THE RETINA OF CEPHALOPODS AND ITS DEGENERATION AFTER OPTIC NERVE SECTION

By J. Z. YOUNG, F.R.S.

Department of Anatomy, University College London

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CONTENTS

Each retinal cell of *Octopus* carries a rhabdomere on two opposite faces. Rhabdomeres from four cells combine to make a square rhabdome. The cells are mainly arranged with their axes in approximately either the vertical or horizontal plane as the eye is usually held in the head. Counts show that there are about twice as many retinal cell nuclei as there are rhabdomes. There are altogether about 2×10^7 retinal cells in each eye, with a density of about 50000/mm^2.

The retinal cells at the centre of the retina are longer and thinner than those at the periphery. There is a strip of longer, thinner cells running horizontally along the equator. These often have less pigment in their distal ends than do the cells dorsally and ventrally, but other distributions of the pigment are seen, depending on the previous illumination.

There are several types and sizes of retinal cell and not all are associated in fours to make rhabdomes.

The proximal segments carry fine collateral twigs, these interdigitate and may allow mutual interaction between neighbours. The main meshes of the retinal plexus are not formed by fibres of the retinal cells but by the axons of cells in the optic lobes, presumably efferents.

After severing the optic nerves to any region of the retina all the retinal cells undergo retrograde degeneration, leaving only the supporting cells intact. The retinal nerve plexus disappears almost completely, but a few fibres remain. At the boundary between a region with severed and intact nerves the plexus continues for some distance into the denervated region.

After removal of all the optic lobe except a portion of its outermost (plexiform) zone the retinal receptors do not degenerate completely but are reduced in length. Their axons have not been interrupted by the operation and this is therefore a partial transneuronal retrograde degeneration.

1. Introduction

The early accounts of the cephalopod retina, though satisfying in many respects, leave uncertain various questions that are of importance for the understanding of the ultrastructure and functioning. Some problems dealt with in the present work are:

(1) the arrangement of the receptor elements (retinal cells and rhabdomes) in relationship to the main symmetry planes of the animal;

(2) their number and density of distribution;

(3) the numbers of the various types of nuclei in the retina;

(4) the nature of the nerve plexus in the retina and of the endings of centrifugal (efferent) fibres there.

(5) in addition it was found that after section of optic nerve fibres the retinal cells, from which these fibres originate, rapidly degenerate. Some details of this interesting retrograde degeneration are described. Inferences can be drawn from it about the nature of the various cells in the retina.

A problem of nomenclature arises in relation to the orientation of 'inner' and 'outer' in the eye. The rhabdome-carrying segments of the retinal cells, directed towards the light, will be called the distal (outer) segments, the nuclear region being proximal (inner)

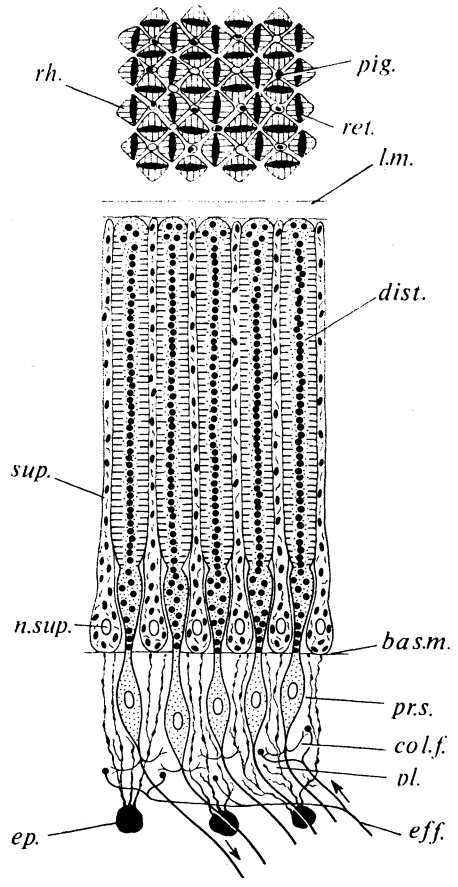

Figure 1. Diagrams of some features of the retina of *Octopus*; above as seen in tangential section and below in radial section. The cells are shown with considerable simplification, especially the supporting cells and epithelial cells.

(figure 1). This gives the tubule-containing photosensitive region the same name as the comparable region in vertebrates ('outer segment'), although the latter points away from the light. To avoid confusion the terms inner and outer have been used as sparingly as possible.

ABBREVIATIONS USED ON TEXT-FIGURES AND PLATES

ax.	axon of retinal cell.
bas.	basal pigmented region of distal segment.
bas.m.	basal membrane.
ch.	choroid layer.
col. ?	long fibre that may be a collateral.
col.f.	fine dendritic collateral of retinal cell.
col.l.	large collateral, perhaps an artifact.
dist.	distal segments.
eff.	ending of efferent fibre in retina.
ep.	epithelial cell.
gl.	glial material around proximal segments.
l.m.	limiting membrane.
mac.	spaces in degenerating retina (? occupied by macrophages).
mac.dist.	macrophages in position of distal segments.
mac.prox.	macrophages in position of proximal segments.
n.bas.m.	nuclei of basal membrane.
n.f.	nerve fibre near sclera, perhaps innervating retinal muscle.
n.ret.	nuclei of retinal cells.
n.sup.	nuclei of supporting cells.
o.l.	optic lobe.
o.n.	optic nerve.
pig.	granule of pigment at centre of rhabdome.
pl.	retinal nerve plexus.
pl.^{1}	outer portion of the nerve plexus where the fibres collect together and run tangentially.
pr.s.	proximal segments of retinal cells.
r.	ring of cells at edge of retina attached to limiting membrane.
ret.	retinal cell.
ret.c.	pigmental protoplasm of retinal cell.
rh.	rhabdome.
rm.	rhabdomere.
sc.	sclera.
str.	strip where there is little pigment in the distal region of the retina.
sup.	processes of supporting cells.
t.	distal pigmented tip of retinal cell.
u.t.	region where the distal tips of the retinal cells are not pigmented.
u.t.^{1}	transition region where there is some pigment in the distal tips of the retinal cells.
v.	retinal vein.

2. METHODS

Young *Octopus vulgaris* (100 to 500 g) were mainly used and, immediately after killing by decapitation, the eyes were fixed by immersion in 10% neutral formol in sea water. They were mostly stained by Cajal's method (Young 1939), embedded in paraffin and cut 5 μ thick in either radial or tangential planes. Some of the eyes were measured after fixation. Pieces were then cut from various parts of the retina, each piece being rectangular so that the orientation of elements in different parts of the eye was obtained.

Some sections were bleached with chlorine and then stained either with haematoxylin and eosin, Masson's trichrome stain or Holmes's silver method. The Kopsch variation of the Golgi method provided some very useful preparations.

Degeneration of the retina was studied after section of some or all of the optic nerve fibres under urethane anaesthesia.

Some observations were made on sections of the eyes of other octopods and of *Sepia*.

3. Arrangement of the rhabdomes

Schultze (1869) called attention to the rather regular arrangement of the elements of the cephalopod retina, forming a pattern of squares, though earlier workers such as Babuchin (1864) and Hensen (1865) had already shown some evidence of this. Grenacher (1883–6) showed that each square could be compared with an arthropod rhabdome and that the basic units were cells with thickenings on two sides (figure 1). Each 'rhabdome' is thus composed of the halves of four cells. It has been shown that the individual thickenings ('rhabdomeres') consist of sets of tubules (Wolken 1958; Moody & Robertson 1960). Several of the early reports show that the rhabdomes are arranged in fairly regular rows, and further examination now shows that these rows lie mainly in the vertical and horizontal directions. This may be of importance in connexion with the capacity of the animals to detect the plane of polarized light (Moody & Parriss 1960, 1961).

It is thus suggested that the true unit of the retina is the retinal cell, including the rhabdomeres belonging to two neighbouring rhabdomes and a proximal segment with nucleus. Although there is still no complete proof of this, the data here provided, especially the counts of the numbers of rhabdomes and nuclei, make it probable.

At their extreme distal (posterior chamber) ends the pigment-containing regions project for a short distance as distinct rounded caps (figure 2, plate 1). Each of these is interpreted as being the outer end of a retinal cell. Slightly more proximally the rhabdomes assume the characteristic pattern of squares (figure 3, plate 1). The pigmented portions appear oval in section and are set mainly approximately in vertical and horizontal directions, as the eye is normally held with the pupil horizontal (Wells 1960). The sections show many deviations from a regular arrangement, though it is difficult to decide how far these are the result of distortion during preparation. Individual pigmented regions may be inclined at slight angles to the main planes. Neighbouring elements are lined up to make short rows, but the whole area does not present the appearance of a completely regular grid. Moreover, there are probably many retinal cells not associated in fours to make a rhabdome, that is to say the unit retinal cells with their two rhabdomeres may remain separate from each other. This applies especially to the smaller ones (p. 8).

Here and there a small round granule of pigment appears at the centre of a rhabdome (figure 3). These may perhaps lie in the processes of supporting cells, which extend between the retinal cells (p. 10). Some of them may be small retinal cells, which other evidence suggests exist among the large ones that form the square rhabdomes (p. 8).

In the more proximal parts of the distal segments the square pattern is less apparent (figure 4, plate 1). The pigment is here less abundant (in a light-adapted retina) and forms narrow lines of granules, on either side of which appears a material lightly stained with silver, which is presumably the rhabdomere. The fact that these lie in pairs is more readily apparent at this level than any other. The reverse picture of the retinal cells is seen if the section has been bleached and stained with haematoxylin and eosin (figure 6, plate 2). The rhabdomeres now appear more darkly stained than the bodies of the cells. The arrangement in pairs can again be seen, with many departures from regularity.

At the innermost end of the distal segment the rhabdomes cease and there is a zone heavily loaded with pigment (figure 8, plate 2). This was called by Grenacher (1883–6)

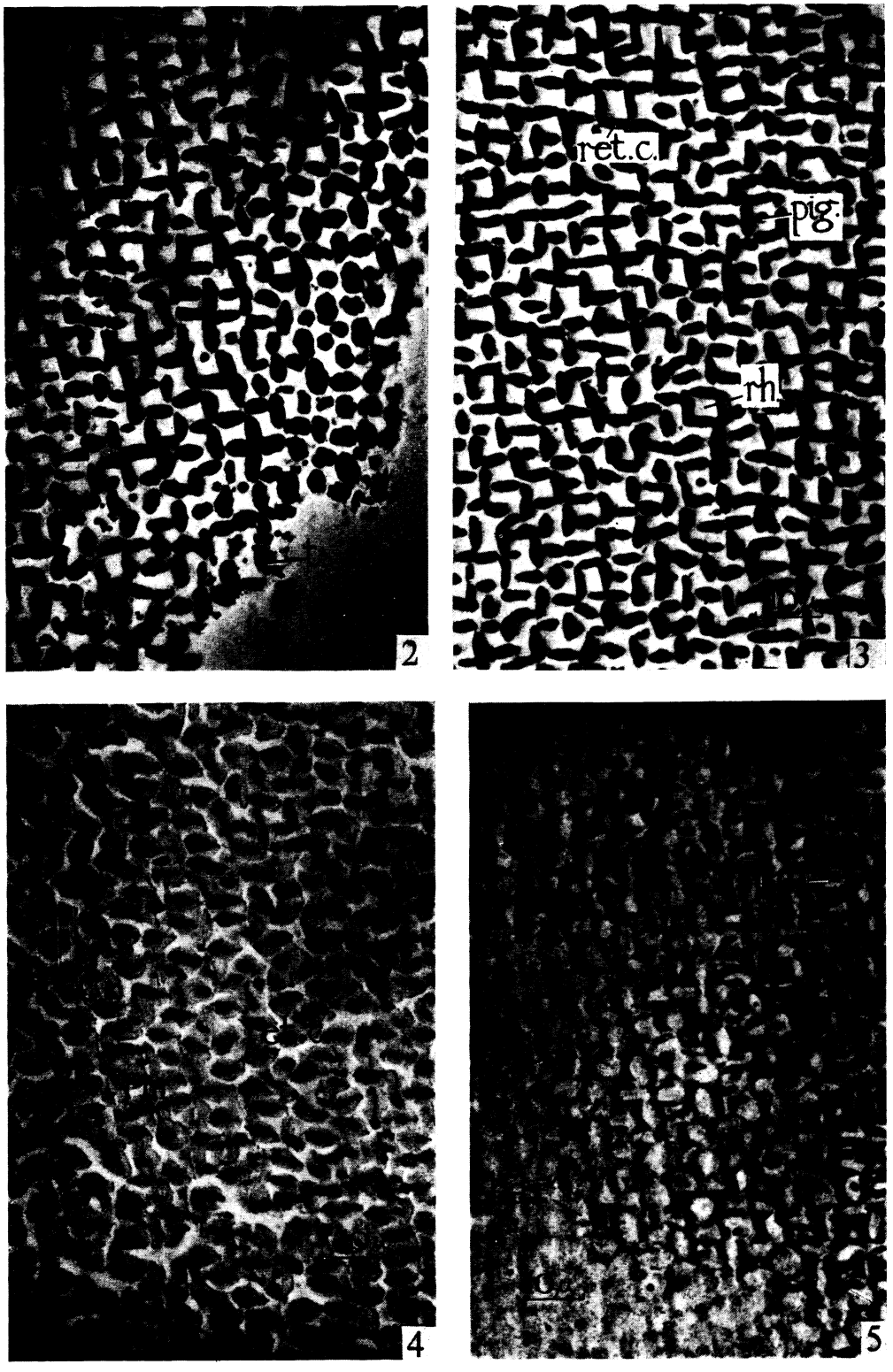

FIGURE 2. Tangential section at extreme distal margin of light-adapted retina. To the right are seen the separate pigmented tips of the distal segments (*t*). To the left the retinal cells are largely grouped to make rhabdomes. In this and the next three figures the long axis of the figure is approximately in the vertical plane. Cajal's stain.

FIGURE 3. Tangential section more proximal than figure 2, showing the rhabdomes. Cajal's stain.

FIGURE 4. Tangential section still further proximally. Here there is less pigment in the retinal cells. The square rhabdomes are now less evident and the unit retinal cells with their two rhabdomeres can be seen. Cajal's stain.

FIGURE 5. Tangential section at the base of the distal segments after bleaching and staining with haematoxylin and eosin. At the top and right the rhabdomeres can still be seen, darkly stained. Towards the bottom left the outlines of the basal pigmented regions (spindles) appear faintly.

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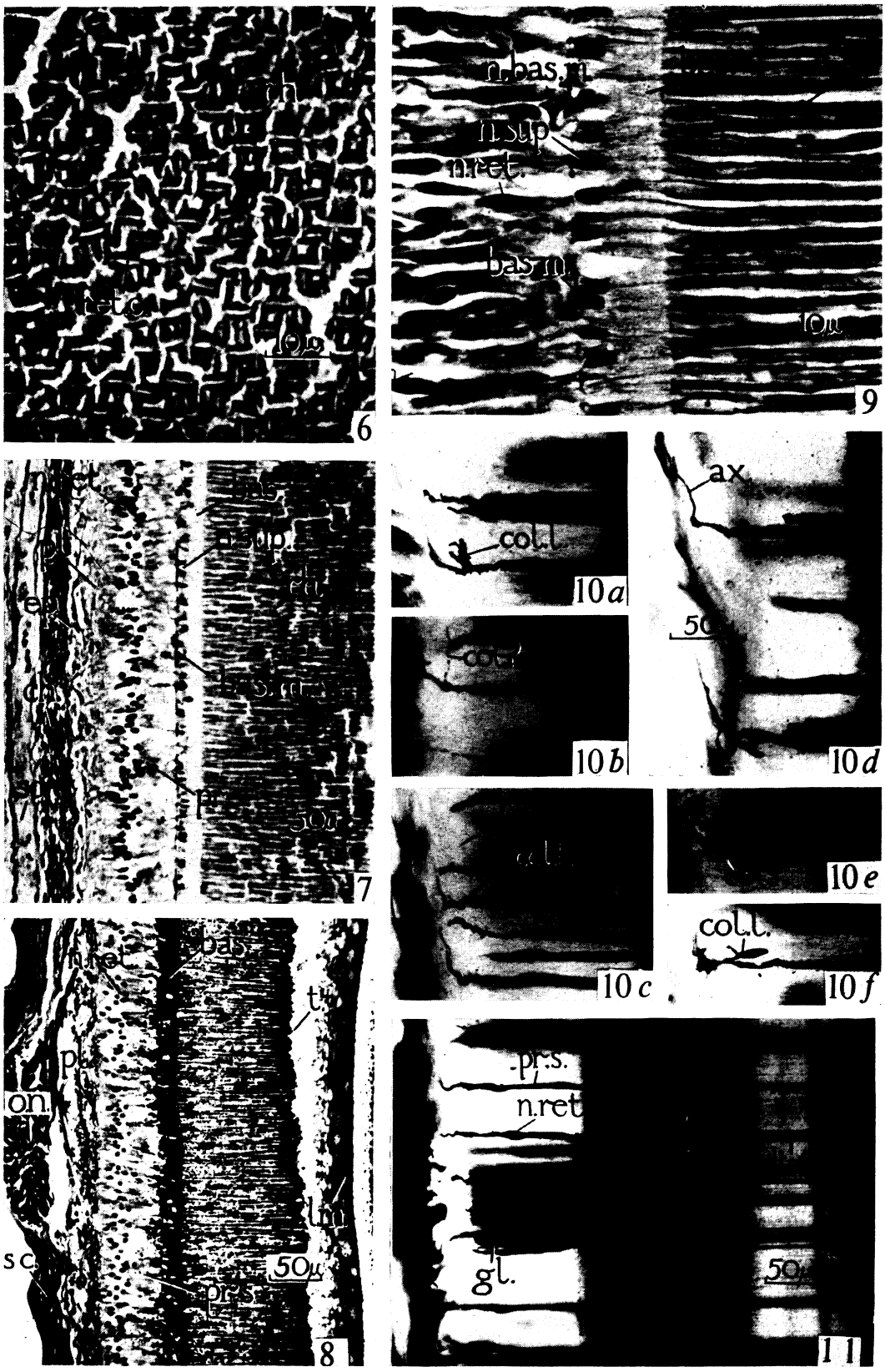


FIGURE 6. Tangential section at middle of distal segment to show rhabdomes after bleaching and staining with haematoxylin and eosin.

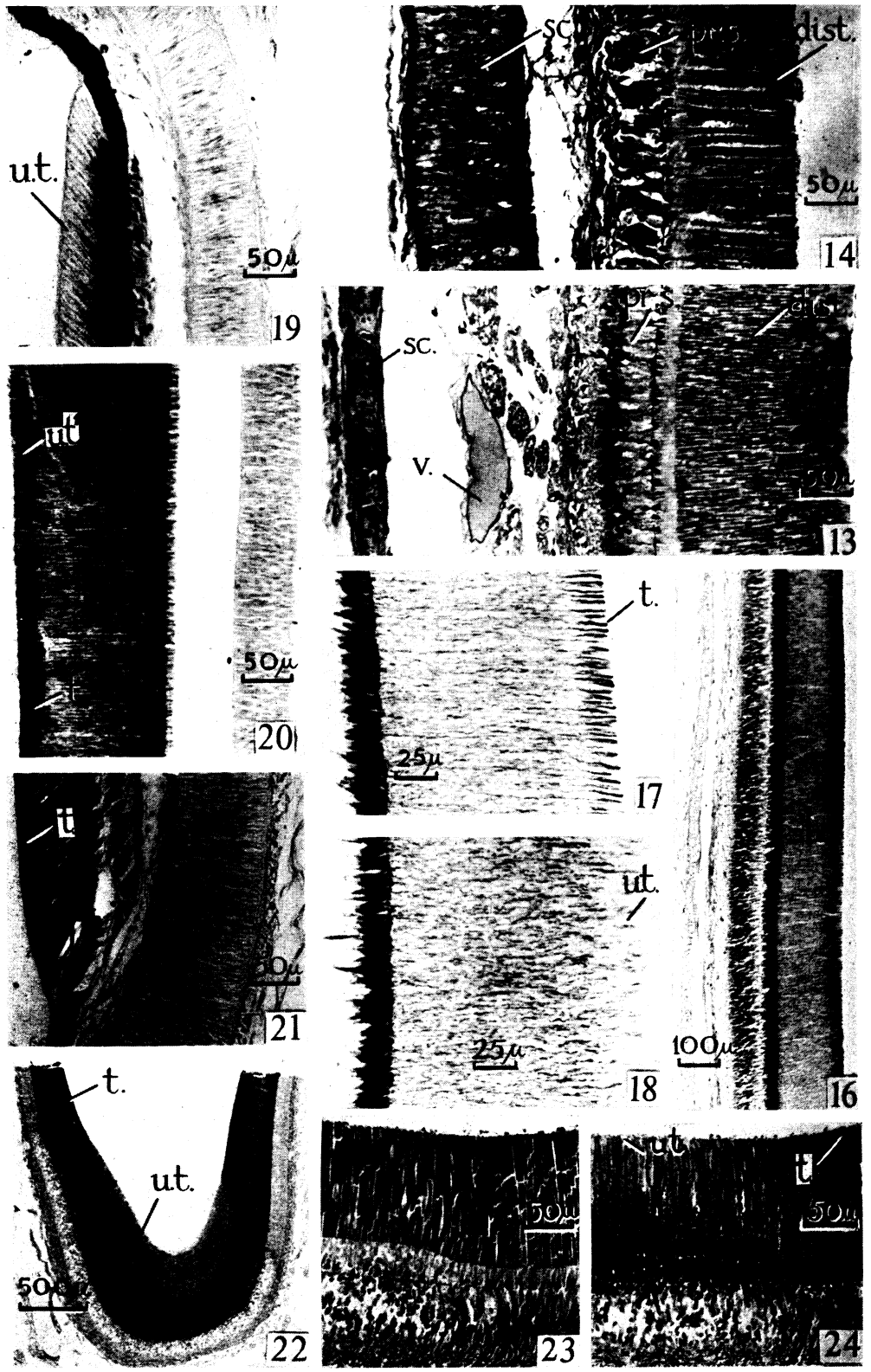
FIGURE 7. Radial section to show the various components of the retina. (Formol fixed, bleached, haematoxylin and eosin.)

FIGURE 8. Similar section to figure 7 but unbleached and stained with Cajal's stain.

FIGURE 9. Higher magnification of preparation similar to figure 7 to show the inner ends of the rhabdomes, supporting cells and proximal segments.

FIGURE 10*a* to *f*. Proximal segments of various retinal cells showing their axons and collateral dendrites of various shapes. (Golgi–Kopsch.)

