. M.

Semi thin sections for light microscopy were cut at 0.5 to 1 μm and stained with Toluidine Blue.

Results

I. Light Microscopy

The peripapillary and peripheral areas of the retinas were examined in detail in this study. Semi thin sections showed the pig's retina to resemble that of man, with the exception of the abundance of cones distributed among the rods (Fig. 1). No fovea nor a capillary free area was observed. The thickness of the 2 nuclear layers varies very little throughout the retina, except near the peripapillary region where they may be several rows thicker.

The inner layers in the pig's retina tend to vary in thickness according to their proximity to the optic nerve. The inner plexiform layer measured 15 to 30 μm in thickness.

The thickness of the ganglion cell layers varied not so much in the number of rows of cells but in their size and proximity to each other—very large, more closely packed ganglion cells can be found closer to the peripapillary area.

The nerve fiber layer was found to be thicker than in man (Hogan *et al.*, 1971), near the optic nerve with measurements up to nearly 50 μm thick.

We found the vascular system to be mainly trilaminar with the capillary network extending externally to the outer part of the inner nuclear layer, and internally to the ganglion layer, except in the peripapillary area where capillaries are also found in the nerve fiber layer.

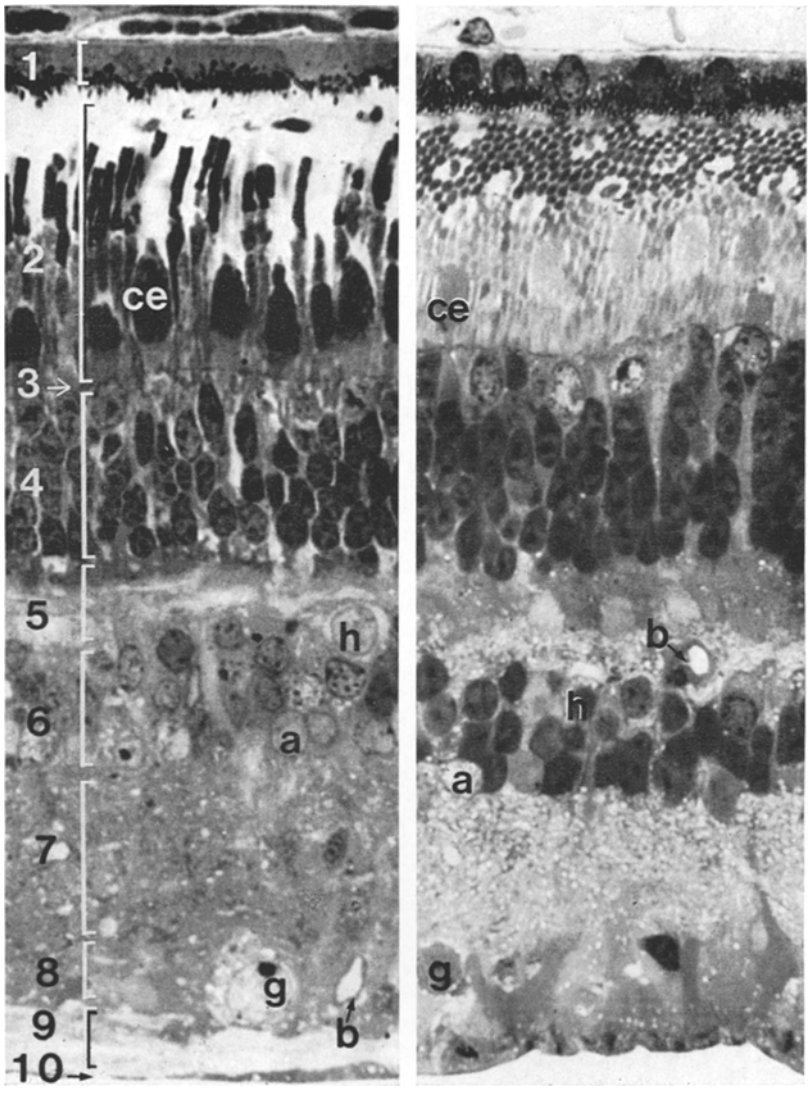


Fig. 1. Semi-thin section of pig's retina (left) and human's retina (right). The thickness of the different layers correspond quite closely (the human outer segments are cut slightly obliquely). *1* pigment epithelium; *2* outer rod and cone layer; *3* outer limiting membrane; *4* outer nuclear layer; *5* outer plexiform layer; *6* inner nuclear layer; *7* inner plexiform layer; *8* ganglion cell layer; *9* nerve fiber layer; *10* inner limiting membrane. *ce* cone ellipsoid; *h* horizontal cell; *g* ganglion cell; *a* amacrine cell *b* blood vessel

II. Ultrastructure

A. Pigment Epithelium

The pigment epithelium measures between 6 and 10 μm in thickness in the central retina; its basement membrane measures 400 Å in width (Fig. 2).

The cytoplasm is found to be rich in smooth endoplasmic reticulum, (ER), and different sized mitochondria; free ribosomes can also be seen scattered throughout the cell. The pigment granules are seen mostly concentrated in the apical portion of the epithelium cell and can measure up to 3 μm in length.

Liposomes as well as phagosomes can also be seen. No annulate lamellae were observed. A Golgi apparatus and rough ER could often be seen located near the nucleus. Lysosomes were quite noticeable in the more apical parts of this layer.

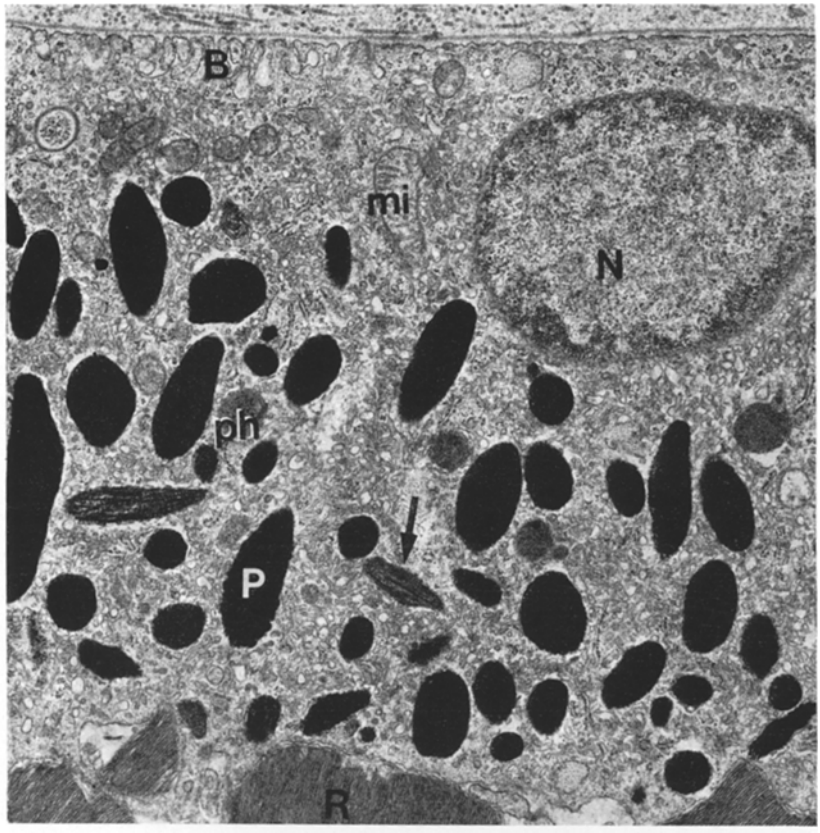
The junctional complex between adjacent cells consisted of an apical gap junction, a well developed zonula adherens (Fig. 4) with a multitude of tonofibrils (Fig. 3) and intermittent zones of cell membrane fusion (zonula occludens, Fig. 4). Microvilli surround the outer segments of the rods extending approximately $^1/_3$ their length (Fig. 5).

