THE OPTIC LOBES OF *OCTOPUS VULGARIS*

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CONTENTS

The optic lobes provide a system for coding the visual input, for storing a record of it and for decoding to produce particular motor responses. There are at least three types of optic nerve fibre, ending at different depths in the layered dendritic systems of the plexiform zone. Here the optic nerve fibres meet the branches of at least four types of cell. (1) Centripetal cells passing excitation inwards. The dendrites of these are very long, with fields orientated more often in horizontal and vertical than in other directions. (2) Numerous amacrine cells, with cone-shaped dendritic fields but no determinable axon. (3) Centrifugal cells conducting back to the retina. (4) Commissural fibres from the opposite optic lobe, and other afferents.

After section of the optic nerves the plexiform layer of the corresponding part of the optic lobe becomes reduced, but the tangential layers of dendrites remain. There is a reduction in the thickness of the layers of amacrine and other cells and a shrinkage of the whole lobe. Conversely the tangential layers can be degenerated, leaving the optic nerve fibres, by severing the arteries to the optic lobe.

The centre of the optic lobe contains cells with spreading dendritic trees of many forms. Some run mainly tangentially, others are radial cones. Those towards the centre send axons to the optic tract. Small multipolar cells accompany the large neurons of the cell islands.

About 2×10^7 optic nerve fibres visible with the light microscope enter the lobes but only $0{\cdot}5 \times 10^6$, or less, leave in the optic tract, these being distributed to some ten centres in the supraoesophageal lobes.

It is suggested that the variety of shapes of the dendritic trees within the optic lobes provides the elements of the coding system by which visual input is classified.

1. Introduction

The optic lobes of cephalopods have been the subject of excellent investigations by v. Lenhossék (1896) and Cajal (1917), as well as others. The abundant data provided by these workers are of the greatest value, but it now appears that there are both regularities and complexities that they did not suspect in the branching systems of the cells of the lobes. Moreover, these regularities may be related to the mechanism for discrimination of shapes by analyzing their vertical and horizontal extents (Sutherland 1957, 1960). There is therefore need for even more detailed knowledge of the arrangement and numbers of the many types of cell that are present. The dendritic fields of these cells are often most elaborate and it is very difficult to obtain sections that show their form. Much remains to be done, and the present work serves only as an introduction to some aspects of a most complicated subject, which will need to be fully explored if we are to understand the functioning of the visual system.

2. Methods

Nearly all the work here described has been with *Octopus vulgaris*, but much material from *Eledone*, *Argonauta* and other octopods and decapods has been available for comparison. There are important differences between the optic systems of cephalopods, and these may provide valuable clues to the relation between methods of using the eyes and the forms of the cells concerned. Nevertheless, there is a basic similarity among them all, as will appear when the present data are compared with those of Lenhossék on *Eledone*, Kopsch (1899) on *Loligo* and Cajal on *Sepia*. A variety of histological techniques has been used, mainly after fixation by immersion, but sometimes by injection through the cephalic aorta. Material must be fixed immediately after killing, as post-mortem changes are rapid. Cajal's method after formol fixation provides a good general method, staining axons, dendrites and nuclei (Young 1939). For detailed estimates of sizes and numbers the material was embedded in celloidin and sectioned at 5 and 15 μ. Much has been gained by cutting sections at widely different thicknesses and comparing sections of plexuses, dendrites, etc., made in various planes.

Details of the cells were obtained from Golgi methods, of which several have been tried. The most generally useful has been the Kopsch modification, used as follows:

Fixation in

(1) 3·5% potassium bichromate (in sea water), 80; 40% formaldehyde, 20; for 24 h.

(2) 3·5% potassium bichromate for 3 to 6 days.

(3) 0·75% silver nitrate for 1 to 2 months.

This gives good impregnation of complete neurons, including their axons, sometimes also of glia and blood vessels.

Good results have also been obtained with Golgi methods applied to material fixed in formol, even after some months. The pieces are placed in 2·5% potassium bichromate at 34 °C for 2 days and then in 2% silver nitrate for 1 to 2 days.

Classical rapid Golgi methods with osmium-bichromate fixation gave, on the whole, less good but still some useful results, as also did long fixation with bichromate or Muller's fluid. Cox methods gave useful impregnations of dendrites and glia.

3. Degeneration techniques

It was possible to confirm several features of the pathways by suitable operations, such as severing the optic nerves or optic tract, or making incisions into the optic lobes. Operations were done under urethane anaesthesia. Degeneration is very rapid, at least with small fibres, and for summer water temperatures (20 to 26 °C). Severed optic nerve fibres became granular, as seen with Cajal's stain, a few hours after injury, even at a distance from the lesion. The reaction is at its maximum after two days and shortly after this all trace of the fibres has disappeared.

4. Optic nerves

These consist of numerous bundles of fine fibres proceeding from the back of the eyeball to the surface of the optic lobes. They form chiasmata, the bundles interweaving so that fibres from the dorsal part of the retina enter the optic lobe ventrally and vice versa (figure 1). The central fibres, projecting to the middle region of the optic lobe, are thus shorter, the more peripheral ones are longer and reach to the regions close to the hilum of the optic lobe. The longest nerves are some 2 cm long in a medium-sized octopus.

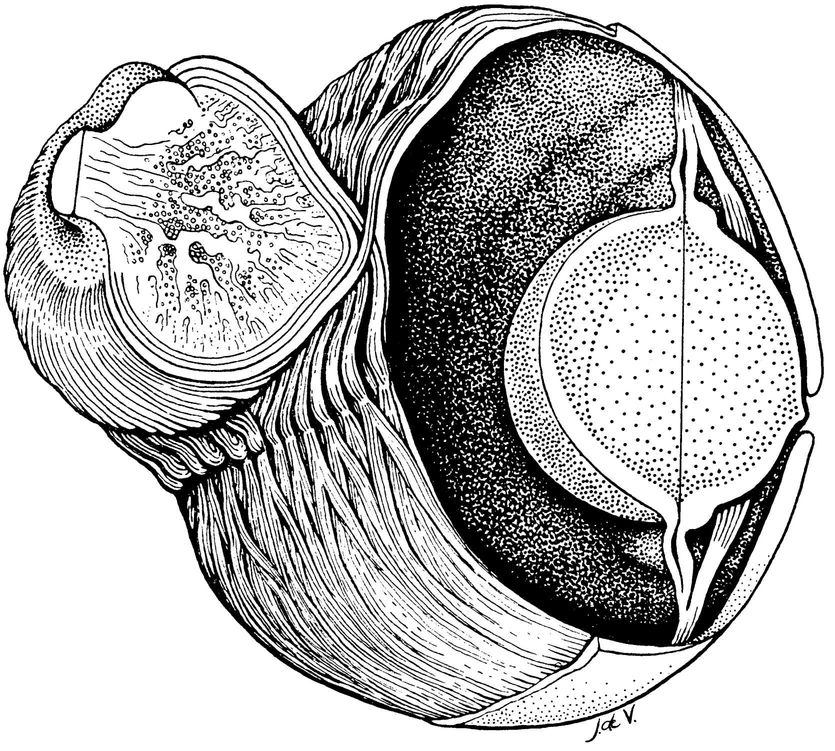


Figure 1. Drawing of a dissection of the eye and optic lobe of *Octopus*, to show the arrangement of the optic nerves and their chiasmata.

The optic nerves contain the axonal processes of the retinal cells after the latter have passed through a plexus in which there may be synaptic interactions (Lenhossék, Cajal, Young 1962*a*). The optic nerves also contain fibres whose cell bodies lie in the optic lobes and even further centrally (see later).

5. ORGANIZATION OF THE OPTIC LOBES

Each optic lobe lies behind the eye in an 'orbit' bounded by cartilage and a tough fibrous membrane ('extra orbital sack'). It is cushioned by a mass of 'white body', lying in a system of orbital sinuses, which are controlled by special valves (Boycott & Young 1956). The optic lobe is a bean-shaped structure, with its long axis in the antero-posterior direction, as the eye is usually held. The head and eyes are, of course, highly mobile, but with the information provided by the statocysts they are usually held with the slit-like pupil horizontal, whatever the position of the animal (Wells 1960; Dijkgraaf 1961). The 'horizontal plane' of the optic lobe will be held to be that parallel to its upper surface. 'Sagittal' and 'transverse' are then the two planes at right angles to this. Radial planes will be considered to be those proceeding from the centre of the lobe, and tangential planes are at right angles to these. The optic nerves enter the lobe over four-fifths of its surface, that is everywhere except at the median border, where there is the optic tract (figure 2, plate 7). The latter is a very large bundle containing fibres running both ways between the optic lobe and supra- and suboesophageal centres and many commissural fibres running between the two optic lobes.

On the dorsal surface of the optic tract lie two nervous structures and a gland—the peduncle and olfactory lobes (figures 2, plate 7 and 75, plate 13) and the optic gland (Boycott & Young 1956). The peduncle lobe receives many fibres from the optic lobes and its function is not known but may perhaps be concerned with the control of motor responses to visual changes. The olfactory lobe receives the olfactory nerve and is connected with the dorsal basal lobe, of the supra-oesophageal mass (Boycott & Young 1962). The optic gland receives nerve fibres from the dorsal basal region and is itself concerned in the regulation of the onset of sexual maturity (Boycott & Young 1956; Wells & Wells 1959).

Attached to the optic lobe is a curious strand of tissue, the subpedunculate organ (Thore 1939; Boycott & Young 1956). This is closely related to the blood vessels of the lobe, but its nature remains an enigma.

6. DIVISIONS AND LAYERS OF THE OPTIC LOBE

The lobe is sharply differentiated into an outer regularly arranged cortex, the 'deep retina', and a central medulla, composed of irregular islands of cells, separated by tracts of neuropil and nerve fibres (figure 3, plate 7). The cell islands become progressively fewer approaching the optic tract. In the cortex is the plexiform zone, a region consisting only of nerve fibres, including the endings of the optic nerve fibres. This is covered externally by a layer of small cells, the outer granule cell layer, and on its inner side is an inner granule cell layer, merging into the cell islands of the medulla.

The optic lobe may seem at first sight not to have the organization typical of molluscan ganglia, that is to say an outer layer of unipolar nerve cells whose fibres proceed into a central neuropil. Closer inspection shows, however, that this plan is basically followed, but the neuropil is broken up and distributed. The whole plexiform zone may be considered as one mass of neuropil, receiving the fibre trunks of unipolar cells of the outer and inner granule cell layers. From these trunks dendritic collaterals arise and some of them have axons that run back through the inner granule cell layer to the medulla of the lobe (*u.p.* figure 4). Some of the cells of the inner granule layer are bipolar, however, and in addition to the fibres that they send to the plexiform layer (dendrites) they also send one or more axons inwards towards the medulla (*bi.* figure 4).

The medulla itself may be considered as consisting of numerous islands of unipolar nerve cells, whose branches pass outwards to their neuropil, rather than inwards as in a typical ganglion. They show wide-spreading branching dendritic systems, from which an axon then proceeds either to some other part of the medulla, or to the optic tract.

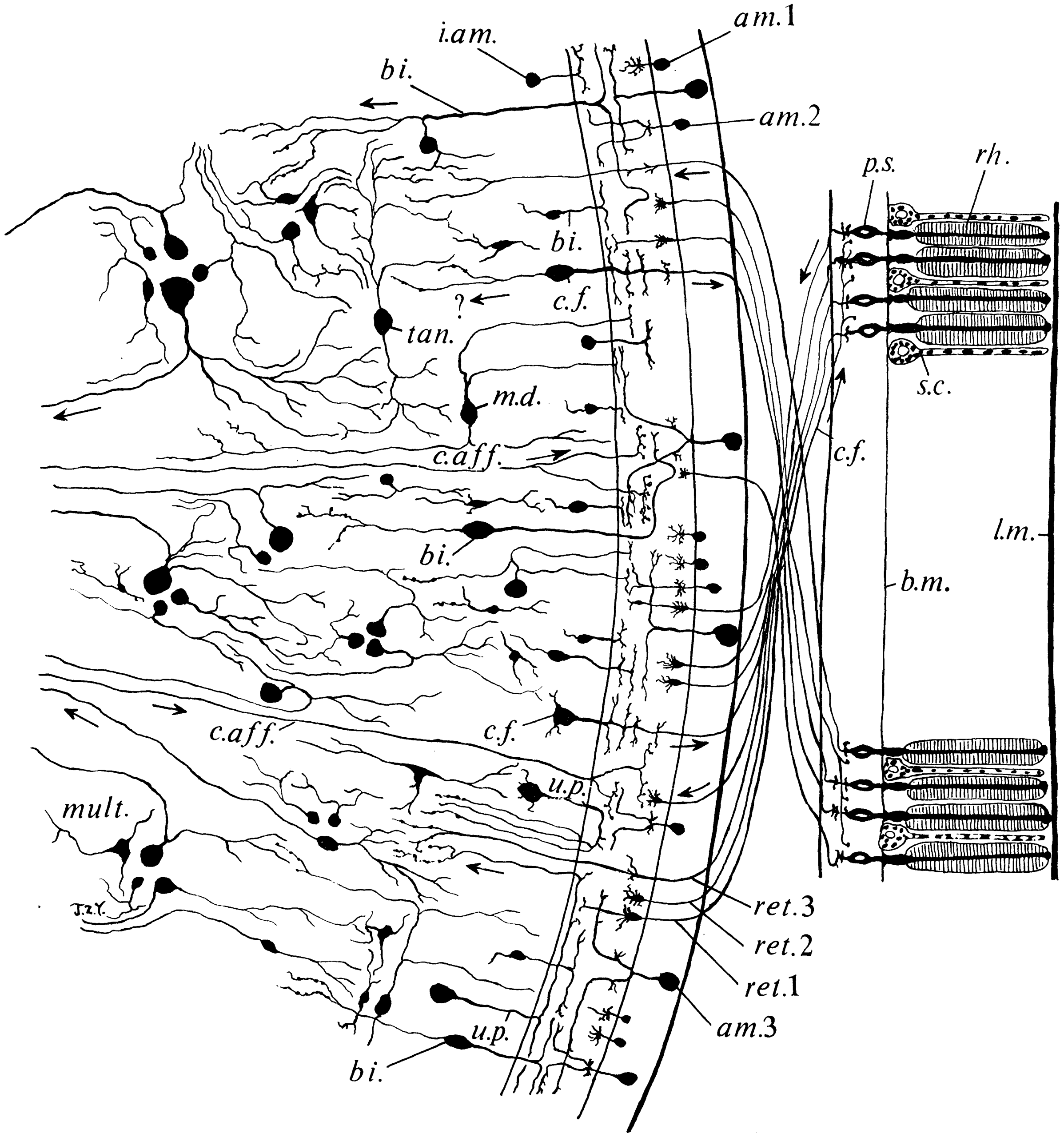


FIGURE 4. Diagram of the connexions of the outer portion of the optic lobe.

While the basic plan can thus be recognized, it is often difficult to identify which are dendrites and which axons, where all spring from a common trunk. In some places the dendrites are very long and little-branched except at their tips. Characteristic thin axons can often be recognized, ending in beaded terminal networks. However, there are many cells whose branches all appear alike. When these branches are well stained and all apparently included in one section it is difficult to believe that any one of them is an 'axon'.

7. NUMBERS OF CELLS IN THE OPTIC LOBES

These have been determined approximately in two series of sections, by methods described elsewhere (Young 1962*b*) and are summarized in table 1. Those in the two granular layers are mostly very small, though a few larger ones occur at the outside of the outer layer, and others deeper in the inner one. This arrangement confirms that the plexiform zone may be compared with a typical ganglion elsewhere in the nervous system of cephalopods or other molluscs, where the larger cells are furthest from the neuropil. There are calculated to be some 2×10^7 retinal cells in the eye, each bearing presumably one fibre that enters the optic nerves (Young 1962*a*). There is, therefore, about one small cell of the outer and inner granule cell layers for each retinal fibre.

TABLE 1. NUMBERS OF CELLS WITH NUCLEI OF THE DIAMETERS GIVEN, AT VARIOUS DEPTHS IN ONE OPTIC LOBE OF AN OCTOPUS OF ABOUT 500 GRAMS

	number of nuclei (10^6)			
layer	$< 5\ \mu$	5–10 μ	$> 10\ \mu$	total
outer granular	18·3	0·5	—	18·8
inner granular	15·6	0·3	—	15·9
central 1	15·8	0·4	0·04	16·2
2	6·2	0·3	0·04	6·5
3	2·7	0·9	0·03	3·6
4	2·5	0·7	0·02	3·2
total	61·1	3·1	0·13	64·2

In order to assess how many fibres leave the lobe in the optic tract we may assume that all cells with nuclei over 10 μ carry axons that do so—namely, 130000. But this is probably an underestimate of the total if smaller cells also contribute, and we may provisionally use a figure of $0{\cdot}25 \times 10^6$ for the fibres leaving the lobe in the tract. The reduction between the optic nerves and the tract thus approaches 100 times.

The cell islands towards the centre of the lobe contain large and small cells, with an increasing proportion of the former. The measurements were not sufficiently precise to determine whether there is an increase of maximum cell size passing inwards. It would be useful to know this to discover whether there is any functional division within the medulla. Probably it is best regarded as a homogeneous entity, with cells at all levels giving rise to fibres that enter the optic tract, but with proportionately more of these towards the centre. Large cells certainly occur even in the outer islands of the medulla, and it is probable that fibres of the optic tract arise from these. Electrical stimulation produces movements of the animal if the electrode is in the medulla but not if it is in the cortex (Boycott 1961).

The centre of the lobe contains few neurons and the nuclei recorded in this region are probably mainly those of glia, blood vessels and the subpedunculate tissue (p. 23).

In the retina there is a strip of cells somewhat different from the rest lying along the equator. There is no obvious comparable differentiation in the optic lobe but no detailed investigation has been made of possible minor differences. The plexiform layer is thinner at the edges of the lobe and increases gradually to a maximum at the centre; but the differences are small.

ABBREVIATIONS USED ON TEXT-FIGURES AND PLATES

am. 1–3	amacrine cells of outer granule cell layer
ax.	axon
b.m.	basal membrane
bas.d.	basal dendrites
bi.	bipolar cell
b.p. 1, 2	bipolar cells conducting away from the plexiform zone
c.f.	centrifugal cell of inner granule layer.
c.aff.	afferent to plexiform layer from central regions
col.	collateral fibres coming from the axon
den.	dendritic field of bipolar cell
dors.bas.	dorsal basal lobe
*f.tan.*1	fibre running a long course in the first tangential layer
gl.	glial fibres investing a large cell of inner granule layer
i.am.	amacrine cells of the inner granule cell layer
i.b.l.	inner basement layer
i.gr.	inner granule cell layer
inf.fr.	inferior frontal lobe
l.m.	limiting membrane
lat.ped.	lateral pedal lobe
m.d.	cell with many dendrites proceeding outwards
med.	medulla of optic lobe
m.p.	multipolar cell with many dendrites reaching to plexiform layer
mult.	small multipolar cells
o.b.l.	outer basement layer
o.gl.	optic gland
o.gr.	outer granule cell layer
olf.l.	olfactory lobe
o.n.	optic nerves
o.tr.	optic tract
p.s.	proximal segment
ped.l.	peduncle lobe
pl.	plexiform zone
r. 1–4	radial layers of plexiform zone
rec.	cell with recurrent axon leading away from plexiform zone
ret.sw.	swollen region of retinal fibre in first radial layer
ret. 1–3	retinal nerve fibres of three types
rh.	rhabdome
stat.	statocyst
s.c.	supporting cell
subv.	subvertical lobe
sup.fr.lat.	lateral superior frontal lobe
t. 1–4	tangential layers of plexiform zone
tan.	tangential cell of outer medulla
u.p.	unipolar cells with a fibre running to the plexiform zone and axons returning from this
vert.	vertical lobe

8. THE CORTEX OR DEEP RETINA OF THE OPTIC LOBES

The cortex of the optic lobes shows some striking similarities to the outer regions of the vertebrate retina (figures 5, 15, plates 7, 8). The optic nerve fibres run radially through the outer granule cell layer to the plexiform zone, where they mostly end. Here they meet (1) dendritic branches of amacrine cells of the outer and inner granular layers, these being cells that have not been shown to have axons; (2) dendritic branches from cells in the inner granular layer and deeper in the lobe, whose axons run into the centre of the optic lobe (centripetal cells); (3) dendritic branches of centrifugal (efferent) cells of the inner granule layer whose axons run out through the outer granule layer and, presumably, to the retina; (4) the terminations of axons of cells lying deeper in the lobe, in the opposite optic lobe, in the subvertical lobe, and in other lobes of the supraoesophageal mass.

All of these classes of fibre run radially through the plexiform zone and then turn to run obliquely or fully in the tangential direction for varying distances. The completely tangential fibres are grouped into rather well-defined layers, of which four may be recognized, alternating with four 'radial' layers (figures 5, 15). Of course, radial fibres run through the tangential layers and the radial layers contain many oblique fibres.

9. Plexiform zone

In this region, therefore, many types of fibre influence each other and no doubt here processes occur by which signals conducted in the optic nerve fibres interact and are appropriately coded. The region shows distinct layers, which have been variously named by previous workers. The stratification is certainly an important feature of the functional organization and requires an exact description, freed as far as possible from terms applicable only to the appearance seen with particular techniques or planes of section (e.g. 'light zone', 'horizontal layer'). The plexiform zone contains a preponderance of radial fibres in its outer half and tangential fibres in the inner half (figure 5). We shall recognize eight main layers, four predominantly radial and four tangential, which for some purposes can be conveniently grouped in three zones, thus:

	Outer granule cell layer	
	Outer basement layer	
1.	1st radial layer	outer zone
2.	1st tangential layer	middle zone
3.	2nd radial layer	
4.	2nd tangential layer	inner zone
5.	3rd radial layer	
6.	3rd tangential layer	
7.	4th radial layer	
8.	4th tangential layer	
	Inner basement layer	
	Inner granule cell layer	

The eight layers are of unequal thickness. The first three are easily distinguished. The other five, divisions of the inner zone, with many tangential fibres, are less sharply separated but there is no doubt that they exist as distinct entities, and may be of great importance in the coding system. The tangential layers consist largely of the dendrites of the cells that carry signals onwards into the lobe and they persist after degeneration of the optic nerve fibres (see figure 23, plate 9).

The second tangential layer is thick and sharply demarcated internally. The third radial layer, though thin, is always readily visible as a zone with few tangential fibres. From here inwards the tissue is nowhere free of tangential fibres and might all be described as a single layer. However, it is always subdivided by a 'fourth radial layer', not free of tangential fibres but with relatively fewer of them (figures 22, 23, plate 9).

10. Vessels and glia of the optic lobe

The optic lobe is supplied by its own arteries, running with the optic tract. These form a dense network of arterioles and capillaries at the centre of the lobe, from which almost straight radial branches run to the plexiform zone (figure 6, plate 7). The regular arrangement of these capillaries suggests a special provision for a functional system in which the topographical conditions are important. The venous system is open, consisting of ill-defined spaces between the cells and fibres. It presumably communicates with the surrounding orbital sinus and there are large venous sinuses at the centre of the lobe.

Between the outer granular layer and the plexiform layer is an 'outer basement layer' containing many spaces, presumably venous (figures 20, 23, plate 9). There is a similar 'inner basement layer' between the fourth tangential layer of the plexiform zone and the inner granular layer (figure 23). The sections often split along the lines of these basement layers.

Although the plexiform layer contains no nerve cell bodies, numerous glial cells are present; some run mainly radially, others tangentially. The radial glial cells, described by Lenhossék (1896) and Cajal (1917), have cell bodies mainly near the inner border and several thick processes with fine twigs (figure 7, plate 7). The branches are especially abundant in the first radial layer, among the endings of the optic nerve fibres. They do not usually extend into the outer granule layer (though other glial cells are present there). Other radial glia cells have cell bodies in the first tangential layer. There are no glia cell bodies in the first radial layer. The tangential glia cells are numerous in the layers of the inner zone, where they make webs of fine processes, often varicose, radiating in all directions from the cells (figures 8, 9, plates 7, 8). Some glia cells with short varicose processes are also present (figure 10, plate 8).

The glia cells in the more central part of the lobe follow the main lines of the fibre tracts. Thus in the region of the inner granule cell layer, where the fibres run mainly radially, the glia cells have long beaded fibres, streaming in that direction (figure 11, plate 8). Some of these fibres seem to end with attachments to arteries (figure 12, plate 8). At the centre of the medulla, where the nerve cells are arranged in islands, the glia fibres run in bundles in the neuropil between the islands (figure 13, plate 8). The similarities in many respects between the glia of cephalopods and vertebrates is one of the many striking examples of parallelism in their nervous system, presumably resulting from separate evolution for similar purposes (Jakubski 1915).

11. ENDINGS OF THE RETINAL CELLS IN THE OPTIC LOBE

These endings in *Octopus* are similar to those described by previous authors for other cephalopods. Much information is therefore available about them, but many important problems remain. All are agreed that many of the fibres end in the plexiform zone and that there is a thickening of most of the fibres in the outer radial layer, from which a further fibre may continue to the deeper layers. The differences in the descriptions are concerned with the depths at which the fibres end and the collaterals given off along their course. Lenhossék and Cajal believed that in young animals the swelling carries collaterals, but that these are reduced and even disappear in the adult ('experimentando uno especie di atrofia') except at the periphery of the lobes, where the juvenile type persists. A few of these peripheral endings they showed to be restricted to the first radial zone. In addition Kopsch and Cajal described a few fibres ending in wider arborizations, either deep in the plexiform zone or beyond it in the inner granule layer.