FIGURE 11. Radial section of whole retina after Golgi–Kopsch staining. Complete units are stained, the distal segments being very straight, the proximal more irregular.



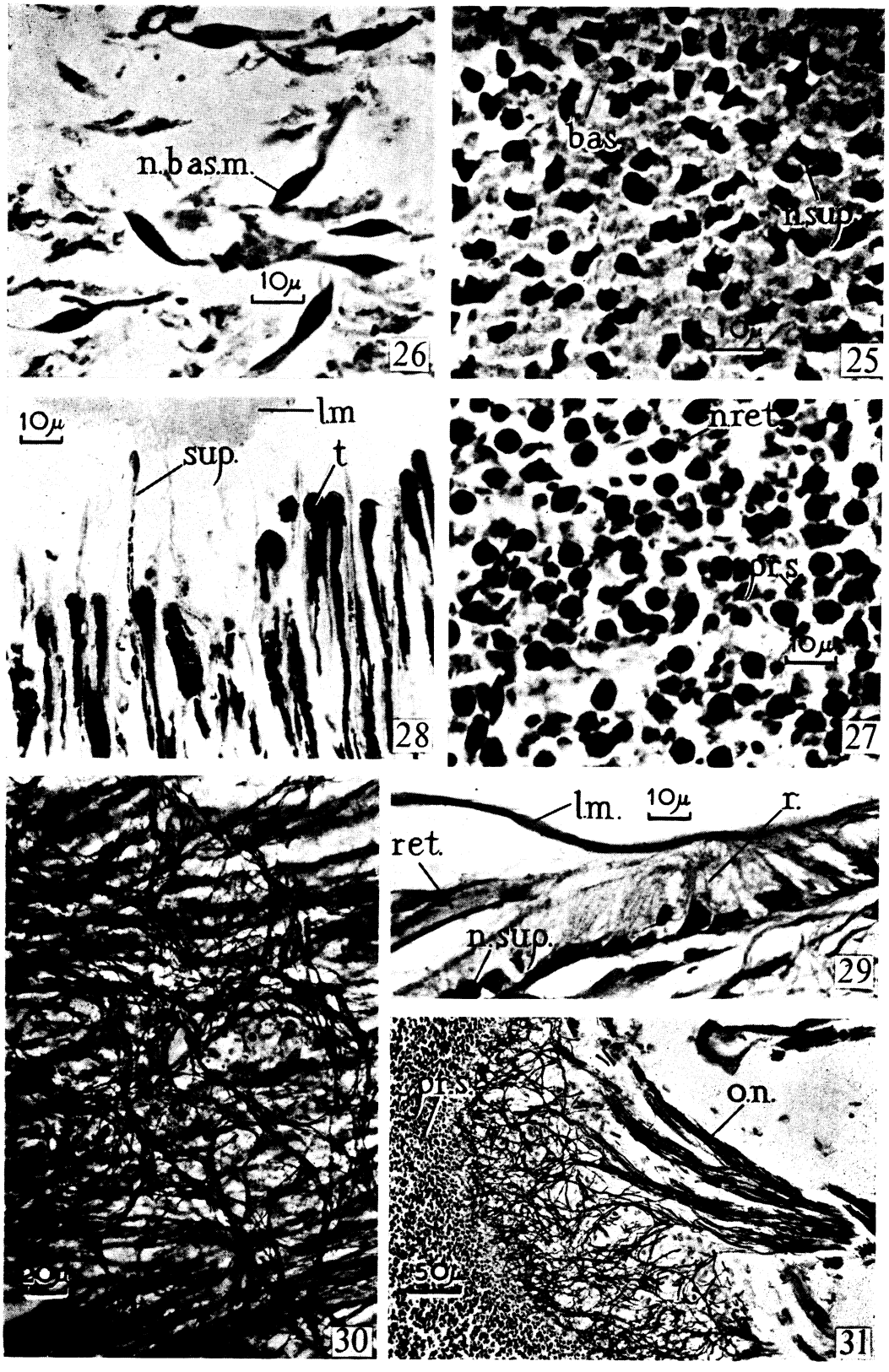
FIGURES 13 and 14. Radial sections from one retina to show differences between the central and peripheral regions, in preparations fixed in formalin, bleached, and stained with haematoxylin and eosin.

FIGURE 16. Centre of the light-adapted retina of *Eledone* to show the strip in which there is little pigment in the distal ends of the retinal cells. (Formalin, haematoxylin and eosin.)

FIGURES 17 and 18. Regions of the light-adapted retina of *Octopus* with and without pigment in the distal ends of the retinal cells. (Formalin, no staining.)

FIGURES 19 to 21. Sections from the dorsal, central and ventral regions of the retina of an octopus where there was distal pigmentation ventrally but not dorsally. (Bouin, haematoxylin and eosin.)

FIGURES 22 to 24. Sections of a region of the retina in the anterior dorsal quadrant where the pigment had retreated locally from the distal regions and there were also changes in the proximal segments. Figure 23 is from a section bleached and stained with haematoxylin and eosin.



FIGURES 25 to 27. Tangential sections of the nuclei of the supporting cells (25), basal membrane cells (26) and retinal cells (27). (Formalin, bleached, haematoxylin and eosin.)

FIGURE 28. Radial section near the margin of the retina where the retinal cells have shrunk away from the limiting membrane, leaving some fibres of the supporting cells, containing pigment. (Formalin, unstained.)

FIGURE 29. Radial section of the margin of the retina. Beyond the last retinal cell (*ret.*) the layer of supporting cells continues and makes a ring of cells (*r.*) apparently attached to the limiting membrane. (Formalin, bleached, haematoxylin and eosin.)

FIGURES 30 and 31. The retinal nerve plexus and origin of the optic nerves. (Cajal.)

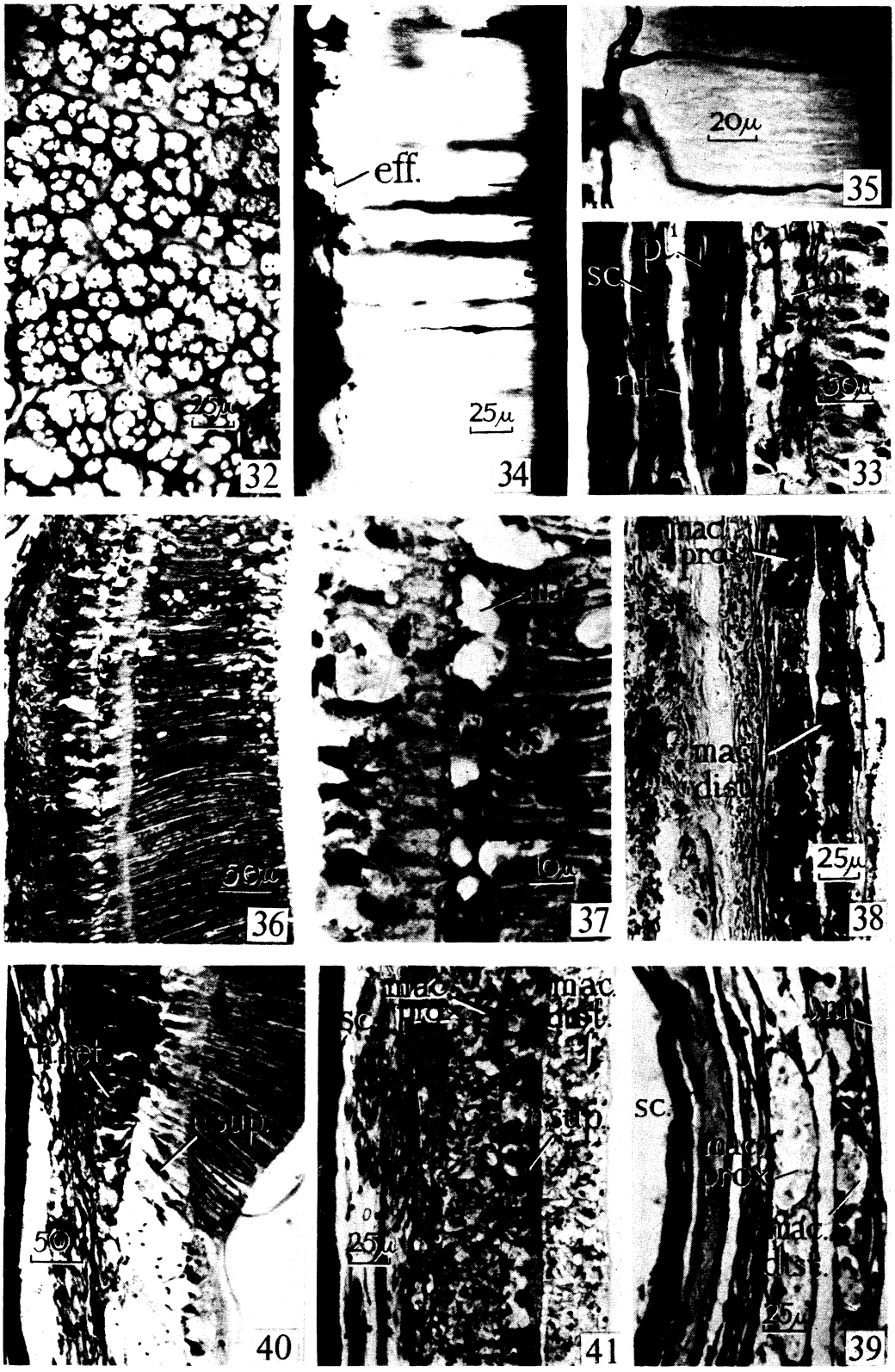


FIGURE 32. Tangential section of basal membrane showing the holes through which the retinal cells pass. (Golgi–Kopsch.)

FIGURE 33. Radial section of retinal nerve plexus to show its inner 'synaptic' and outer 'collecting' components. Isolated nerve fibres near the sclera perhaps innervate retinal muscles. (Cajal.)

FIGURE 34. Radial section to show fine beaded fibres running tangentially. These are probably the endings of the efferents to the retina. (Golgi–Kopsch.)

FIGURE 35. Radial section showing capillaries among the proximal segments. (Golgi–Kopsch.)

FIGURE 36. Radial section at the boundary of normal and denervated regions in a retina where the optic nerves had been cut 10 days previously and degeneration is beginning. (Formalin, bleached, haematoxylin and eosin.)

FIGURE 37. Higher magnification of the degenerating region of figure 36.

FIGURES 38 and 39. Radial section of retina 31 days after section of the optic nerves. (39 is bleached and stained with haematoxylin and eosin.)

FIGURE 40. Margin of normal and degenerated regions 32 days after severing some optic nerves. The retinal cell nuclei have disappeared from the denervated region but the layer of supporting cells continues. (Formalin, bleached, haematoxylin and eosin.)

FIGURE 41. Retina 9 days after severing the optic nerves. The retinal cells have disappeared leaving the supporting cells. (Formalin, bleached, haematoxylin and eosin.)

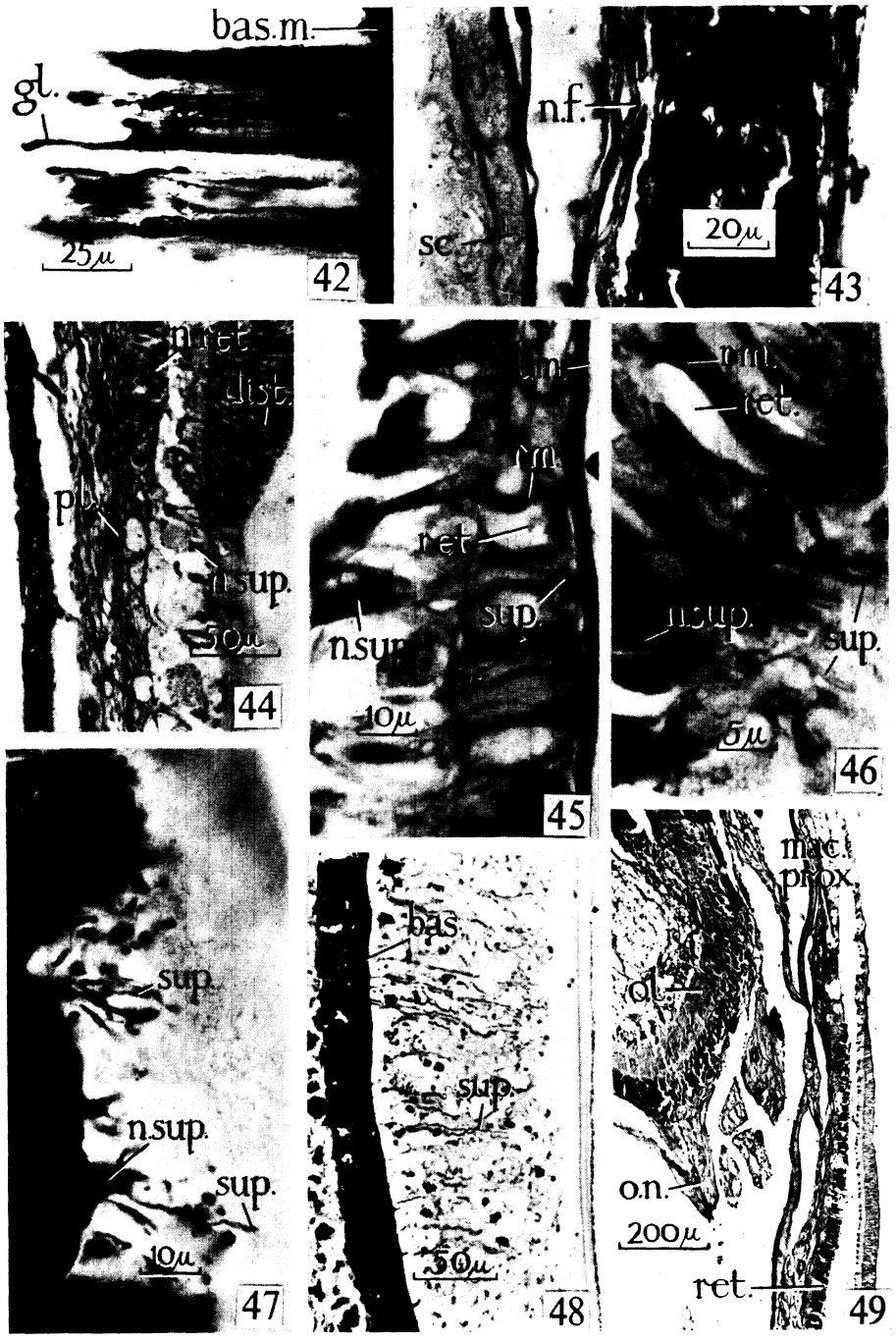


FIGURE 42. Sheets of supporting tissue (glia) that lie around the proximal segments and are perhaps produced by the epithelial cells. (Golgi–Kopsch.)

FIGURE 43. Nerve fibre persisting in retina 42 days after section of the optic nerves. (Cajal).

FIGURE 44. Extension of plexus beyond margin of intact and denervated regions 39 days after section of the optic nerves. (Cajal.)

FIGURE 45. Region where the retinal cells are much reduced in height (see figure 49). The processes of the supporting cells can be seen between them, proceeding to the limiting membrane. (Formalin, bleached, haematoxylin and eosin.)

FIGURE 46. Supporting cells with many processes at the boundary of innervated and denervated region 39 days after section of some optic nerves. (Formol, Mallory.)

FIGURE 47. Supporting cells and their processes at margin of intact and denervated areas 39 days after severing optic nerves. (Cajal.)

FIGURE 48. Persistent processes of supporting cells during the course of degeneration of the retinal cells nine days after severing the optic nerves. (Cajal.)

FIGURE 49. Persistence of part of the periphery of the optic lobe 31 days after severing the optic tract. The retinal cells have survived where they are connected with intact optic lobe tissue, but they are much reduced in length. (Formalin, bleached, haematoxylin and eosin.)

the 'Stäbchensockel', by v. Lenhossék (1894) 'Stäbchenspindel'. We may keep the name 'spindle region' or 'basal spindle'. After bleaching and staining, the place at which the rhabdomeres end can be seen clearly and both radial (figure 9, plate 2) and tangential sections (figure 5, plate 1) show that more proximally the central part of each unit continues as a single fibre-like structure.

Each fibre can be traced inwards through a basal membrane (figure 32, plate 5) to become a single proximal retinal fibre, with a nucleus near the middle of its length. The nuclei are oval in radial section (figure 9), circular in tangential section (figure 27, plate 4). Although they are collected at the middle of this zone they do not form a single row, but are packed at slightly differing levels. The proximal segments have in general a cylindrical form, the smaller ones being dilated at the nucleus. Each of them is sheathed in glial material (see below). This glia terminates proximally at the level of the retinal nerve plexus and here the inner segment swells slightly and shows an irregular outline in Golgi preparations, carrying numerous short collateral branches, some terminating in swellings (figures 10, 11, plate 2). There can be little doubt that these collaterals make synaptic contact with the efferent fibres that end in the retina and perhaps also with each other (see later). Proximal to this region of synapses in the nerve plexus the inner segments taper to form axons. They run directly into an optic nerve nearby, without entering into any crisscrossing arrangement in the plexus. Each retinal cell thus consists distally of a cylinder of protoplasm, carrying two rhabdomeres, and attached to a nucleated proximal segment from which dendritic collaterals and an axonal fibre arise. This structure can be especially well seen at the periphery of the retina, where the distal segments are short. The central protoplasm is here relatively more voluminous. In bleached sections stained with haematoxylin a striated appearance can be seen in the rhabdomeres, which presumably corresponds to the tubules. The rhabdomeres do not extend over the distal ends of the cells in the direction from which the light enters.

In these peripheral regions of the retina the processes of the supporting cells can often be seen separating the rhabdomeres (figure 28, plate 4). Nevertheless, the rhabdomeres of neighbouring cells are often associated to form square rhabdomes here as at the centre, and these are orientated approximately in the vertical and horizontal directions. Only the last few cells at the edge of the retina may be almost separate from each other, though never standing quite alone as they do in the vestigial retina of the blind octopod *Cirrothauma*, figured by Chun (1915).

4. Regional differences in the retina

The question of whether there is any form of 'central area' or fovea of the retina is obviously of first importance and the literature on the subject is confused. Chun (1903, 1915) figures one or more regions with greatly elongated rhabdomes at the centre of the eyes of deep-sea cephalopods, especially those such as *Amphitretus* that have telescopic eyes. It is doubtful whether these regions can be considered comparable to the 'strip' ('Streif') extending horizontally along the equator of the eye, described by earlier authors, especially Hesse (1900) and Hess (1905). They found, especially in *Sepia*, that the rhabdomes are taller and more densely packed in the 'strip' and that the pigment migration that occurs

with change of illumination proceeds in the strip more slowly during light adaptation and faster during dark adaptation than in the remainder of the retina.

There are certainly marked differences within the retina (*a*) in the length of the rhabdomes and (*b*) in the distribution of pigment. The latter differences are inconstant, depending upon the condition of illumination at the time of killing; different distributions have been seen in animals of the same species.

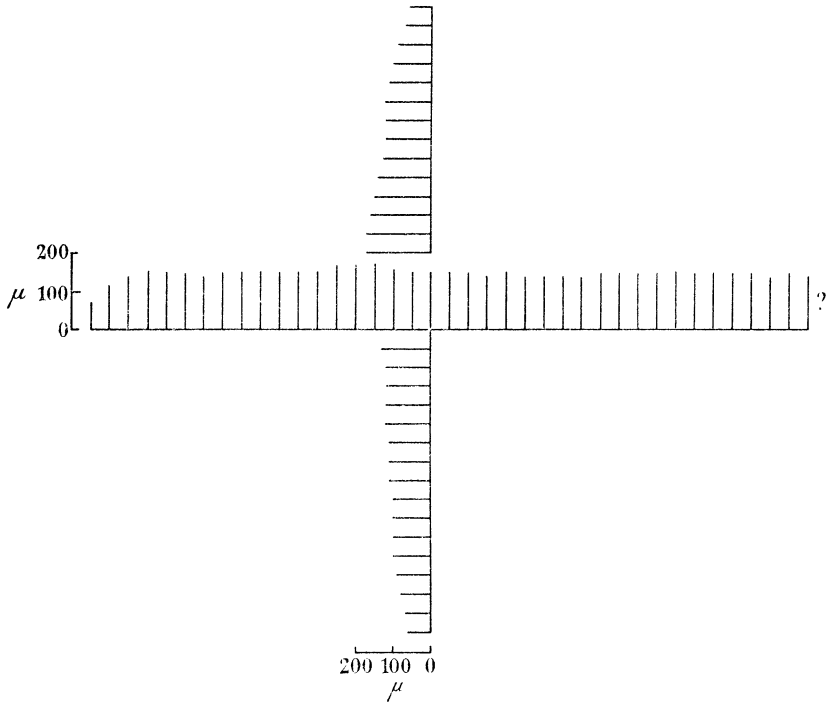


FIGURE 12. Lengths of the rhabdomes of an octopus eye measured on sections taken at various points along the antero-posterior and dorso-ventral axes.

In *Octopus* the retinal cells are much longer and narrower at the centre of the retina than at the periphery (figures 13 and 14, plate 3). At the extreme margins the rhabdomes are less than half the length of those at the centre (figure 12). At the anterior and posterior edges of the retina the length rapidly increases passing from the periphery. Dorsally and ventrally, however, there are larger areas of short rhabdomes. In this sense there is a 'strip' of longer cells running along the horizontal equator. The longest rhabdomes also occupy the central area. This can hardly be said to constitute anatomically a fovea, however, for there is no obvious sharp change, nor has any clear structural difference been seen between the central and marginal cells. The peripheral cells have shorter proximal segments than the central ones and the nerve plexus is thinner peripherally. The shorter cells show a larger proportion of cytoplasm and less of rhabdome than those at the centre (figure 13).

Under various conditions a strip either lighter or darker than the rest of the retina is seen when the eye is opened and examined with the naked eye, or at low magnification. Thus, in both light- and dark-adapted eyes of *Eledone* a light strip is sometimes seen; in other individuals the strip is darker than the rest of the retina. The conditions for the two

appearances have not been fully defined but they depend upon the time and intensity of previous illumination.

When either a light- or dark-adapted eye of *Octopus* is examined immediately after opening no such differentiation is at first apparent but a *transient* strip of lilac-whitish colour appears after 1 or 2 min along the equator. Its margin then spreads peripherally and the centre reverts to a chocolate colour. The meaning of these changes is obscure and is being investigated. When fixed eyes of *Octopus* are examined a strip is sometimes suspected but none readily identifiable with the naked eye is present. Nevertheless, sections show regional differences in the distribution of pigment in this genus as in the other cephalopods.