B. Photoreceptors

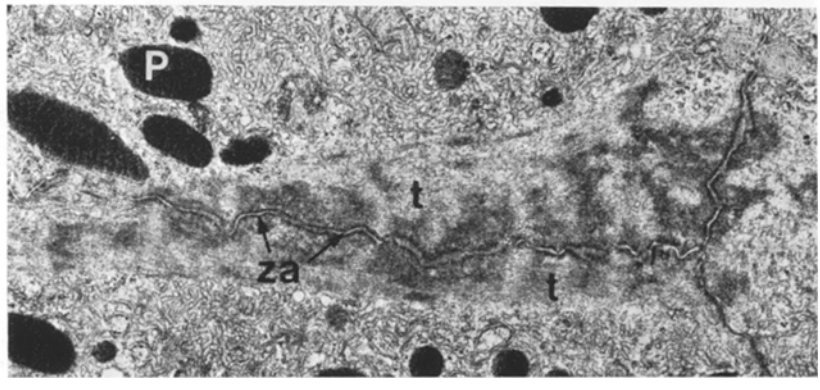
1. Outer Segment. The proportion of cones to rods was approximately 1 to 7. These values were obtained from tangential sections of the retinas of three different animals (Fig. 6). The external segment of the rods can measure up to 36 μm in length and up to 12 μm in length for the cones. The rod disc membrane measured 60–85 Å in thickness and that of the cones measured from 70 to 100 Å in thickness (Fig. 8a and b). There were approximately 25–28 discs per μm for the cones and between 30–35 per μm for the rods.

2. Ellipsoid. a) The rod ellipsoid could be measured up to 20 μm in length with the mitochondrial cristae oriented both transversally and longitudinally (Fig. 7a). Microtubular structures were seen in 18 out of 21 animals examined (Fig. 7 inset). These structures extended more or less down the axis of the cell and were observed through to the synapses. When the tissue, however, was fixed with only 2% OsO_4, these structures were not observed.

b) The cone ellipsoid, cone shaped and very well developed, can have a length up to 15 μm. It is located more internally than that of the rod, being at the same level as the rod myoid. Its diameter does not noticeably increase towards the peripapillary area. The mitochondria stain darker than those of the rods and were very voluminous, taking different shapes (Fig. 7). The cristae were generally oriented trans-



2



3

Fig. 2. Pigment epithelium. *B* basal infoldings, *ph* remnants of a phagosome, *arrow* immature melanin granule. Magnification ×11925

Fig. 3. Pigment epithelium; tangential section. Note the presence of the large number of tonofibrils (*t*) surrounding the junctional complexes. *za* zonula adherens. Magnification: ×11925

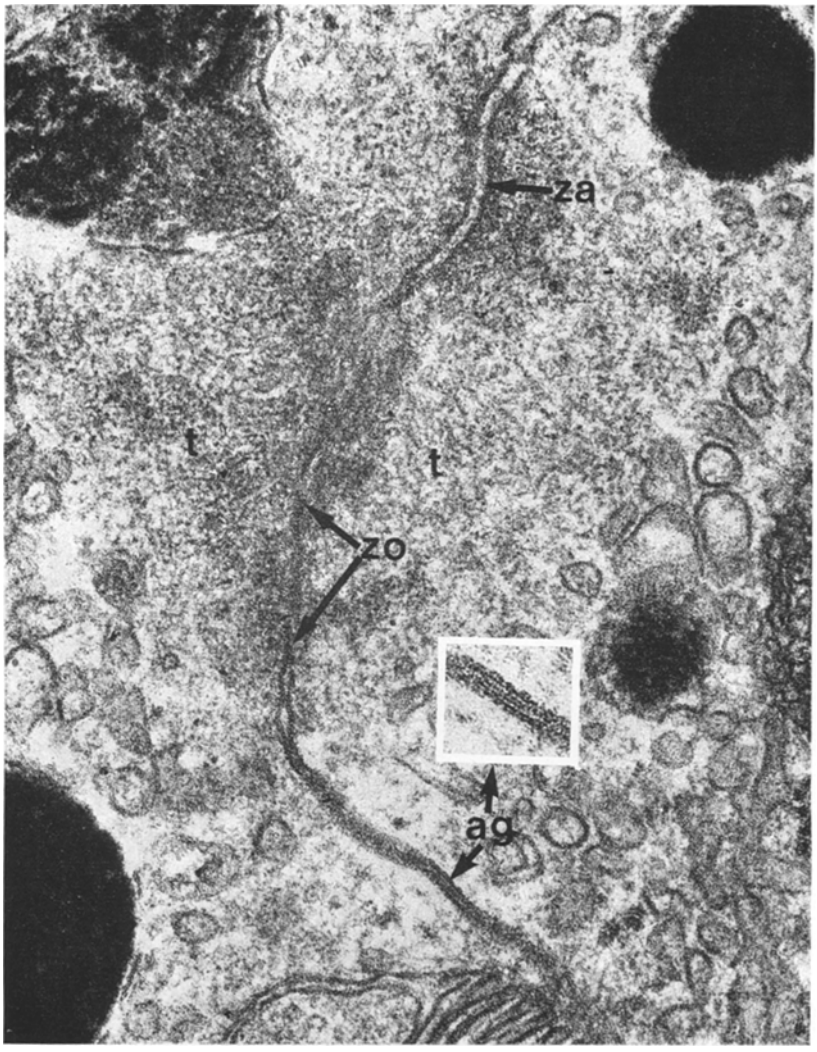
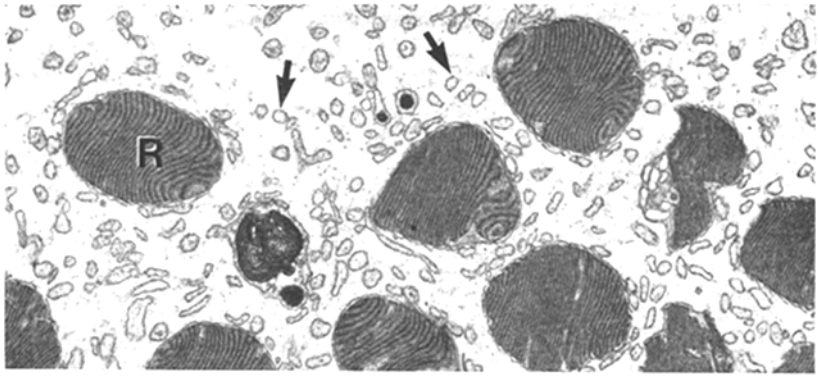