In the present material three types of ending can be distinguished (figure 14): (1) those that reach only to the outer radial layer; (2) about an equal number ending more deeply in the plexiform zone; (3) a few passing through to end deeper in the optic lobe.

The bundles of optic nerve fibres divide as they enter the outer granule cell layer, making smaller and smaller bundles, which pursue sinuous courses until they enter the plexiform layer as separate single fibres (figure 15, plate 8). Immediately within the outer basement layer many of the optic nerve fibres form the expansions that have been described by all authors.

In Golgi preparations this region of the fibre appears as a thickened rod, smooth immediately within the basement layer and then carrying several lateral branches that proceed for a few microns in oblique or tangential directions as the fibre passes through the first radial layer (figures 18, 19, plate 8). The rod may be varicose, showing swellings along its length, especially where the lateral twigs arise. Sometimes the rod appears pitted, as if indented by the presence of a series of knobs near its surface. The number and length of the lateral branches vary considerably. There may be one or a few of up to 10 μ long (figure 18). Usually there are numerous very fine fibres and spines. The longer lateral twigs are mostly found towards the inner end of the first radial layer. There are no striking differences between these forms in the fibres that end in the first radial layer and those that pass beyond it. The former rods are often, but not always, slightly broader (figures 14; 19, plate 8). At their inner ends there may be a slight expansion, with tangential twigs.

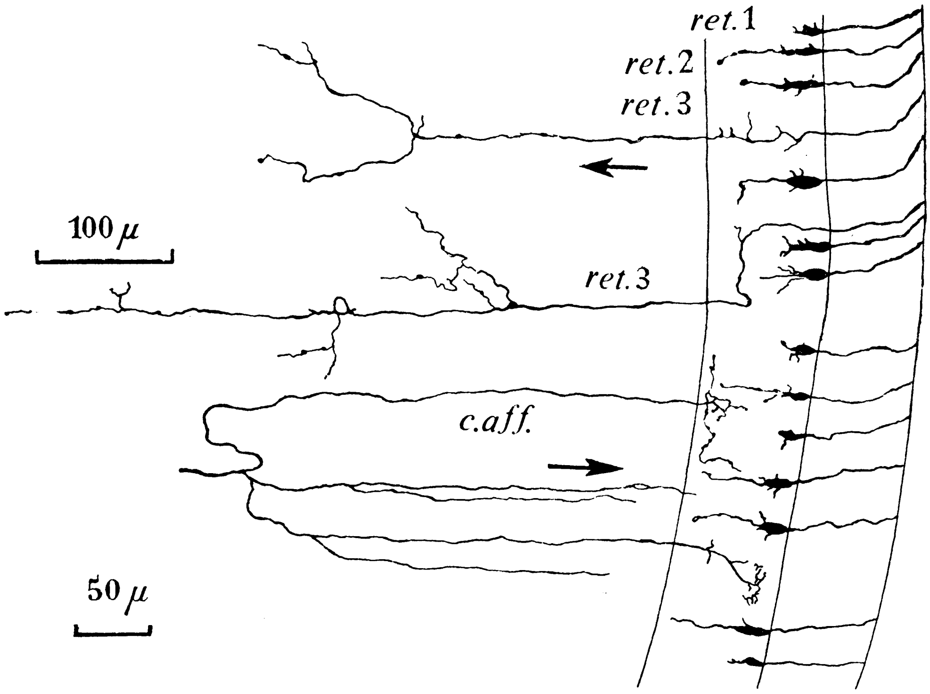


FIGURE 14. Drawings of the three types of ending of the retinal nerve fibres in the optic lobe. The type labelled *ret.* 1 ends only in the first radial layer; *ret.* 2 extends to the deeper parts of the plexiform zone and *ret.* 3 passes beyond the plexiform zone to end in branches more deeply. A fibre reaching to the plexiform zone from a central source is also seen (*c.aff.*) (Golgi–Kopsch).

When preparations stained with Cajal's method are examined, the portion of the optic nerve fibres in the outer radial layer at first seems to lack the thickening that is seen in Golgi preparations (figures 15, 22, plates 8, 9). The explanation appears from study of serial sections 4 μ thick, cut tangential to the surface of the optic lobe, that is to say at right angles to these fibres. Within the outer granule cell layer each fibre appears as a single darkly staining homogeneous thread (figure 20, plate 9). These fibres are separated by the clear spaces of the outer basement layer already mentioned. Immediately beyond this level each fibre is surrounded by a ring of orange-stained material (*ret.sw.* figure 20). This presumably constitutes the smooth, swollen portion of the fibre as seen in Golgi preparations. Then, a few microns deeper still, each unit contains several fibrils, presumably formed by branching of the original one. Sometimes these finer fibrils form a ring around the periphery of the unit, leaving a lighter centre. Still further inwards the fibres become smaller and the main outlines of the unit disappear, this being presumably the region at which the diameter becomes sharply reduced in Golgi preparations. Beyond this level the fibres enter the first tangential layer and are seen as sharply discrete dots dispersed among other fibres (figure 21, plate 9).

Cajal shows in his drawing of *Sepia* a considerable degree of interweaving between neighbouring fibres in the deeper parts of the outer radial zone and passage through the first tangential zone. The fibres certainly do not necessarily pass straight inwards, but there is no sign of systematic interweaving (figure 22, plate 9), nor does this appear in the low-power photograph that Cajal himself gives. It may be concluded that the relations between the optic nerve fibres remain in the main unchanged throughout the plexiform zone.

The course of those optic nerve fibres that pass beyond the first tangential layer can be followed clearly in Golgi preparations (figures 18, 19, plate 8). They run through the second radial layer, usually without branching, but occasionally with some beading. A few seem not to extend beyond this layer (figure 19, bottom). The majority enter the tangential layers of the inner zone and divide there into a small number of terminal twigs, running for short distances ($\sim$ 20 μ) in oblique or tangential directions. These terminal portions are often beaded. There is often a distinct swelling nearly at the end, sometimes with one or two very fine filaments running from it. These swellings have also been seen in Cajal preparations after degeneration of the rest of the tissue of the optic lobe (p. 30), although they are not usually stained in normal Cajal material.

These terminal portions of the optic nerve fibres lie mainly in the second tangential layer, or slightly deeper. They do not usually extend to the innermost parts of the plexiform zone. The endings are, therefore, presumably in relationship with the very long dendrites of the bipolar and other centripetal cells, which lie largely in the second tangential layer.

Of the endings that are limited to the plexiform zone about half are limited to the first radial zone, while the other half reach to the inner tangential zones. The two types occur mixed together in about equal numbers in all parts of the optic lobes. The short ones are not limited to the peripheral parts of the lobe as Cajal believed his 'juvenile type' to be. Conversely, also, longer fibres are present close to the periphery of the lobe.

Examples of the third type of optic nerve ending, running beyond the plexiform layer towards the centre of the lobe are seen in figures 14; 16, 17, plate 8 and 32. They differ from the other endings in the absence of any swelling where they pass through the first radial layer. However, they sometimes provide lateral branches both in that layer and in the third tangential layer (figures 14; 17, plate 8). They have been seen to run for a short distance in the tangential direction in this layer (figure 14). They pass through the inner granule cell layer, usually without further branching and then more centrally they end with a number of fine branches among the islands of cells at the centre of the lobe (figure 14). The endings are characteristic fine tapering fibres, with a few beadings and can be seen at the left of figure 17, plate 8. Since the beading is present only near the tips it seems likely that it is significant in the synaptic functioning of the fibres. The longer of these fibres extend for about 500 μ beyond the plexiform zone.

This third type of optic nerve ending is not numerous, perhaps less than 1/100th of the others. However, there is no way of proving that staining has not biased the sample and longer fibres will in any case be seen less often than shorter. These deeply ending fibres may have a special function by their direct effects on the deeper parts of the centripetal cells (p. 41).

12. Degeneration of optic nerve fibres after section

If the optic nerves are cut the endings of the fibres within the lobe rapidly degenerate. They break into granules within a few hours and after a few days no trace of them remains (figure 23, plate 9). If some only of the optic nerves are cut there is usually a sharp boundary between the parts of the plexiform layer with intact fibres and those with none (figure 24, plate 9). One or two small intact bundles may be seen at a short distance from the rest, but there is no evidence that bundles close together in the optic nerves spread widely to distant parts of the lobe.

The fibres in the tangential layers remain intact after section of the optic nerves (figures 23 to 26, plate 9), as would be expected since they are branches of cells within the optic lobes (p. 38).

Several weeks after the operation, therefore, the first radial layer becomes so shrunken that it almost disappears. This can be seen well at the boundary between denervated and intact areas (figure 25). The tangential layers on the other hand remain about as thick as in a normal region, but are less clearly separated, because of the collapse of the radial layers between. There are also further secondary effects of the operation. The optic lobe as a whole shrinks, and after a month of denervation has two-thirds of its normal volume or less. The outer granular layer is thinner than in a normal lobe (figure 26). Presumably there are further losses throughout the lobe to account for the great shrinkage in volume. The spaces of the outer basement layer, between the outer granule and plexiform layers, are very conspicuous after optic nerve section (figures 23 to 26).

13. Degeneration of the tangential layers of the plexiform zone

The converse experiment of degenerating the tangential fibres while leaving the radial ones can be accomplished by severing the optic tract, which carries the arteries for the optic lobe. When these have been cut the tissues of the lobe degenerate, except for the optic nerve fibres, whose cell bodies are maintained by the independent blood supply of the retina. The retinal fibres can then be seen to end as knobs in the inner zone of the plexiform layer (figure 27, plate 10). None has been seen proceeding further, but they may of course have been damaged by the degenerating tissues around them.

14. External granule cells

All the cells of the external granule layer send their branches into the plexiform zone and only rarely have they been seen to extend beyond this. The cells are mostly rather small, but increase passing outwards, the largest having nuclei up to 10 μ in diameter. The branches proceed to various depths within the plexiform layer (figure 28). Some of the smallest cells have only a single fine trunk, giving off a very few branches in the first radial layer, among the branches of the optic nerve fibres. Such very small cells are seen at *a* in figure 28. The branches may be limited to a few short tangential twigs, or they may form a quite elaborate bush-like floss of fine threads (figure 30, plate 10).

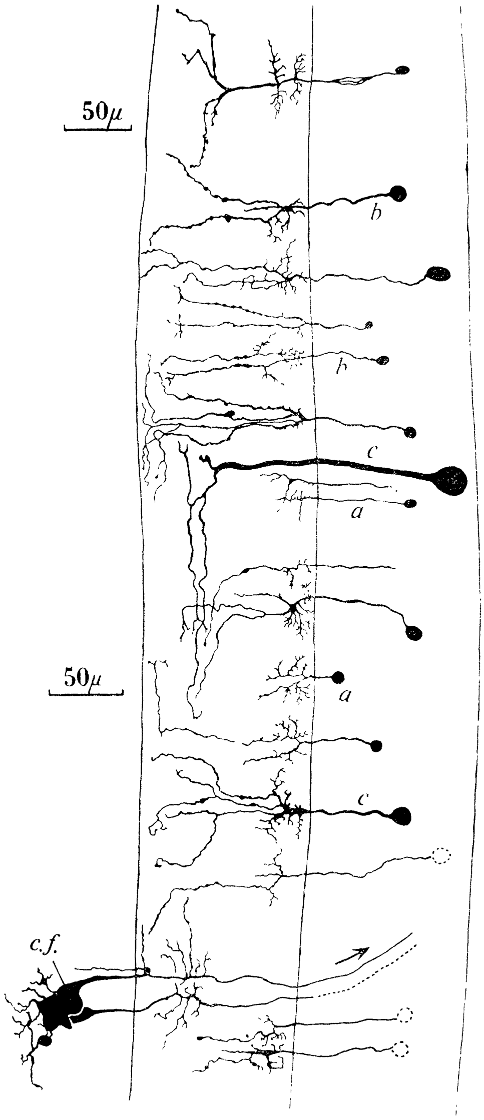


Figure 28. Drawings of cells of the outer granule layer as seen after Golgi staining. *a*, Cells with processes limited to first radial layer; *b*, small cells with two branches; *c*, larger cells, spreading widely in the deeper tangential layers. The picture is a composite from many drawings. The scale covers a slight range as shown by the changing thickness of the plexiform zone; the two scales shown indicate the range (Golgi–Kopsch).

Other small cells bifurcate in the first radial layer, giving off some twigs, and then proceed through the second radial zone with few branches, but often two swellings (figure 28, *b*; figure 31, plate 10; figure 33*c*). Where they arrive at the second tangential layer they may end in a few fine terminal branches or turn into the tangential plane to run for a short distance as fine beaded terminals.

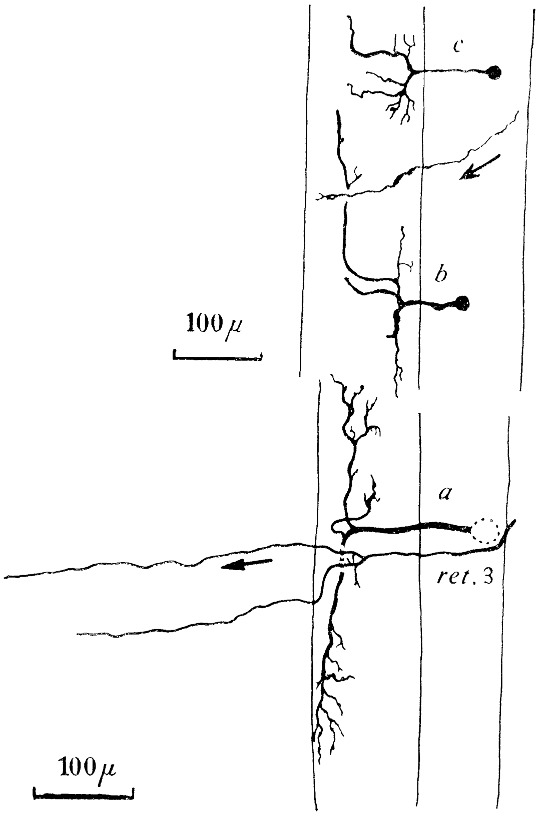


FIGURE 32. Large cells of outer granule layer, with branches spreading widely in the tangential plexiform layers. *a* is restricted to the deeper layers, *b* and *c* have branches in several layers. *ret.* 3 is a retinal nerve fibre passing beyond the plexiform zone (Golgi–Kopsch).

The larger cells towards the outer part of the external granular layer are in general similar, but their branches spread more widely in the inner tangential layers (figures 28*c*, 32*a*). They may or may not have branches in the outer radial layer. Often they have a single main trunk, dividing only upon reaching the inner tangential layers. It is not easy to be certain whether their branches are ever restricted to a single one of the tangential layers. Probably the limitation is not strict, so that individual cells may have their main lower branches at either one or several levels.

A very few of the branches of the outer granule cells have been seen proceeding for a short distance into the region of the inner granule cells (figure 33). The form seen in figure 33*d*, with a process running for a long distance in the plexiform layer and then into the deeper layers, was seen only once. Most of the fibres from these cells that pass beyond the plexiform layer end after a short distance (figure 33*a*, *b*). It seems likely that these deeper branches are aberrations, but it is possible that they are significant types that are rarely stained. Certainly the majority of the large number of external granule cells examined end within the plexiform zone. Cajal described in decapods some outer amacrine cells with branches ending deep to the inner granule cell layer, in the 'estria fibrillar intermedia'. This is not present as a distinct layer in octopods, but it is possible that some of the tangential fibres seen in this region correspond to it, and they may include the processes of the few outer amacrines that have the form shown in figure 33.

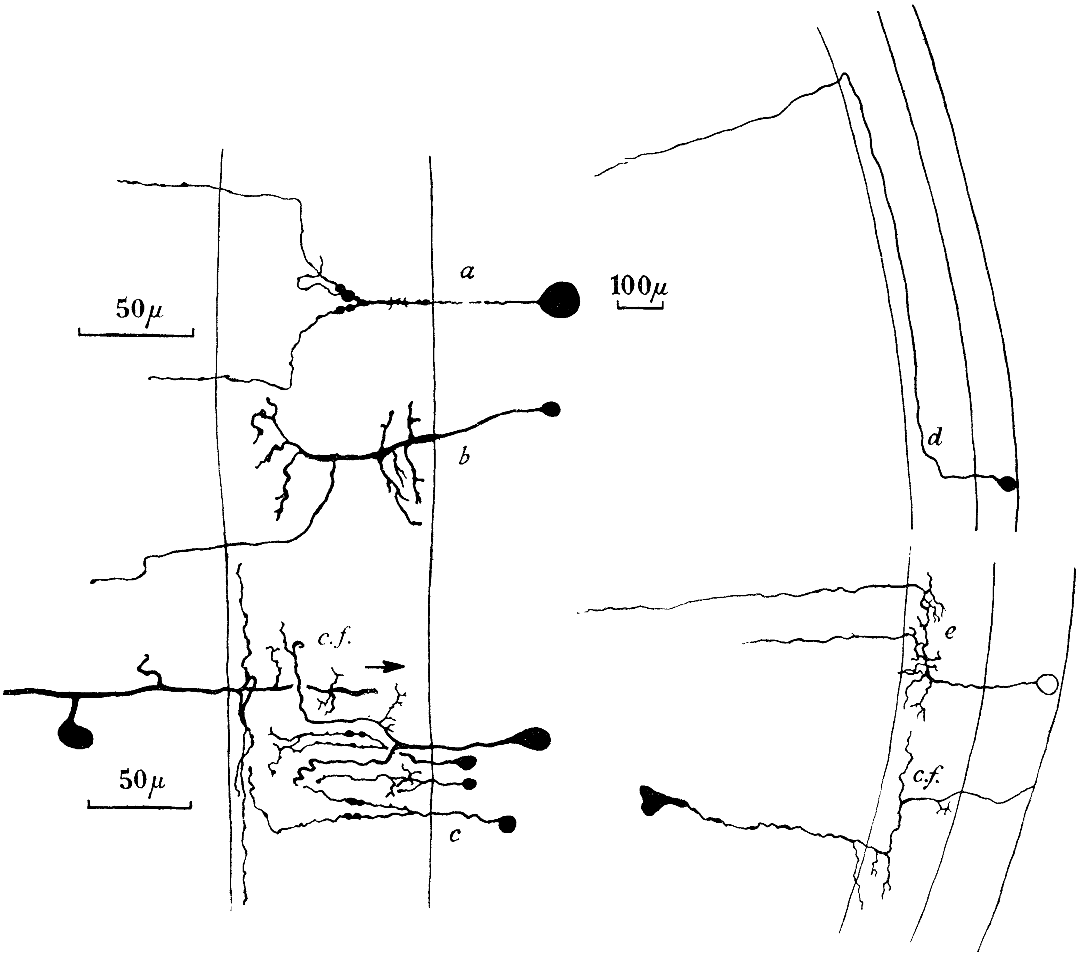


FIGURE 33. Cells of the outer granular layer whose fibres pass beyond the plexiform zone. In *a* and *b* the fibres only proceed a short distance within the inner granule layer. Cells of types *d* and *e* were seen only once each. *c* is a smaller cell of the type of figure 31, plate 10 (Golgi–Kopsch).

Cajal also described in *Sepia* cells with tangential branches ending within the outer granule cell layer itself. Only a few doubtful cells of this type have been seen in the present study. A few cells have been seen in the outer parts of the layer with two branches at opposite ends, both passing down to the plexiform layer, as much as 100 μ apart.

In none of the outer granule cells is there seen any one branch distinguishable from the others as being an axon. Moreover, none has been described by the three authors who have made extensive investigations of these cells in other cephalopods. It remains, of course, possible that one (or more) of the branches is in some way functionally differentiated as an axon or that such axons are present but unstained or below the limit of resolution. However, it may provisionally be concluded that these cells play their part in the events in the plexiform layers without propagation into any differentiated axon. It is surely significant that their more proximal collateral branches occur among the synaptic endings of the optic nerve fibres in the first radial layer. The more distal branches, where present, are among the deeper synapses of the optic nerve fibres. The greater length and spread of the branches at greater depths also suggests a significant regularity.

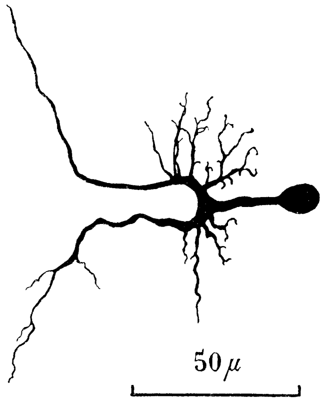


FIGURE 34. Small cell of outer granular layer whose branches in the plexiform zone were all approximately in one plane (the plane of the paper).

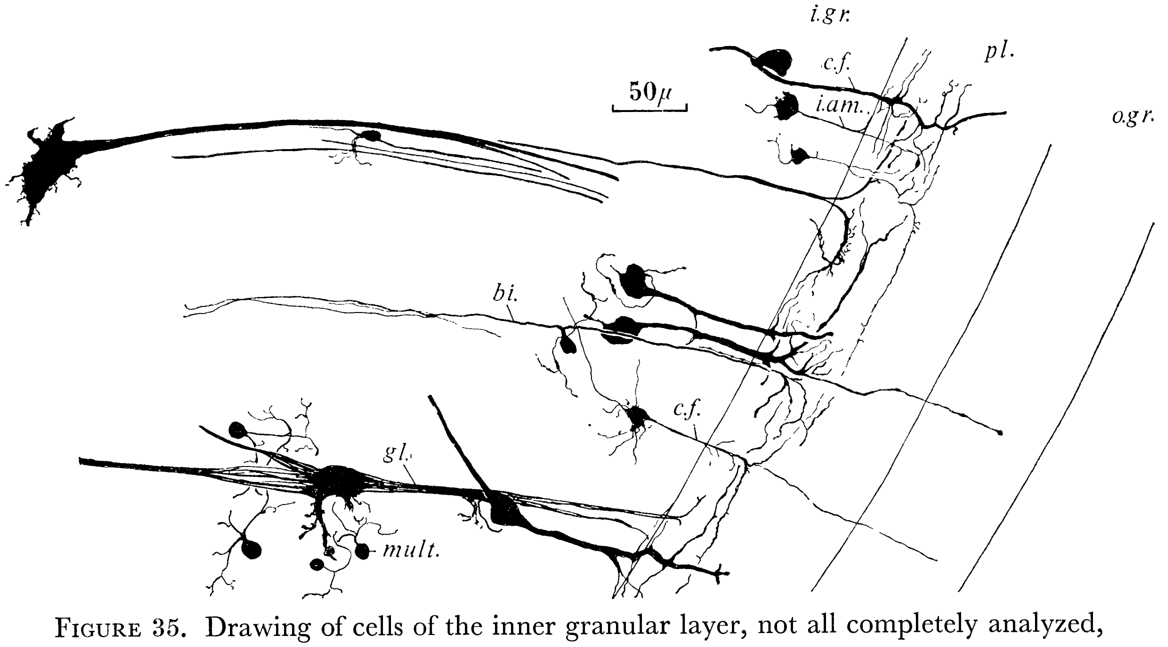


FIGURE 35. Drawing of cells of the inner granular layer, not all completely analyzed, to show the general arrangement (Golgi–Cox).

It has not been possible to make a critical study of the spread of the branches of these cells in the tangential directions. In thick sections it can be seen that in some cells the ramifications proceed in several directions. On the other hand, cells have also been seen in which they appear to be all in one plane (figure 34). It is not known whether any particular plane is involved.

The shapes of these 'dendritic' fields may be of great importance. At present all we can say is that they provide a fabric of branching fibres of various lengths and diverging increasingly with depth. Most of them are thus stimulated by a relatively few optic nerve endings that lie close to each other in the outer part of the plexiform zone, and then encounter a wider group of endings more distally, at the level where these are passing on excitation to the dendrites of both centripetal and centrifugal cells in the inner tangential layers. If the fibres are not restricted to single planes they form an interlocking system of cone-shaped fields.

15. INNER GRANULE CELL LAYER

There is less agreement about the structure of this region than any other part of the optic lobe. Certainly there are large differences here between decapods and octopods. In both groups there are, in this layer, centrifugal cells, whose axons proceed to the retina. Lenhossék described, in *Eledone*, numerous bipolar cells, with dendrites in the plexiform zone and axons proceeding centrally. Kopsch and Cajal were unable to find these in decapods, but described an inner fibrillar layer and a palisade layer of cells.