The effect of a lighter area is produced, as Hess (1905) showed, by the reduced quantity of black pigment in the distal ends of the cells (figures 16 to 18, plate 3). In the light-adapted retinas of three *Eledone* and three *Sepia* that have been sectioned this condition was confined to a horizontal strip. The distinction between the two types of retinal cell is sharp in some *Sepia*, but in the octopods the pigment gradually becomes less and is minimal at the centre (figure 18). No other sharp difference between the cells of the two areas has been detected. Those in the 'strip' are slightly longer (both proximal and distal segments), being from the most central part of the retina.

In sections of *Octopus* the situation is complicated. Differences in the distribution of pigment are present, but they are inconstant and do not always form any regular pattern or 'strip'. Figures 19 to 21, plate 3, are from a series through the whole head of a young *Octopus vulgaris* (about 150 g) in which both retinas show almost no distal pigmentation in their dorsal halves, but heavy pigmentation ventrally, the transition occurring rather sharply at the equator (figure 20).

This condition is an exception in our series, however. In many *Octopus* even though no 'strip' can be seen with the naked eye, examination of sections shows that the cells at the centre of the retina contain less distal black pigment than the cells of the dorsal and ventral periphery (figures 17 and 18, plate 3). As in *Eledone* the degree of difference varies. Sometimes even the central cells show a considerable amount of pigment distally. Presumably the condition is related to the state of illumination at the time of death. Some pigment is always present in the distal part of the retina and there is some evidence that in the strip region it lies in the fibres of the supporting cells that lie between the rhabdomeres but these are so fine that it is hard to be certain of this. Presumably the differences are due to the previous treatment and experiments over considerable periods are evidently needed.

Occasionally, sharp changes in the distribution of pigment and other features of the retina have been seen in limited areas. Thus in the eye shown in figures 22 to 24, plate 3, the pigment in most of the retinal cells was mainly concentrated in two layers, namely, in the basal region and at the distal ends of the distal segments. In one sharply defined area in the dorsal, anterior part of the retina, the cells contained little pigment at their distal ends and the more proximal pigment formed a broader band, extending into the proximal segments and scattered in the more proximal parts of the distal segments. It is not clear whether these differences are due to differences of illumination or even to pathological processes.

Some data from other species are available. Sections of the light adapted retinas of a small *Octopus defilippi* showed dense black pigment throughout the rhabdomes except for a narrow horizontal strip at the equator where the distal ends were free of it. In sections of the eyes of several *Argonauta argo*, however, the ventral part of the retina was found to be deeply pigmented throughout, the dorsal part to have less pigment in the distal ends of the cells. These animals of course are subjected to strong illumination from above.

5. Different types of retinal cell

A further question is whether there are distinct types of retinal cell such as might have different sensitivities or connexions. In the Golgi preparations, in which complete retinal cells are picked out, marked differences in diameter are seen (figures 11, plate 2, and 15). The holes in the basal membrane also show the passage of elements of various sizes (p. 10).

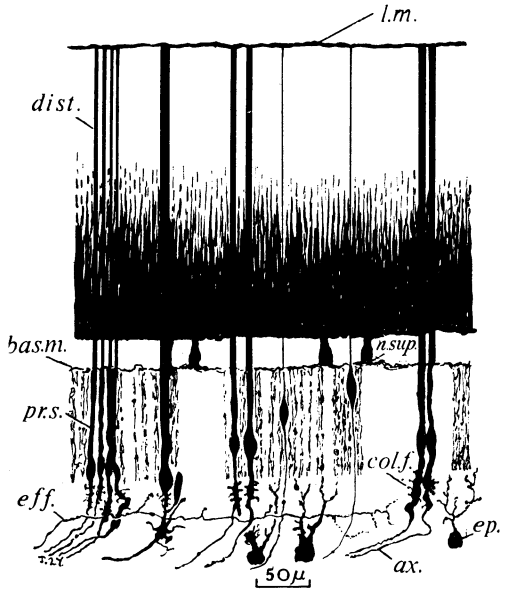


Figure 15. Drawing of a radial section of the retina after staining with the Golgi–Kopsch technique.

In the smaller retinal cells the nucleus lies rather far distally and the whole proximal segment has a characteristic spindle appearance (figure 15). It tapers off into a very fine beaded axon, often with no visible collateral synaptic twigs (they may well be beyond resolution). These small retinal cells seem to occur alone, not grouped in fours.

The Golgi method may show two or more retinal cells closely associated. Whenever several cells are associated they can be seen to terminate in the appropriate number of nerve fibres, again emphasizing that the retinal cell is the functional unit. The synaptic twigs of the members of one unit may lie very close to each other in the nerve plexus and might influence each other, or share the same centrifugal influences.

It seems likely therefore that there are several types of retinal cell and that whereas some at least of the smaller ones are single isolated entities (presumably each with two rhabdomeres), the larger ones are mostly associated in fours to make the rhabdomes. It is not unlikely that these different types would signal different changes in illumination.

6. Number of retinal elements and nuclei

Hess (1905) estimated in *Eledone* 81 000 retinal cells/mm^2 in the strip and half that number at the periphery. In *Sepia* the density in the strip was 105 000/mm^2. Heidermanns (1928) seems to suggest 62 500/mm^2 at the centre and many times less at the periphery. Wolken's '2000 rhabdomes per retina' is obviously a misprint, since he gives the diameter of each at 1·0 to 1·5 μ.

The retinal elements change progressively in size and density and the change is especially rapid towards the dorsal and ventral edges. It is therefore obviously important to specify the position of samples exactly. The values that Hess gives for the density in the 'Streifengebiet' and 'ausserhalb des Streifs' differ by a factor of two. This applies only to the extreme edges of the retina, however. In *Octopus* over the greater part of the area actually used in vision the differences between centre and periphery, though present, are less than twice.

In the present study pieces were taken at the centre of the retina and near to but not quite at the periphery in front, behind, dorsally and ventrally.

Table 1

	numbers/0·0025 mm^2		
region of retina	rhabdomes	proximal segments	supporting cell nuclei
centre			
Cajal	89	162	—
haematoxylin	59	123	45
periphery (anterior)			
Cajal	89	156	—
haematoxylin	67	142	58
periphery (dorsal)			
Cajal	74	137	—
haematoxylin	60	126	48

The number of proximal segments was found to be close to twice that of the rhabdomes, agreeing with the suggestion that the rhabdomeres are mostly associated in pairs. Counts of the rhabdomeres were made on sections tangential to the retina, stained with Cajal's method (table 1). These sections show the nuclei as well as the retinal elements, but some of the nuclei are much obscured by pigment. The sections were therefore bleached and stained with haematoxylin, and the counts repeated. Counts were made on photographs at 200×, using an area corresponding to 50 × 50 μ (figures 25 to 27, plate 4). In estimating the number of proximal segments a level with many nuclei was used (such as figure 27), and the fibres not carrying nuclei at that level were also counted, to give as nearly as possible a total count of the proximal segments that are present. The rhabdomes and proximal segments are not easy to count on the bleached and stained material and the estimates may be low. In the Cajal-stained material, the rhabdomes and proximal segments are clearer and provide better estimates. On the other hand the estimates for the supporting cell nuclei should be sound in the stained preparations. We may therefore take as approximations figures of 75 rhabdomes, 150 inner rod segments and 50 supporting cell nuclei/0·0025 mm^2 for the central part of the retina.

The figures do not suggest great differences in the various parts of the retina, though no doubt these exist, especially at the extreme edges. We may provisionally take a single estimate for the whole eye. The area of the whole retina of the animal used for table 1 was estimated as 400 mm^2. If we take an estimate of 150 proximal segments/0·0025 mm^2, this gives a density of 70000/mm^2 and a total of $2{\cdot}8 \times 10^7$. This estimate is probably high, because the area of the whole retina was measured after fixation but before embedding in wax and the counts were therefore made after considerable further shrinkage. Moreover no account is taken of the lower densities at the periphery. Therefore $2{\cdot}0 \times 10^7$ may be an approximate estimate for the number of proximal segment fibres, that is, of the presumed units of the retina.

7. Supporting cells

The cells whose nuclei lie among the pigmented spindle bases of the distal segments have been given many names (Stäbchenkörner by Hensen, Limitanszellen by Grenacher, Stutzzellen by v. Lenhossék, pigment corpuscles or intercalary cells by Cajal (1917)). Supporting cells is perhaps the most suitable English name.

Their bases lie immediately distal to the basal membrane (figure 9, plate 2), to which as Cajal has shown they may be attached by expanded feet (figure 15). Distally they stretch up between the rhabdomes and Hensen, Grenacher and Cajal have all suggested that they continue between these. Grenacher first suggested that they reach to the surface of the retina and secrete the limiting membrane there. Moody (1961) has seen very fine fibres between the rhabdomes, and these are probably the processes of the supporting cells.

In the peripheral regions of the retina these processes between the rhabdomes can often be seen with the light microscope (figure 28, plate 4); probably they are thicker here than at the centre. They contain pigment granules. At their distal ends they often remain attached to the limiting membrane even where this has pulled away from the retina cells. It may well be therefore that they secrete this membrane. At the extreme edges of the retina the supporting cell layer continues beyond that of the retinal cells (figure 29, plate 4). Here it can clearly be seen that the limiting membrane is attached to a ring of these cells, which surrounds the retina.

After degeneration of the retinal cells rather coarse finger-like processes can be seen attached to the supporting cells (p. 14). These are presumably the thickened remains of the normally finer tubules.

The nuclei of the supporting cells appear as ovals in radial section but in tangential sections they are polygonal and sometimes curved, as if wrapped around the bases of the retinal cells (figure 25, plate 4). The number of supporting cell nuclei is roughly equal to that of the rhabdomes, but of course each cell may have several processes.

8. Basal membrane

This is a conspicuous sheet of fibrous material, which stains with light green or aniline blue and with silver by Holmes's method. No collagen fibres are seen here by electron-microscopy, however (Moody, personal communication).

In tangential sections stained with Golgi methods it appears as a fenestrated lamina (figure 32, plate 5), the holes presumably serving for the passage of the bases of the retinal cells. They vary in diameter from 20 to 2 μ or less.

On the proximal side of the membrane lie some large cells, placed at wide intervals and having the appearance of fibrocytes (figure 26, plate 4). Presumably these produce the membrane. Similar cells also occur scattered among the nuclei of the proximal segments and strands of material staining like collagen are seen among the glial processes that are described below.

9. Retinal nerve plexus

At the inner ends of the proximal segments there is an elaborate plexus of nerve fibres at the back of the retina (figures 30, 31, plate 4). The nature of this plexus, the source of its fibres and of the interactions that it allows are now beginning to be clear. The plexus may be considered to consist of two layers (figure 33, plate 5). In the more distal one, immediately adjacent to the proximal segments of the retinal cells, fibres interweave in many directions and there are synapses between the collaterals of the retinal cells and the endings of the centrifugal (efferent) fibres of the optic nerves (figure 15). The outer layers of the retinal plexus consist of fibres running mainly tangentially and then uniting to make the bundles of the optic nerves. These latter are formed as collections of fibres from neighbouring points of the plexus (figure 31). They run through the thin bundles of fibres of the retinal muscles and then through the cartilage of the sclera at the back of the eye-ball (Alexandrowicz 1927).

The axons of the retinal cells run through the plexus, without interweaving, directly to the optic nerves (figure 15). As they pass through the plexus these fibres carry numerous very fine collateral ('dendritic') twigs (figures 10, 11, plate 2). These are probably only the bases of still finer fibres below the limit of resolution with the light microscope. Occasionally appearances suggesting longer thinner collaterals have been seen (figure 10*b*), but it is hard to exclude that these are segments of fibres of the nerve plexus, superficially attached to the inner segments. The collateral twigs of neighbouring retinal cells frequently interlace and it may well be that they have synaptic influences upon each other, such as have been shown in *Limulus* (Miller 1957; Ratliff, Miller & Hartline 1958).

One or more larger irregular collateral swellings are often seen attached to the proximal segment (figure 10). Their irregularity suggests that they may be artifacts or a normal component enlarged by the Golgi stain. No collaterals were seen turning back among the proximal segments as they were described by Cajal in *Sepia*. This may of course be only a result of incomplete staining or resolution, but as v. Lenhossék also described only very short collaterals in *Eledone* it is provisionally concluded that most of them have this form in octopods, whatever may be the condition in decapods. There is almost certainly interaction of the collaterals with the other components of the plexus, the centrifugal fibres. The whole elaborate plexus seen in Cajal preparations is not made up of the axons of retinal nerve cells, nor even probably of their collaterals, but of the endings of fibres running from the optic lobes to the retina. Numerous centrifugal cells with such a course are known to lie in the inner granular layer of the lobe (Young 1962).

If the retinal cell axons run direct to the optic nerves and the centrifugal fibres make a plexus, it is obviously important to discover the nature of the branching system there. This may provide clues to the functioning of these efferent fibres. The meshes of the plexus are formed by bundles of fibres that run only for a short distance in one direction and then,

meeting another bundle, diverge in a new direction. In Cajal preparations single fibres cannot usually be followed for long distances, in marked contrast to the plexuses in the optic lobes (Young 1960). Points of branching, at which fibres separate and run in different directions, are common. Golgi preparations show that single individual fibres bifurcate. The fibres of the plexus do not, so far as they can be followed, run in any particular direction in relation to the axis of the eye, and measurements of the angles made with the horizontal by the fibres within a given area show no preferred directions. By contrast, the fibres of the plexuses of the plexiform layers of the optic lobes are largely orientated in vertical and horizontal directions (Young 1960). No nerve cells have been seen within the retinal nerve plexus.

In a few preparations with the Golgi–Kopsch modification nerve endings that presumably belong to the efferent fibres have been seen (figures 15 and 34, plate 5). Single fibres sometimes run in a tangential direction in the plexus for 300 μ or more. They carry fine lateral twigs and end as very thin, branching fibres, often beaded (figure 15). Most of the endings that have been seen lie among the dendritic collaterals of the retinal cells. A few branches seemed to pass up between the nucleated regions of the proximal segments, but it was difficult to distinguish between these branches and those of the epithelial cells.

The epithelial cells are the glia cells described by Cajal and others. Their nuclei are seen in figure 7, plate 2. As Cajal showed in *Sepia* the cells have branches in the plexus itself and extending among the proximal segments of the retinal cells (figure 15). Cajal compared them with the Mullers fibres or retinal glia of vertebrates.

They have been seen imperfectly stained in some Golgi preparations in *Octopus* (figure 15). Between the proximal segments there also appear sheets of material that stains yellow-brown with Golgi–Kopsch (figures 15 and 42, plate 6). The sheets are strengthened by thickenings that run radially. They show granules along their length and larger masses occur at intervals. This material presumably belongs to the epithelial cells, but as mentioned already there are other nuclei (besides those of the proximal segments) in this region. The material between the proximal segments is often not obviously in continuity with the epithelial cells. Indeed it usually ends abruptly where the plexus begins, though this may be an artifact of the Golgi stain.

On the other hand, the glial material is very different from the fine tangential fibres described above in the plexus, and the two occur side by side in the same section. It is concluded that the tangential fibres are nervous and are the endings of the efferent fibres that are known to run into the optic nerves from the 'centrifugal cells' of the optic lobes (Young 1962).

In the most proximal part of the plexus, almost against the sclera, run a few isolated nerve fibres that probably innervate the retinal and scleral muscles (figure 33, plate 5).

10. The outer layers and blood supply of the retina

Outside the layer of 'epithelial cells' that limits the retinal plexus is a 'choroid' layer of connective tissue, blood vessels and muscles (Schöbl 1878; Alexandrowicz 1927). Outside this again lies the cartilaginous sclera, which readily separates from the rest. The layer of retinal muscles is especially well developed at the periphery and there the retina remains more firmly attached to the sclera. Where the retinal elements cease, the layer of muscle is

continuous with that of the ciliary body. The bundles of nerves innervating the retinal muscles are continuous with those of the ciliary muscles and arise from the ciliary nerve ring.

The cartilage of the sclera is thickened at the periphery of the retina (figure 14, plate 3) but elsewhere it is less than 25 μ thick. It is pierced by the numerous bundles of optic nerve fibres and by arteries and veins. Arteries of diminishing size are present in the proximal layers of the retina and capillaries extend as far inwards as the basal membrane (figure 35, plate 5). None has been seen among the distal segments. The whole length of the rhabdomes ($>150\,\mu$) must be nourished by the supporting cells or by diffusion from the basal or limiting membranes.

The retinal veins are thin-walled vessels (figure 13, plate 3) presumably emptying into the orbital sinus.

11. Degeneration of the retinal cells after optic nerve section

The retinal elements degenerate completely in any part of the retina whose optic nerve fibres have been sectioned. The degenerative process consists of a break-up of both distal and proximal segments of the retinal cells, the whole region becoming vacuolated and invaded by macrophages (figures 36 and 37, plate 5). The rhabdome-containing layer gradually contracts and finally collapses and disappears altogether. The supporting cells, however, do not degenerate but remain, loaded with pigment. After full degeneration they appear as rather short cylindrical cells, lying between the basal and limiting membranes (figures 38 and 39, plate 5). That the limiting membrane remains intact after the disappearance of the distal segments confirms that it is a product of the supporting cells.

The boundary between an innervated and denervated region is not quite sharp. A few rhabdomes of reduced height are seen, the proximal segment layer also gradually reducing (figure 40, plate 5).

After full degeneration the region proximal to the basal membrane is reduced to a narrow layer of macrophages, filled with pigment, occupying the site of the proximal segments and retinal nerve plexus.

The speed of the degeneration varies considerably. No consistent signs of changes were seen in animals examined up to 2 days after operation. In one examined after 9 days the retinal cells had almost completely disappeared (figure 41, plate 5). Degeneration may have been exceptionally fast in this animal. In other octopuses killed 10 days after operation, the retinal cells had not been wholly destroyed. The retinal cell nuclei were shrunken and irregular in outline and the cytoplasm and rhabdomes were shrunken and wavy and in process of being invaded by macrophages.

After degeneration of the retinal cells is complete a few nerve fibres can still be seen in the outer region of the retina (figure 43, plate 6). They may be traced for short distances and there is no reason to doubt their nervous nature. They represent only a few per cent. of those normally present, but can be seen in all properly stained sections of retinae even 2 months after complete removal of the optic lobe. Probably these fibres innervate the retinal muscles and reach the eye through the ophthalmic nerves and ciliary nerve ring (Alexandrowicz 1927).

A most interesting feature is that the retinal nerve plexus does not end abruptly at the boundary between an innervated and a denervated region (figure 44, plate 6). Since the main part of the plexus consists of the efferent fibres this confirms that the action of these is not localized, but in some way distributed, through the plexus, over a considerable area of the retina. In the experiment shown in figure 44 the plexus extended, with gradual attenuation, for at least a millimetre beyond the point at which the rhabdomes ended.

12. Survival of supporting cells and their fibres after degeneration

The boundary region between intact and degenerated retina provides valuable evidence that the supporting cells send thin fibres into the region of the rhabdomes. Where the rhabdomes are greatly reduced in height they also become slightly separated and fingers of protoplasm from the supporting cells can be seen between them (figure 45, plate 6). Beyond the last surviving retinal cell a few of the supporting cells still carry elongated fibres (figures 46 and 47, plate 6). These are presumably the remains of fibres that previously ran between the rhabdomes. They contain pigment granules. There is no evidence to show how many such fibres are related to each rhabdome, or how they are arranged. Several fibres spring from each supporting cell, which has a swollen basal region. They may continue through the entire (reduced) thickness of the distal retina, running between the rhabdomeres of neighbouring retinal cells to the limiting membrane (figure 45). This suggests that they also occupy this position in the normal retina, although they are no doubt much altered during the contraction of the distal layer that accompanies degeneration. It may well be that they become thicker in this process; Moody & Parriss (1961) have indeed found many much finer fibres in this situation. Figure 48, plate 6 shows an intermediate stage, before the remains of the rhabdomes have been completely removed. The processes of the supporting cells form wavy tubes, up to 5 μ in diameter.

13. Partial retrograde degeneration after injury to optic lobe

In one animal in which the optic lobe was removed the cut made at operation had severed a small piece of the lobe, which remained attached to the back of the retina (figure 49, plate 6). The receptors of the corresponding region had become greatly reduced in height, but had not degenerated completely. They were less than half of the length of those in the opposite eye. The portion of the optic lobe that remained intact included only the plexiform zone, the outer granule cell layer and a few cells of the inner granule cell layer. The whole of the central portion of the lobe was absent. The processes of the retinal receptors end mainly within the plexiform layer and they had mostly therefore not been severed by the operation. The small piece of optic lobe remaining was, however, presumably provided with little blood and the terminals of the nerve fibres may have suffered a partial 'metabolic interruption'. The reduction in length of the rhabdomes could well have been the result of this, but may also be a retrograde transneuronal effect, resulting from the reduced connexions in the isolated piece.

14. Discussion

(*a*) *Orientation of the rhabdomes*

Schultze (1869) first suggested that each unit cell of the retina carries a pair of what we now call rhabdomeres. The further study and counts recorded here confirm this suggestion. If the cells are orientated more or less regularly, then there is a possible intra-ocular mechanism for the discrimination of the direction of polarized light discovered by Moody & Parriss (1960). The fact that the retinal cells are mostly arranged in the vertical and horizontal planes can hardly be an accident. It may be correlated with the fact that discrimination of polarization is best in these planes and is poor in oblique directions. It may be that this orientation of the rhabdomes is also related to the fact that octopuses distinguish visual forms largely in terms of their vertical and horizontal extents (Sutherland 1957, 1958). However, it is not yet certain exactly how the projection is made.

(*b*) *The question of the presence of a fovea*

There is some evidence that the retinal cells are not all alike. The smaller ones may not be associated in fours to make rhabdomes. There cannot be many such single ones, however, because the total number of proximal segments is close to twice that of the square rhabdomes.

The problem of whether there is a specially differentiated central area in the cephalopod eye remains unsettled. The distal segments are certainly somewhat longer in a strip of tissue running along the equator of the eye horizontally. In *Sepia* the size and closeness of packing of the retinal cells is different in this region from elsewhere in the eye. In octopods the differences are less, though the retinal cells at the extreme edges are much shorter than the rest. The absence of pigment from the distal ends of the rhabdomes may give the strip region a lighter appearance to the naked eye in *Sepia* and some *Eledone*. There is evidence of a similar strip of cells also in *Octopus*, although the distribution of pigment in different parts of the eye varies. It seems probable that in all cephalopods there is a horizontal central strip of cells in which the movement of pigment in response to changes of illumination is different from that elsewhere. These cells must be at least as strongly illuminated as those elsewhere in the eye and yet they show less distal movement of pigment during light adaptation. In this sense of being less sensitive to illumination they may constitute a fovea comparable to that of vertebrates. It remains to be discovered whether this is in any sense a region of clearest vision or colour vision or whether the fact that it is extended horizontally is related to the finding that the animal can discriminate lengths more readily in the horizontal than the vertical direction (Sutherland 1961).