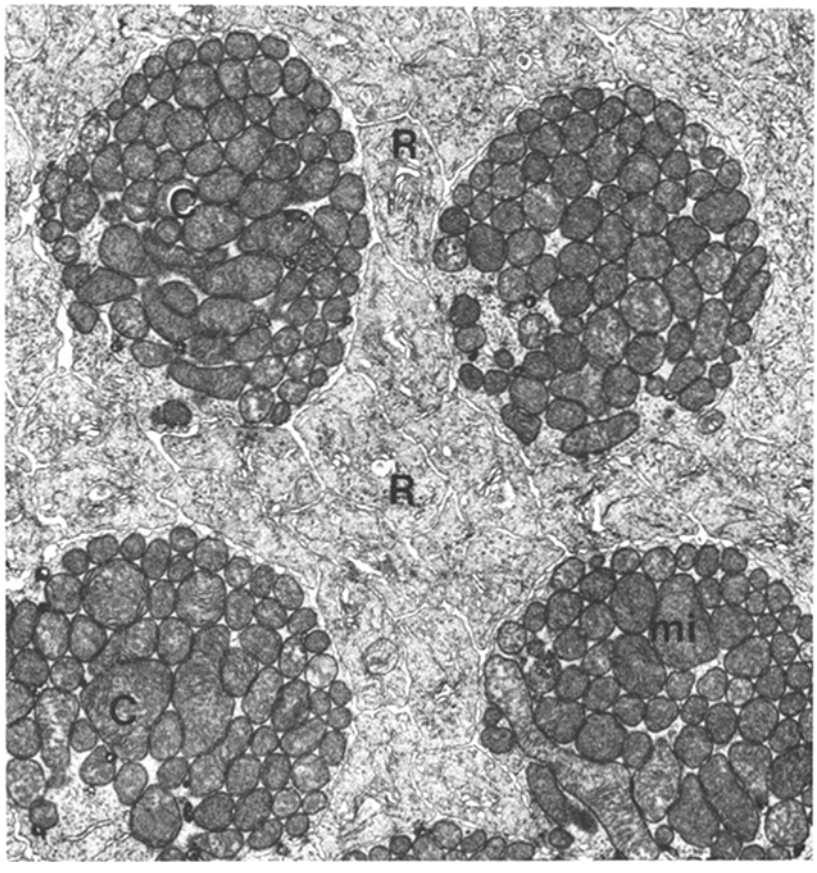
Fig. 4. Pigment epithelium; tangential section showing details of the junctional complex. *ag* apical gap junction, *za* zonula adherens, *zo* zonula occludens, *t* tonofibrils. Magnification ×80000. Inset: apical gap junction. Magnification: ×150000

versally. Neurotubules were sometimes seen in the cytoplasm surrounding the mitochondria. The microtubular structures were seen only once in the cone ellipsoid.

3. Myoid. a) The rod myoid, which can measure up to 20 μm in length, contains many free ribosomes and smooth ER in its cytoplasm.