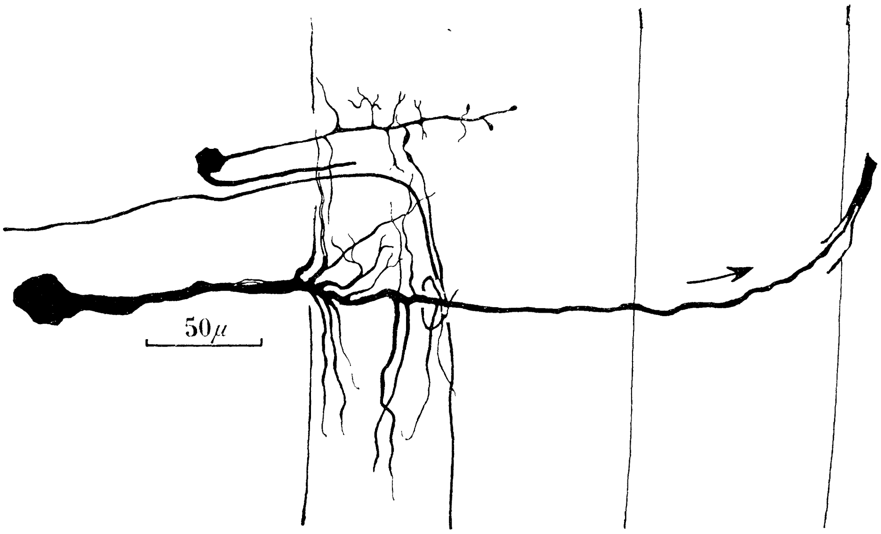


FIGURE 36. Drawing of a centrifugal cell (Golgi–Cox).

In the present work on *Octopus* four types of cell have been found in the inner granule cell layer (figure 35). (1) Centrifugal cells, with branches in the plexiform zone and an axon proceeding into the optic nerves. These presumably conduct from the optic lobe to the retina. (2) Centripetal cells, with branches in the plexiform zone and axons that proceed inwards to the medulla of the optic lobe. Cells of this type are, however, found quite deep within the medulla itself as well as in the internal granule layer. (3) Small multipolar cells. (4) Inner amacrine cells, with branches restricted to the plexiform layer.

16. CENTRIFUGAL CELLS

The centrifugal cells are a characteristic component of the inner granular layer and are frequently well stained by Golgi methods. The cell body lies not far from the plexiform layer, to which it sends a large trunk. This divides into numerous fine branches, each cell often having some branches within each of the inner three tangential layers (figures 36 to 40). These branches do not show any systematic arrangement, though those in the deeper layers are sometimes the longer. They do not extend to great distances away from the main trunk, the whole tree usually showing a diameter of 100 μ or less. The orientation of the dendritic fields has been determined for a few cells (figures 41, plate 10; 42, 43). The fields may be round, but some are certainly elongated in the antero-posterior direction. In some of the cells of figure 43 the fields at different levels in the plexiform layer have different orientations. The data are not sufficient to establish whether such arrangements indicate any systematic orientation.

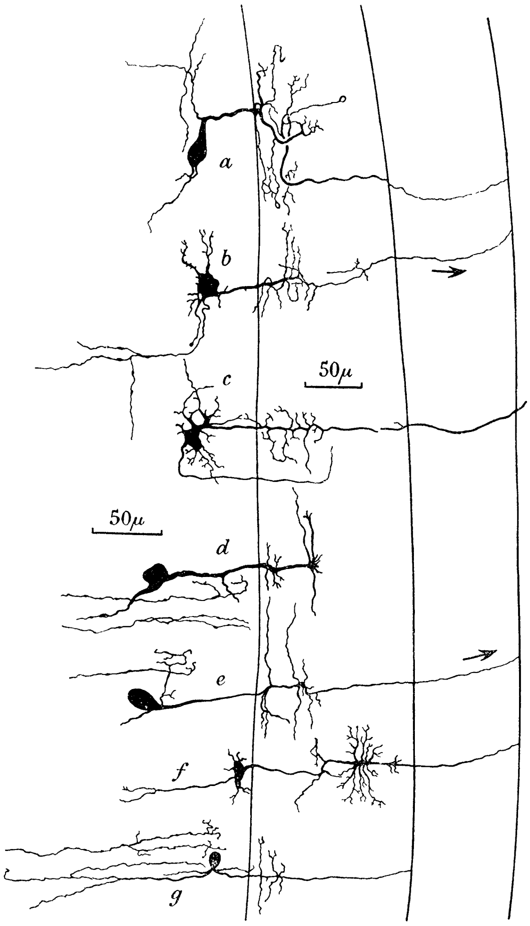
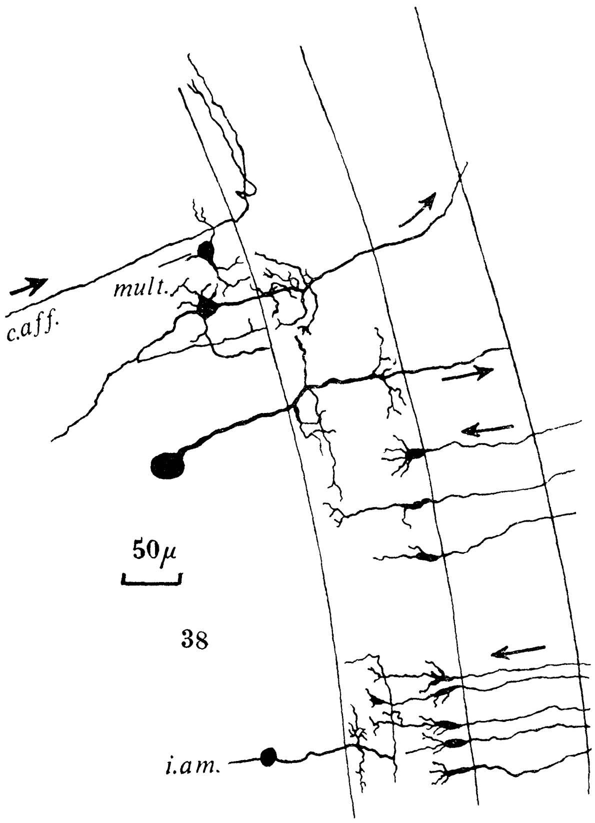


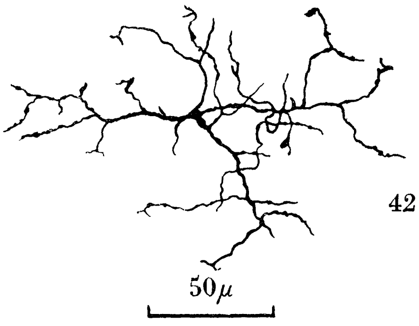
FIGURE 37. Drawings of several centrifugal cells, *a* and *b* at a smaller scale than the others (Golgi–Kopsch).

The cell of figure 37*a* shows a coiled arrangement of the main trunk, which was seen occasionally. Collaterals arise at intervals in different directions. The efferent axon of this cell apparently passes to a region of the retina a short distance from that from which the cell receives optic nerve influences. More commonly the efferent axon and afferent fibres run in the same or very nearby nerves.

The main trunk continues in the centrifugal direction through the plexiform layer and may give further lateral branches, especially in the first radial layer (figure 37*b*, *f*). The fibre then continues through the outer granule cell layer and enters an optic nerve. These fibres remain intact within the stumps of the optic nerves attached to the optic lobes many weeks after these have been severed from the retina. Endings that are presumed to be of these fibres have been found in the retina (Young 1962*a*).

The centrifugal cells may have basal branches arising from the cell body. These are often numerous and run for no great distance, and appear to be dendrites (figure 40*a*, plate 10). The orientation of their fields is not necessarily uniform in all directions. The cells may also carry fine branches (axons?) that proceed towards the centre of the lobe (figures 37; 40*c*, plate 10) or, in a few cases, run up into the plexiform zone parallel to the main trunk of the cell (figures 36, 37*c*). Figure 37*g* shows a cell with apparently several fine basal axons and a centrifugal process that could be traced almost into the optic nerves. Centrifugal cells with such extensive basal branches were not commonly seen, but the existence of these centrally directed fibres raises the suspicion that these cells conduct centripetally as well as peripherally, perhaps indeed, in both directions. They have been called 'centrifugal' here only by anatomical criteria. Recording with micro-electrodes from the cut central stumps of optic nerves has established the presence of fibres conducting outwards (Lettvin & Maturana 1962).





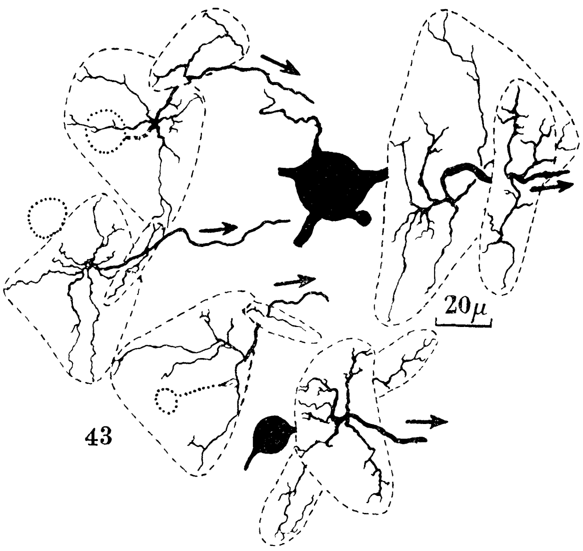


FIGURE 38. Drawing of the centrifugal and other cells shown in figure 39, plate 10.

FIGURE 42. Drawing of the dendritic field of the centrifugal cell shown in figure 41*a*, plate 10.

FIGURE 43. Drawings of several centrifugal cells as seen in a thick section tangential to the surface of the optic lobe. The limits of the dendritic fields at various levels in the plexiform layer have been outlined by dots (Golgi–Kopsch).

17. Bundles passing from the medulla to the optic nerves

Von Lenhossék, Cajal and Alexandrowicz have described bundles of fibres that run right through the optic lobes from the optic stalk and into the optic nerves. Such bundles undoubtedly occur in *Octopus* and probably, as Alexandrowicz supposed, their cell bodies lie within the central nervous system. There are few of them, mostly situated round the edges of the optic lobes (figure 44, plate 11). They contain rather thick fibres and form compact bundles, running among the optic nerves rather than actually joining them.

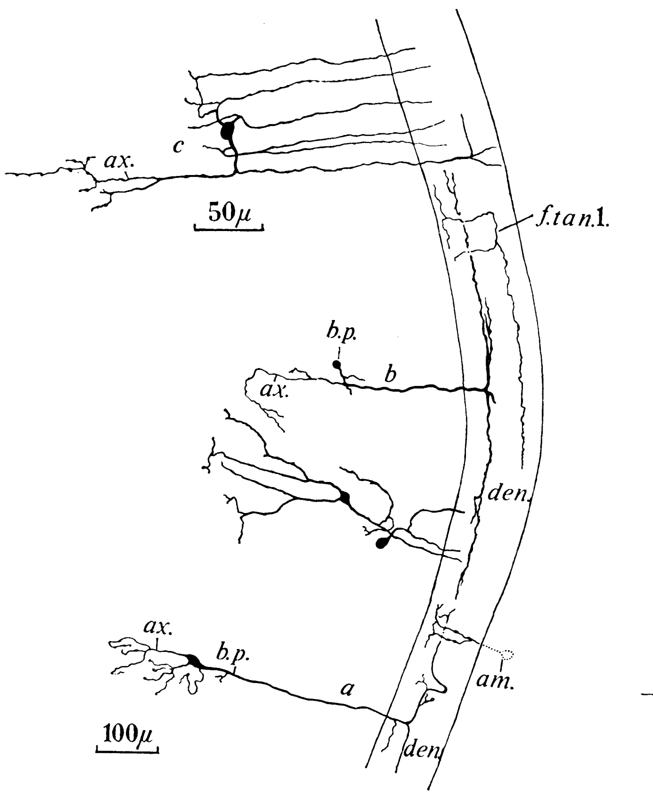


Figure 45

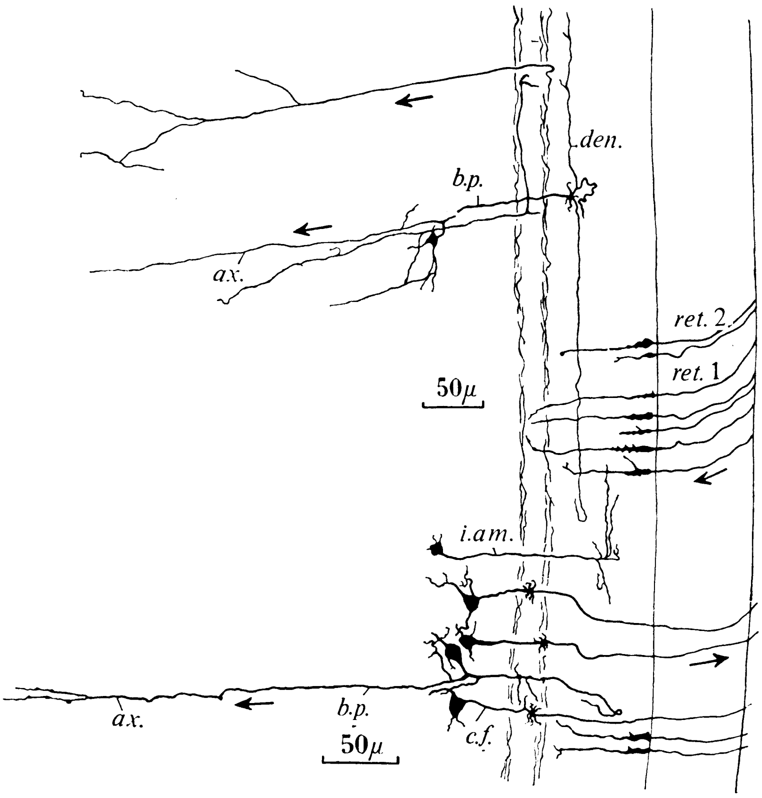


Figure 46

Figure 45. Cells sending dendrites to the plexiform zone; *a* and *b* are bipolars, *c* has several fibres (dendrites?) running to the plexiform zone. *f.tan.* 1 is a fibre seen running for a long distance in the first tangential layer (Golgi–Kopsch).

Figure 46. Cells with dendrites in the plexiform zone (*den.*) and axons (*ax.*) running centrally, also centrifugal cells, endings of retinal fibres and an inner amacrine cell.

After section of the optic nerves these fibres remain intact. It has not been discovered whether their cell bodies lie in the optic lobes or further towards the centre, but they are presumably efferents, probably to the system of ciliary and retinal muscles.

18. Centripetal cells, conducting inwards from the plexiform layer

The question of how impulses are passed inwards from the plexiform layer has much puzzled previous workers. Von Lenhossék and Kopsch described some cells with dendrites in this layer and axons proceeding inwards, but Cajal could not find them in *Sepia*. The situation in *Octopus* is that there are many such bipolar cells, but there are also numerous cells that send fibres up into the plexiform layer to form branches there, from which recurrent fibres then proceed inwards again to the medulla. These are, of course, unipolar cells of the typical form of molluscan neurons, considering the plexiform layer as a neuropil that receives branches from cells around it.

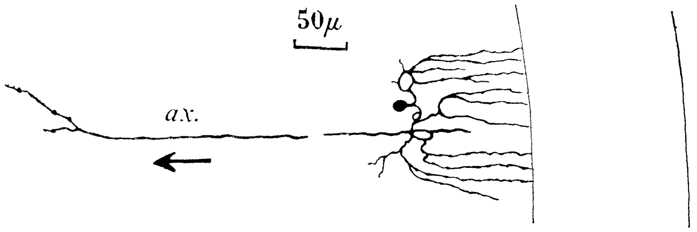


FIGURE 47. Single cell with numerous presumed dendrites running to the plexiform zone and an axon running centrally (Golgi–Kopsch).

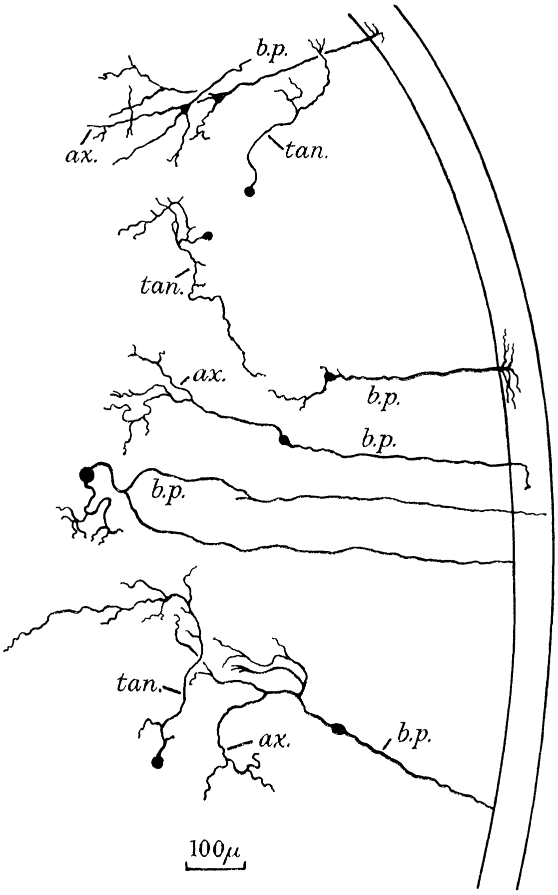


FIGURE 48. Large cells with fibres running to the plexiform zone and presumed to be bipolars (*b.p.*). Also some tangential cells (Golgi–Kopsch).

The bipolar cells may be of simple form, with an apical dendrite reaching outwards and one or more axons going inwards (figures 45, 46). They may have two or more branches proceeding to the plexiform layer and one or several passing inwards (figures 45, 47, 48). The important question of the form of the dendritic trees in the plexiform layer is discussed later (p. 42). The fibres that are considered to be axons have a fine beaded structure

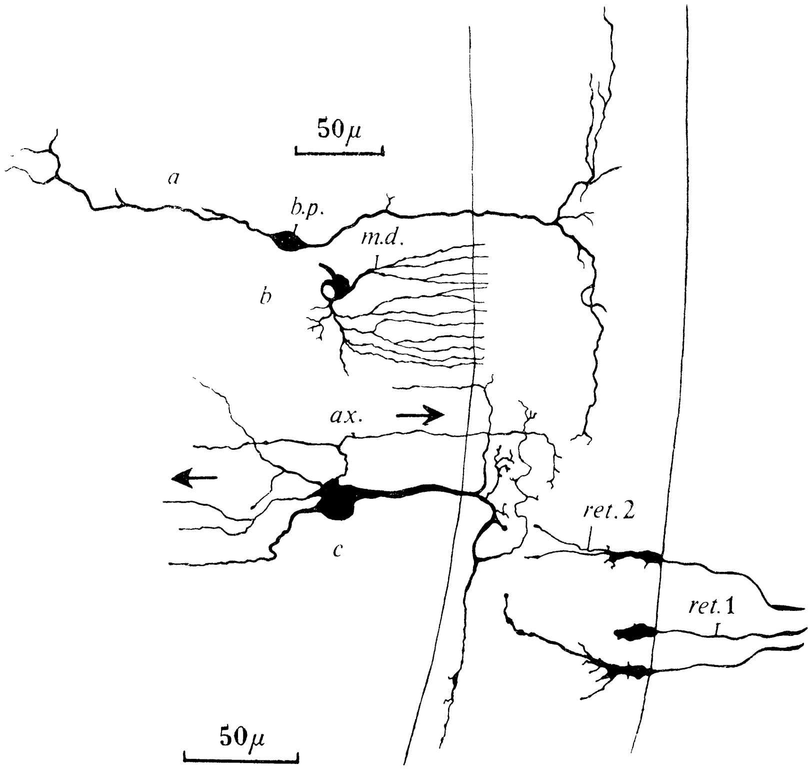


FIGURE 52. Cells sending fibres to the plexiform zone as well as centrally. *a* is a typical bipolar cell; *b* has numerous fibres presumed to be dendrites (see figure 47); *c* has an apical dendrite and several fine basal axons (?), including one that returns to the plexiform zone (Golgi–Kopsch).

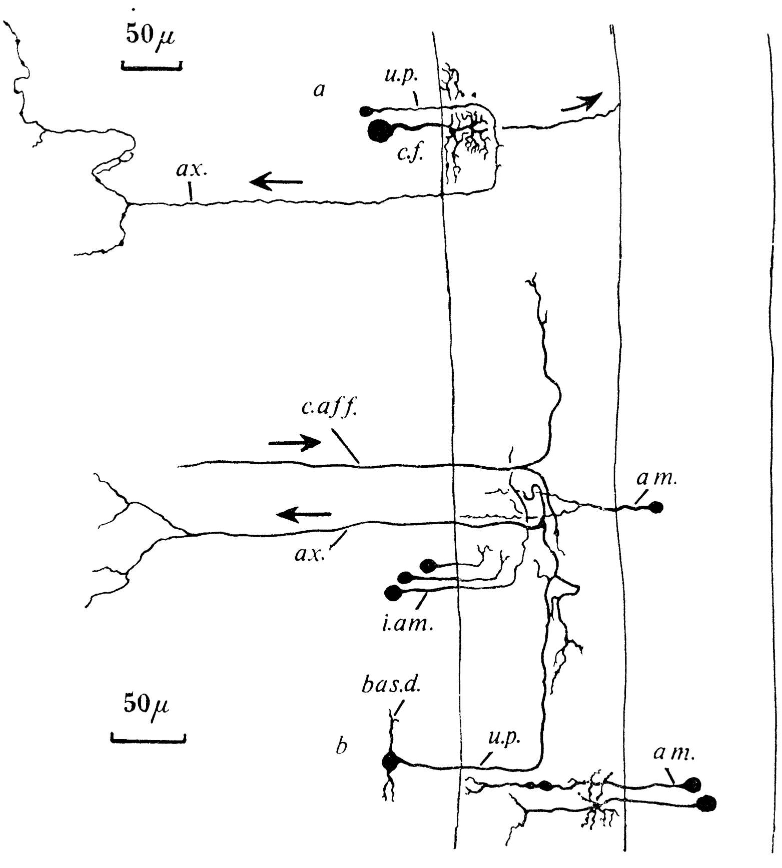


FIGURE 54. Unipolar cells (*u.p.*) with a trunk running to the plexiform zone, where it branches and then gives one or more fibres (axons) that return to the centre of the lobe. Cell *a* has a relatively small field in the plexiform zone. *b* and *c* have wide fields and in addition some basal dendrites (*bas.d.*). Centrifugal cells, amacrines and small multipolar cells are also shown (Golgi–Kopsch).

and pass to varying distances in the medulla before dividing up into relatively few fine terminal branches, often marked by varicose swellings (figures 49, 50, plate 11).

Some of the cells have basal branches in the tangential plane, from which several fibres (?dendrites) proceed outwards to the plexiform zone and others (?axons) inwards towards the medulla (figures 47; 51, plate 11; 52). The nature of these cells with multiple branches is not easy to determine. Some of them might be glial (figure 52*b*), but that in figure 47 seems certainly a neuron. Figure 51, plate 11, gives a good view of the appearance of the numerous branches that are presumed to be dendrites.

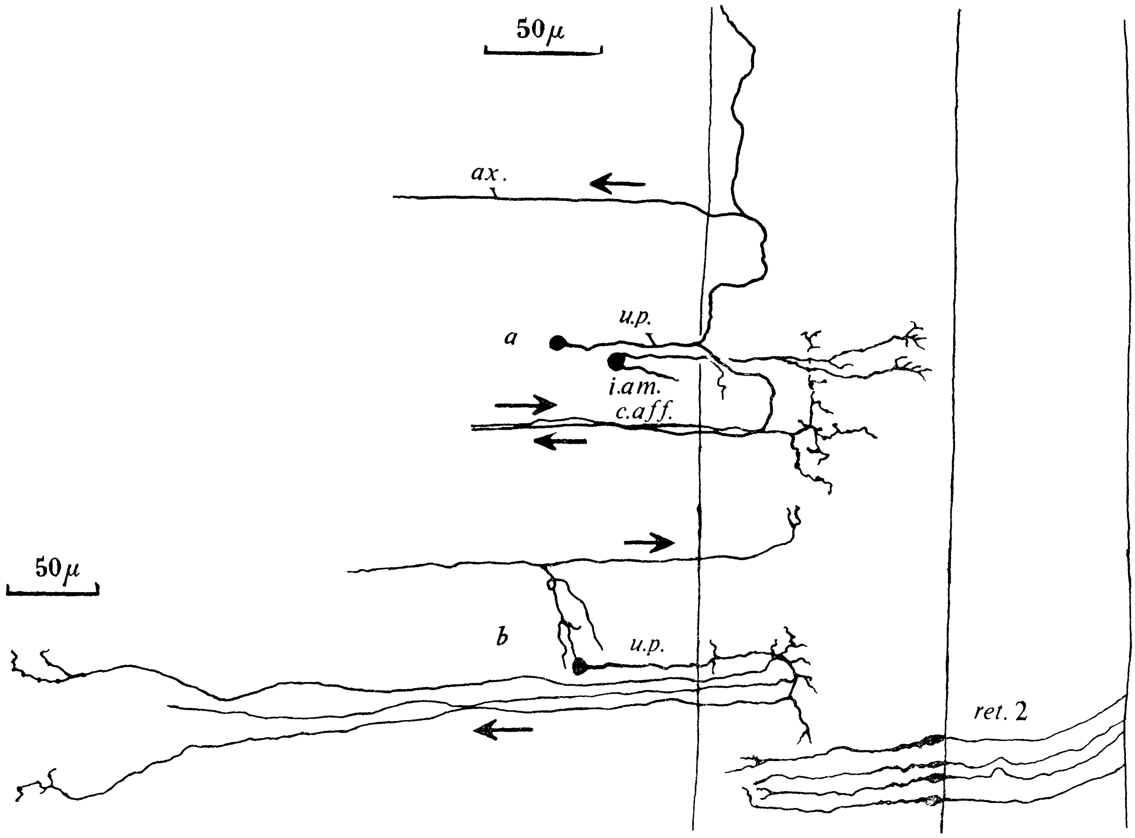


FIGURE 55. Unipolar cells with several axons returning from the plexiform zone. *a* has apparently two of them rather far apart, *b* has several close together and perhaps a recurrent one to the plexiform zone. A fibre reaching the plexiform layer from the centre of the lobe (*c.aff.*) is also shown, and an inner amacrine (*i.am.*) (Golgi-Kopsch).