Such evidence as there is suggests that no single central area is used for fixation. When a food object (crab) is shown to an octopus in the extreme front or back of the visual field the animal may swim towards it either backwards or forwards, with the image held on the part of the retina at which it was first encountered (Packard & James 1962). Steering, or at least aiming, can therefore be accomplished even by the edge of the retina. At the last moment before seizing its food the octopus usually turns, however, so that the image falls on the centre of the retina.

Animals can be taught to discriminate shapes seen only in the back or front of the visual

field. Tests with the previously untrained portion of the retina then show mainly correct performance (Muntz 1961). The most convincing evidence that complex visual functions can be performed with the periphery of the retina is that animals in which the whole central part of the eye has been denervated can still be taught to discriminate between shapes, though performance is less accurate than in normal animals (Wyatt & Young, unpublished). Most of this experimental work has been concerned with vision in the main horizontal plane of the retina. It may be that although all parts of the retina are equivalent in this plane there are differences between the equatorial and the dorsal and ventral regions.

(*c*) *The retinal plexus and efferent fibres to the retina*

Collaterals of the retinal cells were described in *Eledone* as long ago as 1894 by Lenhossék, and Cajal described even more extensive ones in *Sepia*. It seems very likely that they allow interaction between neighbouring retinal cells, which perhaps inhibit each other and increase contrast, as in *Limulus* (Ratliff *et al.* 1958). The problem of the function of the retinal plexus is complicated by the finding that a large part of its mesh-work is made up of fibres whose cell-bodies lie in the optic lobe and are presumably efferents. That there are fibres running into the optic nerves from cells of the optic lobes has long been known. The actual endings in the retina have not previously been seen. Similar efferent fibres have of course been shown in vertebrates (see Maturana 1958), and Autrum (1958) has shown something of their effect on retinal activity in insects. There may thus be a quite complicated interplay of influences within the retinal plexus, between the neighbouring retinal cells and the efferent fibres from the optic lobes. Presumably these are all part of the coding operations by which certain types of information are extracted so that the signals in the optic nerves do not simply repeat the information in the retinal image. Indeed it is likely that it would be difficult to do this accurately and it is for this reason that in cephalopods, as in vertebrates, the coding process begins in an elaborate plexus immediately behind the photoreceptors.

(*d*) *Retrograde degeneration after nerve section*

The retrograde degeneration of the cells of the retina after section of their nerve fibres is similar to that occurring in many vertebrate receptor cells and neurons, but not previously recorded outside the vertebrates. The cut was made some 5 mm or more away from the cell body and the operation itself can hardly have produced direct damage to the retina. It severs some of the arteries to the retina (Schöbl 1878), but does not make the retina obviously ischaemic: moreover the non-nervous cells survive well.

At a place where denervated and intact retina meet the retinal cells show a gradual reduction in height (figure 40, plate 5). This shows that mutual influences between neighbours are involved in maintaining the integrity of the retinal cells. These influences might operate between the retinal cells themselves or by the centrifugal axons upon them. The plexus of centrifugal cells extends into the denervated region beyond the intact rhabdomes. It therefore seems likely that the decreasing height of the latter is due to the absence of mutual influences between the retinal cells themselves.

The presence of even a small fragment of the optic lobe is sufficient to prevent full degeneration of the retinal cells whose axons have not been severed, though these show a marked reduction in size, which is an interesting transneuronal retrograde change.

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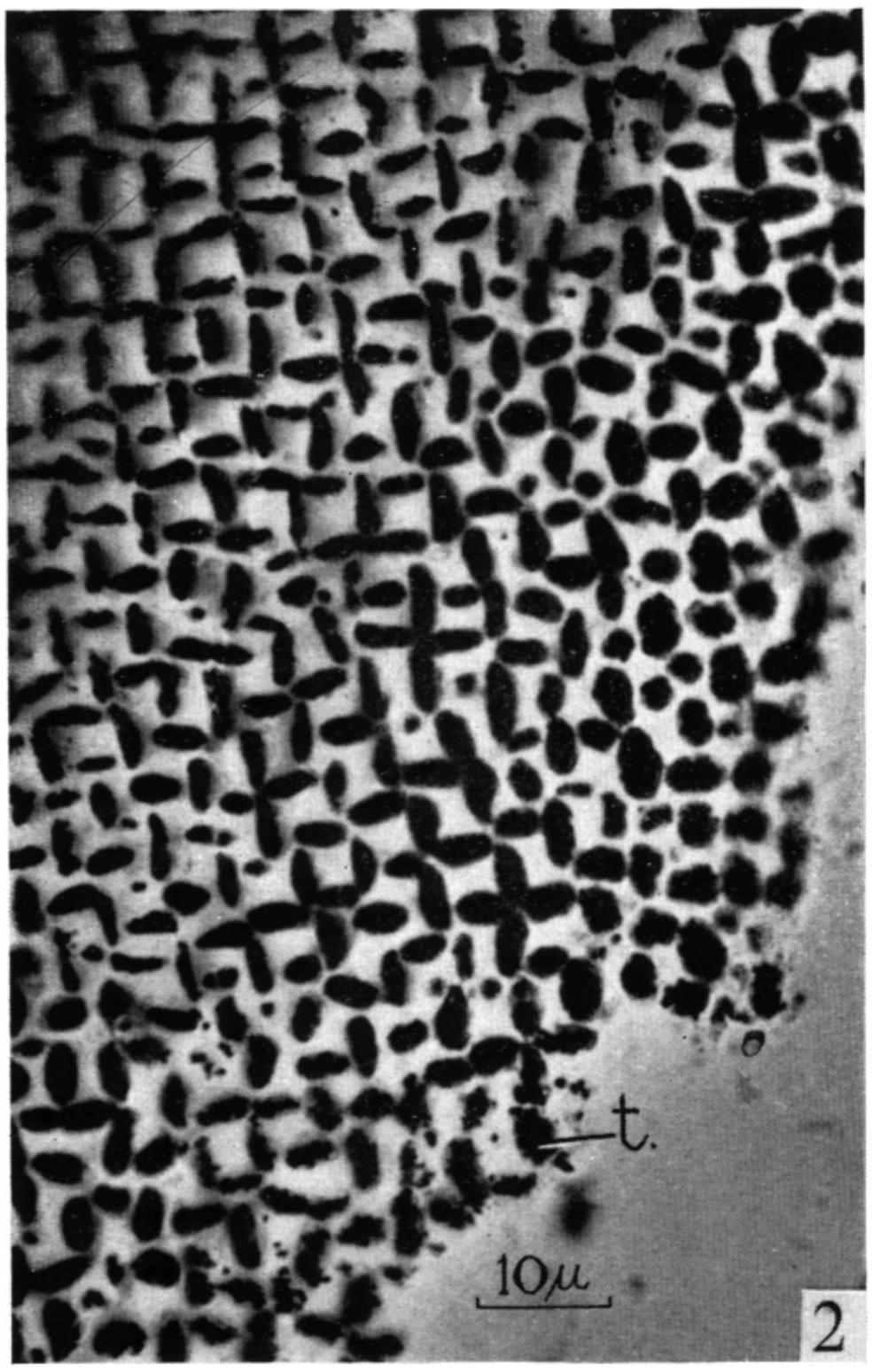
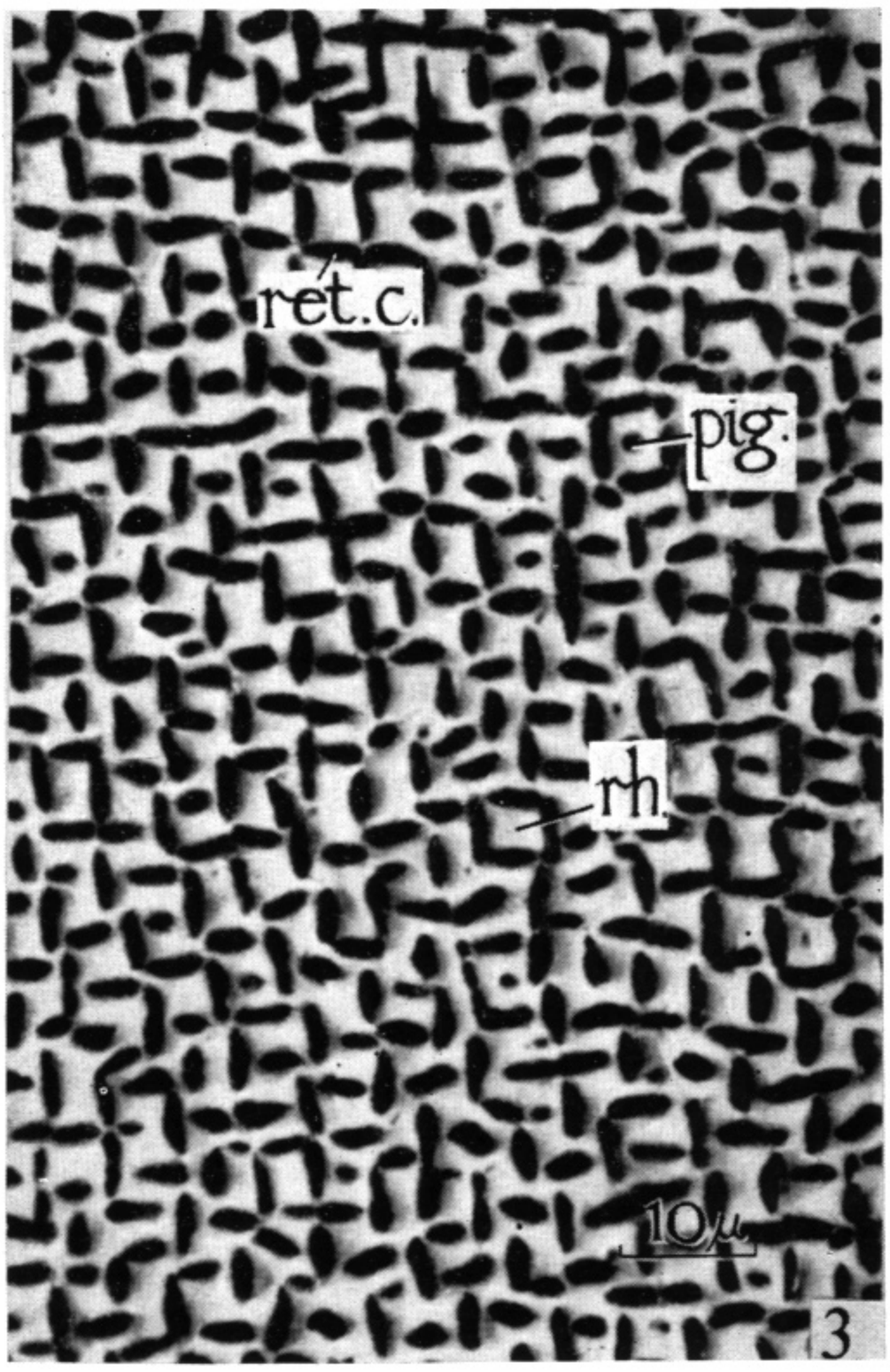
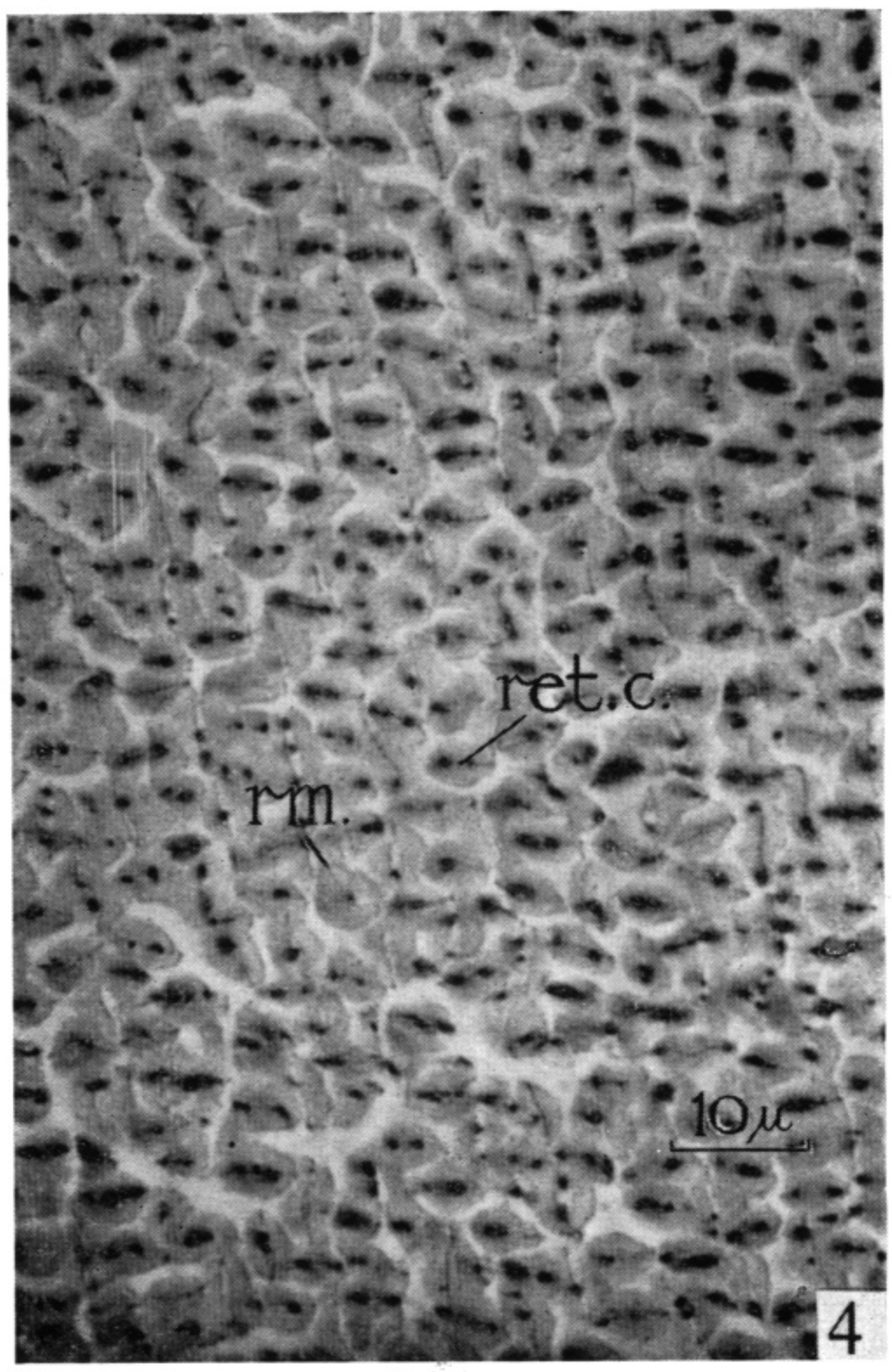






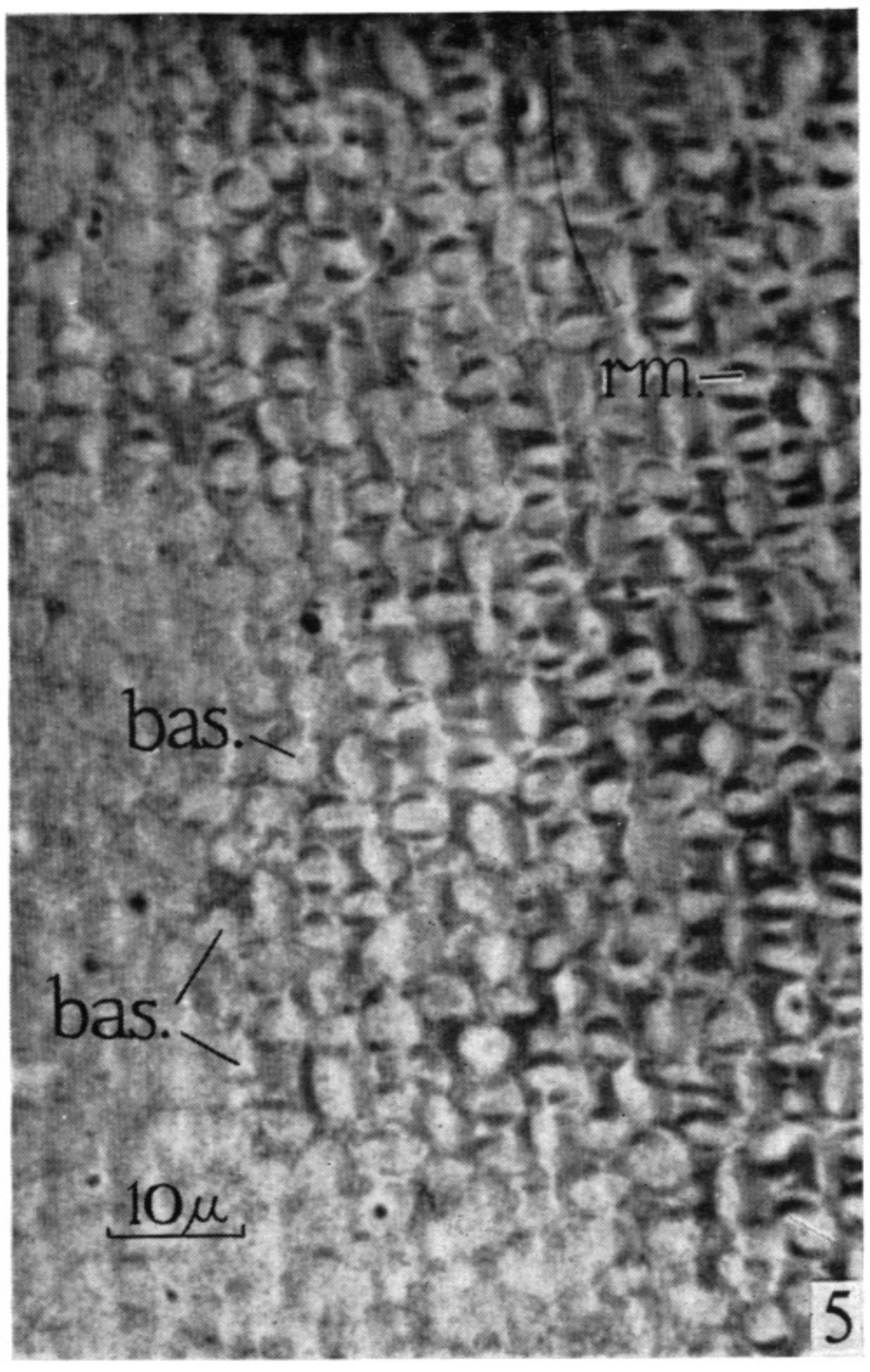
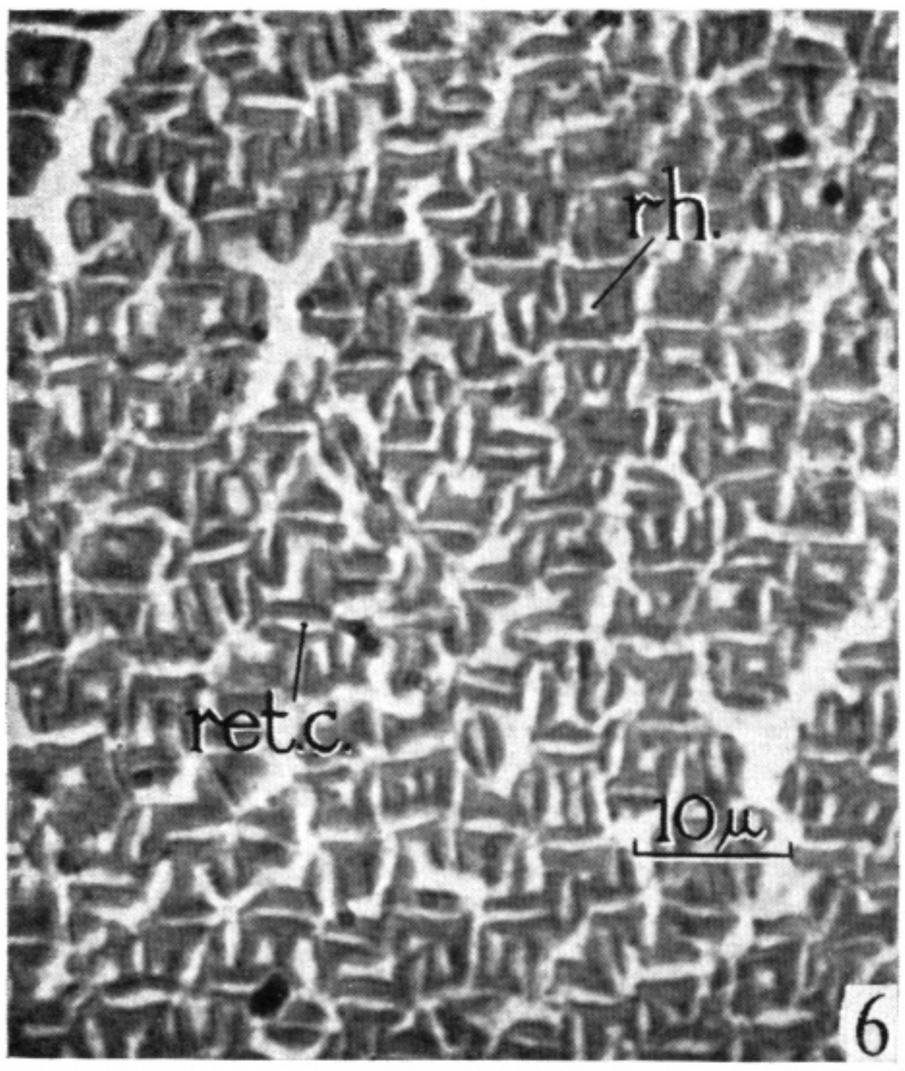


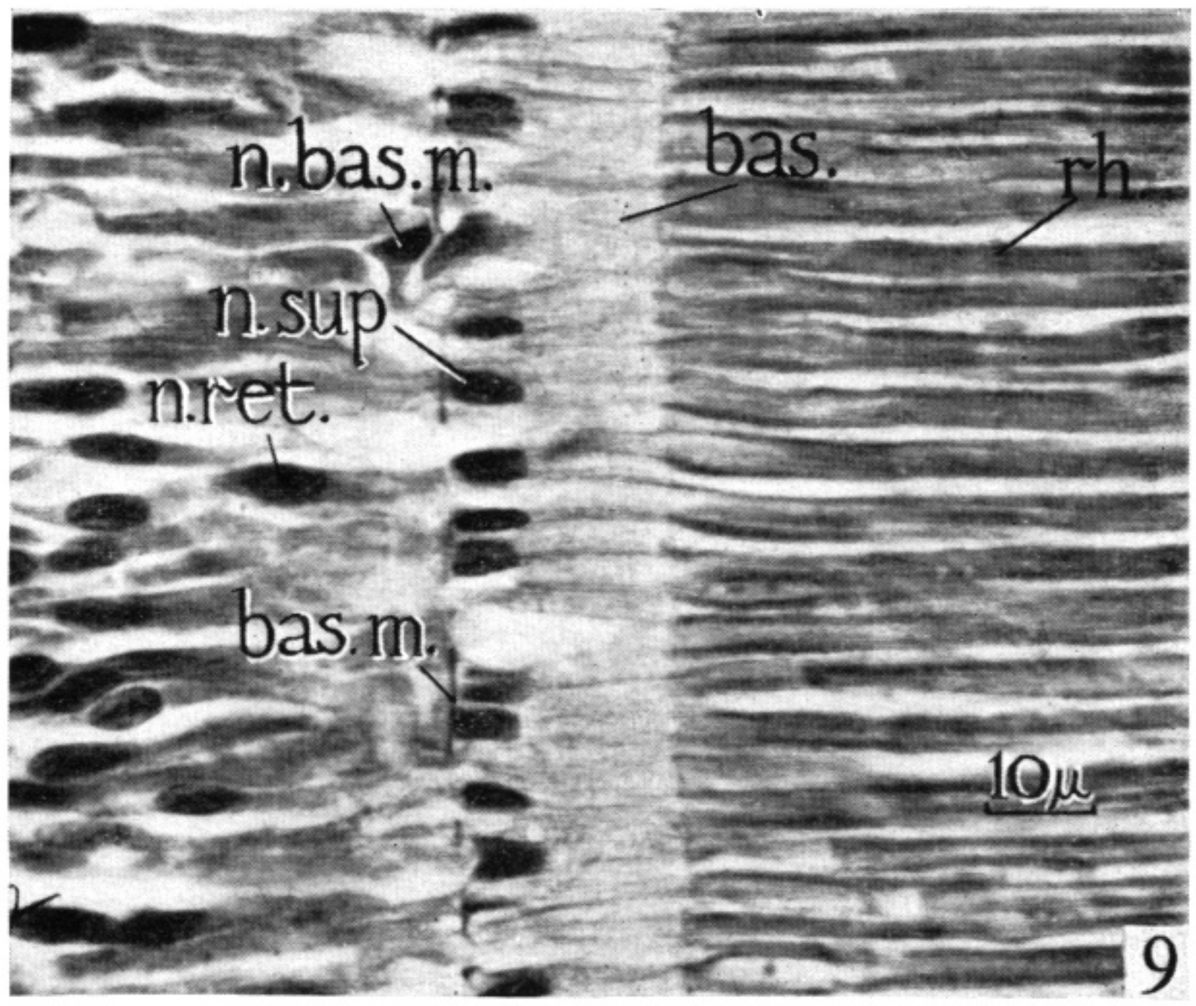
FIGURE 2. Tangential section at extreme distal margin of light-adapted retina. To the right are seen the separate pigmented tips of the distal segments (*t*). To the left the retinal cells are largely grouped to make rhabdomes. In this and the next three figures the long axis of the figure is approximately in the vertical plane. Cajal's stain.