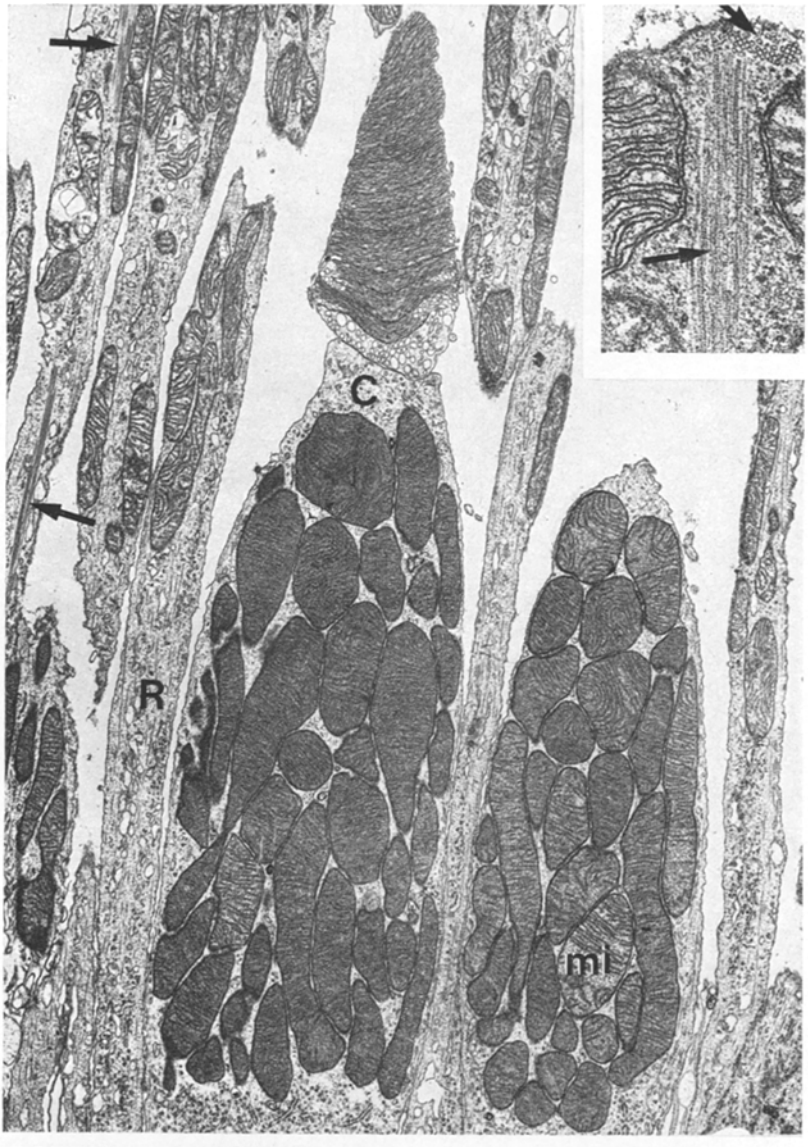
5



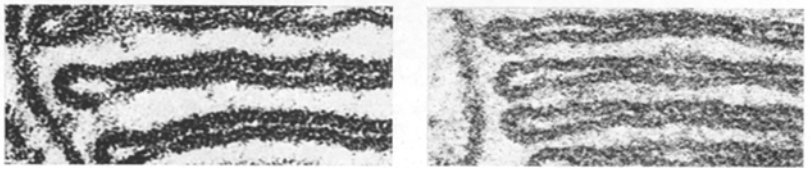
6

Fig. 5. Rod outer segment; tangential section surrounded by pigment epithelial microvilli (arrow). Magnification × 27000

Fig. 6. Tangential section through region of cone ellipsoid and rod myoid. Magnification × 7400



7



8a b

Single microtubules can be seen extending along the axis of the cell. A Golgi apparatus and lysosomes are also present.

b) The cone myoid shows a comparable arrangement of organelles, however it measures only 10 μm in length.

C. Outer Limiting Membrane and Nuclear Layer

The outer limiting membrane is a zonula adherens desmosome junction. Fiber baskets of the Müller cells can be seen surrounding the different photoreceptors at this level (Fig. 9).

The cone nuclei are found to be situated in the more external part of the nuclear layer, whereas the rod nuclei are situated in the internal parts.

D. Outer Plexiform Layer

The rod and cone's axons which extended approximately 12 μm in length down to the synapses, contain many single microtubules having a diameter of 200 Å and running the length of the axis. Smooth ER, free ribosomes and occasional mitochondria can be seen.

The rod spherule contains many synaptic vesicles with a diameter of about 550 Å; free ribosomes and smooth ER aggregates were seen as well as occasional neurotubules (Fig. 10). Synaptic ribbons contained the characteristic 3 dark and 2 clear bands and were measured to be 450 Å thick.

The cone pedicle's cytoplasm was similar to that of the rod's spherule, except for the synaptic ribbons, which were slightly shorter in the cone (Fig. 10).

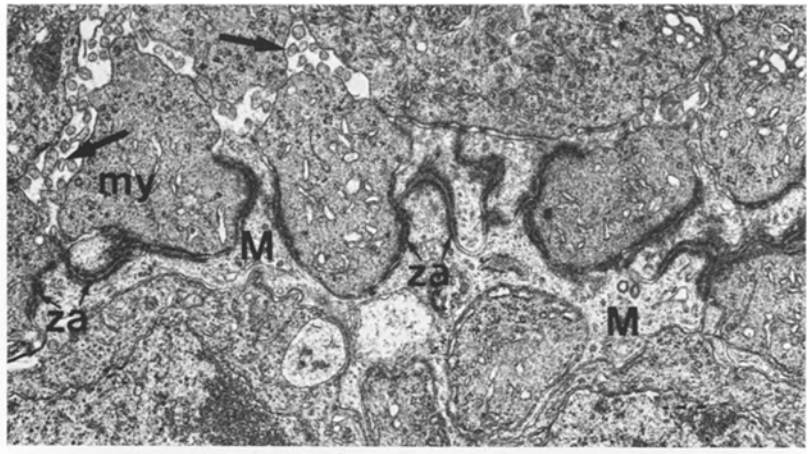
The inner zone of the outer plexiform layer is a complex mixture of horizontal, bipolar and Müller cell processes, the former often being much larger than the others (Fig. 11).

E. Inner Nuclear Layer

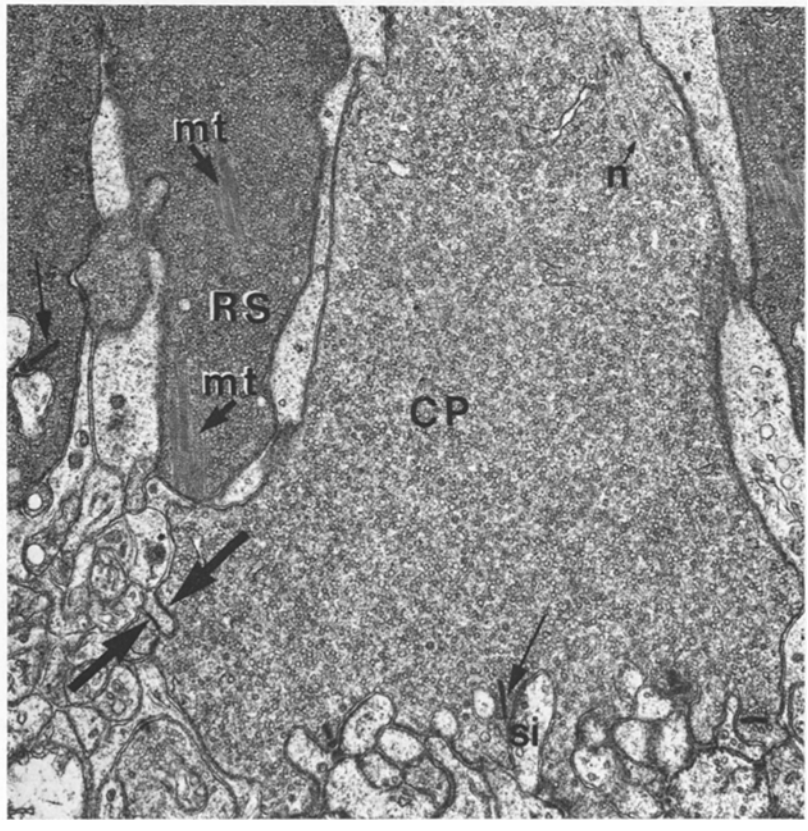
1. Horizontal Cells. These cells in the pig were found to be of an impressive size with a lighter, more regularly dispersed nucleoplasm in comparison with the surrounding cells. Their cytoplasm contains

Fig. 7. Cones surrounded by rod inner segments. Arrows points to microtubular structures in a rod. Note the impressive cone mitochondria with its mainly transversally oriented cristae. Magnification ×6750 Inset: Microtubular structure (arrows) in rod ellipsoid; tangential section. Magnification ×58500

Fig. 8. a Magnified view of cone discs. Magnification ×205000. b Magnified view of rod discs. Magnification ×201000. a and b The disc spacing as well as the thickness appears to be larger in the cones



9



10

numerous mitochondria, rough ER, free ribosomes, Golgi apparatus, single neurotubules and occasional smooth ER (Fig. 11). No crystal bodies, like those found in man (Yoshida, 1965), were observed. The horizontal processes can be very large and can be seen to cover a considerable area in the outer plexiform layer. Synaptic processes can, on the contrary, be small, leading to a more direct contact with the photoreceptor synapses (Fig. 12).