Probably the cells with the larger dendritic fields have cell bodies that lie deeper in the medulla and axons that extend to a greater depth, but it is difficult to determine this relationship exactly. Only in a few fortunate sections has it been possible to see both a wide extent of the dendritic field and the full course of the axon and its branches. Such evidence as there is suggests that the terminal field of each axon covers a relatively small volume, but of course the sampling difficulties will tend to exclude large fields.

The unipolar centripetal cells, with recurrent fibres from the plexiform layer, also show a wide variety. They are called unipolar cells because they have one main trunk and in spite of the fact that they may in addition have several ascending and descending branches.

No cell has ever been seen with dendrites in the plexiform zone and axon in the optic tract, however, and it may provisionally be assumed that they do not occur. If this is so, the axons of the centripetal cells must make synapse with the dendrites of the medullary cells that send axons to the tract.

Figure 68. Cells of the medulla to show the general organization of multipolar cells, with axons directed towards the optic tract (Golgi–Kopsch).

Figure 69. Unipolar cells at the centre of the optic lobe to show dendritic collaterals and axons proceeding towards the optic tract (Golgi–Kopsch).

(figure 58, plate 11). Preliminary study of the distribution of these collaterals suggests that they are rare near the centres of dendritic fields and become increasingly frequent towards the tips. Such a distribution might mean that the cell would only fire nerve impulses in its axon after stimulation from optic nerve fibres covering at least a large proportion of its dendritic area. The number of cells suitable for detailed study of this feature has so far been small.

More reliable quantitative evidence that the dendrites are orientated in vertical and horizontal directions more frequently than in other directions can be obtained from Cajal preparations sectioned tangentially (figure 60, plate 12). Here of course it is not possible to follow the dendrites of each individual cell, but presumably all of the larger dendrites are stained and can be counted. Axons reaching to the plexiform zone from the medulla are also stained, and as they cannot be satisfactorily distinguished from the dendrites they are included in the estimations. Measurements have been made of the lengths of fibre present in sample areas from sections at different levels within the plexiform layer, measuring also the angle that each makes with the horizontal plane, which was determined from the direction of the main axis of the section (table 2). The fibres running vertically are the most numerous and there are also many in the horizontal direction, but there are fewer obliques. The mean length is greatest for the horizontal dendrites, though the differences are not great. The interpretation of these results depends upon knowledge of the full dendritic trees of the individual cells. It may be that there is a preponderance of oval fields, with long axes horizontal and branches proceeding roughly at right angles to the main axis.

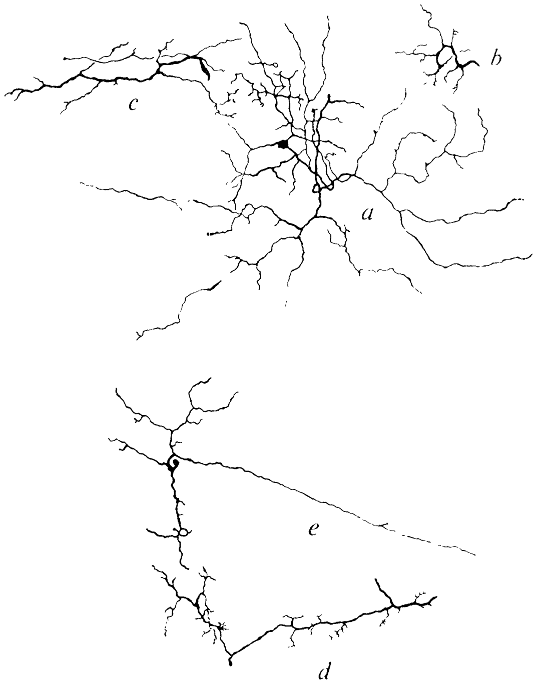


FIGURE 56. Drawings of dendritic fields of several centripetal cells as seen in sections tangential to the plexiform layer. Fields *a* and *b* are approximately circular, the remainder are elongated in the horizontal axis, which corresponds to the short length of the page (Golgi–Kopsch).

Table 2. Number and lengths of fibres in an area of 22 500 μ^2 in the plexiform layers of the optic lobe of an octopus. (Cajal's method)

	degrees from horizontal					
layer of plexus	75–105	105–135	45–75	135–165	15–45	165–180 0–15
2nd tangential						
number	39	8	13	6	5	13
length (μ)	1455	393	462	204	179	531
mean length (μ)	37	49	36	34	35	50
3rd tangential						
number	24	18	11	16	11	19
length (μ)	625	447	373	490	445	664
mean length (μ)	26	25	34	31	41	35
4th tangential						
number	26	14	14	11	13	16
length (μ)	760	450	321	357	359	415
mean length (μ)	29	32	23	32	29	26
total						
number	89	40	38	33	29	48
mean length (μ)	32	32	30	32	34	34

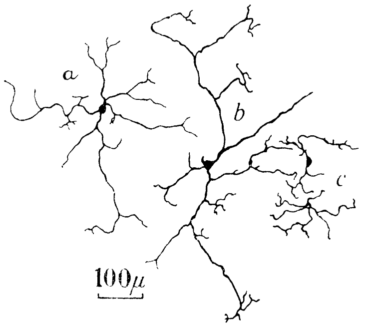
20. Inner amacrine and multipolar cells

One of the problems that has not been fully solved is to decide whether there is any large number of cells in the inner granule layer that send branches only to the plexiform zone. Cells that approach this type are seen in figures 35, 46, 54, 55. Many of them, however, have small branches arising from the cell body. These could conceivably be very short axons (e.g. figure 35), and these would then be bipolar cells, conducting inwards from small areas of the plexiform zone. Lenhossék indeed seemed to be of this opinion, and it might be that where no basal fibres are seen this is a defect of the Golgi stain. If this is so then there is no system of inner amacrines with branches spreading outwards as cones, in the reverse direction to those of the outer amacrines. Since some small cells of this type have been seen (and Cajal describes them in decapods), however, it seems probable that there is such a reverse system. The centrifugal cells themselves indeed may be considered as part of it.

The numerous small multipolar cells of the inner granule cell layer present the same problems as elsewhere in the lobe, since they have no obvious axons (figure 35).

21. Tangential cells in the outer medulla

In decapods there is a well-defined palisade layer of large cells limiting the inner granule cell layer. It is characteristic of octopods that these cells, if present, are not sharply marked off from others with branches running radially. In the deeper parts of the inner granule layer there occur cells with branches spreading widely in the tangential plane (figures 51, plate 11; 61). The fields of some of these cells approach the size of the fields in the plexiform layer, but probably the majority are smaller. The branches are very fine and numerous and carry many side branches. They are not confined to one depth in the lobe but reach up into the inner granule cell layer and down towards the centre of the lobe. The fields that have been seen in tangential section appear to be approximately circular but they have been too few to be certain (figures, 62, 63). It may provisionally be assumed that the fields are flat disks, thicker than those of the plexiform layer, but thinner and more regular than those nearer to the centre of the lobe (see below).



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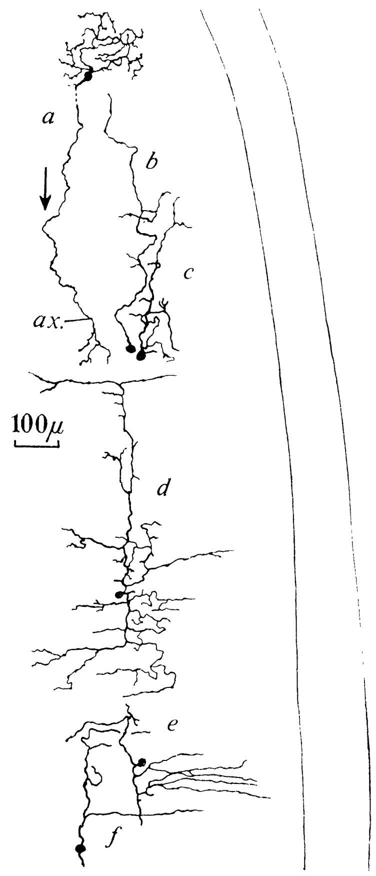

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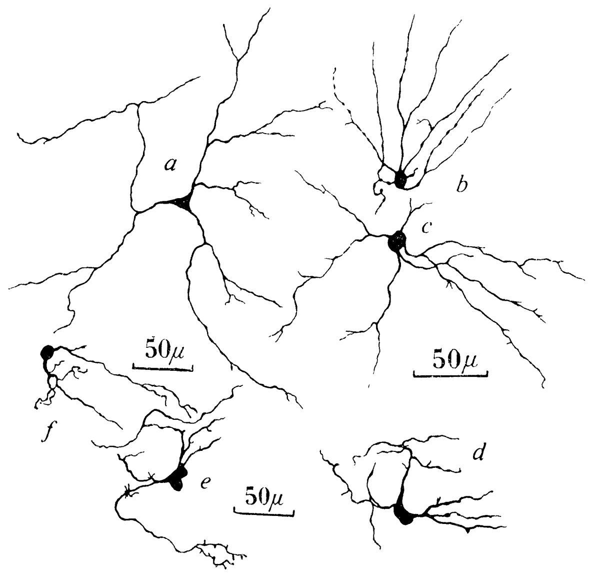

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FIGURE 61. Tangential cells in the outer region of the medulla as seen in a transverse-section (Golgi–Kopsch).

FIGURE 62. Large tangential cells in outer region of medulla in a section cut tangential to the surface of the lobe (Golgi–Kopsch).

FIGURE 63. Smaller multipolar tangential cells from outer region of medulla, in tangential sections (Golgi–Kopsch).

Some of the cells appear to have a definite single axon, running in a tangential direction (figure 61 *a*). In others it is hard to decide which branch, if any, is an axon. Fibres have not been seen proceeding for a long distance centrally from these cells and it is possible that their activities are confined to promoting interaction at one level. Small multipolar horizontal cells, with no obvious axon, are also numerous at this, as at all other levels (figure 63).

22. CELLS OF THE MEDULLA WITH AXONS PASSING INWARDS

The cells that presumably pass on excitation from the level within the inner granule cell layer are not clearly distinct from the tangential cells (figure 64). They have numerous spreading dendrites, running mainly radially outwards, and a fibre that is presumed to be

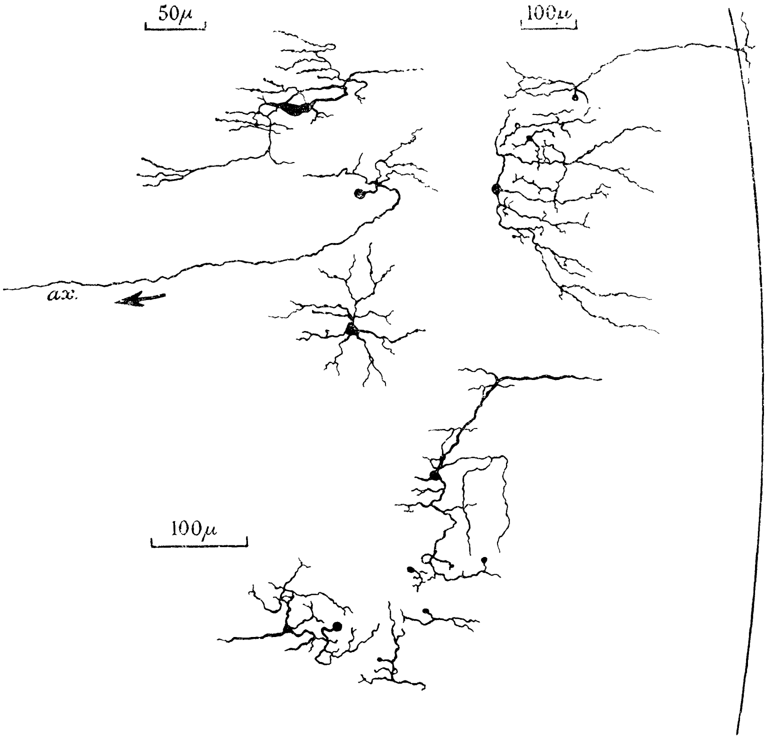

FIGURE 64. Cells of the outer region of the medulla (Golgi–Kopsch).

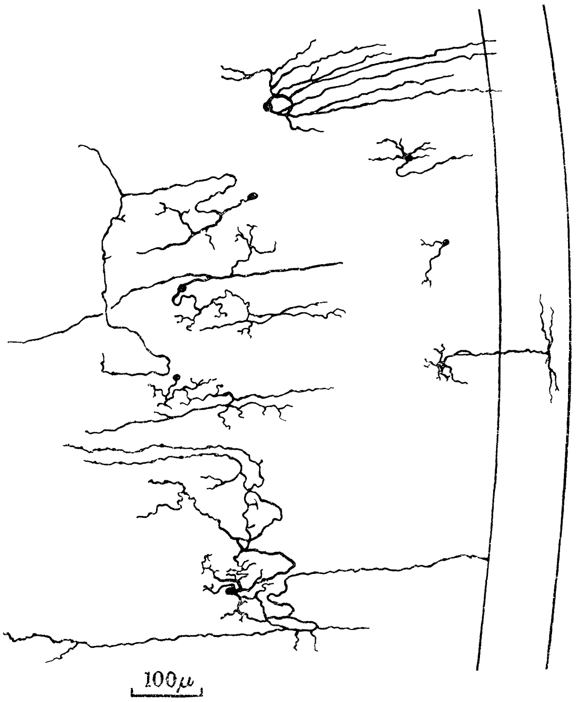

FIGURE 65. Cells of the outer region of the medulla (Golgi–Kopsch).

the axon passing centrally or obliquely, though often not for a great distance. There is sometimes also a fibre proceeding outwards and these may reach the plexiform layer and constitute a recurrent pathway.

The shapes of the dendritic fields of these cells must be both varied and irregular, but they are very hard to study. Often they are cylinders, elongated in the radial direction, sometimes extending as far as the plexiform zone (figure 65). The diameter of the cylinder seems to be 300 μ or less, that is, rather smaller than the larger fields in the plexiform zone. The length of the cylinders is also variable and may approach 0·5 mm. Obviously it is exceedingly difficult to obtain a complete picture of such figures and one can only obtain an approximate idea of their shapes even in the thickest sections. Some of the fields seem to be flattened in one plane (i.e. horizontal or vertical), others tapered to make cones with base upwards or downwards. Many may be quite irregular, with tongue-like projections of the fields, although in most the dendrites seem to occupy a fairly compact volume.

These dendritic fields are presumably activated by the axons of the centripetal unipolar and bipolar cells, which in turn collect from orientated dendritic fields in the plexiform layer. If the dendritic fields of these medullary cells were themselves orientated they would provide a further set of filters, each cell responding only to activation by particular sets of the more superficial cells. However, knowledge of their shapes is too scanty to be more specific.

23. The centre of the optic lobe

The cells just described in the outer part of the medulla, arranged in more or less radial rows, gradually give place to those of the cell islands at the centre of the lobe (figure 66). These are often basically unipolar, the single main branch then dividing into numerous dendrites that run in the fibre tracts between the cell islands. An axon arises from one of these branches and either ends in some other part of the lobe or proceeds to the optic tract.

The form of the dendritic fields of these central cells is hard to determine. Some spread out widely towards the surface (figure 66) and these must be influenced by visual changes in widely distant parts of the retina. Others are multipolar cells, with several branches spreading between the cell islands (figure 67). Often no one of these is clearly distinguished as an axon. This is especially true of the very numerous small cells in the islands. All the stained branches of these can frequently be traced to their ending within the section and it is difficult to believe that any one of them is differentiated as an axon.

Some of the larger cells, on the other hand, carry a distinct smooth fibre that runs towards the optic tract and is presumably the axon (figures, 64, 68, 69; and 70, plate 12). It has not been easy to establish the details of the origins of the fibres of the optic tract, however. Passing inwards through the lobe, there is an increasing proportion of larger cells (table 1) and an increasing predominance of fibre bundles over cells. The whole centre of the lobe is thus a distribution system, ensuring that influences from all parts of the visual field can reach to each of the many centres that are connected with the optic lobe (see below). It has not been possible to discover how far the dendrites of the cells that give origin to these axons reach towards the surface. There is no certain evidence that even one further synapse is necessarily involved between the plexiform zone and the tract.

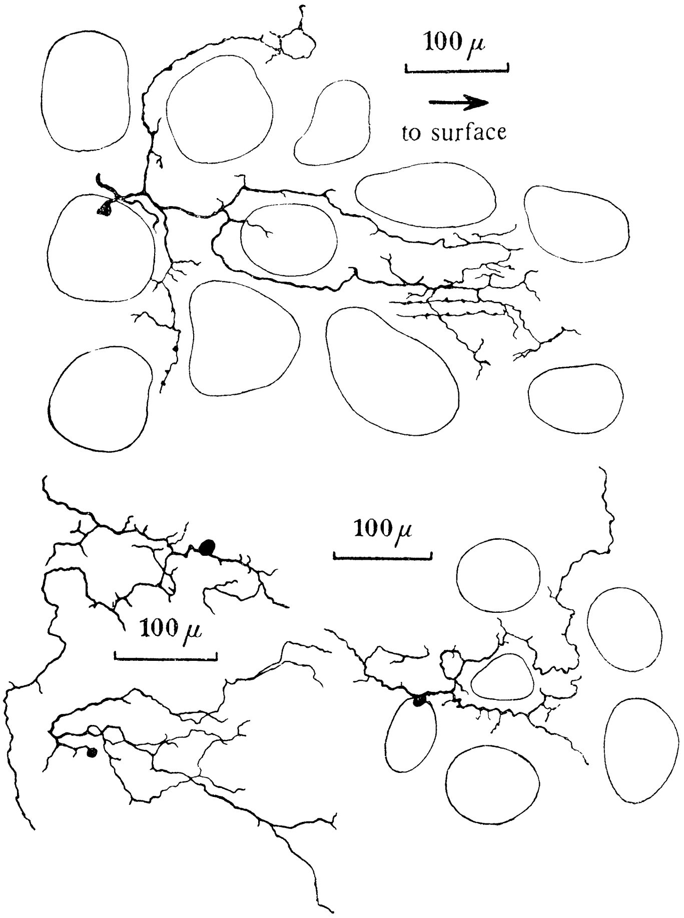

Figure 66. Cell islands of the medulla and their large cells with dendritic trees reaching towards the surface (Golgi–Kopsch).

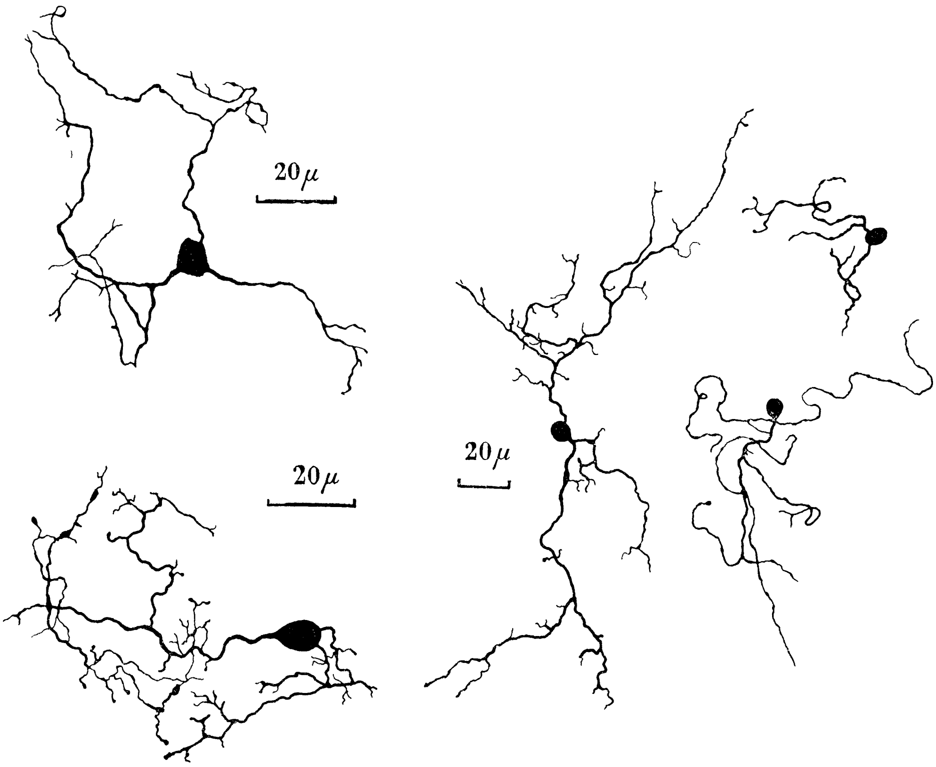

Figure 67. Small multipolar cells from medulla; radial section (Golgi–Kopsch).

No cell has ever been seen with dendrites in the plexiform zone and axon in the optic tract, however, and it may provisionally be assumed that they do not occur. If this is so, the axons of the centripetal cells must make synapse with the dendrites of the medullary cells that send axons to the tract.

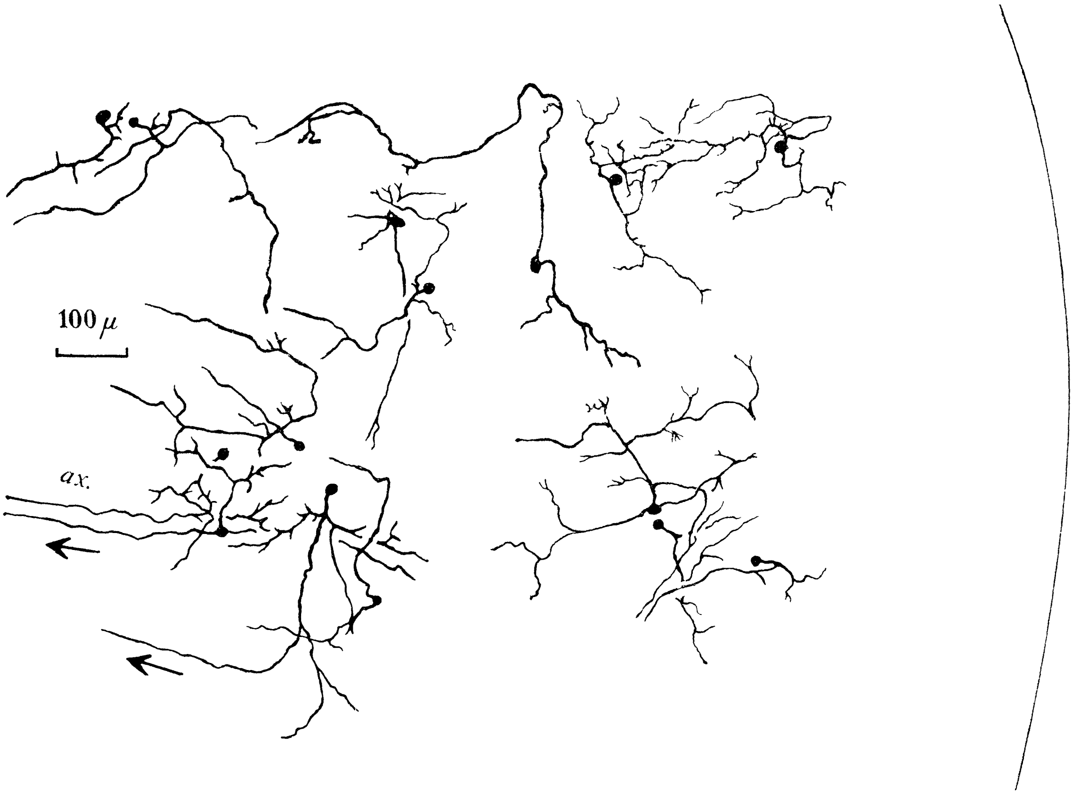

FIGURE 68. Cells of the medulla to show the general organization of multipolar cells, with axons directed towards the optic tract (Golgi–Kopsch).

FIGURE 69. Unipolar cells at the centre of the optic lobe to show dendritic collaterals and axons proceeding towards the optic tract (Golgi–Kopsch).

It does not follow that the pathways between the plexiform layer and the optic tract are necessarily very complicated, though they may well be so. Indeed the maze of fibres between the cell islands suggests that they are (figures 73*a*, plate 12, and 76, plate 13). The cells and fibre tracts look essentially alike throughout the central part of the lobe. They presumably include several sorts of cells, allowing the visual input to produce the appropriate response among the many that are available to an octopus (Boycott & Young 1962). There is also evidence that changes within the optic lobes constitute a major part of the memory store of the animals.