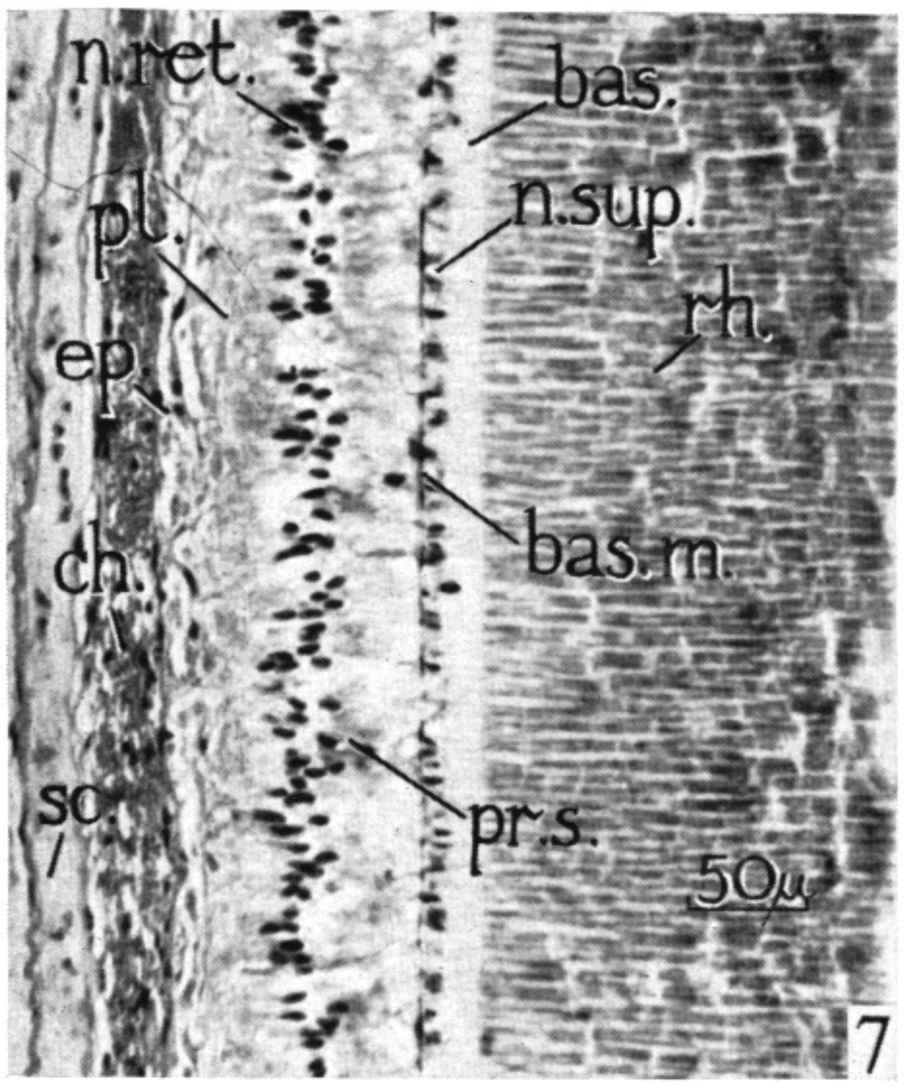
FIGURE 3. Tangential section more proximal than figure 2, showing the rhabdomes. Cajal's stain.

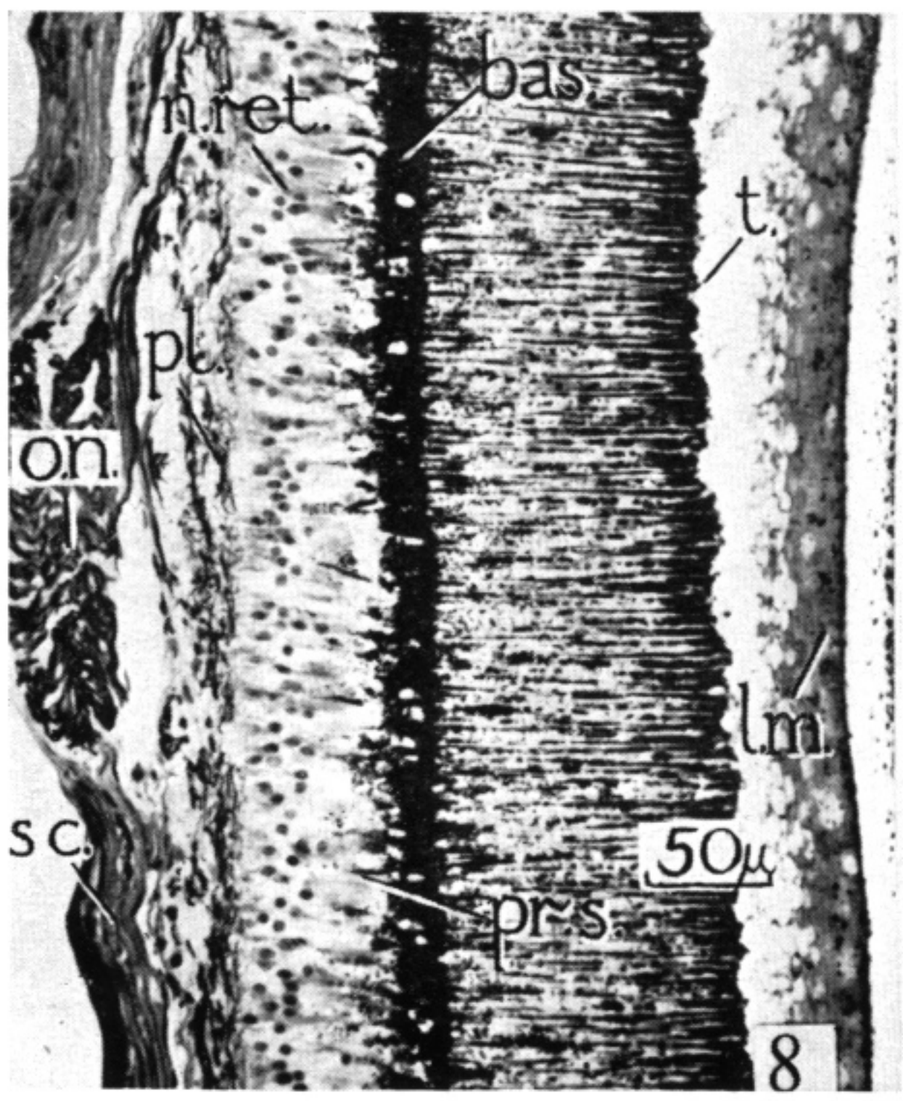
FIGURE 4. Tangential section still further proximally. Here there is less pigment in the retinal cells. The square rhabdomes are now less evident and the unit retinal cells with their two rhabdomeres can be seen. Cajal's stain.

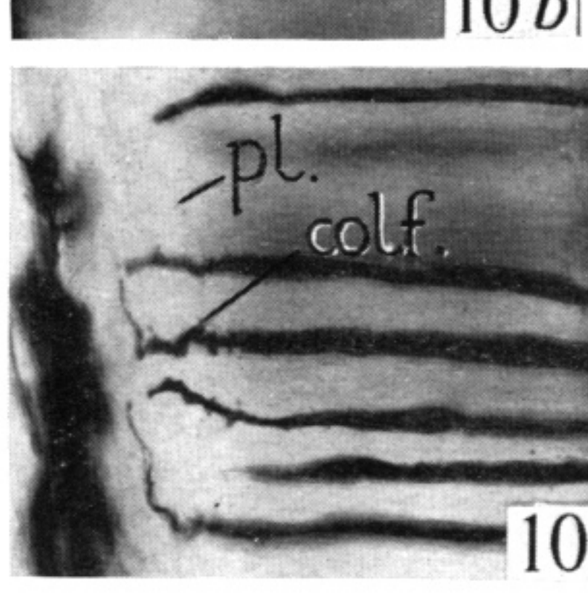
FIGURE 5. Tangential section at the base of the distal segments after bleaching and staining with haematoxylin and eosin. At the top and right the rhabdomeres can still be seen, darkly stained. Towards the bottom left the outlines of the basal pigmented regions (spindles) appear faintly.

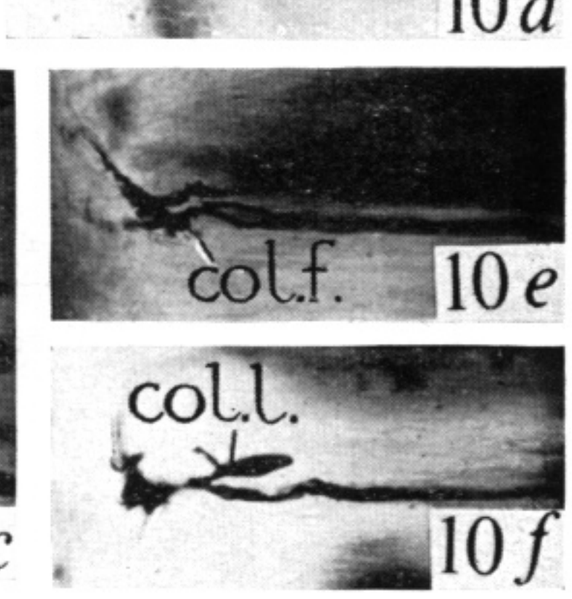












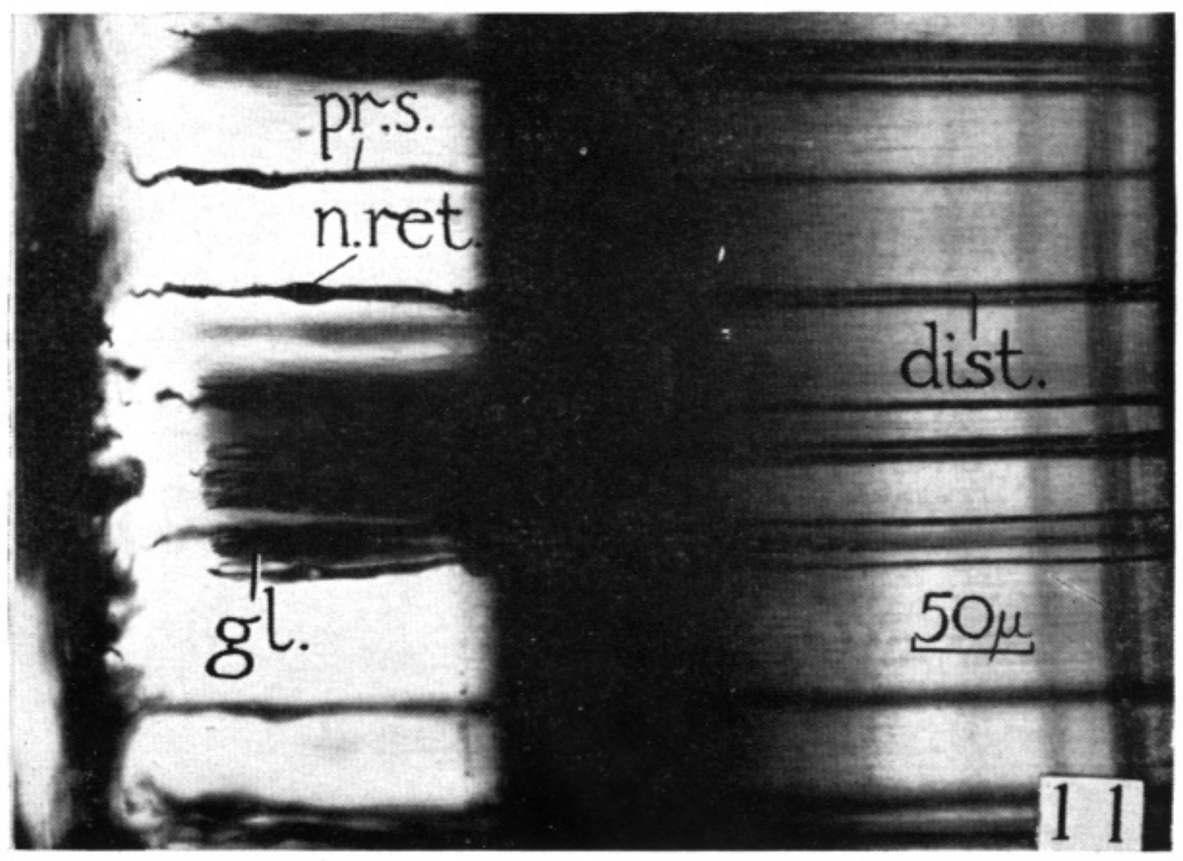


FIGURE 6. Tangential section at middle of distal segment to show rhabdomes after bleaching and staining with haematoxylin and eosin.

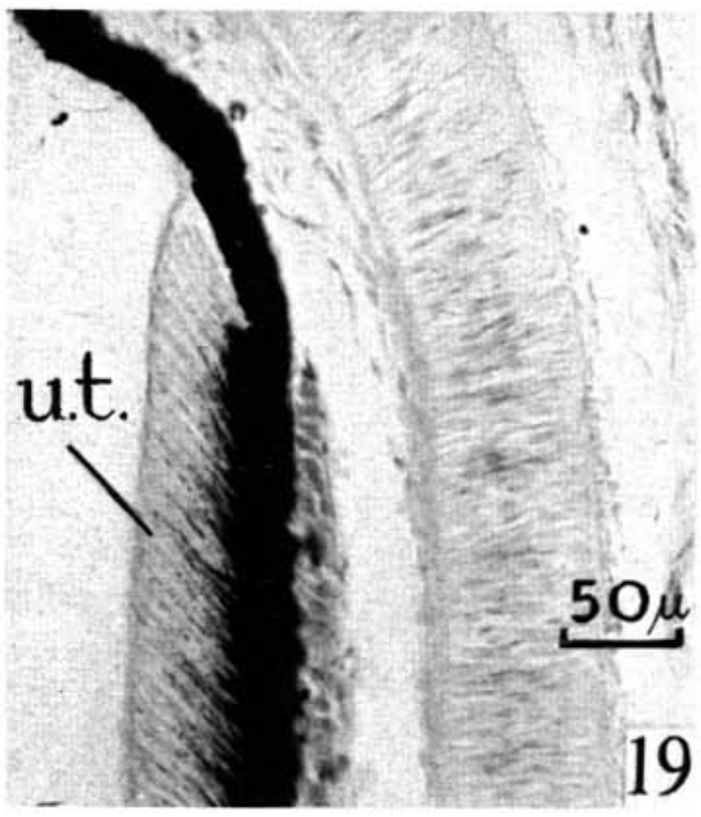
FIGURE 7. Radial section to show the various components of the retina. (Formol fixed, bleached, haematoxylin and eosin.)

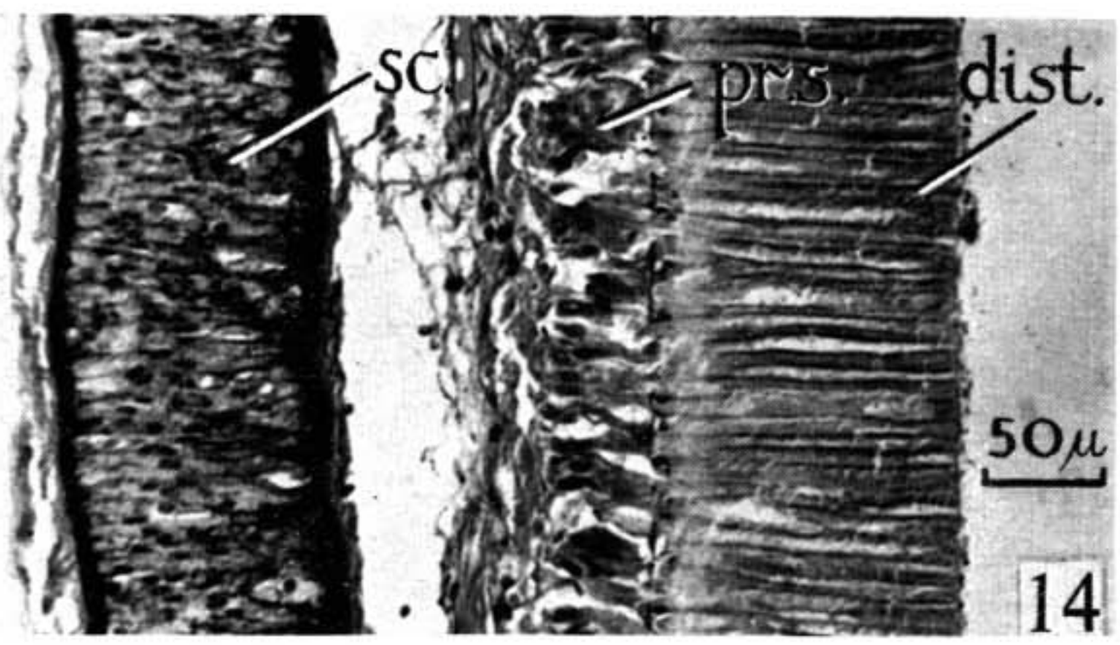
FIGURE 8. Similar section to figure 7 but unbleached and stained with Cajal's stain.

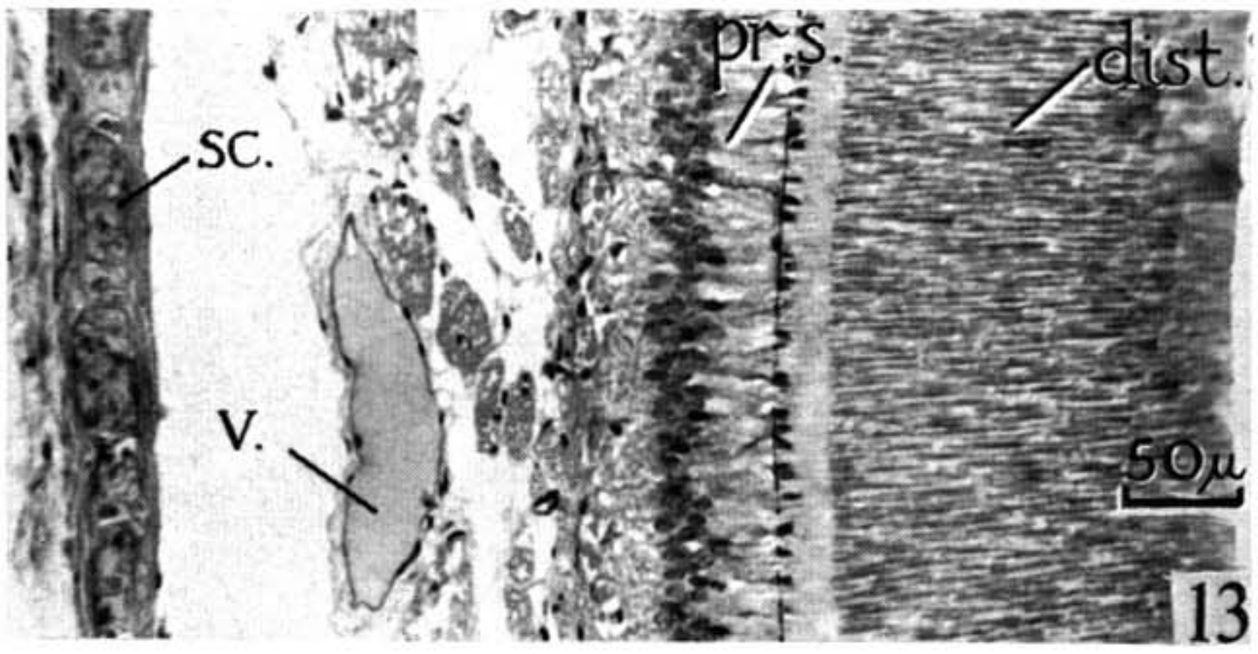
FIGURE 9. Higher magnification of preparation similar to figure 7 to show the inner ends of the rhabdomes, supporting cells and proximal segments.