2. Bipolar and Amacrine Cells. The different types of bipolar cells identified in the primate (Boycott and Dowling, 1969), were difficult to distinguish in the pig. Their cytoplasm contained microtubules and relatively abundant mitochondria (Figs. 11 and 13).

Amacrine cells have indented nuclei, often showing prominent nucleoli (Fig. 13). Their cytoplasm is rich in cell organelles, notably a prominent Golgi apparatus and smooth ER. Dense bodies could also be seen. The mitochondria of the cells were seen to have a clear matrix with well defined cristae.

3. Müller Cells. The nuclei of these large cells is located in this layer. Here the perikaryon, as well as containing numerous smooth ER, was found to have a well developed rough ER. With favorable orientation, the darkly stained cisternae becomes more evident. Mitochondria with a granular ground substance and hardly discernable cristae were always present in these cells (Fig. 13).

F. Inner Plexiform Layer

This layer which tends to be thicker near the peripapillary region contains the neuronal and Müller cell processes, blood vessels and occasional astrocytes. Bipolar dendrites could be identified by the presence of a small synaptic ribbon. The cell processes containing free ribosomes were thought to be ganglion cell processes like that in man (Dowling, 1970); the amacrine processes containing neither ribosomes nor a synaptic ribbon. Granulated vesicles like those identified in the rat (de Iraldi and Etcheverry, 1967), were also seen in ganglion and amacrine cell processes (Fig. 14).

Fig. 9. External limiting membrane; tangential section. This structure is a junctional complex, "zonula adherens" (*za*) between Müller cell and photoreceptor myoid (*my*) cytoplasmic membranes. Note the Müller cell "fiber baskets" (arrow). Magnification ×11925

Fig. 10. Cone pedicle (*CP*) and rod spherule (*RS*), synapses showing synaptic ribbons (arrow), surface contact junctions, (thick arrows), and synaptic invaginations (*si*). Note the presence of the microtubular structures (*mt*). Magnification ×11700

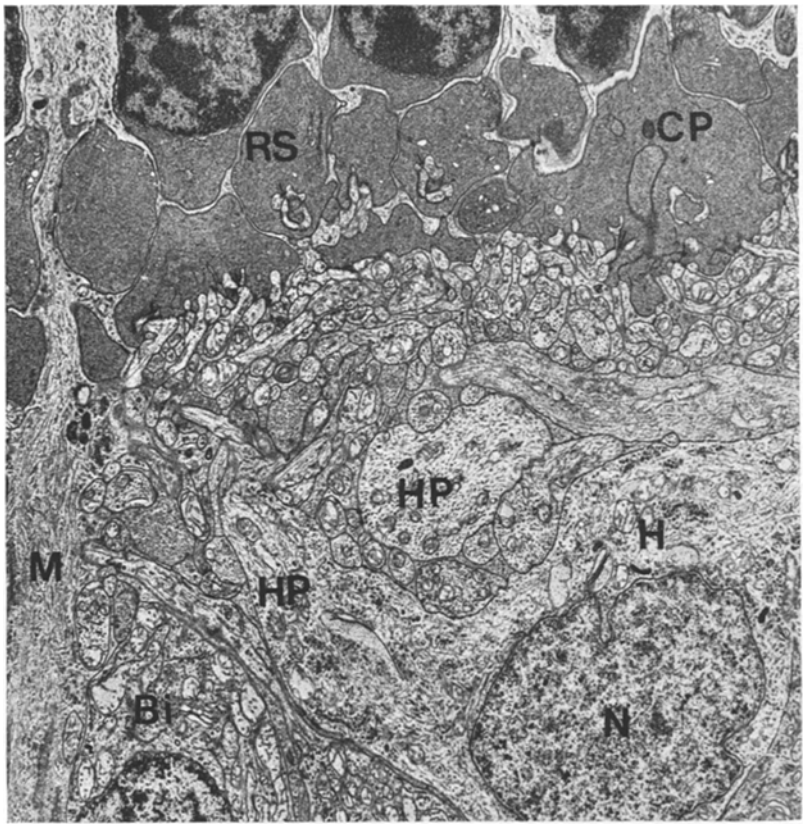


Fig. 11. Outer plexiform layer showing a horizontal cell (*H*), with lateral processes (*HP*), also seen cut transversally. *Bi* bipolar cells, *CP* cone pedicle, *RS* rod spherule. Magnification ×3750

G. Ganglion Cell Layer

This layer contains the different sized ganglion cells, some blood vessels, a few astrocytes and a network of branching Müller cell cytoplasm (Fig. 15). The ganglion cell's cytoplasm is rich in rough ER and free ribosomes, giving it a granular appearance. Mitochondria are also abundant, but we found difficult to preserve. The Golgi apparatus is well developed and lysosomes, neurotubules and smooth ER are found throughout the cytoplasm.

H. Nerve Fiber Layer

The ganglion cell axons contain many microtubules and microfibrils as well as mitochondria. The Müller cell cytoplasm is rich in smooth ER and free ribosomes along with numerous glycogen granules (Fig. 16).