24. ENDINGS OF FIBRES OF THE OPTIC TRACT WITHIN THE OPTIC LOBES

The optic tract contains fibres reaching the optic lobes from many sources (see p. 51). The endings of these can be seen in the plexiform zone and sometimes deeper within the lobes. They have the form of fine, branched, beaded terminals (figures 71; 72, plate 12). Sometimes one fibre seems to have a restricted distribution, but others branch

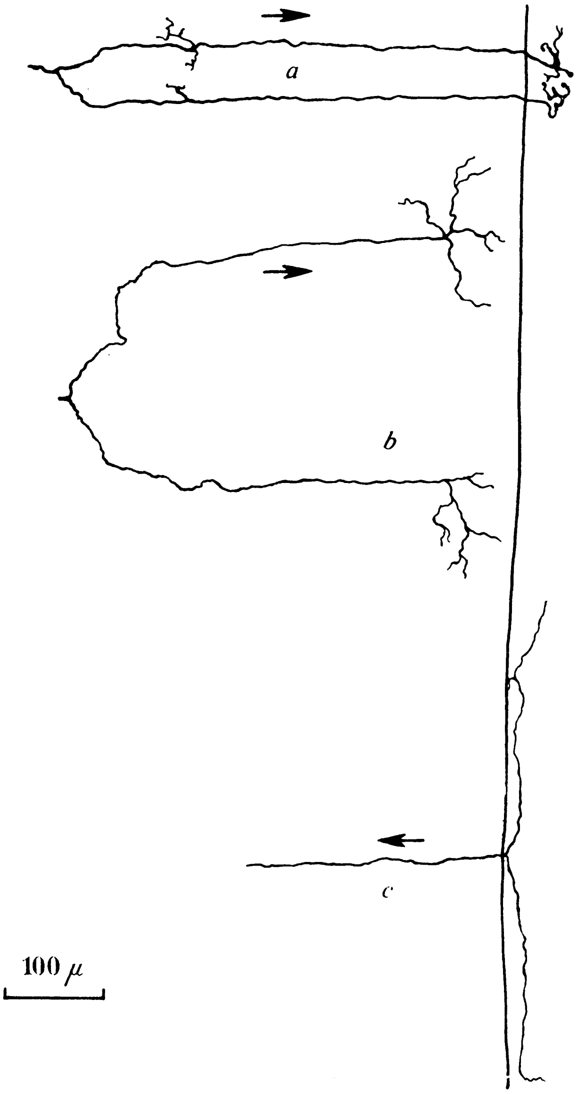

FIGURE 71. Branching fibres in the outer region of the optic lobe. *a* and *b* are presumed to be afferents reaching the lobe from more distant regions. *c* is probably a dendrite (Golgi–Kopsch).

and spread widely. It is not known whether fibres from the different sources listed below end differently within the lobes. There is some evidence that axons from cells at the centre of the lobe pass outwards to end more superficially (p. 46).

25. Degeneration after lesions in the optic lobes

Some evidence about the arrangement of pathways in the lobes can be obtained by placing knife cuts in various planes. Degeneration proceeds very fast and granular fibres, stainable with Cajal's method, can be seen in the first 2 or 3 days after a lesion (figure 73*b*, plate 12) and then soon disappear.

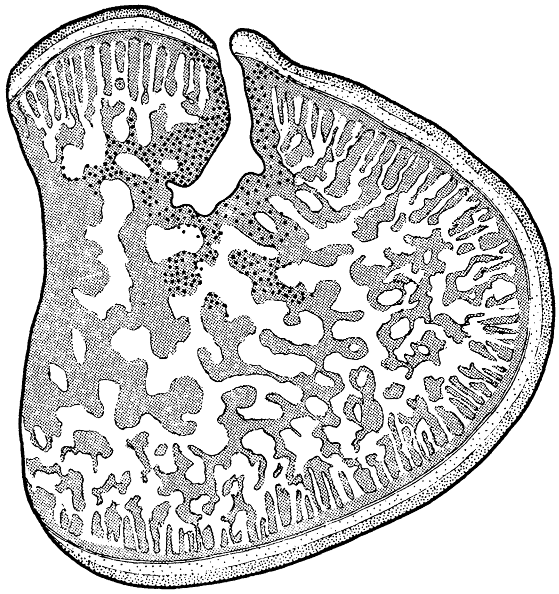

Figure 74. Drawing from a photograph of a transverse section of optic lobe. The large dots show the distribution of degenerating fibres that was seen three days after a stab wound had been placed in the top of the optic lobe. The finely stippled areas represent fibre tracts, the white being cell islands.

After a wound such as that of figure 74 the area of degeneration is narrow near the surface and broadens towards the centre. Few degeneration granules are seen in the plexiform zone (except near the wound), many in the fibre tracts between the deeper cell islands. We may conclude that tangential pathways become more abundant, passing more deeply. It is difficult to detect a few degenerating fibres by this method and it may be that the tangential spread at the deeper levels is wider than figure 74 suggests.

26. The optic tract and the connexions of the optic lobes

A considerable part of the centre of the optic lobe is occupied by the gathering of fibres from all parts of the lobe into appropriate bundles for distribution. Fibres reach the lobe from at least eight distinct sources and leave to ten areas in the brain (see below), so that it is not surprising that the sorting system is complicated (figures 75, 76, plate 13). There is no evidence that fibres for any particular destination arise from one part of the lobe rather than another. However, there must be a degree of regularity in the connexions, for when an image falls on any part of the retina an octopus attacks with the appropriate arms or swims in the right direction (Packard & James, personal communication).

It may be convenient here to summarize the tracts that are known to enter and leave the optic lobes. The evidence for many of these comes from degeneration following lesions elsewhere in the brain (Boycott & Young 1962).

Afferent connexions

(1) Optic nerve fibres originating in the retina and ending as three types of fibre in the plexiform zone and outer part of the medulla (p. 27).

(2) Commissural fibres from the opposite optic lobe.

(3) Fibres from other afferent systems:

(*a*) The brachio-optic tract carries fibres that probably arise in the brachial lobes and bring information from the arms.

(*b*) The inferior frontal to optic tract is a small bundle of large fibres, probably carrying chemotactile information from the buccal region, as well as from the arms.

(*c*) The magnocellular-optic tract may carry information from the back, mantle and viscera.

(4) Fibres from higher motor centres:

(*a*) The anterior basal-optic tract is concerned with the activities of the optic lobe in orientating the eyes and head and in walking movements of the whole animal.

(*b*) The medial basal-optic tract, concerned with the swimming and other movements of the mantle.

(*c*) The lateral basal-optic tract, concerned with colour.

(5) Fibres from the memory centres:

(*a*) The main output of the subvertical lobe reaches the optic lobe, this being the pathway by which the superior frontal and vertical lobes chiefly produce their effects, which are mainly concerned with memory.

(*b*) The superior frontal (lateral) sends a bundle direct to the optic lobe.

Efferent connexions

The optic lobe sends fibres to the retina and to nearly all parts of the supraoesophageal lobes, but not directly to the suboesophageal lobes (except the magnocellular lobe). The paths may be classified as follows:

(1) To the retina, from the centrifugal cells of the inner granular layer.

(2) Commissural fibres to the opposite optic lobe.

(3) To the peduncle lobes, which are placed on the optic tract, and are perhaps concerned with the timing of movements.

(4) To the various higher motor centres.

(*a*) Anterior basal lobes for control of the position of head and eyes and the direction of movement.

(*b*) Medial basal lobes, perhaps for control of the initiation of swimming or walking.

(*c*) Lateral basal lobes for the control of colour change.

(*d*) To the magnocellular lobes to initiate defensive actions, such as the assumption of a dymantic (startling) pattern or the defence posture, with the arms turned back.

(5) To centres controlling motivation and sexual maturation.

(*a*) The dorsal basal lobe may be partly in control of the 'motivation' system and certainly part of it regulates the onset of sexual maturity, through the optic glands.

(*b*) The lateral superior frontal lobe controls the power to attack objects seen at a distance and capacity to stay in a home among the rocks.

(*c*) Fibres from the optic to the subvertical lobe may also assist in this.

(6) To memory centres.

The fibres of the optic to median superior frontal tract provide the visual input to the vertical lobe system.

27. Discussion

The optic lobes act as an analyzing and coding system for the visual input and at the same time as a higher motor centre. Electrical stimulation in the medulla of the lobe will produce movements and complex colour patterns (Boycott 1961). The occurrence of the coding and decoding systems within one lobe provides an opportunity to analyze their workings and emphasizes that neither can be considered alone. Here we have been able to suggest that the coding of some features may depend upon the geometrical arrangement of dendrities in the plexiform layer, but obviously much further work on the anatomy and physiology of the dendritic fields is required.

The general arrangement of the system provides a clue to its functional organization. The input from the axons arising from the retinal cells is first displayed, after inversion in the dorso-ventral plane by a chiasma, over an extended area in the plexiform layer. Here the topological relations of the input fibres are preserved. They meet the processes of a large number of small amacrine cells with branches spreading as cones at various depths. These small cells must have an important effect, perhaps increasing the influence of contours by lateral inhibition. The method of action of such short cells with no apparent axon is unknown. Their occurrence here as well as at similar levels in the visual systems of arthropods and vertebrates must be significant.

At the same level, the visual input meets the branches of centrifugal cells, whose fibres proceed to the retina. This is parallel to the situation in insects, where Autrum (1958) has shown that the effects of these fibres is to increase flicker fusion frequency and hence acuity. The parallel with the vertebrate retina is less clear. Nor is it clear what may be the function of the basal processes of these cells, which seem to be sometimes axons, sometimes dendrites (p. 37).

The layering of the plexiform zone again suggests parallels with both arthropods and vertebrates but here we have no real clue to the significance. It may be connected closely with the coding system, various types of fibre producing different responses according to the depths at which they end. This is an especially attractive view since these layers contain the dendrites that provide the pick-up that conducts to the next level. The fact that the optic nerve fibres end at differing depths is also suggestive. These endings have here been classified as at three levels (1st radial layer, inner plexiform zone, inner granular layer, p. 27). Perhaps finer divisions could be made according to the level of ending in the plexiform and inner granular layers. There may be a distinction between the fibres ending in the plexiform layers, perhaps concerned with form discrimination, and the more deeply ending fibres, which may signal brightness.

The regular arrangement of the dendrites in the plexiform layers and the possible shapes of their dendritic fields are perhaps the most challenging features of the system. If the fields have different orientations they may serve to signal the extent of figures in the vertical and horizontal directions, which Sutherland (1960) has shown to be of special importance for recognition of shape. It is not impossible that by suitable combinations of fields of different sizes, with axons projecting to corresponding depths, this could provide the coding system for visual patterns. If the cells at the centre of the lobe also have orientated fields they may serve to extract ratios of extent in different directions. Deutsch (1960) has suggested that the fibres of the plexiform zone serve to measure the vertical extent of figures, apparently by converting it to a frequency code.

Further speculation is perhaps not profitable until we know more of the anatomy and physiology of these cells. In many of the cells of the optic lobes the distinction between axons and dendrites is difficult. We do not know whether a cell such as that of figure 53, plate 11, whose main trunk first functions as a dendrite and then becomes an axon, acts differently from bipolar cells such as those of figure 50, plate 11. The cells of the lobe show a great variety of forms and one can only suggest at present that it is this variety itself that constitutes the elements of the code. If this is so then the details of the lengths of the dendrites and distribution of their branches are presumably features of fundamental importance in deciding the conditions under which a cell fires.

If there are cells specifically responsive to particular configurations of visual input we must suppose that each can initially produce the action pattern of either attack or retreat. Pathways from the arms and mouth to the optic lobes are available to carry fibres whose action may be to 'switch' those optic lobe cells that are active at a time when either food or pain impulses prevail. In this way the optic lobes would come to contain the representations that produce appropriate response in the future (Young 1960).

Much more is undoubtedly involved, and the vertical lobes play a large part in the recording process. Pathways responsible for generalization from one part of the visual field to others must also be considered (Muntz 1961). More information is needed before the complete mechanism can be seen, but the general plan of the system and the details of the dendritic fields suggest that specific topographical arrangements will prove to be an important feature.

The material for this work has been collected over many years at the Stazione Zoologica at Naples, to whose Director, Dr P. Dohrn, and staff I am most grateful for continual help. The Nuffield Foundation has provided assistance during several of the years of work. The research reported in this and the previous paper has also been sponsored in part by the United States Air Force Office of Scientific Research. I am indebted to Mr B. B. Boycott for help and advice at all stages of the work. Dr E. G. Gray, Mr M. Moody and Miss J. Parriss kindly read the MS. I am also indebted to Mr J. Armstrong and Miss P. Stephens for making many of the preparations, and to Mrs Astafiev for help with the drawings.

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DESCRIPTION OF PLATES 7 TO 13

PLATE 7

FIGURE 2. T.s. optic lobe to show the optic tract and the lobes on it (Cajal).

FIGURE 3. Portion of t.s. optic lobe to show plexiform layer, radial bundles and medulla (Cajal).

FIGURE 5. T.s. surface of optic lobe to show the divisions of the plexiform layer (Cajal).

FIGURE 6. T.s. to show arterial tree at the surface of the optic lobe (Golgi–Kopsch).

FIGURE 7. T.s. showing three glia cells with radial fibres running throughout the depth of the plexiform zone (Golgi–Kopsch).

FIGURE 8. Section tangential to surface of optic lobe, showing glia cells with long processes radiating in the inner tangential layers of the plexiform zone (Golgi–Cox).

PLATE 8

FIGURE 9. Section tangential to surface of optic lobe, showing glia cells with long processes radiating in the inner tangential layers of the plexiform zone (Golgi–Cox).

FIGURE 10. Similar section to figures 8 and 9, glia cell with short blunt processes.

FIGURE 11. T.s. of inner granule cell layer, showing glia cells with long fine fibres running mainly radially (Golgi–Cox).

FIGURE 12. Artery from inner granule cell layer with glial fibres attached (Golgi–Kopsch).

FIGURE 13. Glial cells from neuropil between the cell islands towards the centre of the optic lobe (Golgi–Cox).

FIGURE 15. T.s. surface of optic lobe to show arrangement of incoming bundles of optic nerve fibres (Cajal).

FIGURES 16 and 17. T.s. surface of optic lobe to show endings of the retinal nerve fibres, mainly in the plexiform zone. Two fibres that pass beyond this zone are seen. In figure 17 the fine terminal branches of one of these are seen at the left (Golgi–Kopsch).

FIGURES 18 and 19. Endings of retinal nerve fibres in the plexiform zone. Some end within the first radial layer, others pass beyond it (Golgi–Kopsch).

PLATE 9

FIGURE 20. Section obliquely tangential to surface of optic lobe to show the appearances of the retinal nerve fibres as they emerge from the outer granule cell layer (at right). Immediately within the first radial layer they are swollen (*ret. sw.*) with a darker core and lighter cortex. More deeply (to the left) the central fibre divides into several fibrils and the cortex disappears (Cajal).

FIGURE 21. Section tangential to surface of lobe at level of first tangential layer. The retinal nerve fibres appear as compact dots (Cajal).

FIGURE 22. T.s. plexiform zone to show passage of optic nerve fibres through the first and second radial layers (Cajal).

FIGURE 23*a*. Plexiform zone of an optic lobe 5 days after severance of the optic nerve fibres.
b. The plexiform zone of the opposite side of the animal. 23*a* and *b* stained together (Cajal).

FIGURE 24. T.s. surface of optic lobe at the boundary between a normal area and one whose optic nerves had been cut 9 days previously (above). Note absence of fibres from the first radial layer (Cajal).

FIGURE 25. Boundary between normal optic lobe and region denervated 45 days previously (below). Note shrinkage of outer granule cell layer (Cajal).

FIGURE 26*a*. Portion of optic lobe whose optic nerves were cut 45 days previously.

b. Opposite optic lobe for comparison (Cajal). Note shrinkage of outer granule cell layer and plexiform zone, especially its first radial layer. The inner granule cell layer is also shrunken and disorganized.

PLATE 10

FIGURE 27. T.s. plexiform zone of an optic lobe whose optic tract had been cut 7 days previously. Only the optic nerve fibres and outer granule cells are intact; the central part of the lobe has degenerated (to the left) (Cajal).

FIGURE 29 *a*, *b* and *c*. Cells of the outer granule cell layer seen after staining with the Golgi–Kopsch method. Some of the cells have been drawn in figure 28.

FIGURE 30. Outer granule cell with bunch of very fine fibres in first radial layer (Golgi–Kopsch).

FIGURE 31. Outer granule cell with fine twigs in first radial layer and two branches, each carrying two swellings in the second radial layer (Golgi–Kopsch).

FIGURE 39. T.s. optic lobe showing centrifugal cells and optic nerve fibre endings.

FIGURE 40*a* to *d*. Centrifugal cells with various forms of basal dendrite and of branches in the plexiform zone (Golgi–Kopsch).

FIGURE 41*a* and *b*. Dendritic fields of centrifugal cells in the plexiform zone. The longer axis of the page represents the vertical, the shorter the horizontal plane.

PLATE 11

FIGURE 44. Edge of optic lobe as seen in horizontal section, showing two bundles of fibres passing from the medulla through the plexiform zone into the optic nerves.

FIGURE 49. Portion of t.s. optic lobe to show a 'bipolar' cell, with two dendrites passing to the plexiform zone and an axon directed centrally (Golgi–Kopsch).

FIGURE 50. Photograph of a cell drawn in figure 46 to show the appearance of the centrally directed fibres that are presumed to be axons (Golgi–Kopsch).

FIGURE 51. Cell with many fibres (?dendrites) proceeding to the plexiform layer, also a tangential cell below it (Golgi–Kopsch).

FIGURE 53. Cell with a fibre reaching to the plexiform zone, giving short branches there, and then turning back into the centre of the lobe (Golgi–Kopsch).

FIGURE 57*a* to *c*. Dendritic fields of three centripetal cells as seen in sections tangential to the plexiform zone. Orientation as figure 41. The main axes lie in the horizontal plane (Golgi–Kopsch).

FIGURE 58. Portions of three dendrites from a dendritic field in the plexiform zone to show collateral twigs, more frequent towards the tips (Golgi–Kopsch).

PLATE 12

FIGURE 59. Plexus of fibres in the inner tangential layers of the plexiform zone (probably mainly second tangential) in a Golgi–Kopsch section tangential to the surface of the lobe. The long fibres are mainly dendrites of centripetal cells. Glia cell bodies are seen as black smudges. In this and figure 60 the horizontal axis of the lobe is that across the page.

FIGURE 60. Plexus in second tangential layer in a Cajal-stained section cut tangential to the surface of the lobe. The thicker fibres are mainly dendrites of centripetal cells, but axons are also stained by this method.

FIGURES 70*a* and *b*. Unipolar cells from the centre of the optic lobe, showing dendritic collaterals (*col.*) and axons directed towards the optic tract (Golgi–Kopsch). These cells are drawn in figure 69.

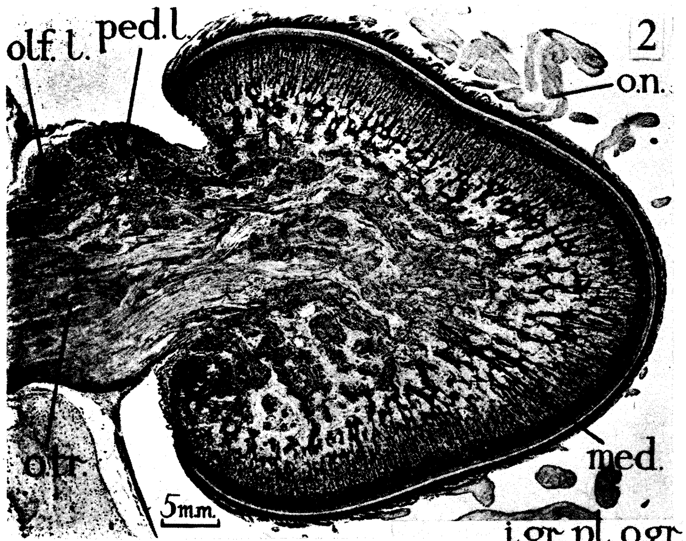
FIGURE 72. T.s. plexiform zone to show afferent fibres reaching it from central sources (*c.aff.*). These end at various levels. Endings of retinal nerve fibres are also seen (Golgi–Kopsch).

FIGURE 73*a*. Fibre tracts between cell islands filled with granules 3 days after a lesion nearby. *b*. Normal lobe (Cajal).

PLATE 13

FIGURE 75. T.s. whole central nervous system at level of optic tracts to show some of their many connexions (Cajal).

FIGURE 76. Thick h.s. at level of optic tract after Golgi stain to show bundles collecting from all parts of the optic lobes and distributing to various supraoesophageal centres.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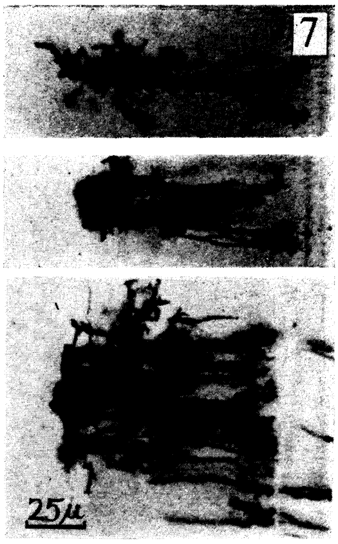
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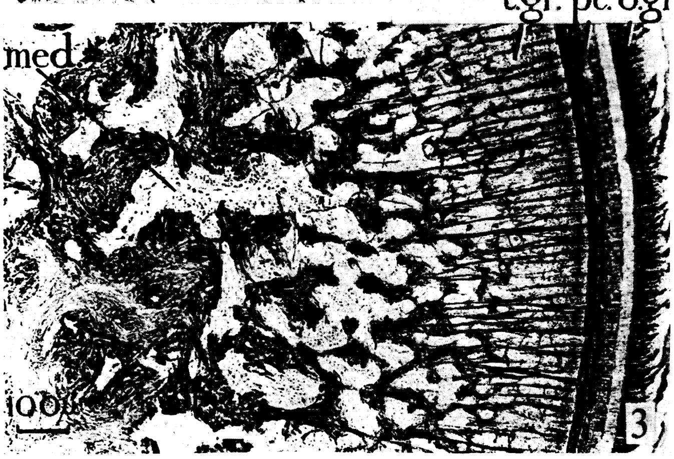
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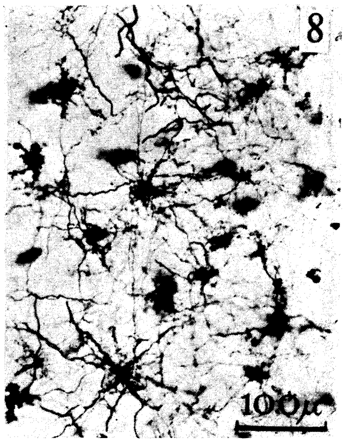
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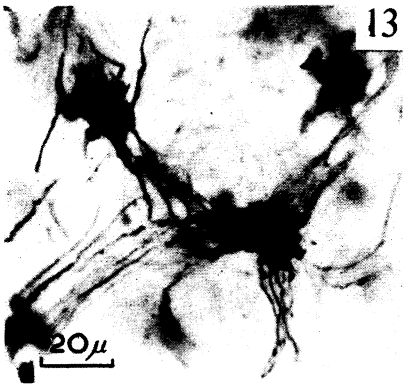
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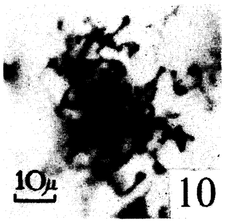
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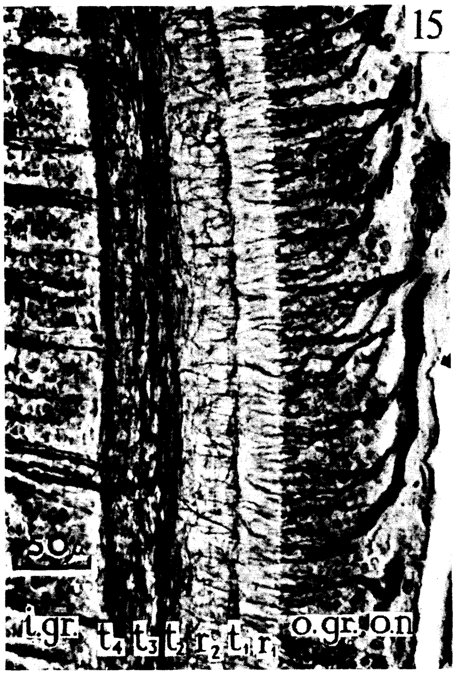
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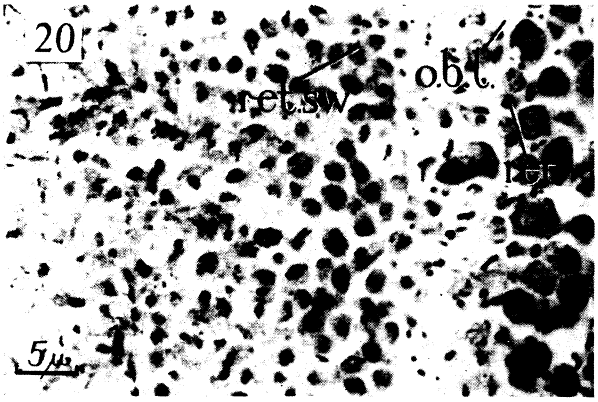
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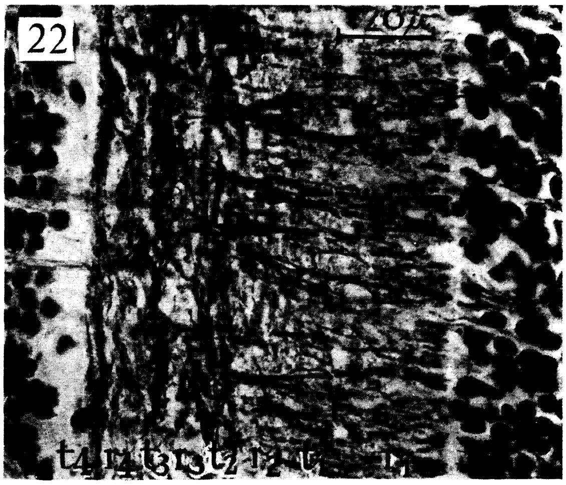
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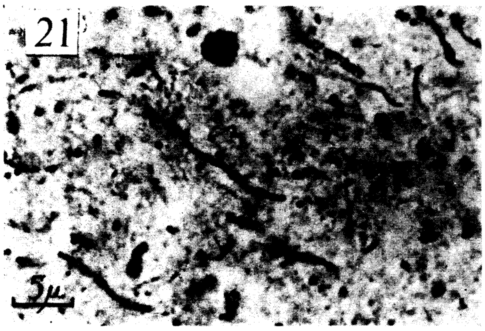
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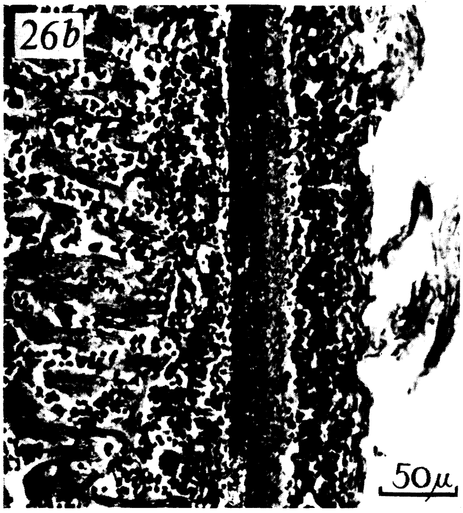
23*b*