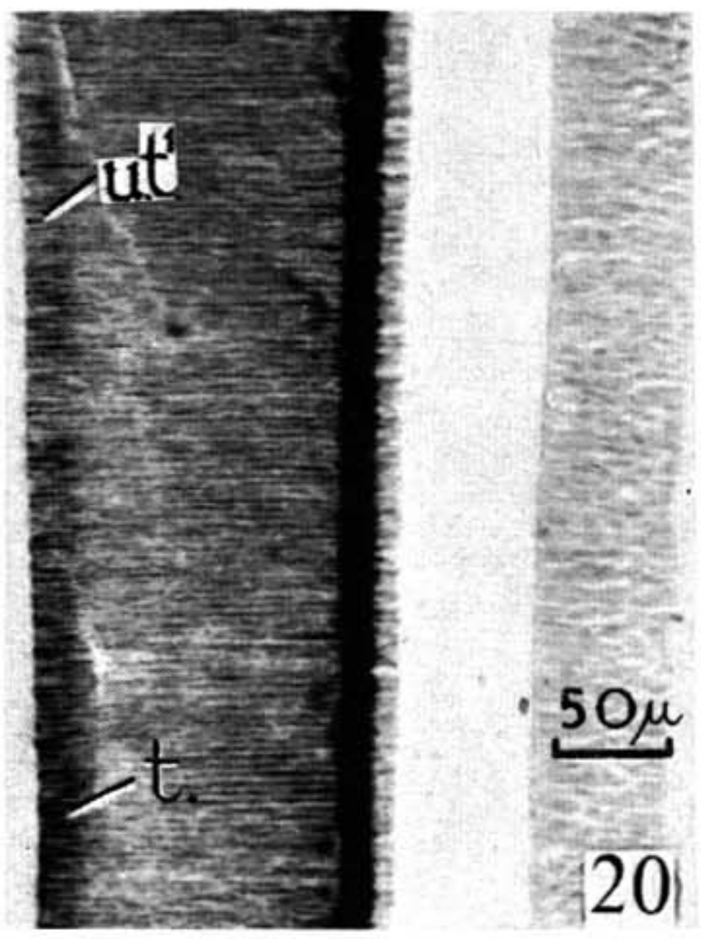
FIGURE 10*a* to *f*. Proximal segments of various retinal cells showing their axons and collateral dendrites of various shapes. (Golgi–Kopsch.)

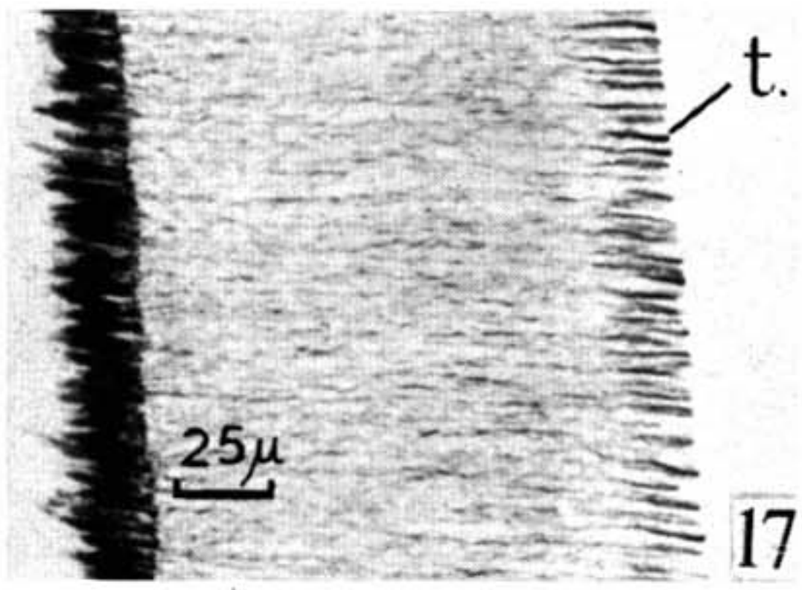
FIGURE 11. Radial section of whole retina after Golgi–Kopsch staining. Complete units are stained, the distal segments being very straight, the proximal more irregular.

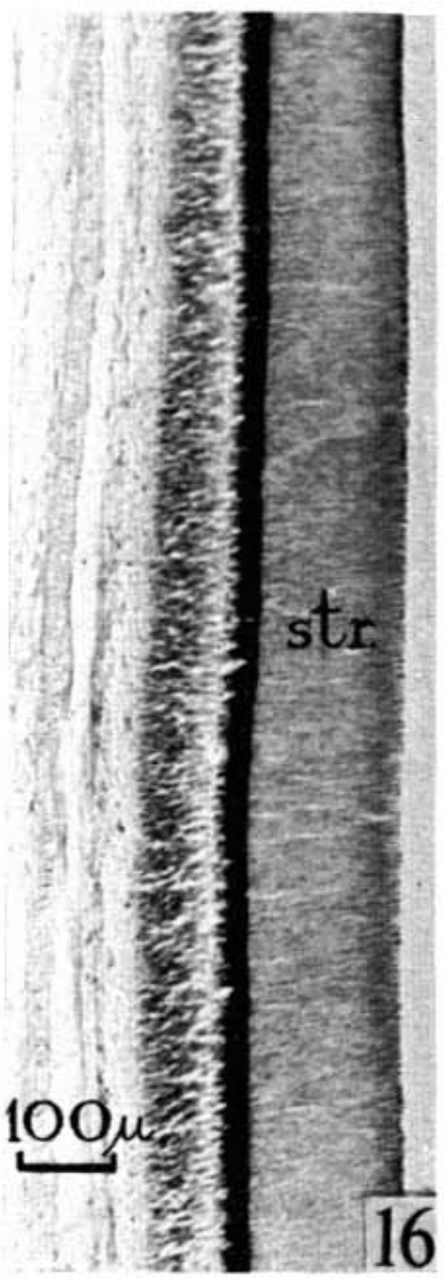


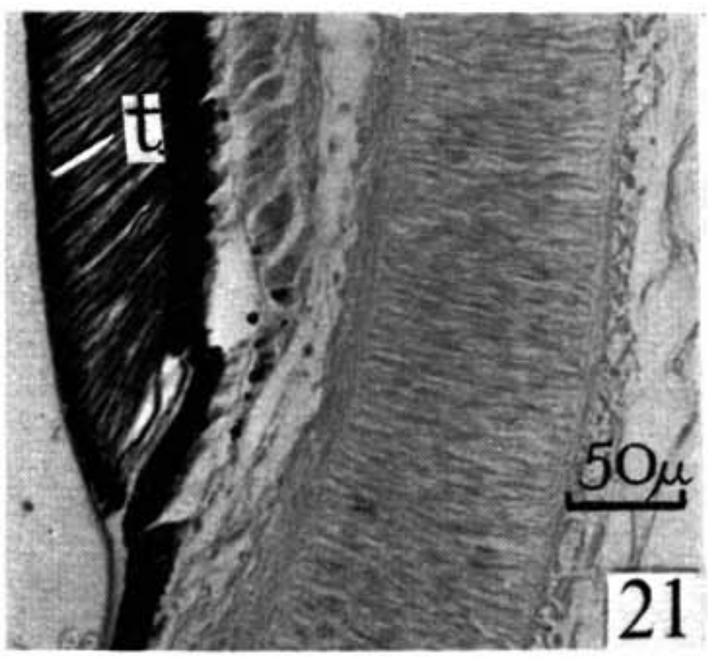


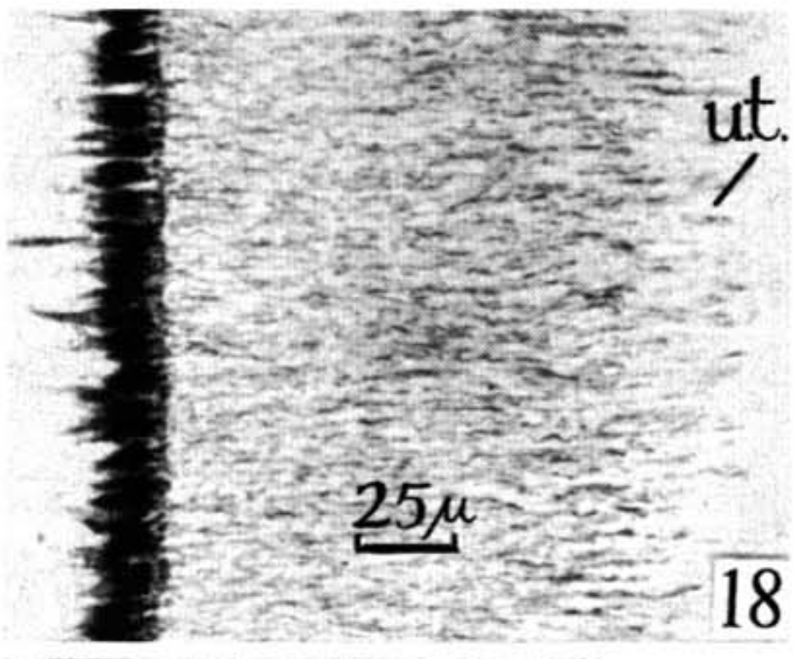


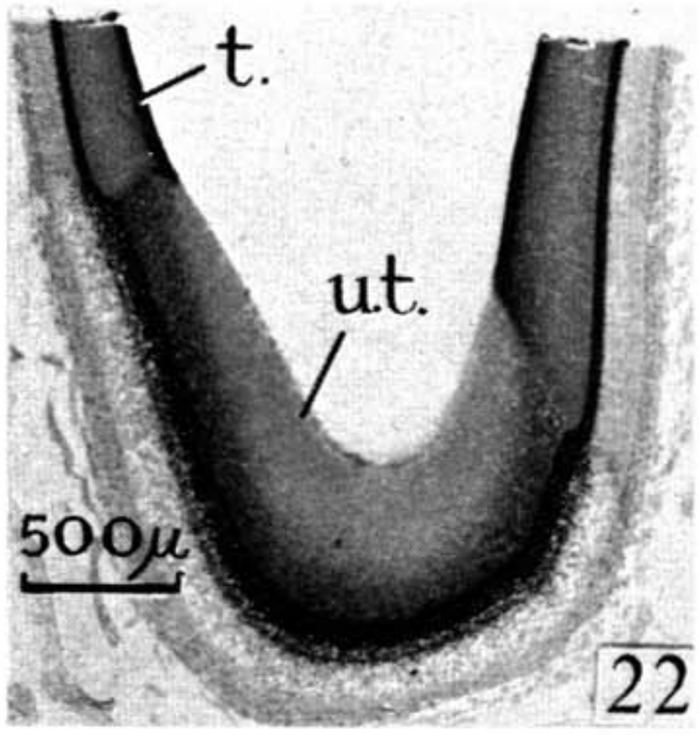


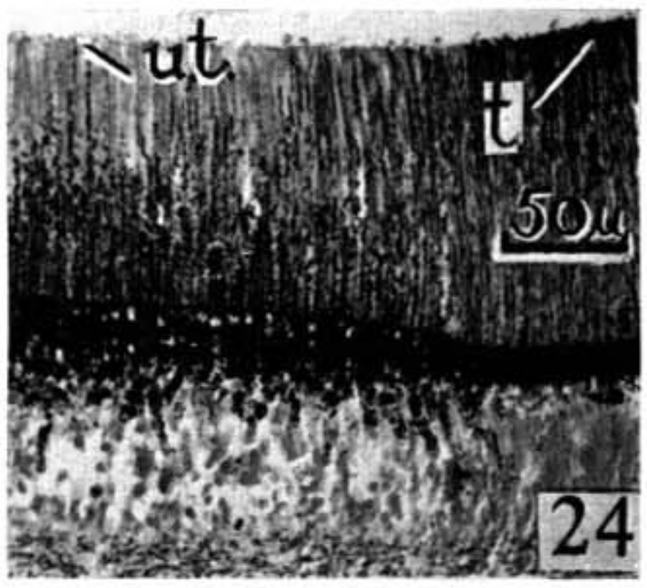












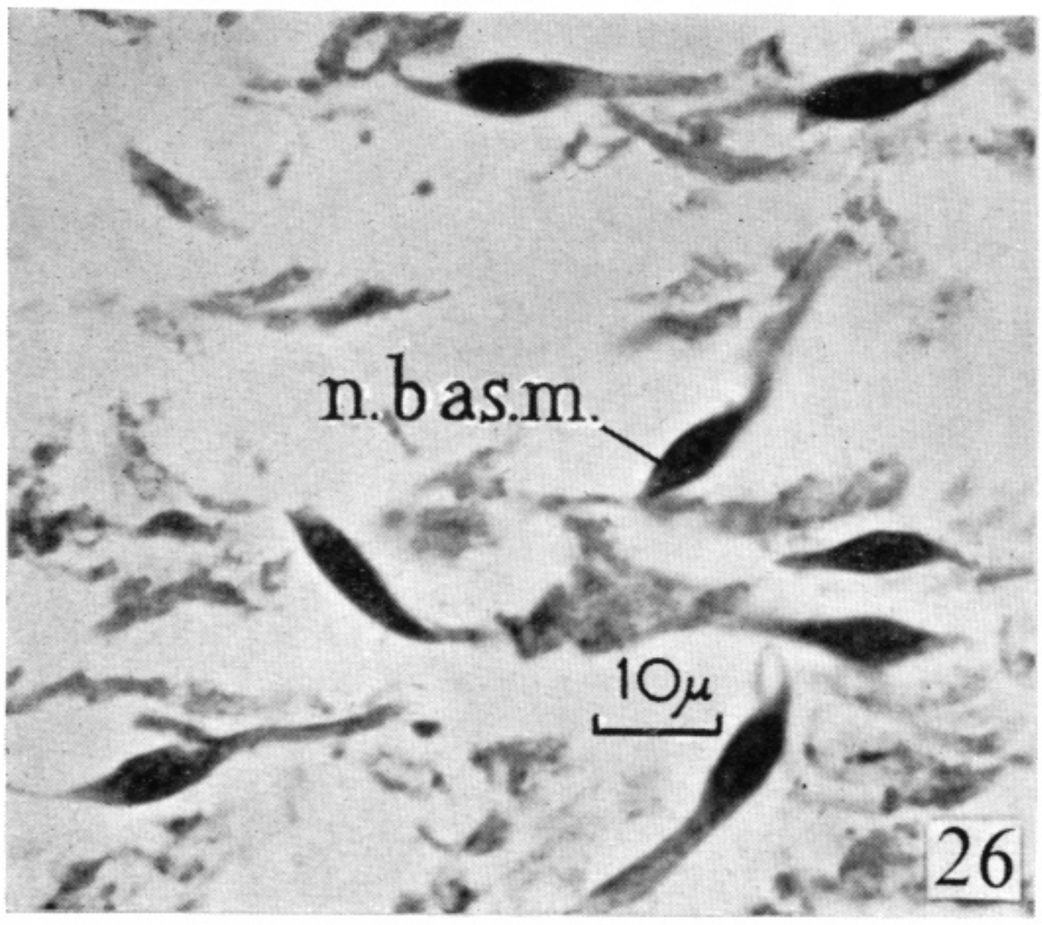
FIGURES 13 and 14. Radial sections from one retina to show differences between the central and peripheral regions, in preparations fixed in formalin, bleached, and stained with haematoxylin and eosin.

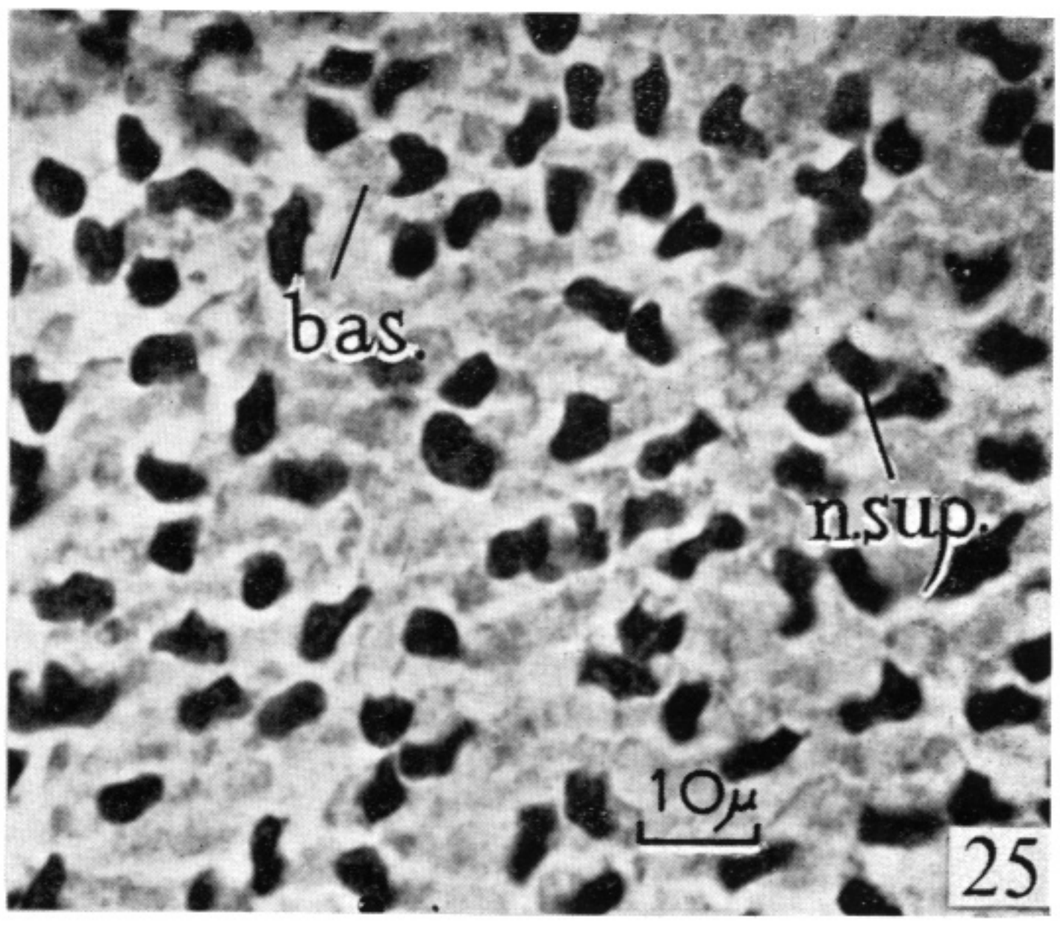
FIGURE 16. Centre of the light-adapted retina of *Eledone* to show the strip in which there is little pigment in the distal ends of the retinal cells. (Formalin, haematoxylin and eosin.)

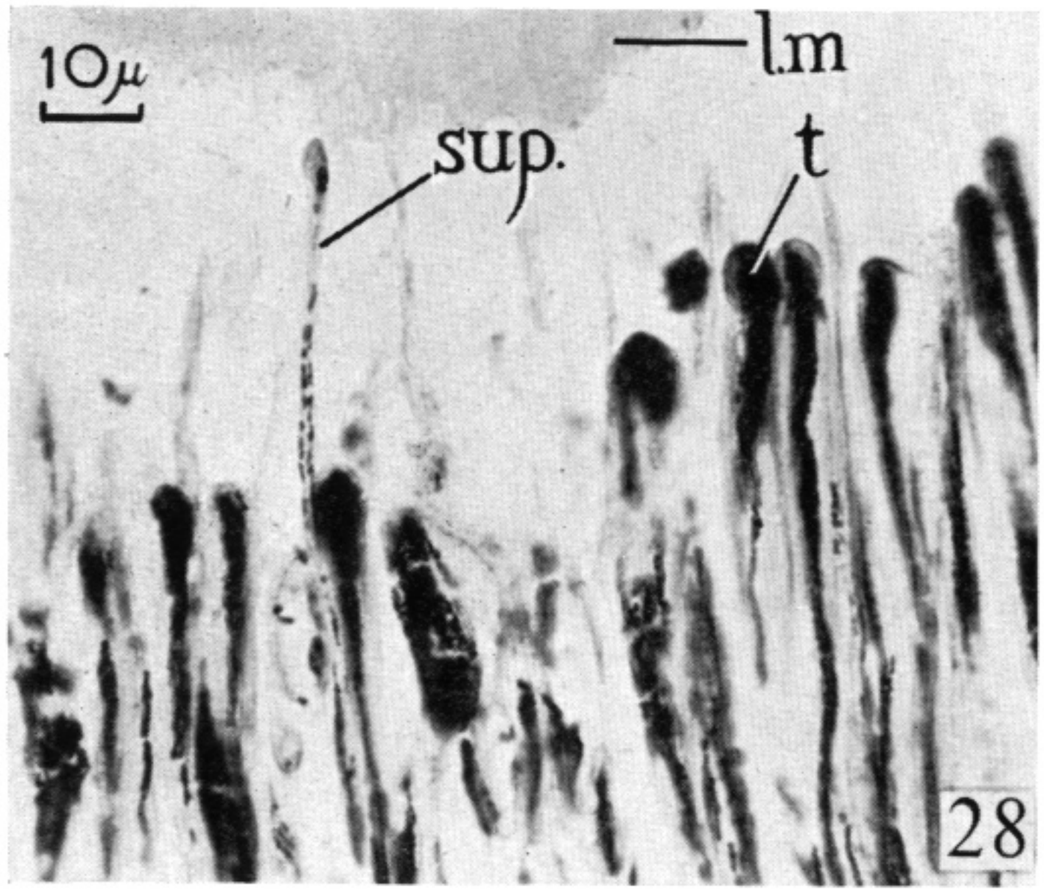
FIGURES 17 and 18. Regions of the light-adapted retina of *Octopus* with and without pigment in the distal ends of the retinal cells. (Formalin, no staining.)