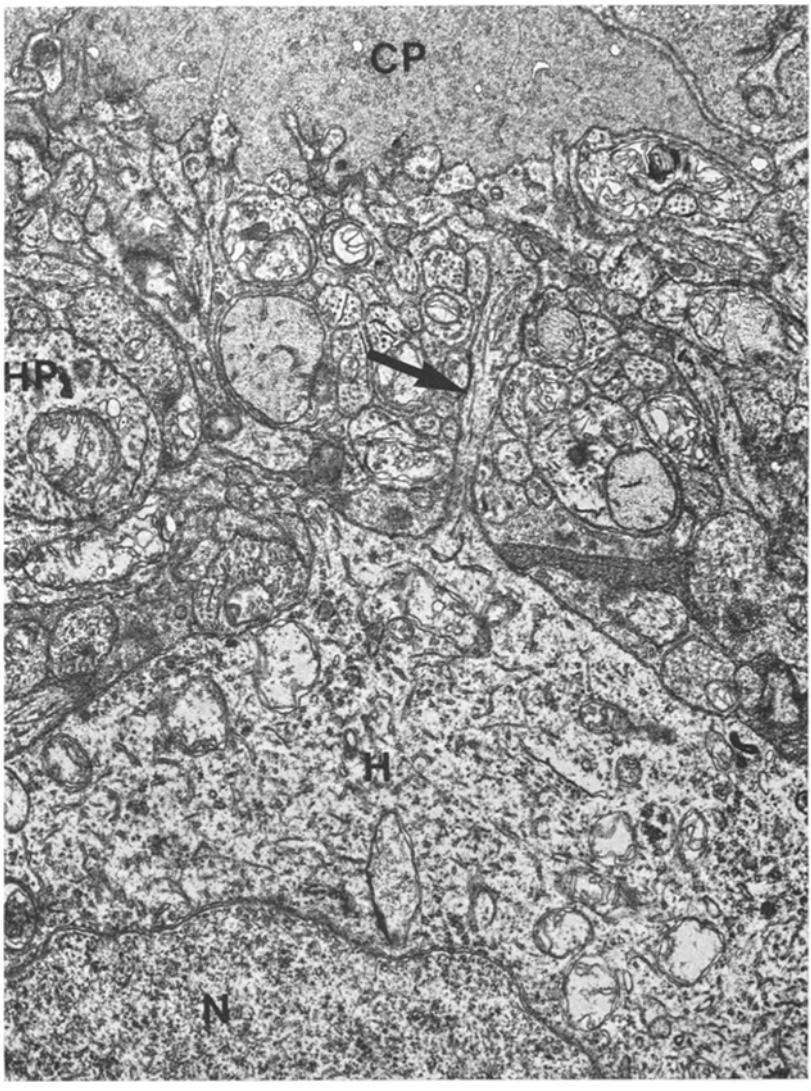
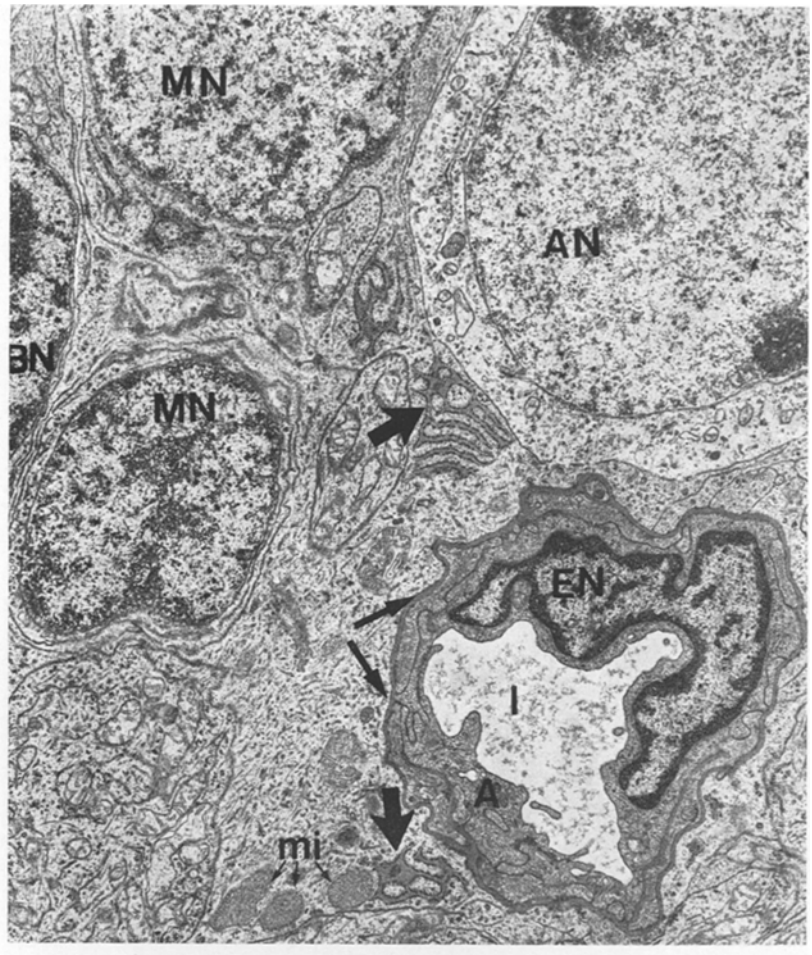
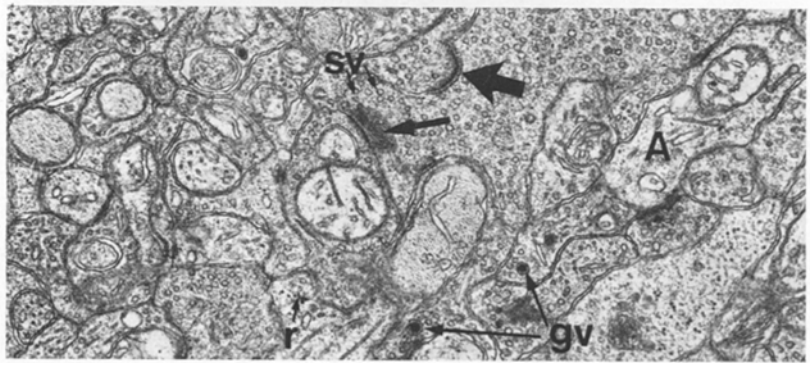


Fig. 12. Outer plexiform layer showing a horizontal cell (*H*), with a small process (arrow), branching toward a cone pedicle (*CP*). *HP* horizontal process cut transversally. Magnification ×12000

A rather large number of astrocytes were found in this layer. They are smaller than the ganglion cells and their nucleoplasm tends to have a darker stain. Their cytoplasm has abundant cell organelles and gives



13



14

off relatively long processes containing numerous microfilaments which branch into the surrounding cells.

The internal limiting membrane is a basement lamina of 250 to 300 Å in thickness, separating the Müller cell membrane or astrocyte membrane from the vitreous. In this region, large blood vessels which are mainly arterial can occasionally be seen lying rather superficially, appearing to protude into the vitreous.

J. Blood Vessels

The capillaries are of the closed type and their fine structural features resemble those of man. The basement membrane is continuous and may split into several layers of varying thickness, enclosing both endothelial cells and pericytes. An intimate contact can be observed between vascular basement membrane and surrounding glial cells (Fig. 13).

The arteries can have up to 10 endothelial cells lining their lumina and these, in turn, are surrounded by layers of smooth muscle fibers which are again enclosed by ramifications of basement membrane. The adventitia is made up of loosely packed collagen fibers.