23*a*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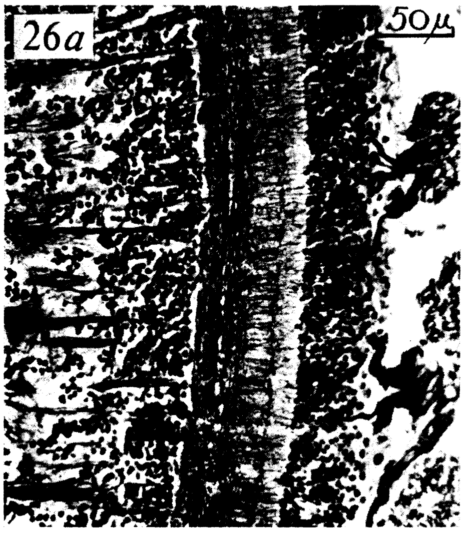
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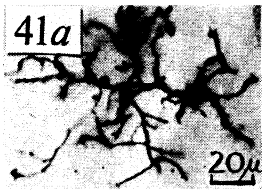
41*a*



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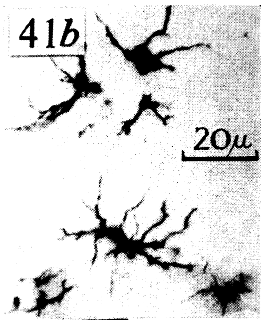

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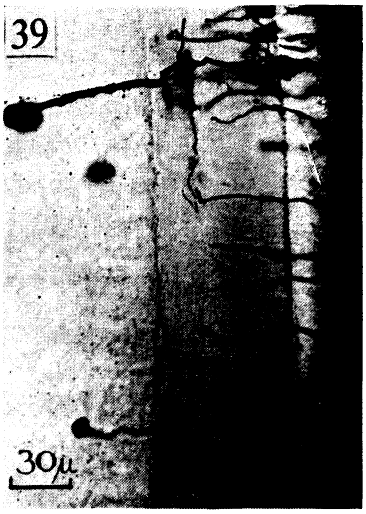
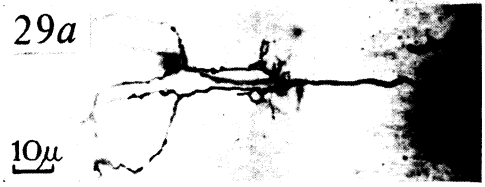
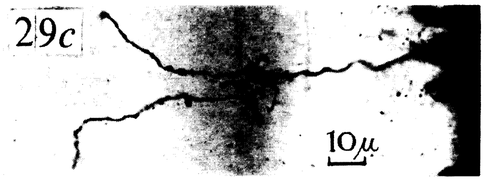


29*a*



29*b*

29*c*



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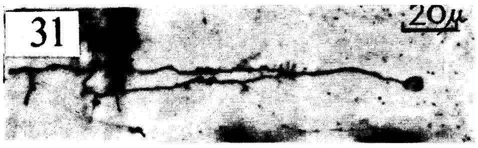

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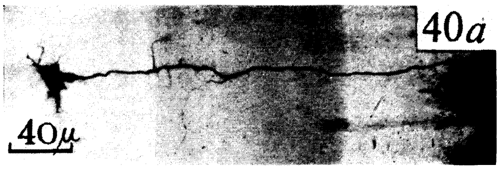

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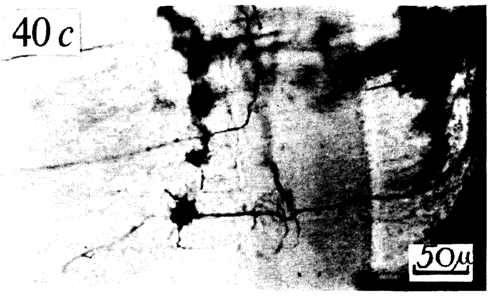

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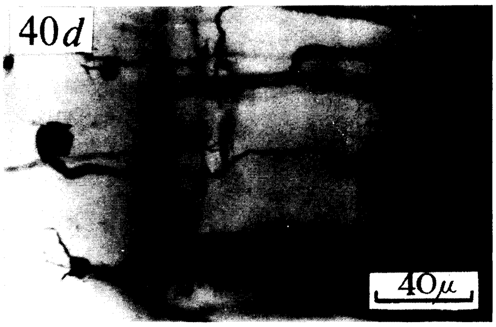

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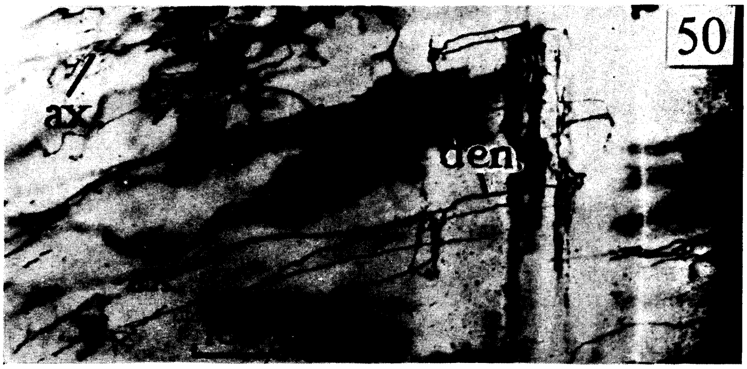

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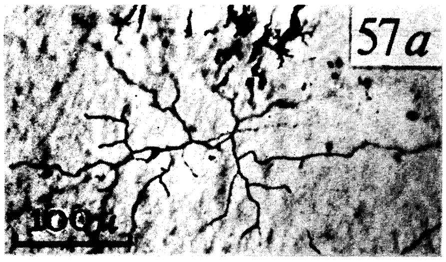

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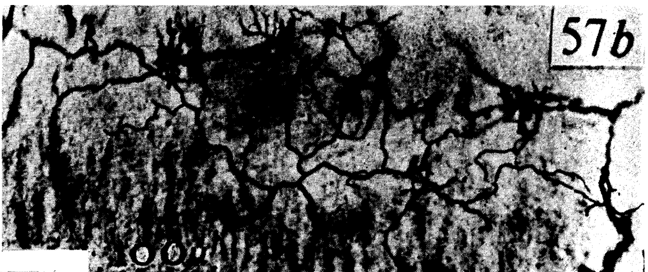

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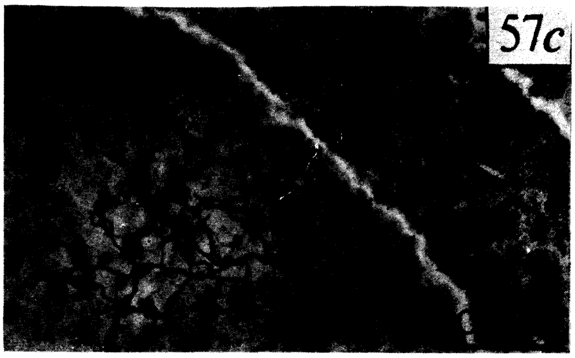

57*c*

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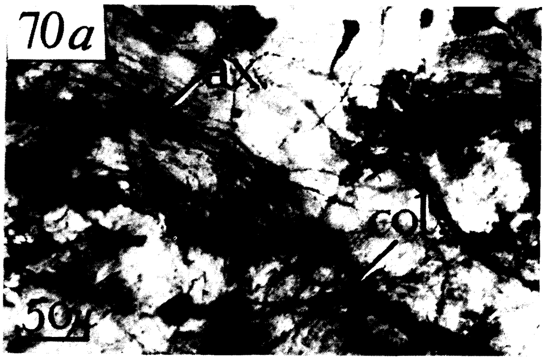
70*a*



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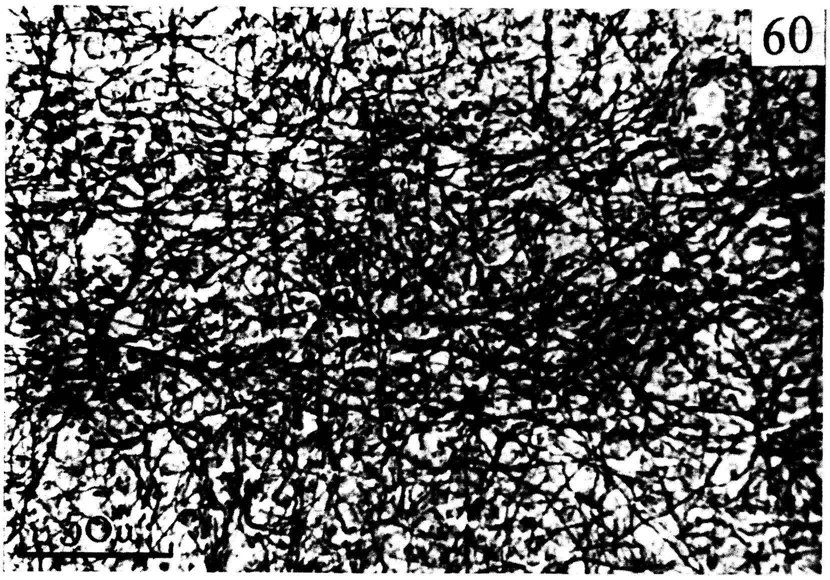

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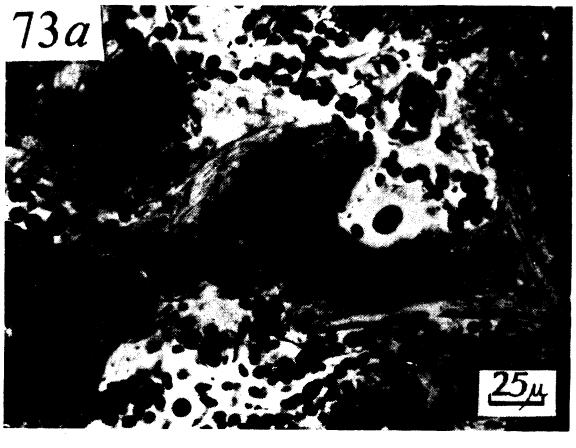