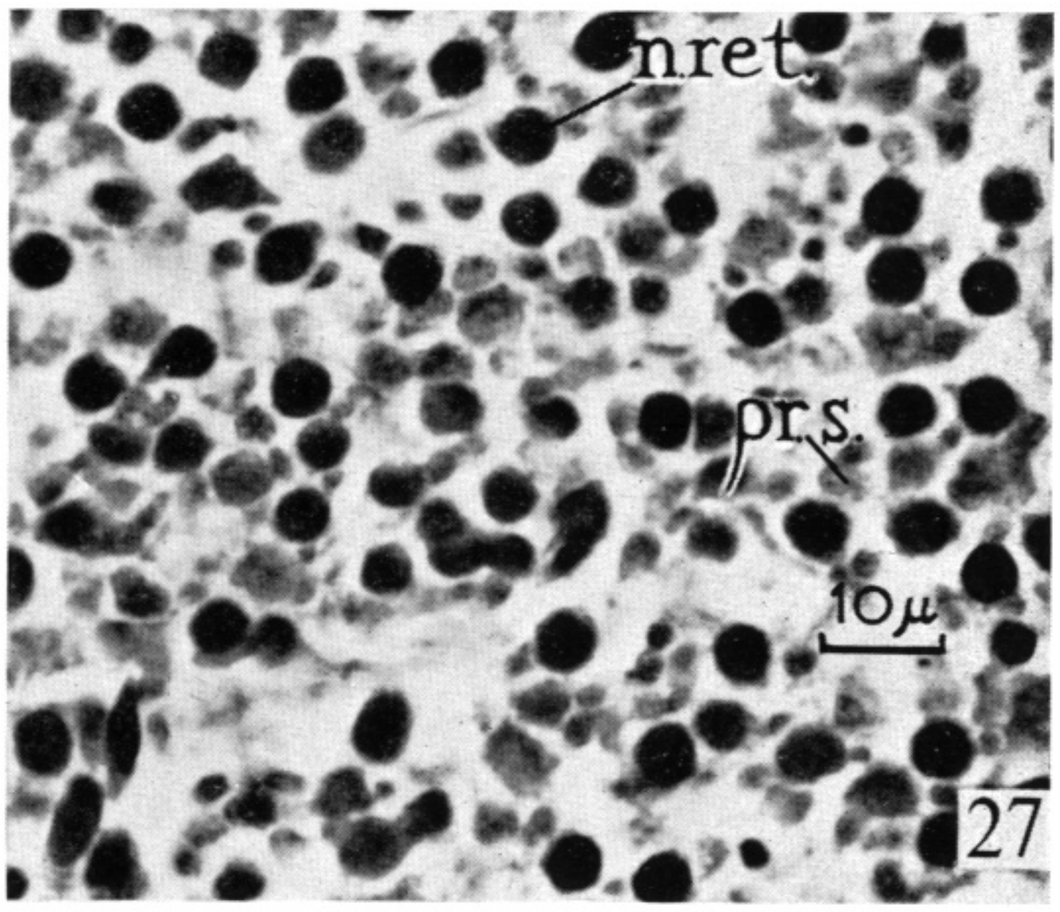
FIGURES 19 to 21. Sections from the dorsal, central and ventral regions of the retina of an octopus where there was distal pigmentation ventrally but not dorsally. (Bouin, haematoxylin and eosin.)

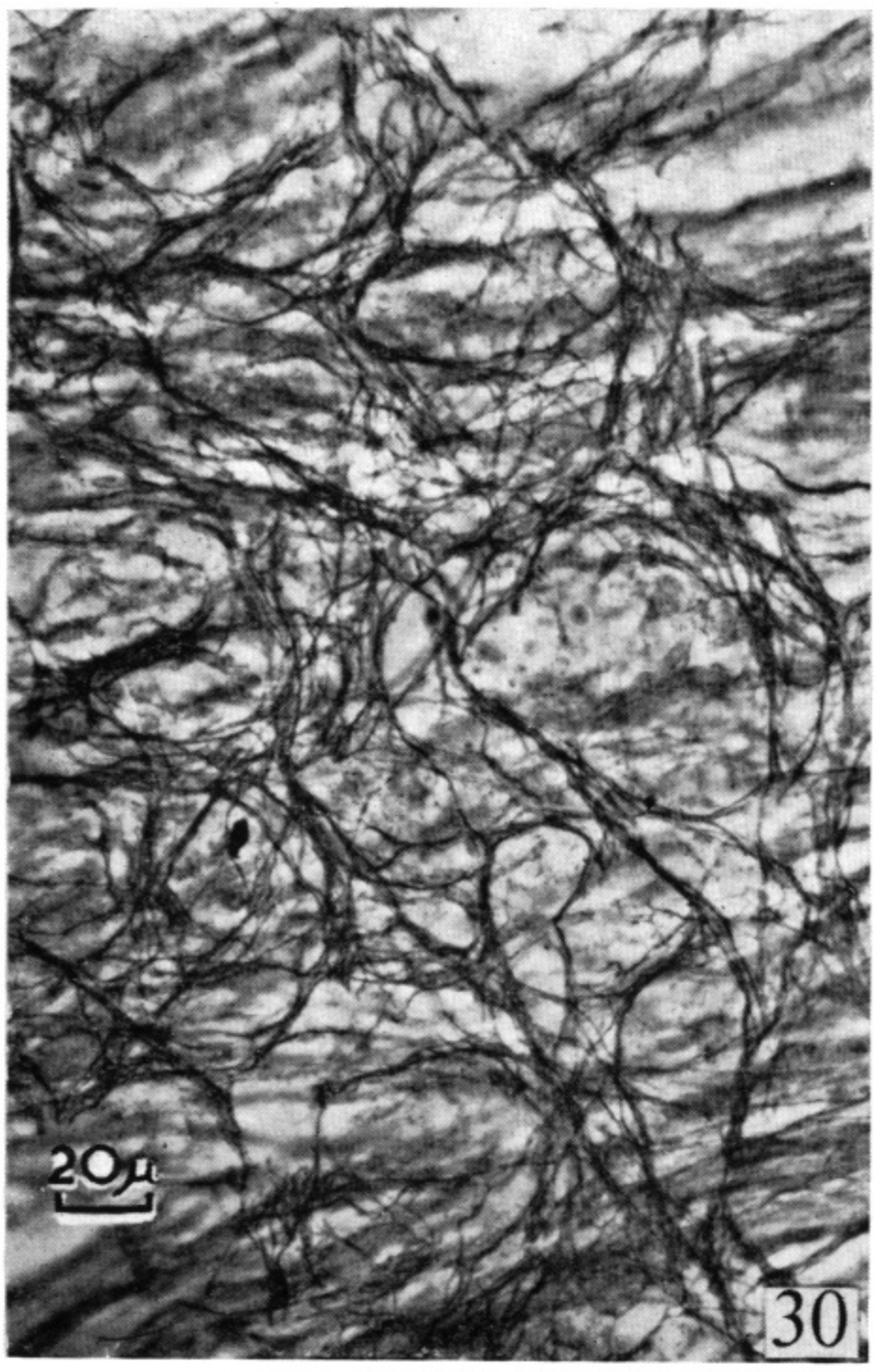
FIGURES 22 to 24. Sections of a region of the retina in the anterior dorsal quadrant where the pigment had retreated locally from the distal regions and there were also changes in the proximal segments. Figure 23 is from a section bleached and stained with haematoxylin and eosin.

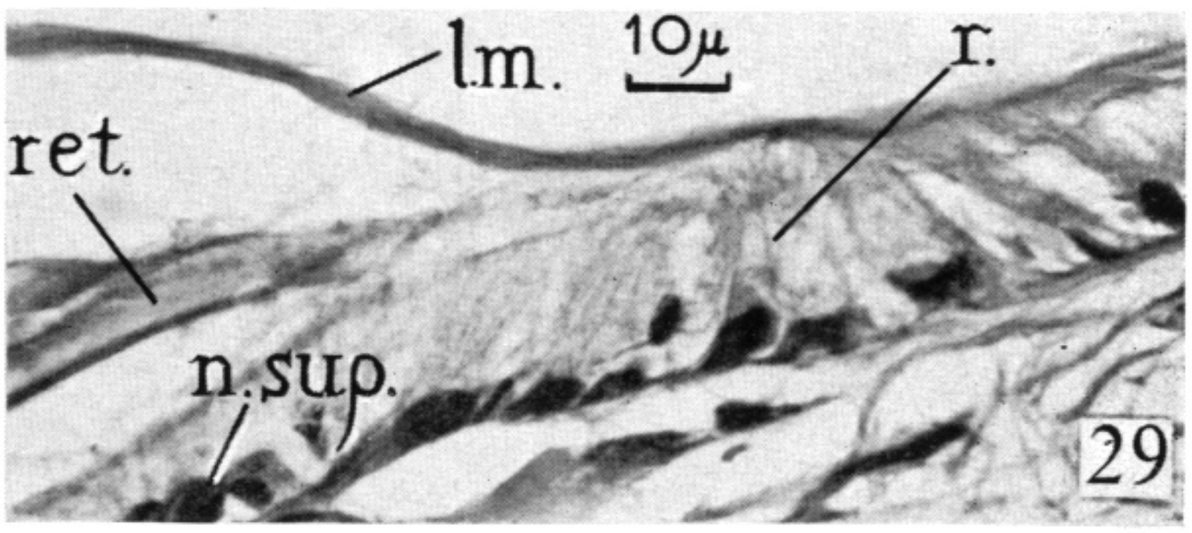


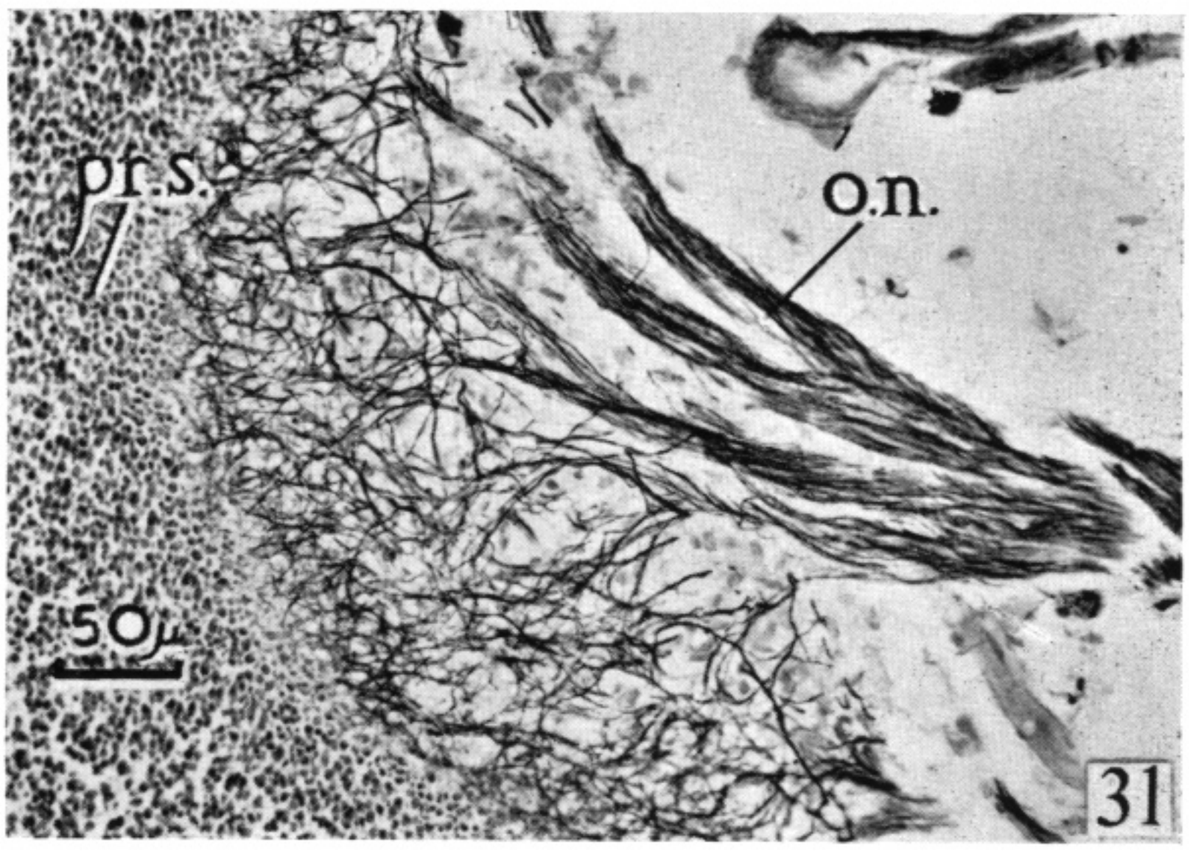










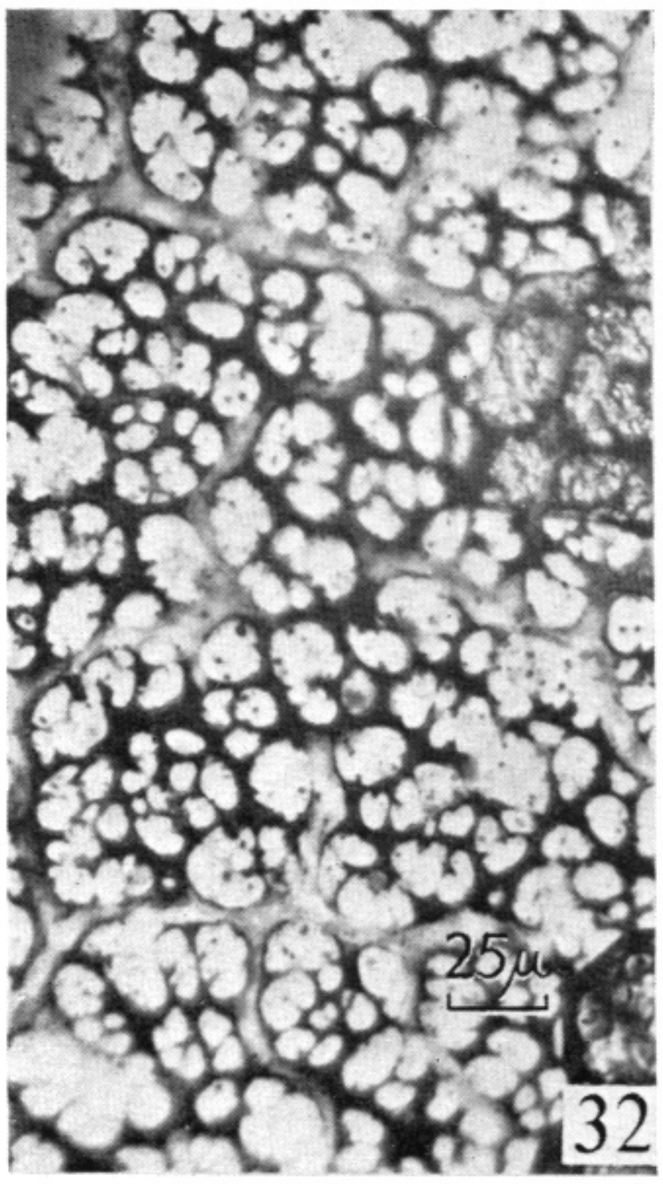


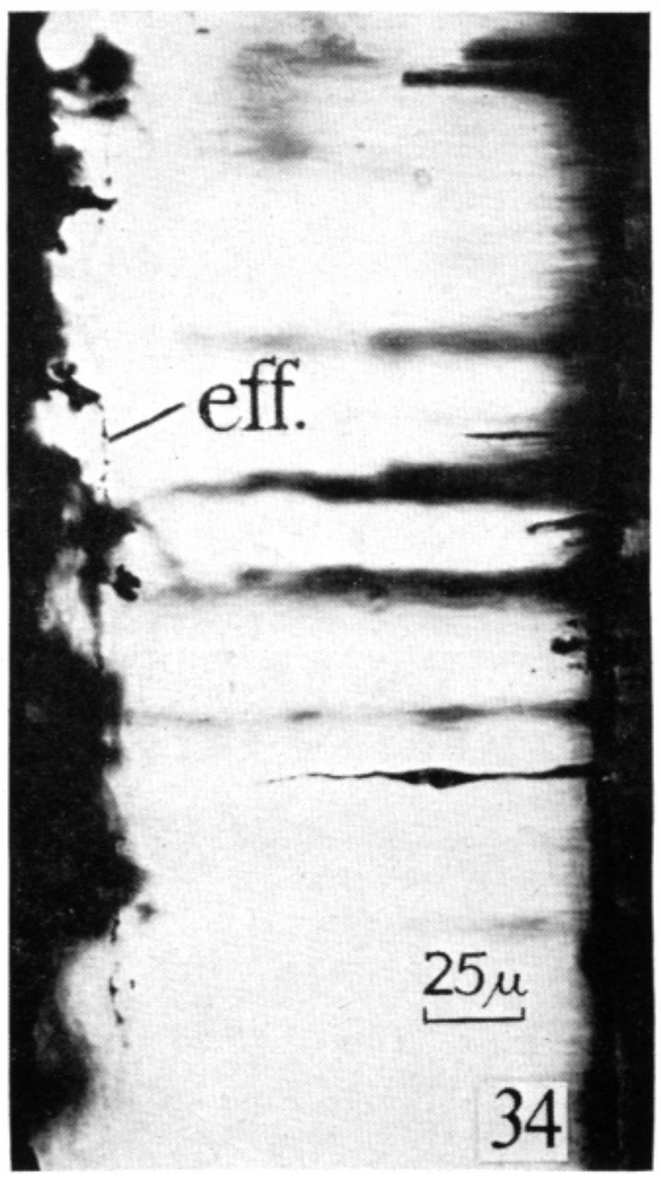
FIGURES 25 to 27. Tangential sections of the nuclei of the supporting cells (25), basal membrane cells (26) and retinal cells (27). (Formalin, bleached, haematoxylin and eosin.)

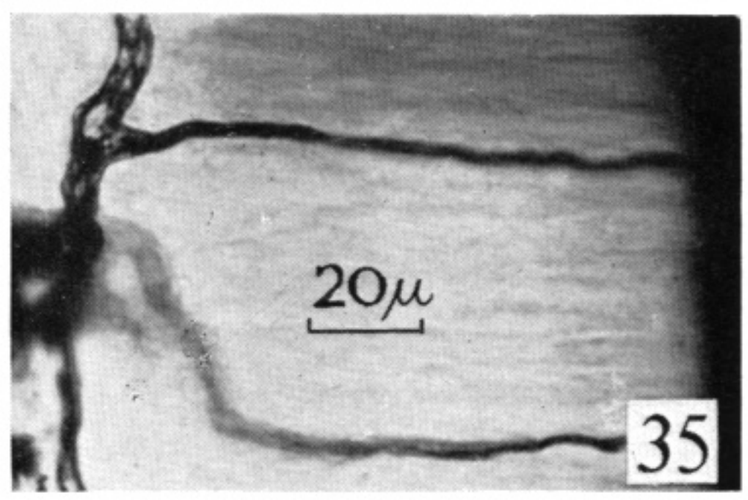
FIGURE 28. Radial section near the margin of the retina where the retinal cells have shrunk away from the limiting membrane, leaving some fibres of the supporting cells, containing pigment. (Formalin, unstained.)

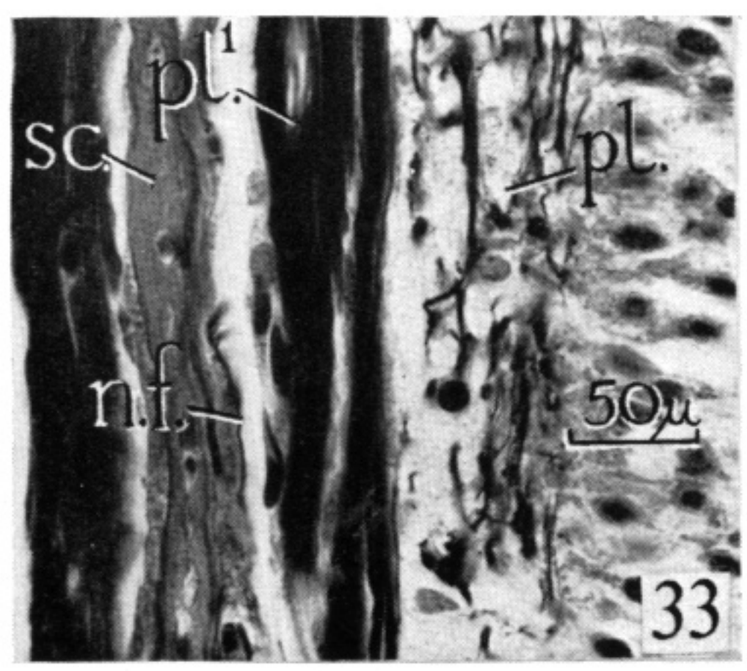
FIGURE 29. Radial section of the margin of the retina. Beyond the last retinal cell (*ret.*) the layer of supporting cells continues and makes a ring of cells (*r.*) apparently attached to the limiting membrane. (Formalin, bleached, haematoxylin and eosin.)

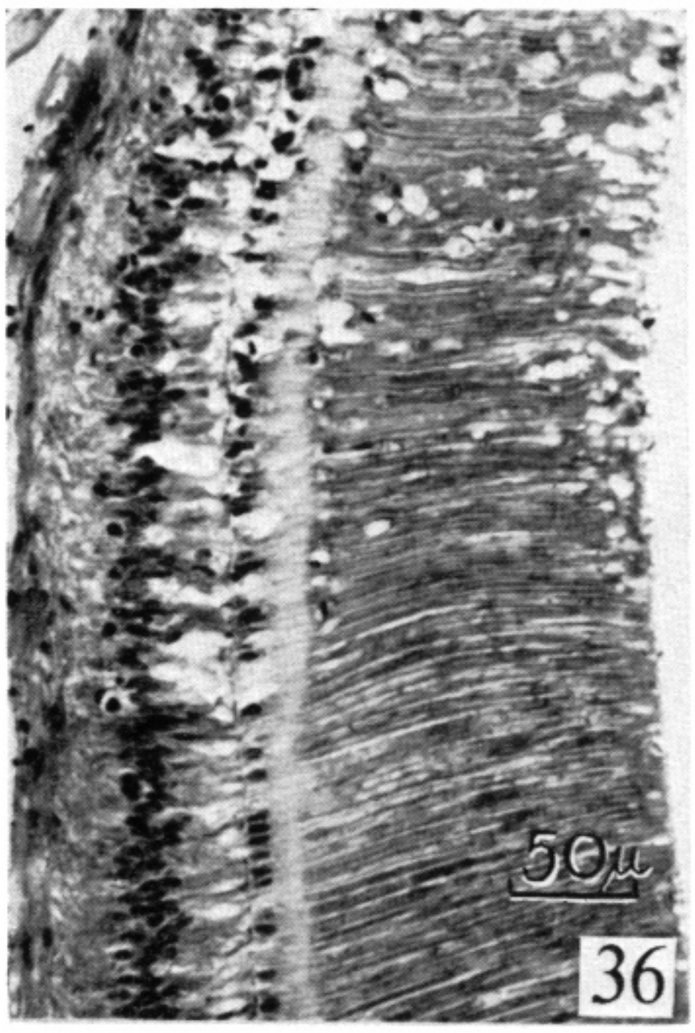
FIGURES 30 and 31. The retinal nerve plexus and origin of the optic nerves. (Cajal.)