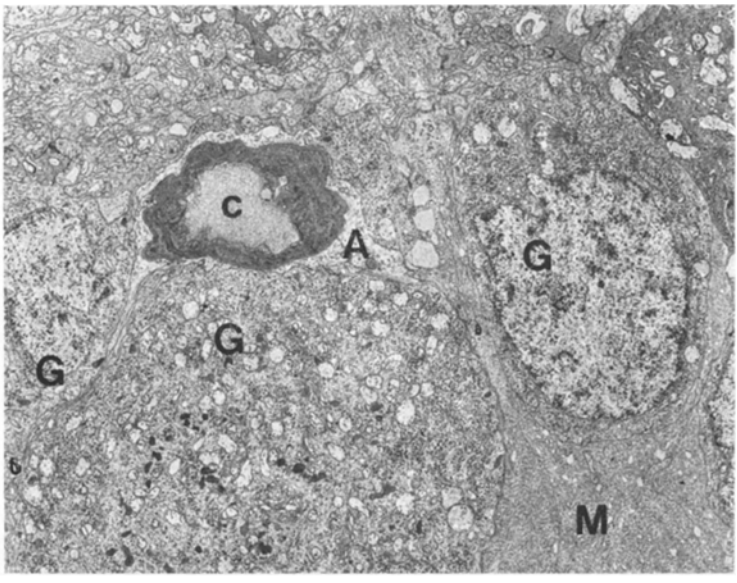
The veins have a larger lumen than the corresponding arteries and tend to have fewer smooth muscle fibers in their walls. They also appear to have a greater number of pinocytotic vesicles than the arterial vessels.

Discussion

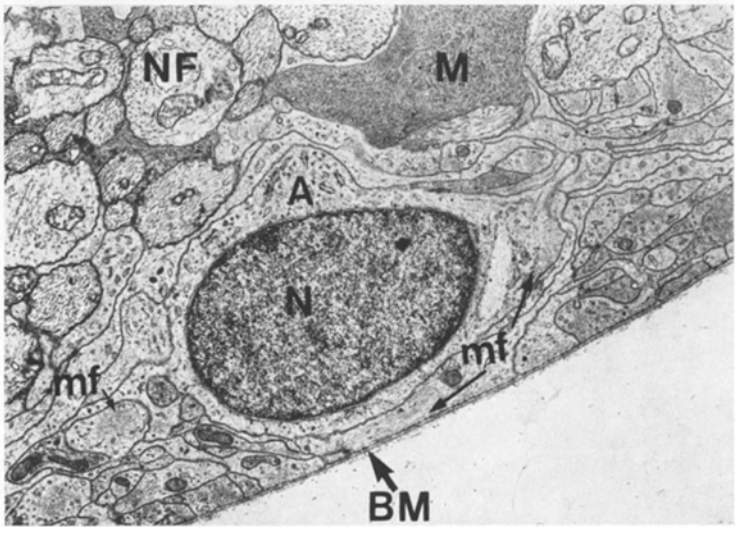
The basic ultrastructure of the pig's retina appears to have a rather typical primate-like architecture with the major exception that there is no fovea (Prince *et al.*, 1961; Bloodworth *et al.*, 1965). Instead the cones are found to be abundantly distributed among the rods throughout the entire retina. With the exception of the nerve fiber layer, the thickness of the different layers were quite parallel to those of man (Missotten, 1965; Hogan *et al.*, 1971). Contrary to Prince and coll. (1961), we found

Fig. 13. Inner nuclear layer showing a small arteriole (*A*), surrounded with a continuous basement membrane (small arrow). Note the well developed rough endoplasmic reticulum with a finely granular electron dense content (thick arrows), as well as mitochondria with a granular matrix and sparce cristae in the Müller cell cytoplasm. *AN* amacrine cell nucleus, *BN* bipolar cell nucleus, *EN* endothelial cell nucleus, *I* vascular lumen, *MN* Müller cell nucleus. Magnification ×6720

Fig. 14. Inner plexiform layer showing a synaptic ribbon (small arrow) and synaptic vesicles (*SV*) of a bipolar synapse along with surface contacts (thick arrow). Free ribosomes can be seen in a ganglion cell dentrite. *A* amacrine cell process, *gv* granulated vesicles. Magnification ×17550



15



16

Fig. 15. Ganglion cell layer showing three different ganglion cells (*G*). Astrocyte cytoplasm (*A*), containing many microfibrils, surround a capillary (*c*). Note the well developed Golgi apparatus and abundant lysosomes, in the ganglion cell cytoplasm. Magnification ×3000

Fig. 16. Nerve fiber layer showing an astrocyte (*A*) with its darkly stained nucleus and microfibril-containing *(mf)* cytoplasmic processes. *BM* inner limiting basement membrane, *NF* nerve fibers. Magnification ×6300

the dimensions of the inner plexiform layer to approach those of man, instead of being twice as thick. In the pig, the rod to cone ratio did not noticeably change throughout the retina.

The cones were found to be more conspicuous, especially the mitochondria of the ellipsoid. Their mainly transversally orientated cristae differed from man whose cristae are mainly longitudinally oriented and not as voluminous (Missotten, 1963a; Hogan *et al.*, 1971). These transverse cristae probably represent a very active metabolism (Karnovsky, 1963).

The presence of the microtubular structures seen mainly in the rods was not clearly understood, however, the fact that they were observed in most cases makes them noteworthy. Different microtubular or microfibrillar structures have been observed in the photoreceptor cells (Mountford, 1964; Sheffield, 1966; Cohen, 1969; Albert *et al.*, 1970; Leuenberger, 1972; Popoff, 1973) or in the synaptic neurons (Orzalesi and Bairati, 1964; Monneron *et al.*, 1965; Seite, 1969; Seite and Zerbib, 1972; Sengel and Stoebner, 1972). With the exception of Cohen (1969), none of these authors found such structures to extend from the ellipsoid level through to the synapes of the rod, as was observed in the pig's retina.

The glutaraldehyde fixative made measurements of the external segments of the rods and cones unsuitable (Borovjagin *et al.*, 1973; Godfrey, 1973), however measurements were made to allow comparative studies between rod and cone.

The tonofibrils of the pigment epithelium appear to be exceptionally well developed in the pig's retina.

The bipolar and amacrine cells appeared to have an ultrastructure quite similar to that of man's (Hogan *et al.*, 1971). The large size of the horizontal cells makes them a distinctive point for the pig.

The Müller cell perikaryon was also rather distinctive in the pig, due to the presence of the well developed rough ER with their fine granular cisternae. The presence of such structures was mentioned by Shakib and Ashton (1966), in the ischaemic pig. We, however, found these in all our pigs, 8 of which had not been under experimental treatment.

The ganglion cell's ultrastructure appears to be similar to man (Hogan *et al.*, 1971). They have approximately 3 sizes and are slightly more concentrated towards the peripapillary area and thin out towards the periphery.