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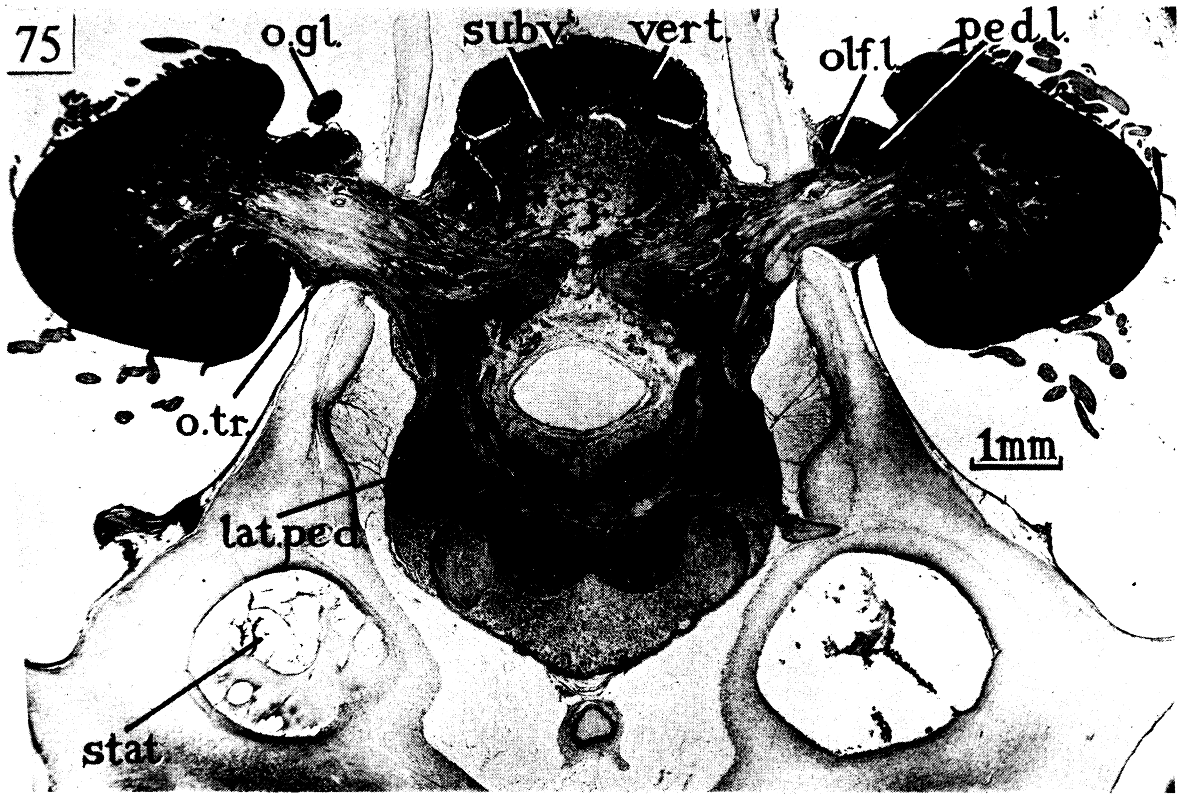
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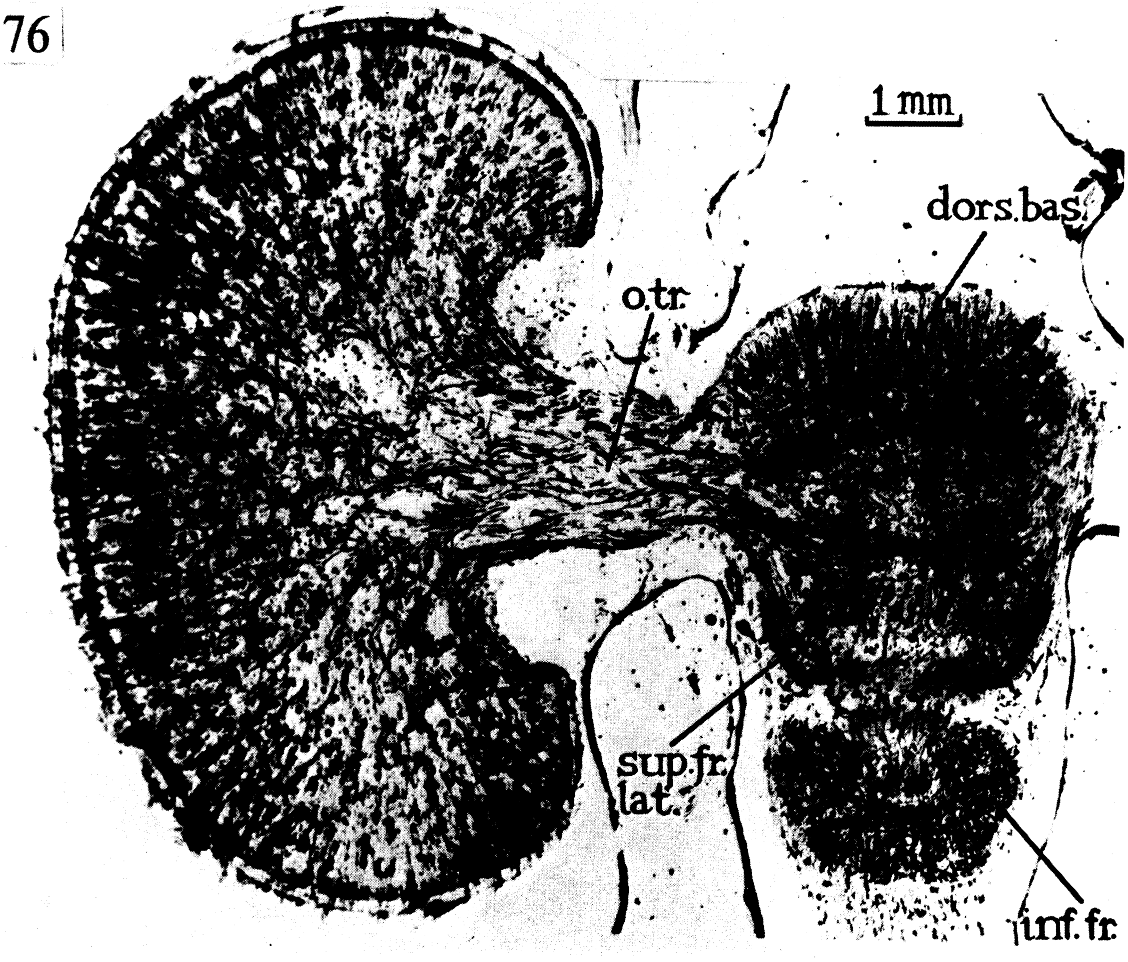
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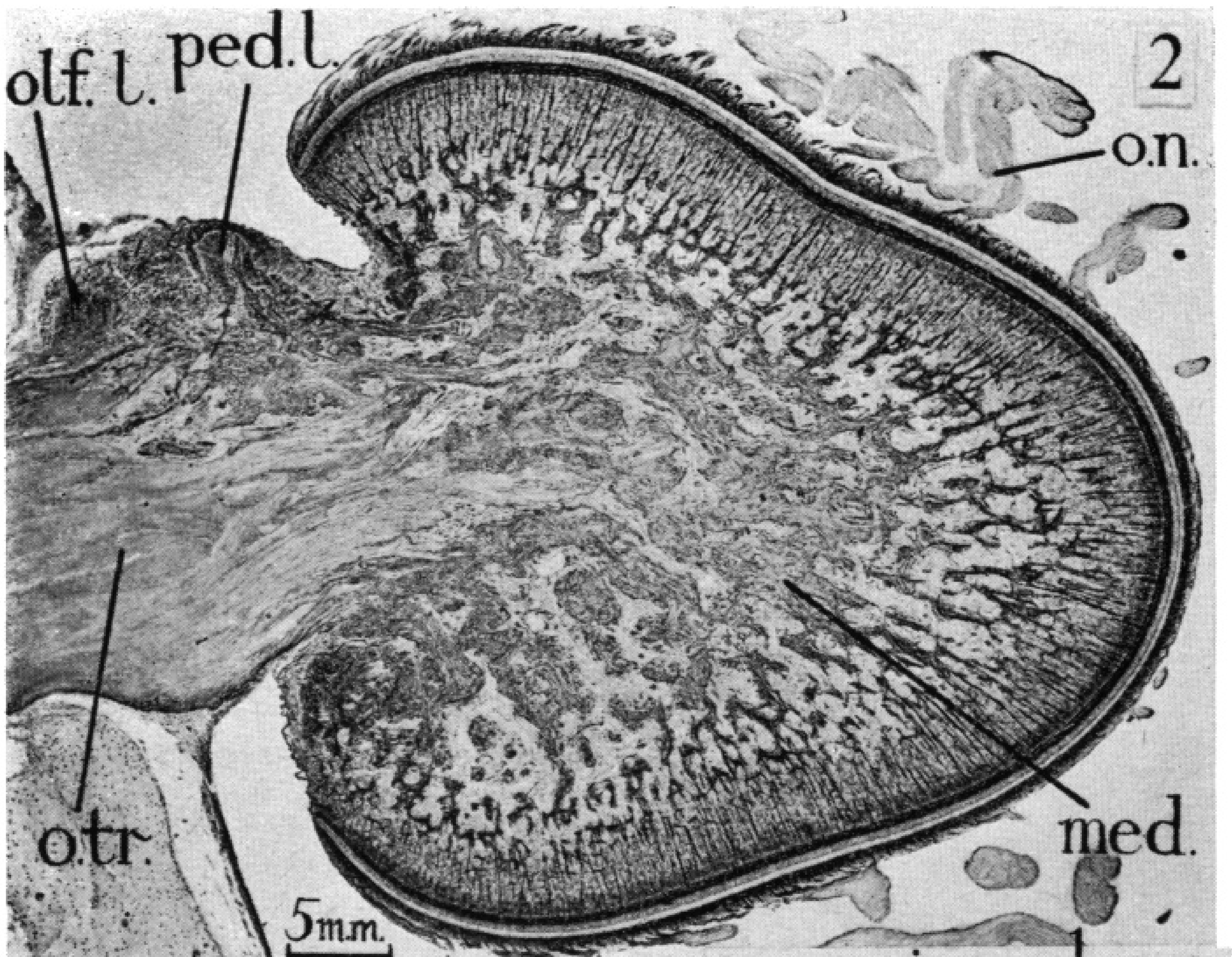
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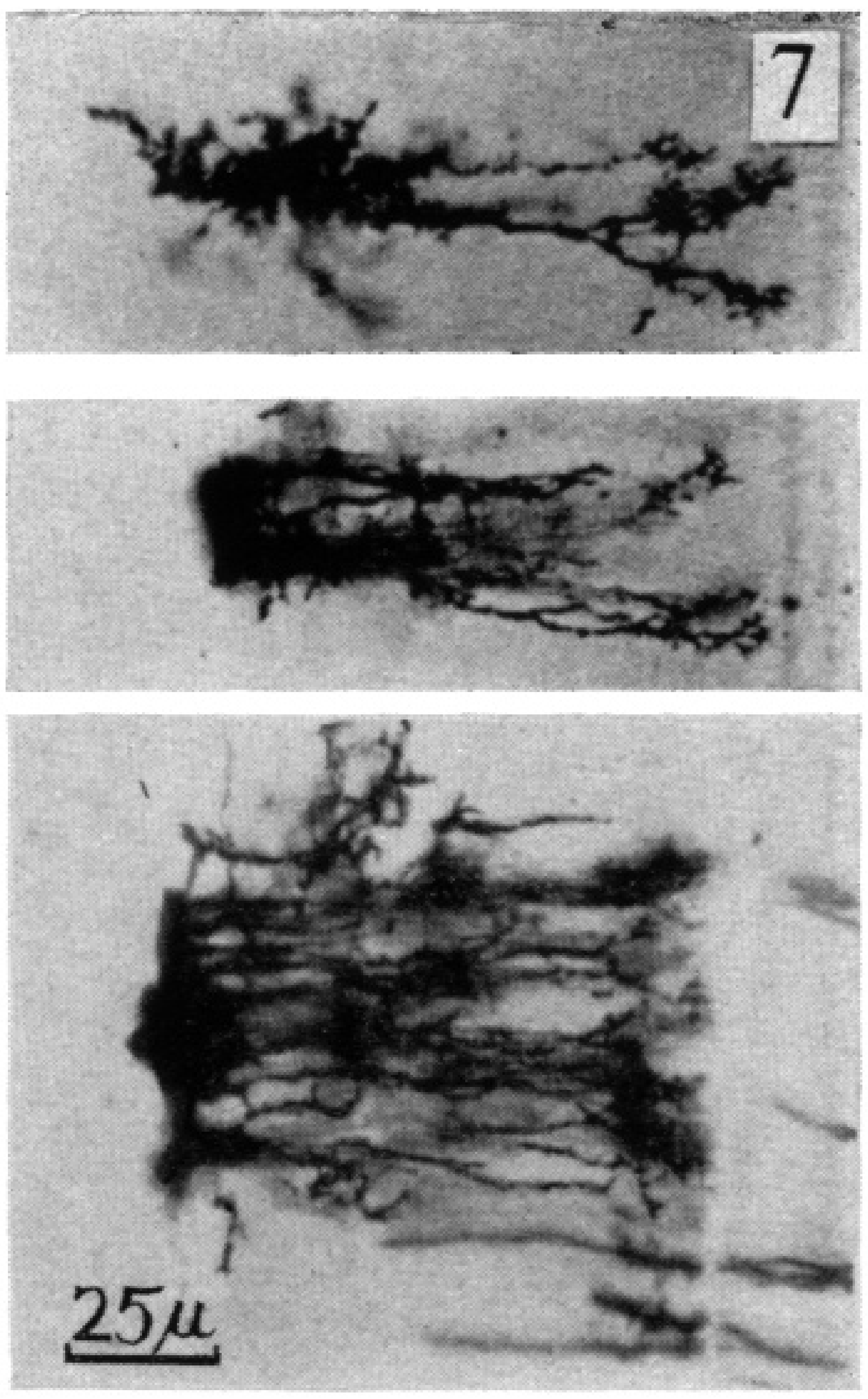
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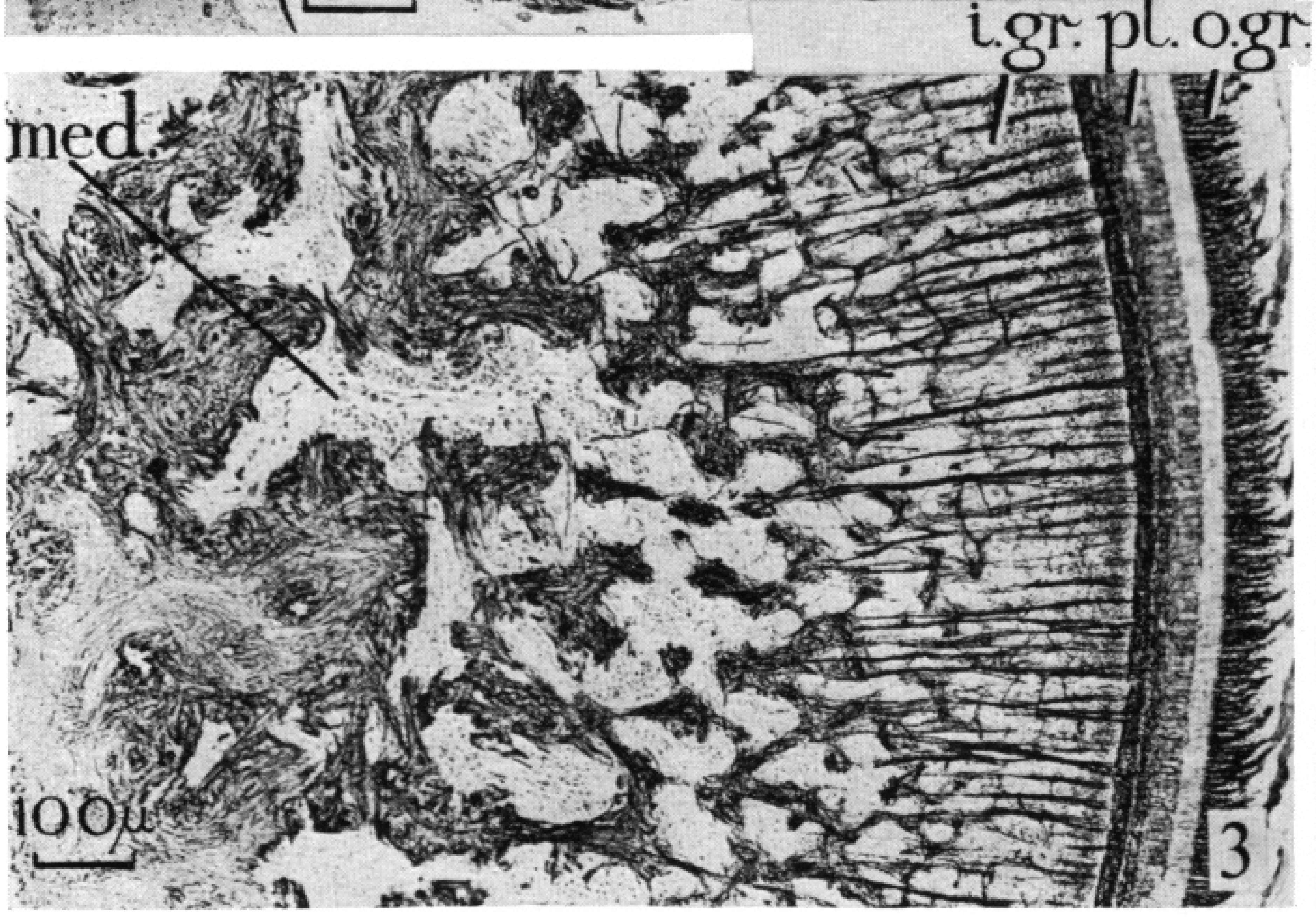
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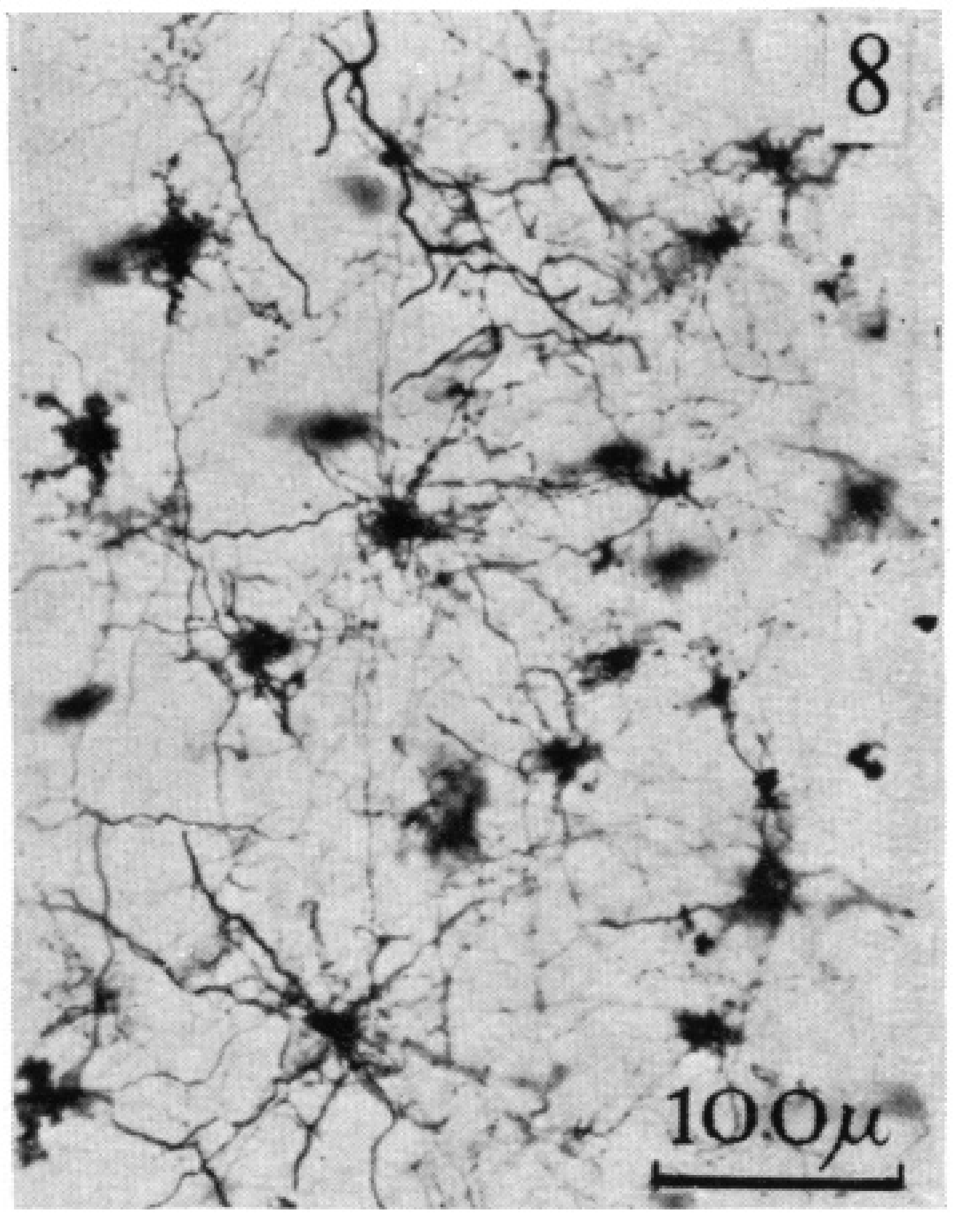
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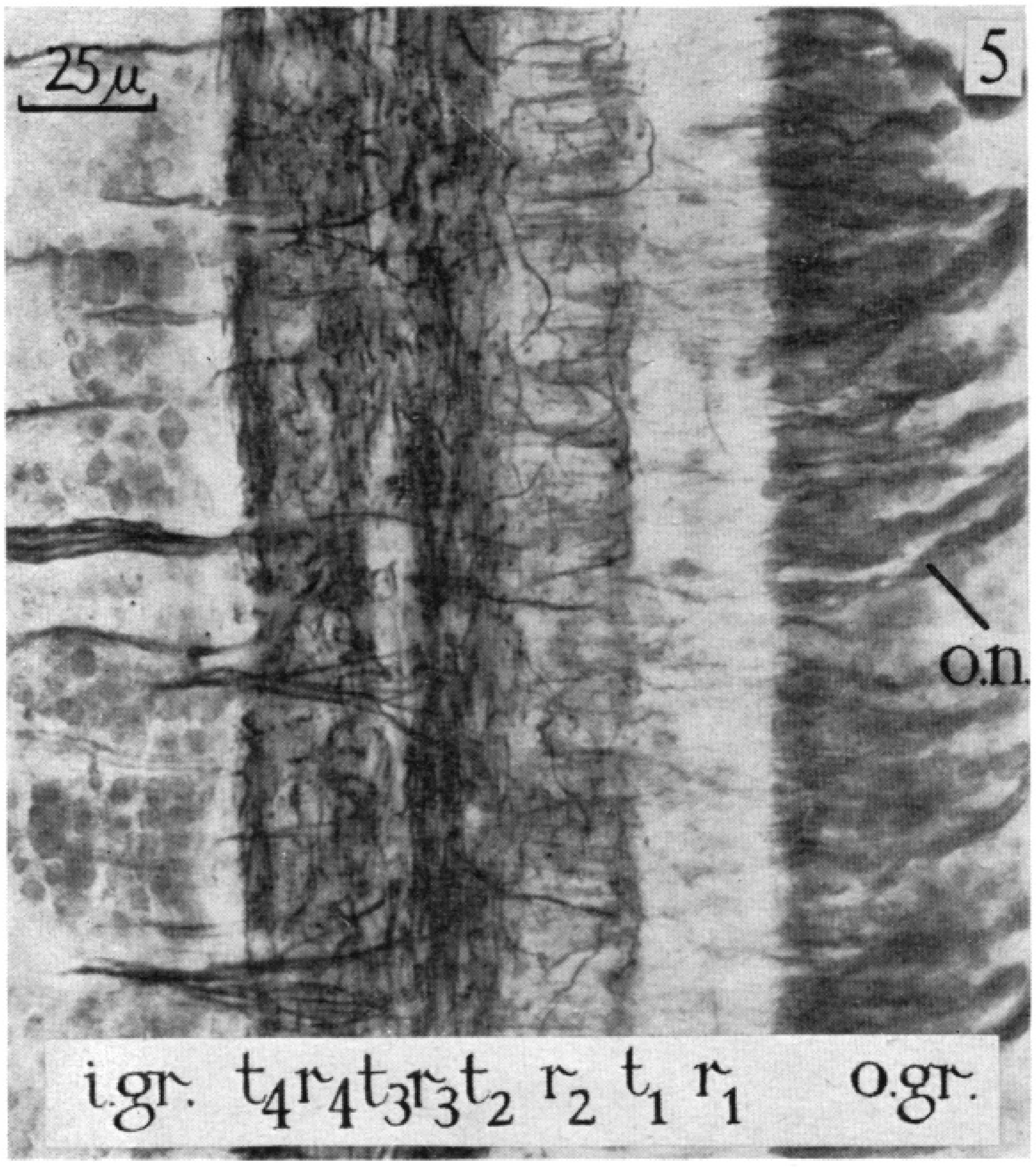
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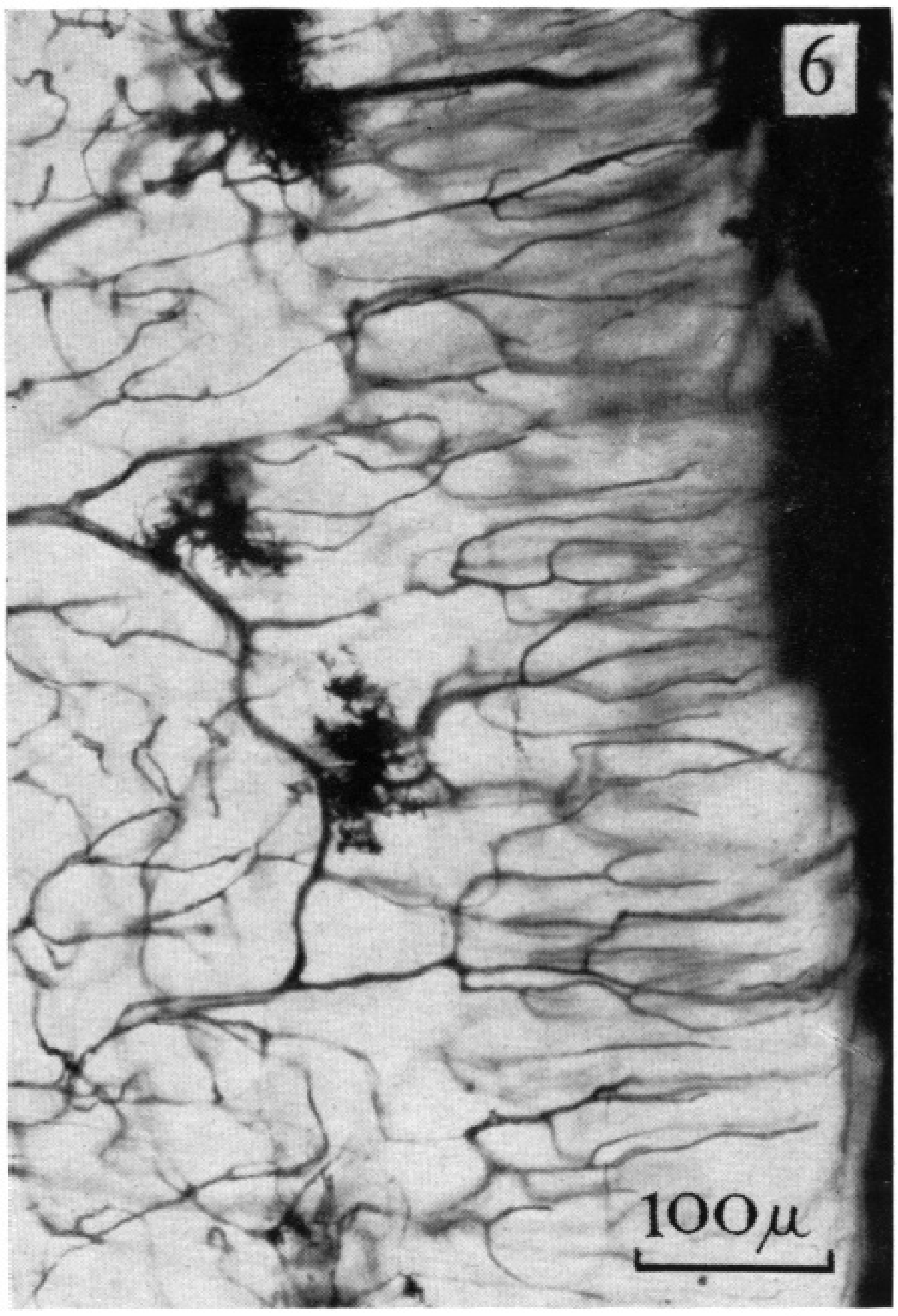
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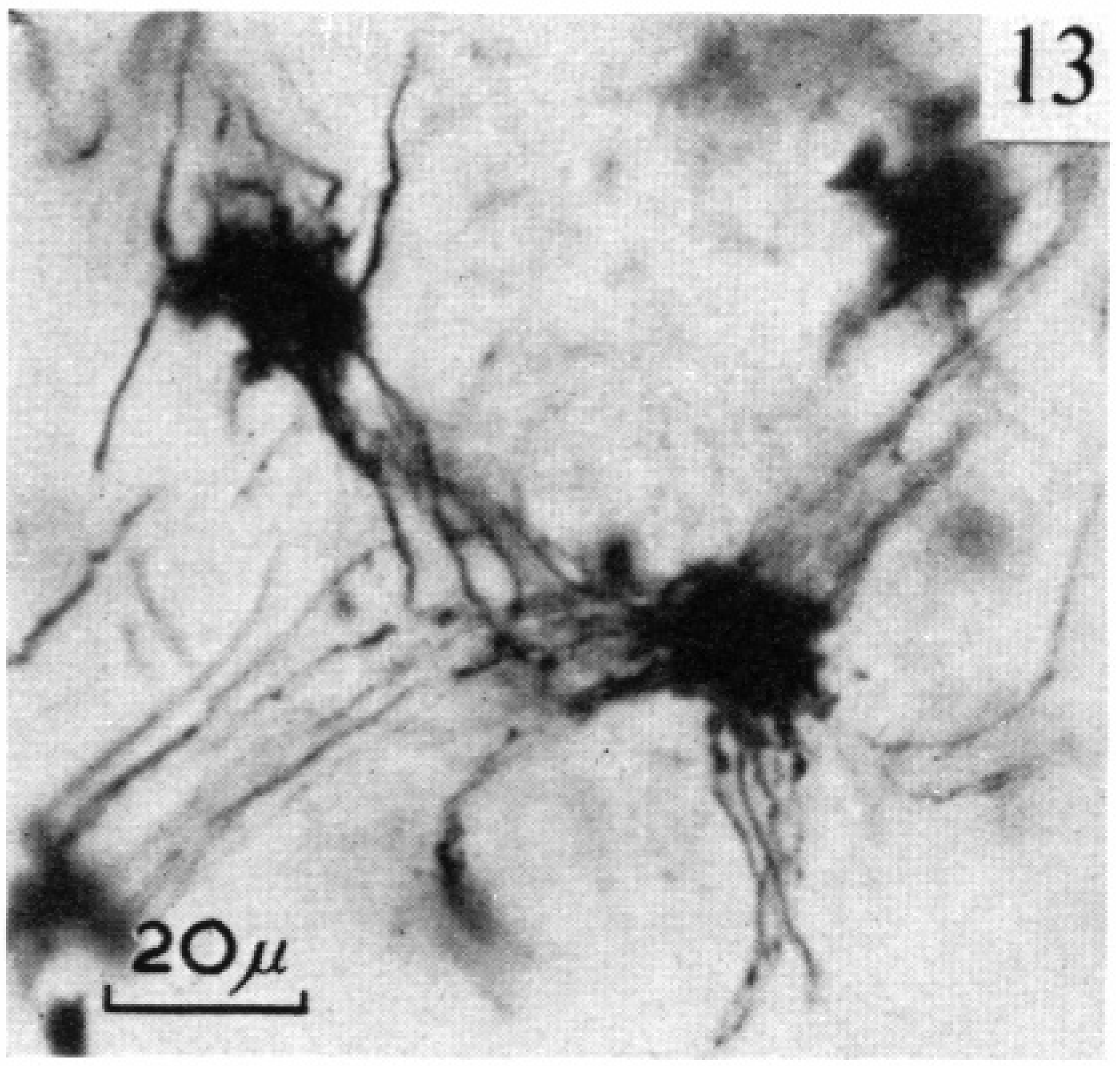
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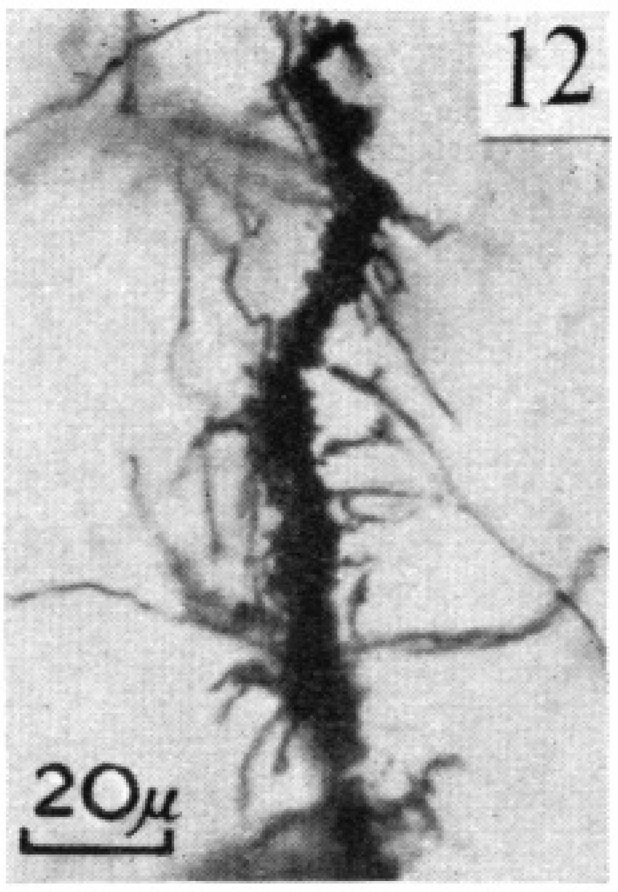
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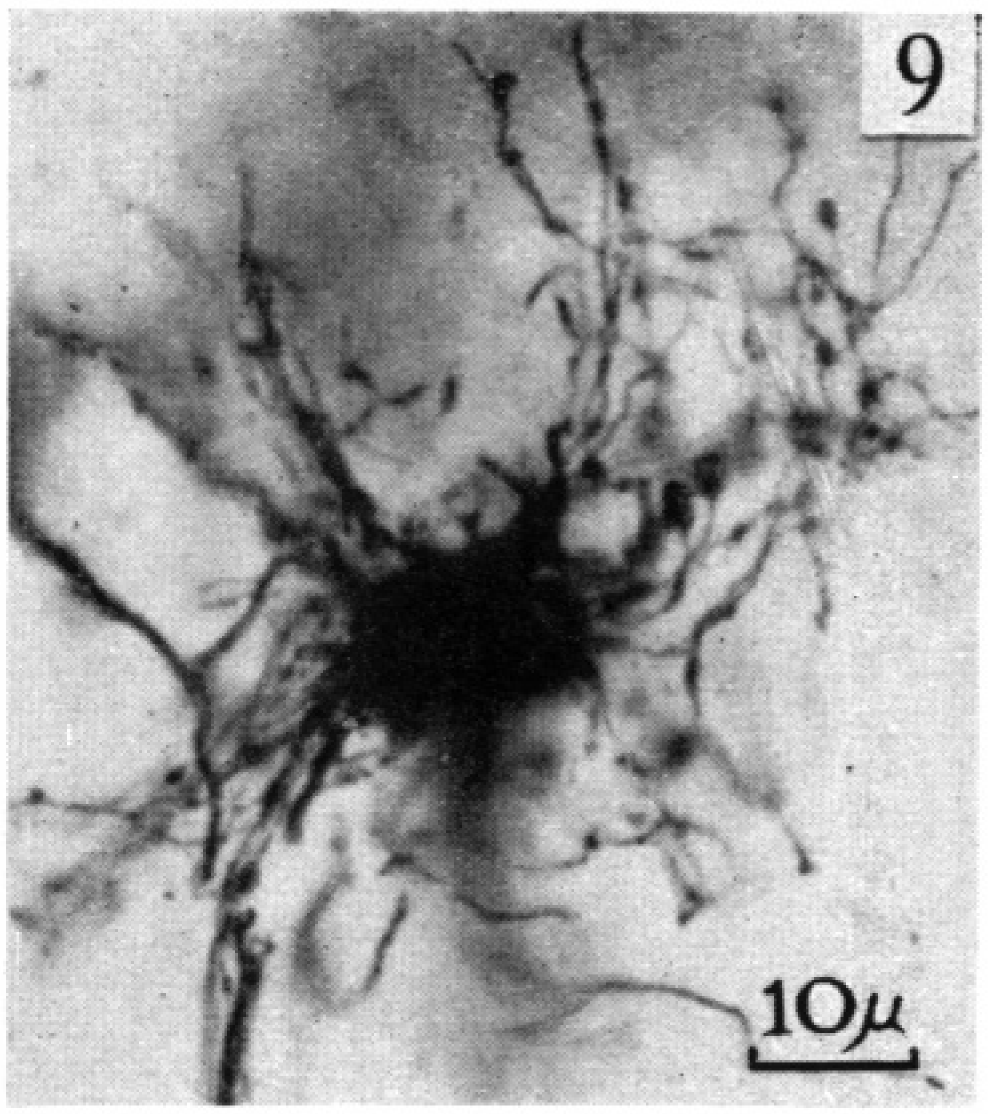
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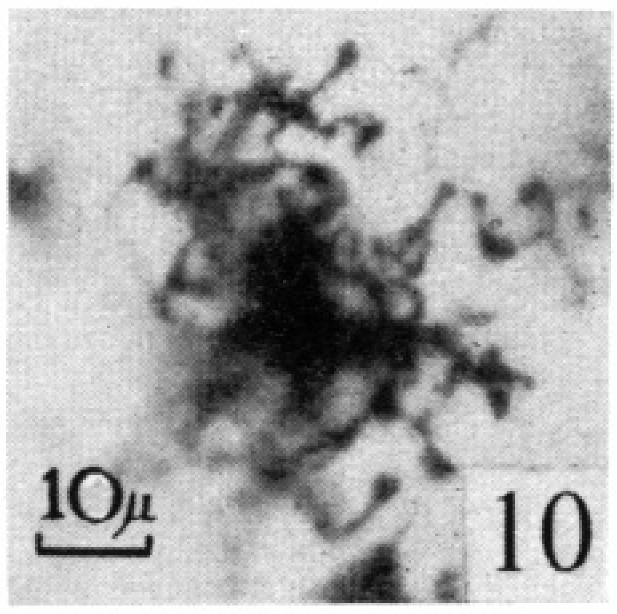
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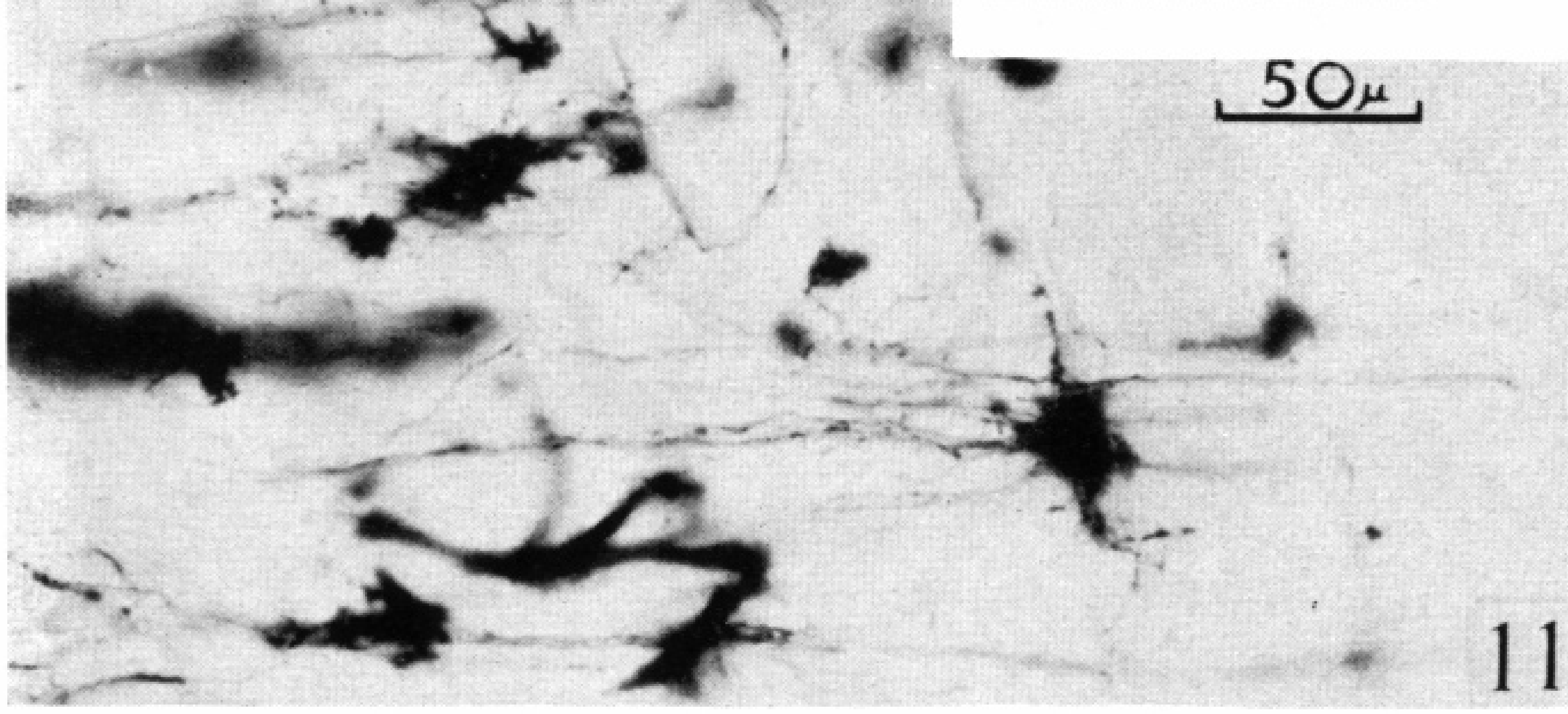
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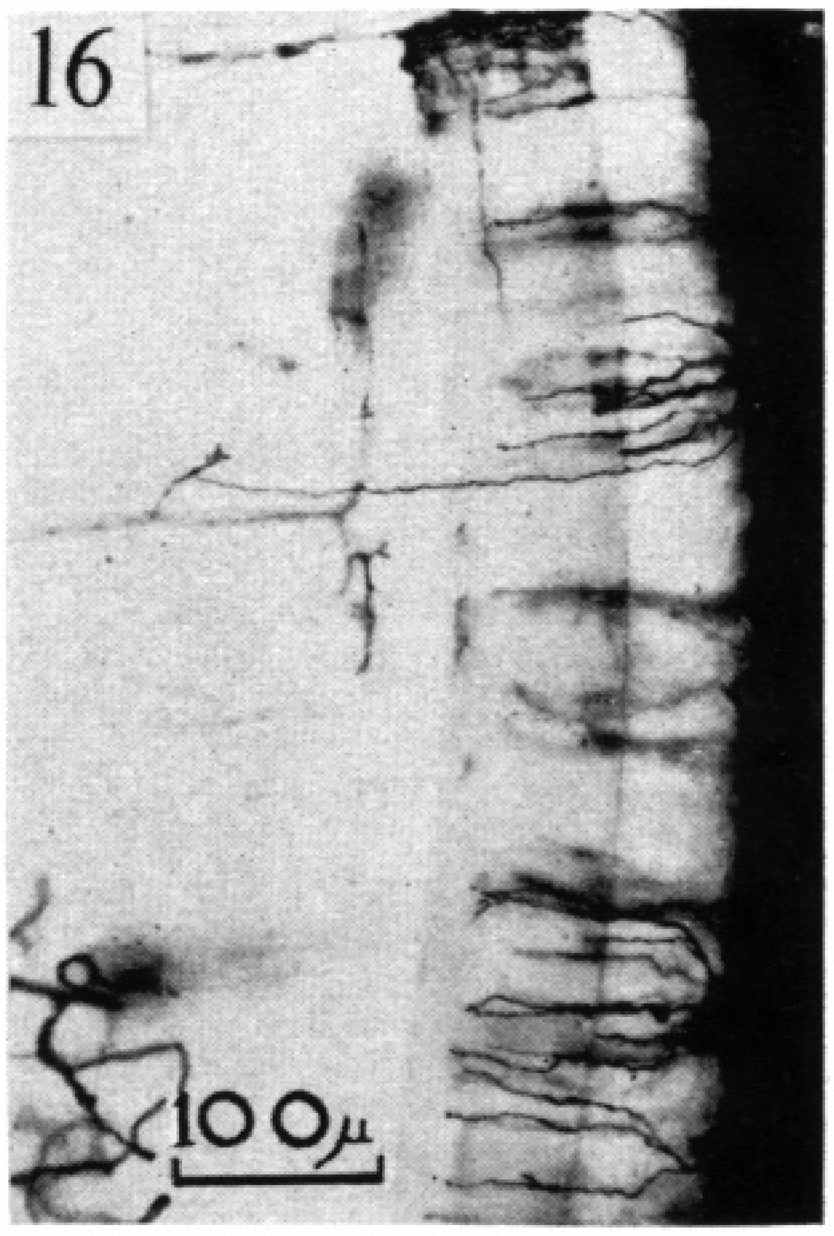
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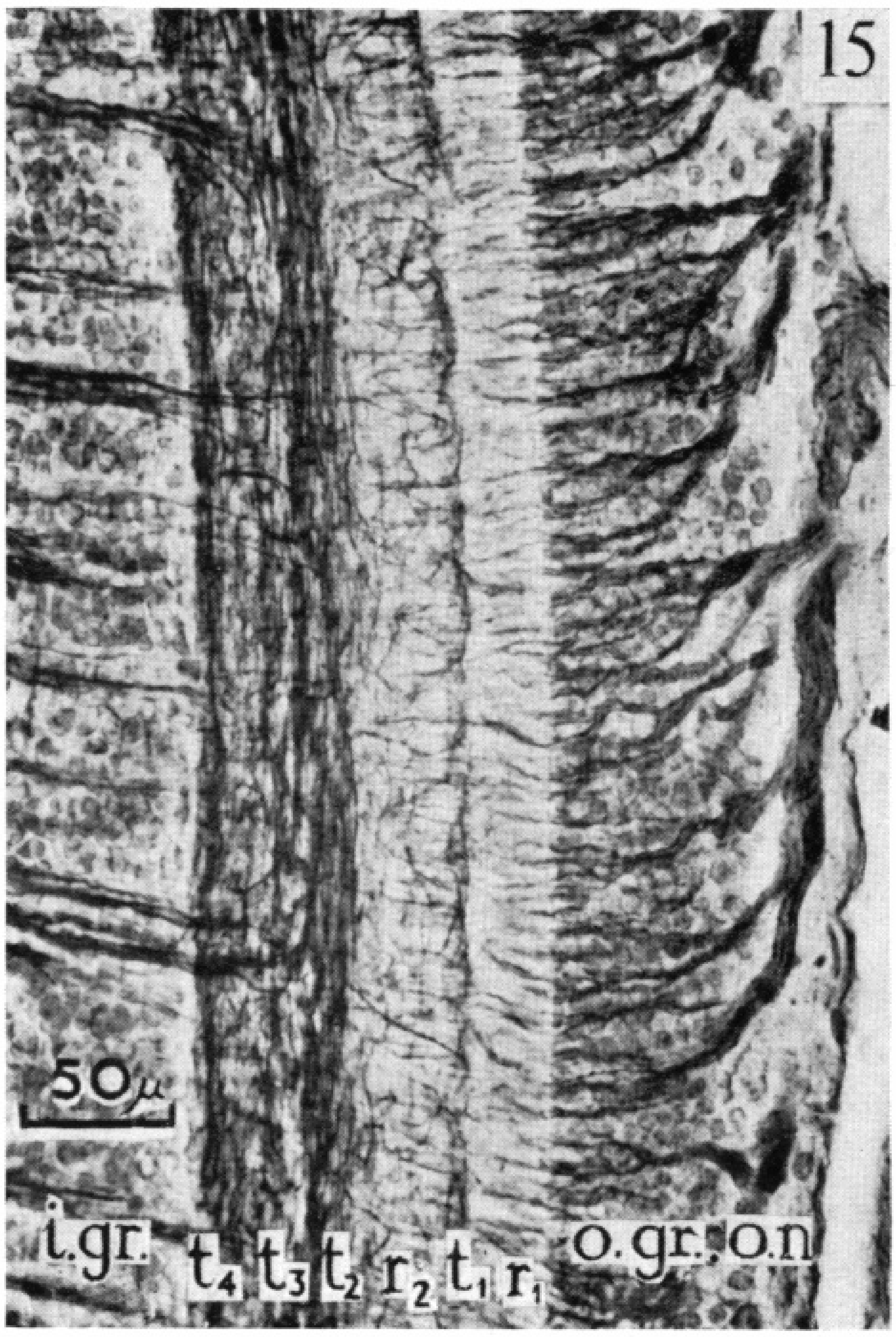
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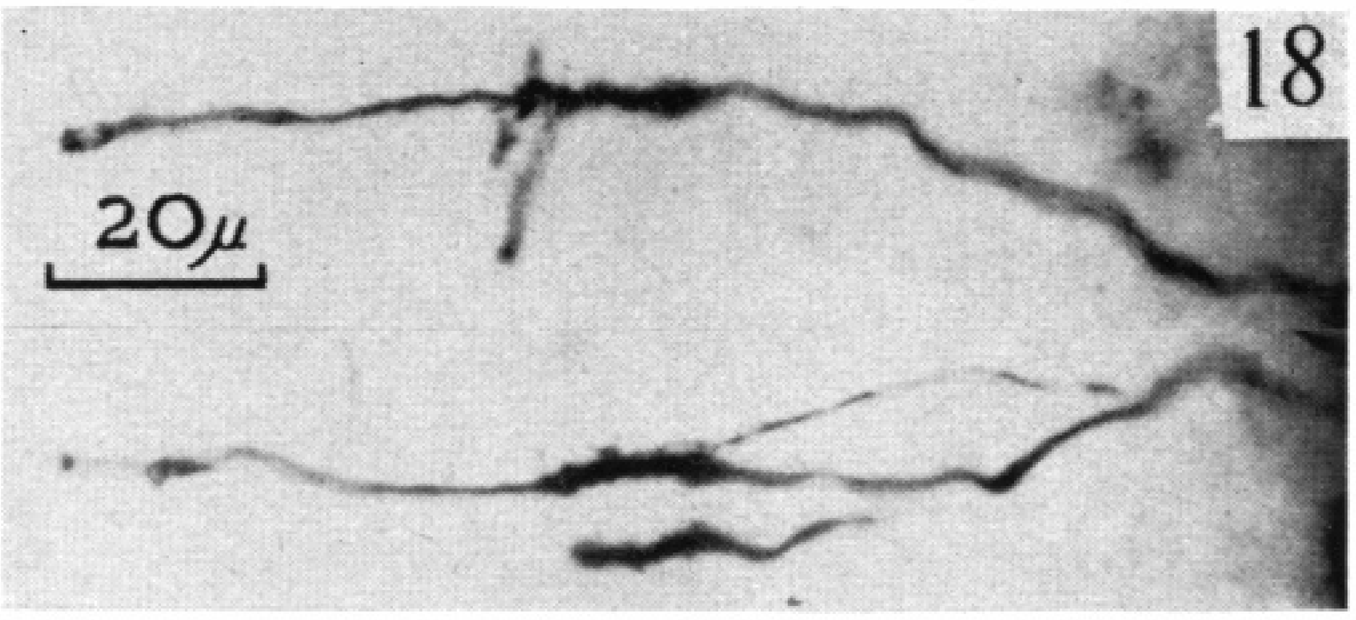
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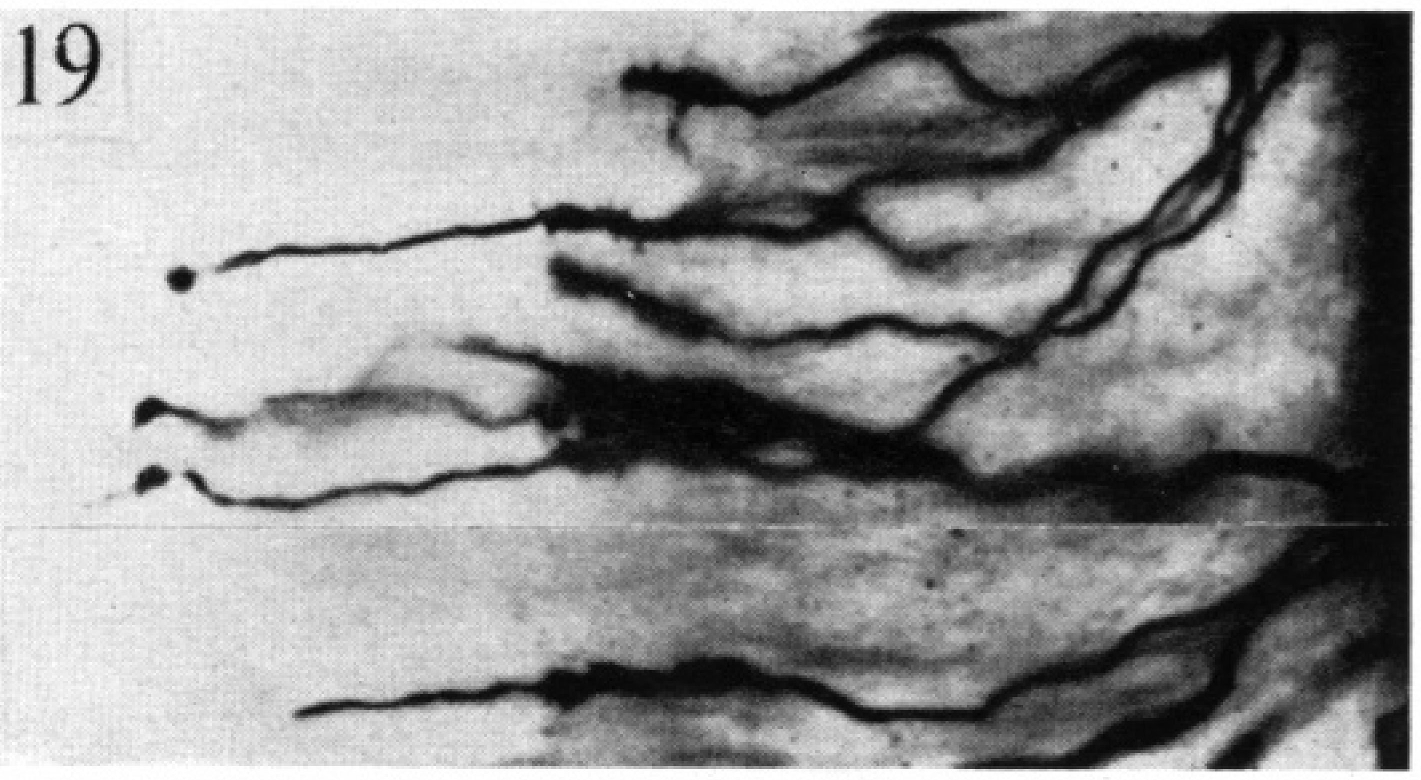
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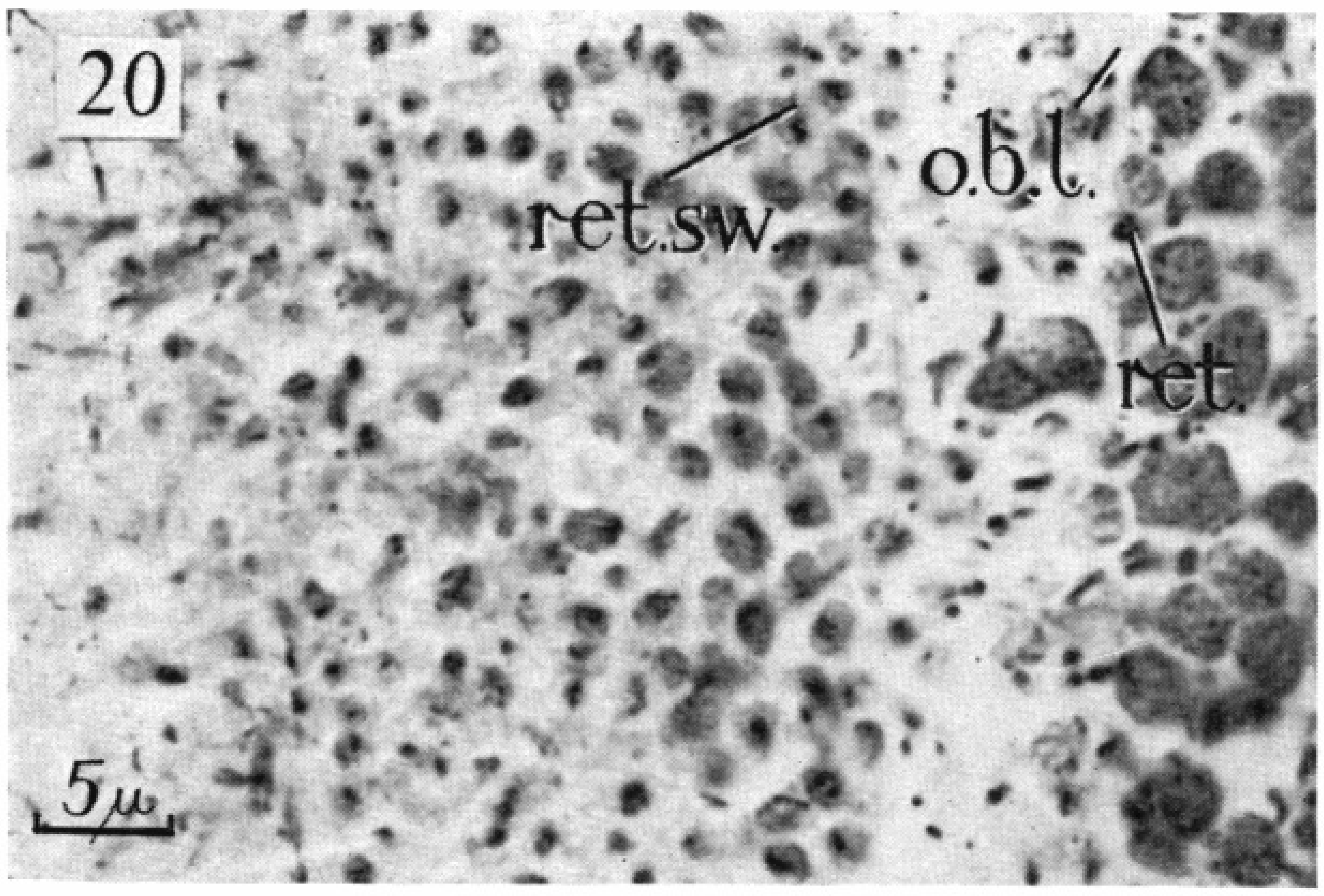