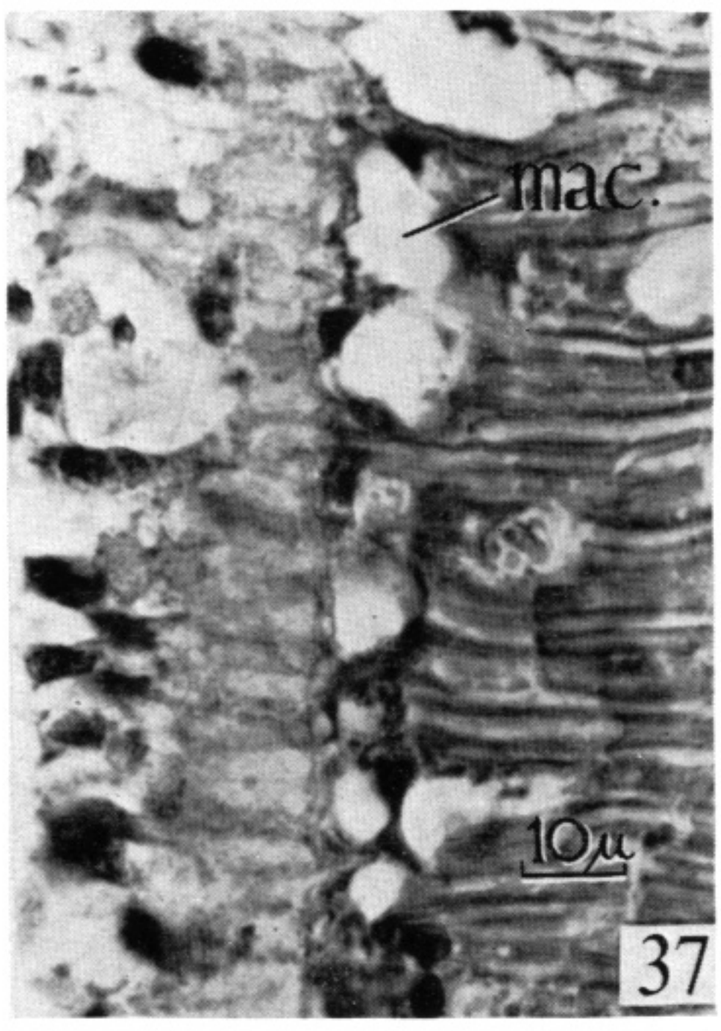












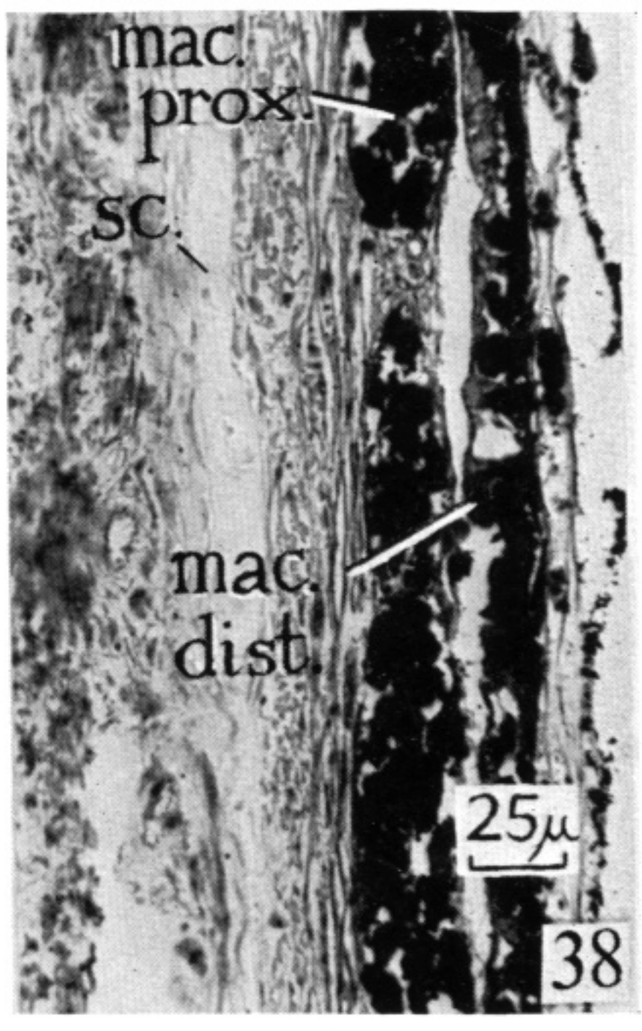


FIGURE 32. Tangential section of basal membrane showing the holes through which the retinal cells pass. (Golgi–Kopsch.)

FIGURE 33. Radial section of retinal nerve plexus to show its inner 'synaptic' and outer 'collecting' components. Isolated nerve fibres near the sclera perhaps innervate retinal muscles. (Cajal.)

FIGURE 34. Radial section to show fine beaded fibres running tangentially. These are probably the endings of the efferents to the retina. (Golgi–Kopsch.)

FIGURE 35. Radial section showing capillaries among the proximal segments. (Golgi–Kopsch.)

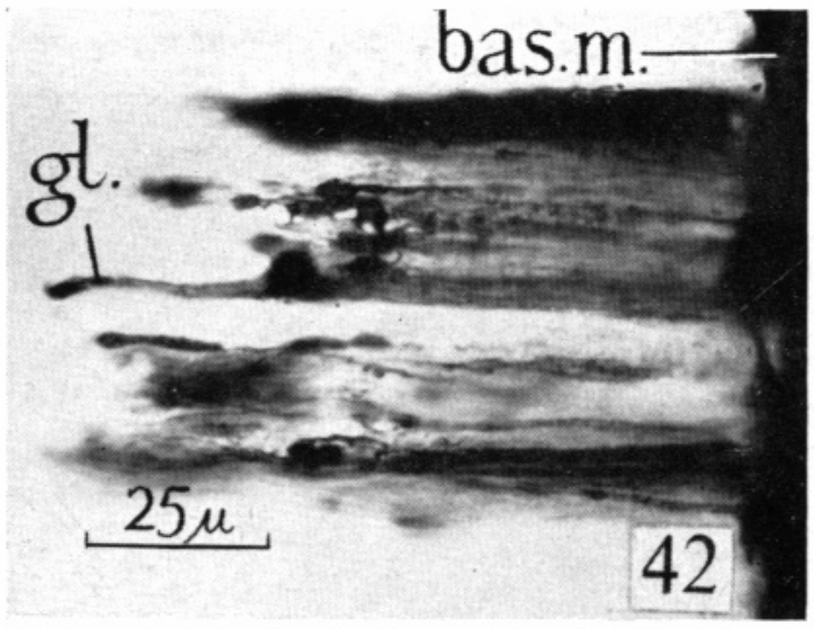
FIGURE 36. Radial section at the boundary of normal and denervated regions in a retina where the optic nerves had been cut 10 days previously and degeneration is beginning. (Formalin, bleached, haematoxylin and eosin.)

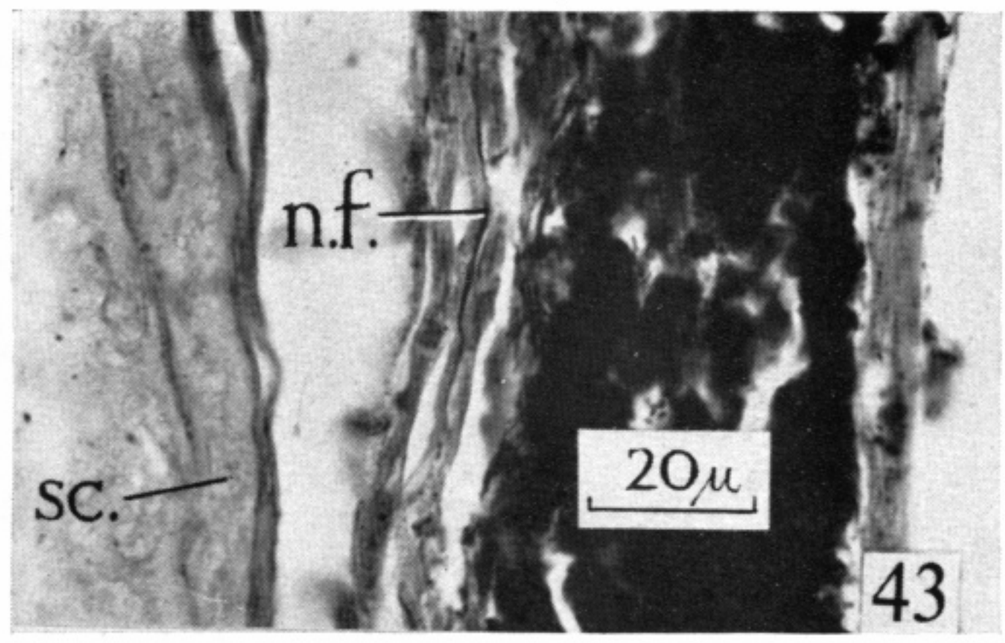
FIGURE 37. Higher magnification of the degenerating region of figure 36.

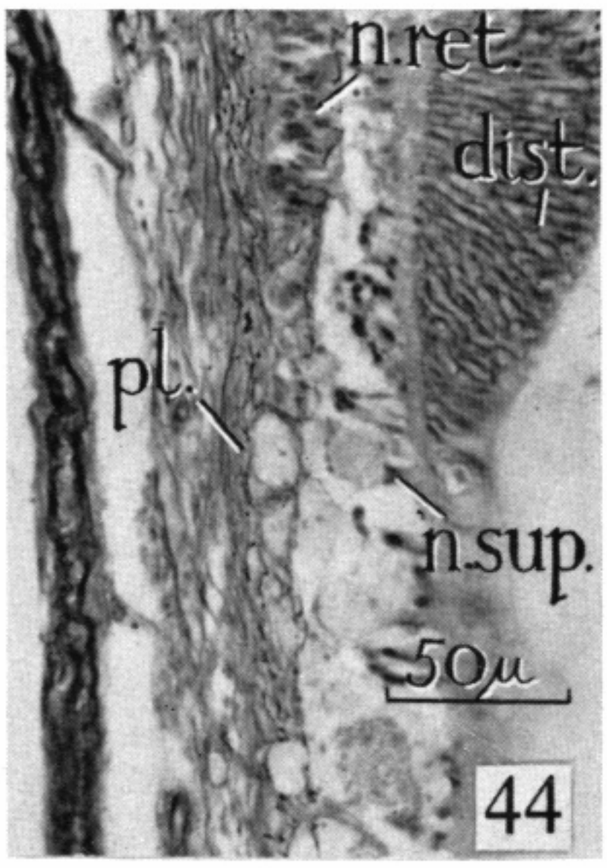
FIGURES 38 and 39. Radial section of retina 31 days after section of the optic nerves. (39 is bleached and stained with haematoxylin and eosin.)

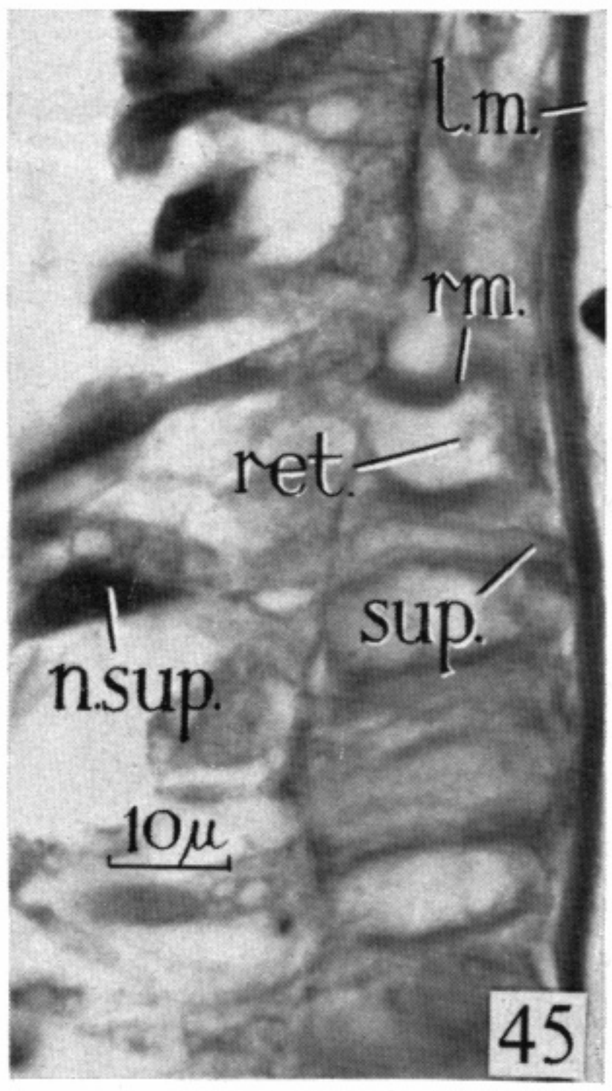
FIGURE 40. Margin of normal and degenerated regions 32 days after severing some optic nerves. The retinal cell nuclei have disappeared from the denervated region but the layer of supporting cells continues. (Formalin, bleached, haematoxylin and eosin.)

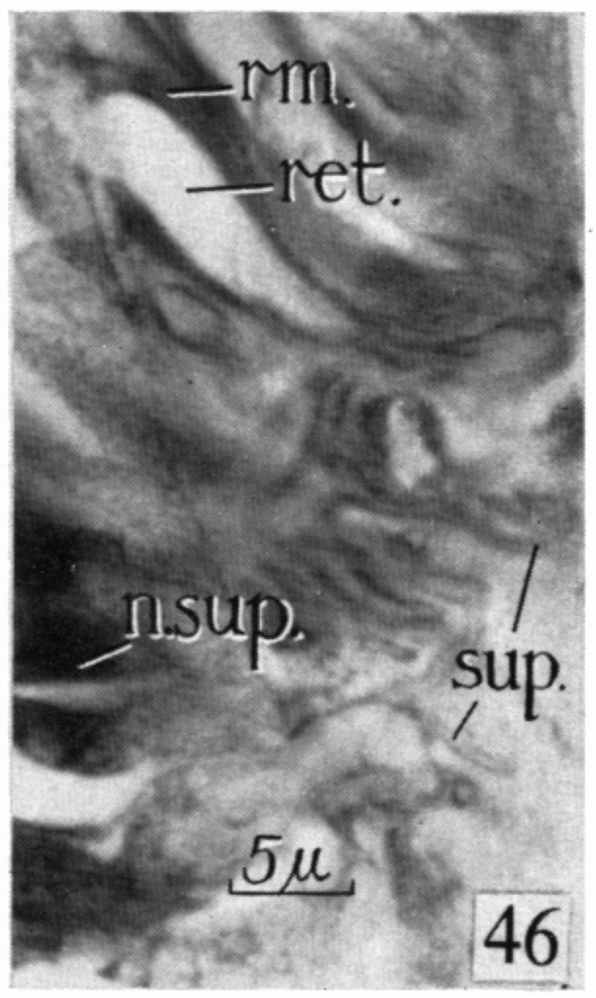
FIGURE 41. Retina 9 days after severing the optic nerves. The retinal cells have disappeared leaving the supporting cells. (Formalin, bleached, haematoxylin and eosin.)

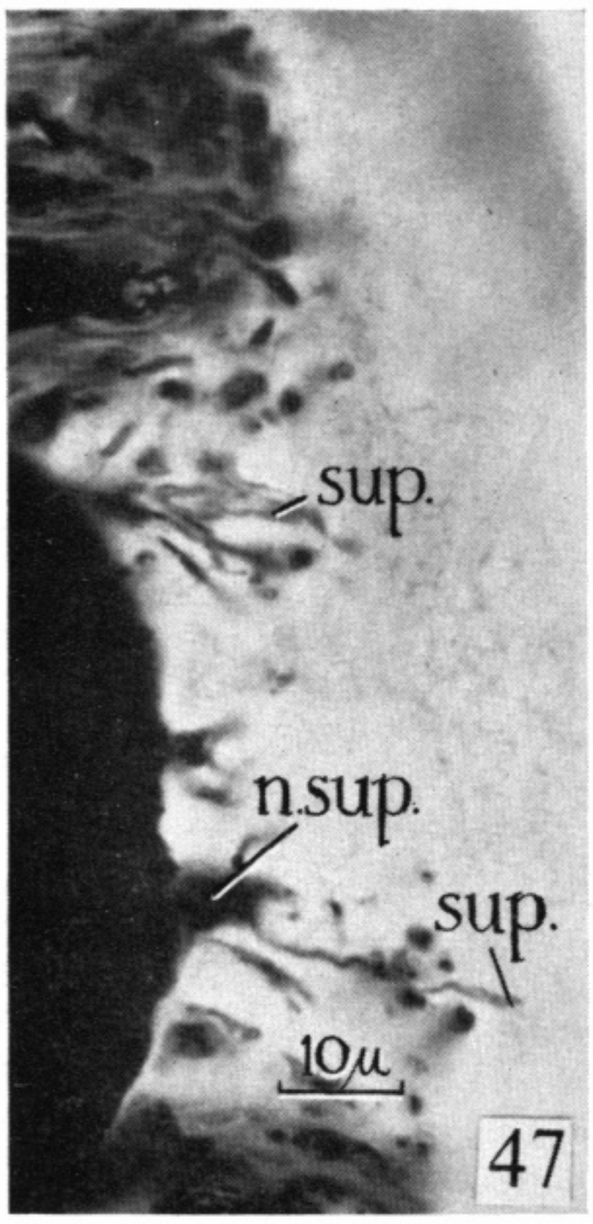


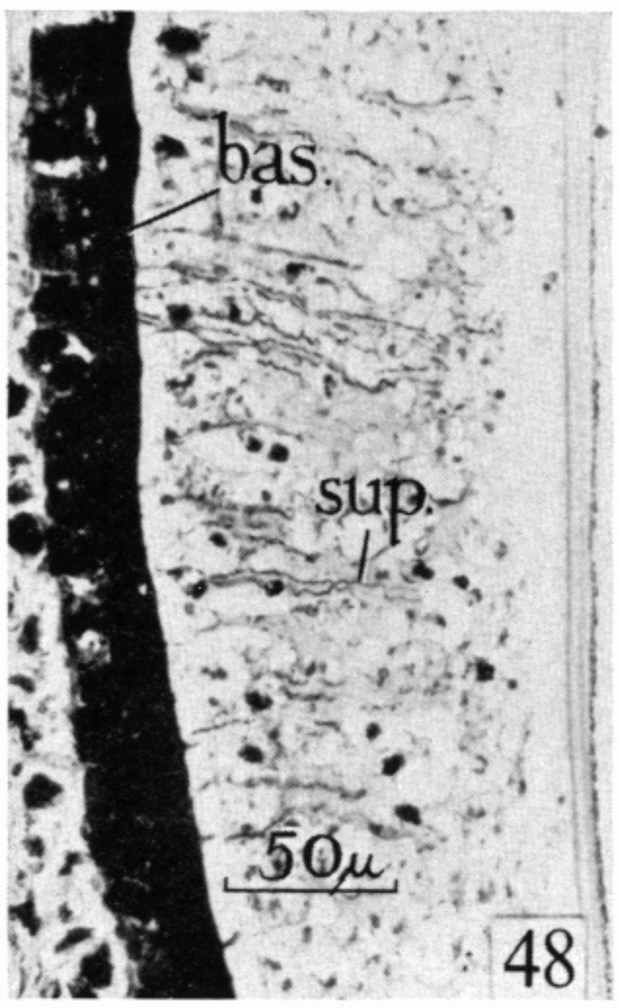












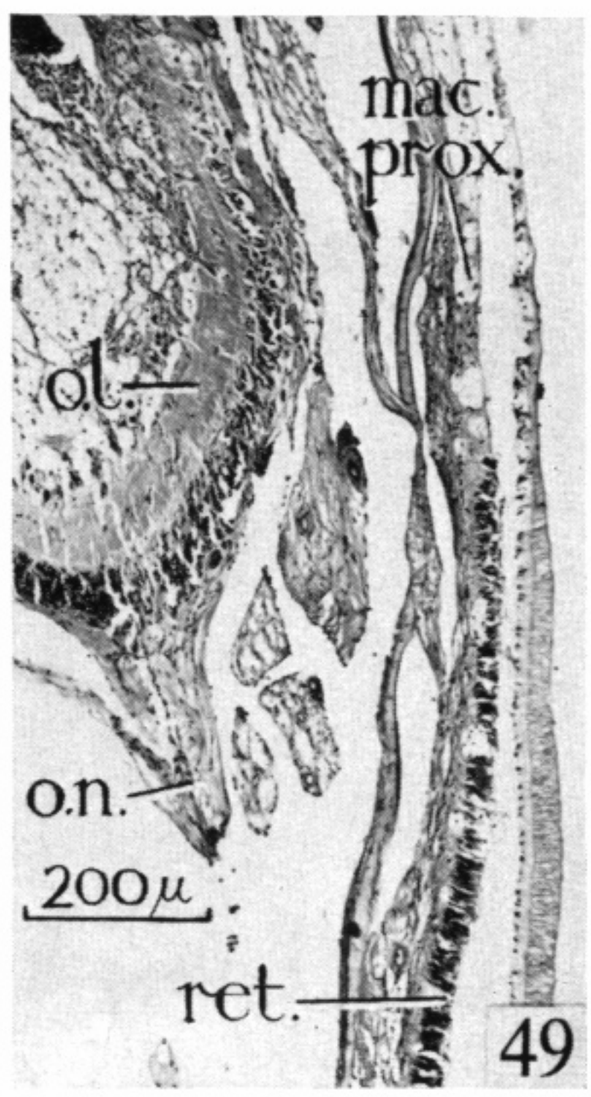


FIGURE 42. Sheets of supporting tissue (glia) that lie around the proximal segments and are perhaps produced by the epithelial cells. (Golgi–Kopsch.)

FIGURE 43. Nerve fibre persisting in retina 42 days after section of the optic nerves. (Cajal).

FIGURE 44. Extension of plexus beyond margin of intact and denervated regions 39 days after section of the optic nerves. (Cajal.)

FIGURE 45. Region where the retinal cells are much reduced in height (see figure 49). The processes of the supporting cells can be seen between them, proceeding to the limiting membrane. (Formalin, bleached, haematoxylin and eosin.)

FIGURE 46. Supporting cells with many processes at the boundary of innervated and denervated region 39 days after section of some optic nerves. (Formol, Mallory.)

FIGURE 47. Supporting cells and their processes at margin of intact and denervated areas 39 days after severing optic nerves. (Cajal.)

FIGURE 48. Persistent processes of supporting cells during the course of degeneration of the retinal cells nine days after severing the optic nerves. (Cajal.)

FIGURE 49. Persistence of part of the periphery of the optic lobe 31 days after severing the optic tract. The retinal cells have survived where they are connected with intact optic lobe tissue, but they are much reduced in length. (Formalin, bleached, haematoxylin and eosin.)