The presence of numerous astrocytes in the more inner layers of the pig seemed to be another rather distinctive point.

The arrangement of the blood vessels in our study corresponded to that of Rootmen (1971). The ultrastructure of the blood vessels we found, like Bloodworth *et al.*, (1965), to be similar to that of man (Hogan and

Feeny, 1963), the lack of the "Swiss cheese effect" in the pig's basement membrane is probably simply a difference in age of the subjects examined.

The pig's retina, therefore, appears to have an ultrastructure that follows a basic mammalian, and often primate, retinal pattern with certain distinctive features, As such, I would conclude by saying that the pig and most notably the miniature pig whose small size is convenient for laboratory handling, appears to be a suitable model for future retinal studies.

Key to Abbreviations

C = cone cell
M = Müller cell cytoplasm
mi = mitochondria
n = neurotubule
N = nucleus
P = melanin granule
r = free ribosomes
R = rod cell

Acknowledgements. I would like to thank Professor J. Babel for his continuous encouragement and interest shown throughout this study, and also Dr. P. Leuenberger for his valuable suggestions and criticism. Thanks also go to Dr. M. Tsacopoulos for his generous contribution of the miniature pig's eyes.

References

Albert, D. M., Dalton, A. J., Rabson, A. S.: Microtubules in retinoblastoma. Amer. J. Ophthal. **69**, 296–299 (1970)

Bloodworth, J. M. B., Gutgesell, H. P., Engerman, R. L., Retinal vasculature of the pig. Light and electron microscopic studies. Exp. Eye Res. **1**, 174–178 (1965)

Borovjagin, U. L., Ivania, T. A., Moshkov, P. A.: The ultrastructural organisation of the photoreceptor membranes and the intradisc spaces of the vertebrate retina as revealed by various experimental treatments. Vision Res. **13**, 745–752 (1973)

Boycott, B. B., Dowling, J. E.: Organisation of the primate retina: light microscopy. Phil. Trans. B **255**, 109 (1969)

Cohen, A. I.: Vertebrate Retinal Cells and their organisation. Biol. Rev. **38**, 427–459 (1963)

Cohen, A. I.: Rods and cones and the problem of visual excitation. In: Straatsma: The retina, p. 31–62. Los Angeles: Unif. Calif. Press 1969

Dowling, J. E.: Organisation of vertebrate retinas. Invest. Ophthal. **9**, 655–680 (1970)

Dowling, J. E., Boycott, B. B.: Organisation of the primate retina. Electron Microscopic studies. Proc. roy. Soc. B **166**, 80 (1966)

Godfrey, A. J.: A study of the ultrastructure of visual cell segment membranes. J. Ultrastruct. Res. **43**, 228–246 (1973)

Hogan, M. J., Alvarado, J. A., Weddell, J. E.: Histology of the human eye. An atlas and textbook. Philadelphia-London-Toronto: W. B. Saunder & Co. 1971

Hogan, M. J., Feeney, L.: The ultrastructure of the retinal vessels. I. The large vessels. II. The small vessels. J. Ultrastruct. Res. **9**, 10–28, 29–46 (1963)

Iraldi, A. P. de, Etcheverry, G. J.: Granulated vessels in retinal synapses and neurons. Z. Zellforsch. **81**, 283–294 (1967)

Karnovsky, M. J.: The fine structure of mitochondria in the frog nephron correlated with cytochrome oxidase activity. Exp. Molec. **2**, 347–366 (1963)

Leuenberger, P.: Mikrofibrilläre, kristallartige Einschlüsse in den Photoreceptorsynapsen der menschlichen Netzhaut. J. Microscopie **15**, 79–84 (1972)

Missotten, L.: L'ultrastructure des cônes de la rétine humaine. Bull. Soc. belge Ophtal. **132**, 472–502 (1963a)

Missotten, L.: The ultrastructure of the human retina. Brussels Arscia Uitaven, N. V., 1965

Monneron, A., Cotte, G., Seite, R.: Corps microfibrillaires dans les axons des neurones vigitatifs de mamifères. J. Microscopie **4**, 91–94 (1965)

Mountford, S.: Filamentous organelles in receptor-bipolar synapses of the retina. J. Ultrastruct. Res. **10**, 205–216 (1964)

Moyer, F. H.: Development, structure and function of the retinal pigmented epithelium, p. 1–30. In: Straatsma: The retina. Los Angeles: Univ. California Press 1969

Orzalesi, N., Bairati, A.: Filamentous structures in the inner segment of the human retinal rods. J. Cell Biol. **20**, 509–514 (1964)

Popoff, N. A.: Filamentous alterations in photoreceptors from human eyes with retinoblastoma. J. Ultrastruct. Res. **42**, 244–254 (1973)

Prince, J. H., Diesem, C. D., Eglitis, I., Ruskell, G L.: Anatomy and histology of the eye and orbit in domestic animals. Springfield, Ill.: Ch. C. Thomas 1961

Rootman, J.: Vascular system of the optic nerve head and retina in the pig. Brit. J. Ophthal. **55**, 808–819 (1971)

Seite, R.: Recherches sur l'ultrastructure, la nature et la significance des inclusions microfibrillaires paracrystallines des neurones synaptiques. Z. Zellforsch. **101**, 621–646 (1969)

Seite, R., Zerbib, R.: «Boules homogènes» de Nageotte et inclusions microfibrillaires dans les neurones sympathiques chez le chien. J. Microscopie **13**, 107–108 (1972)

Sengel, A., Stoebner, P.: Inclusions microfibrillaires paracristallines intraneuronales chez l'homme. J. Microscopie **15**, 395–398 (1972)

Shakib, M., Ashton, N.: Focal retinal ischaemia. Part II. Ultrastructural changes in focal retinal ischaemia. Brit. J. Ophthal. **50**, 325–384 (1966)

Sheffield, J. B.: Microtubules in the outer nuclear layer of the rabbit retina. J. Microscopie **5**, 173–180 (1966)

Sjöstrand, F. S.: Electron microscopy of the retina: the structure of the eye, ed. G. K. Smelser, p. 1–28. New York: Academic Press 1961a

Tsacopoulos, M., Baker, R., Johnson, M., Strauss, J., David, N. S.: The effect of arterial P_{CO_2} on inner retinal oxygen availability in monkeys. Invest. Ophthal. **12**, 449–455 (1973)

Yoshida, M.: The fine structure of the so-called crystalloid body of the human retina as observed with the electron microscope. J. Electron Micr. **14**, 285–289 (1965)

Marie Louise Beauchemin, B. Sc.
Clinique Universitaire d'Ophthalmologie
CH-1205 Genève
Schweiz