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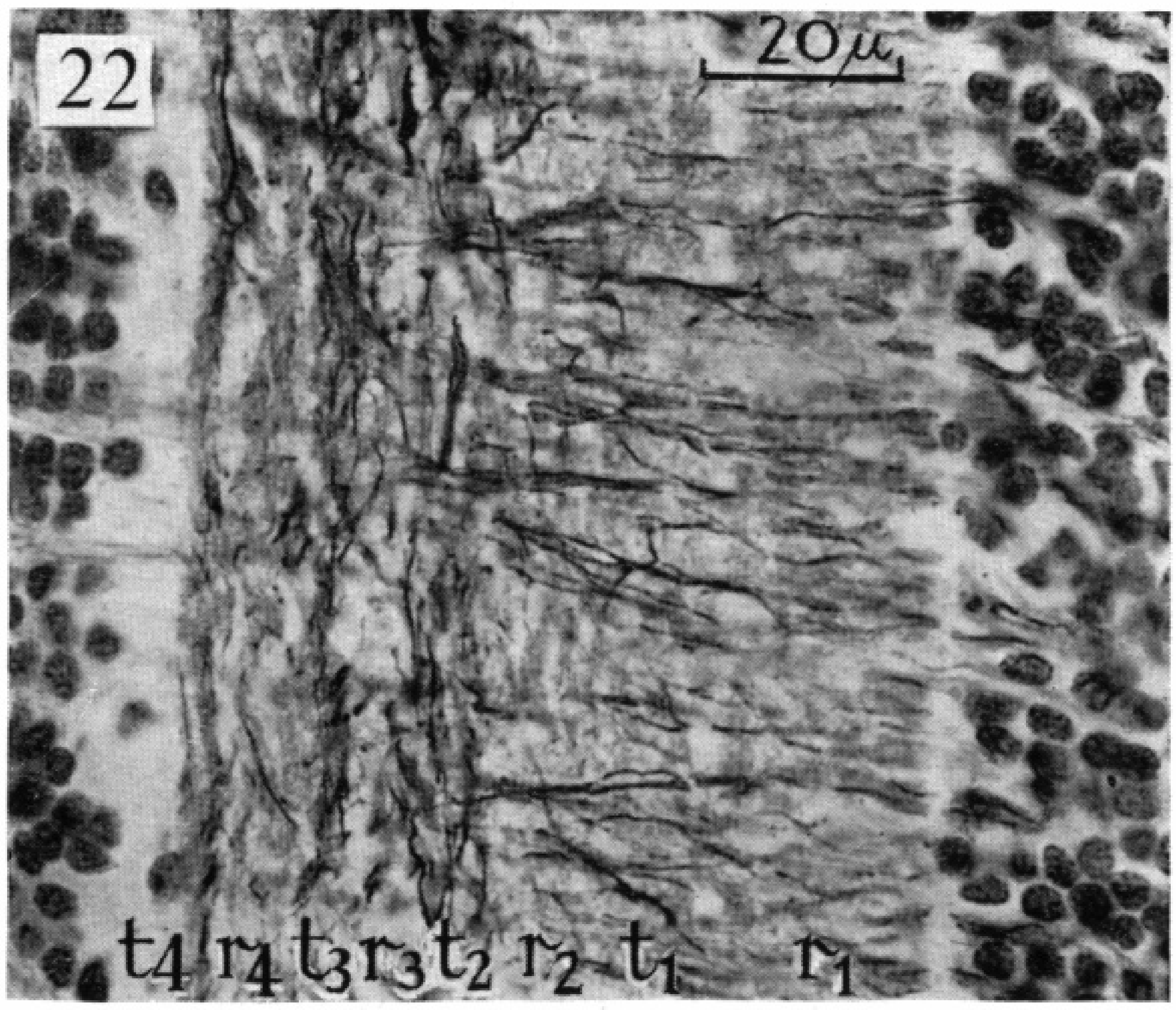

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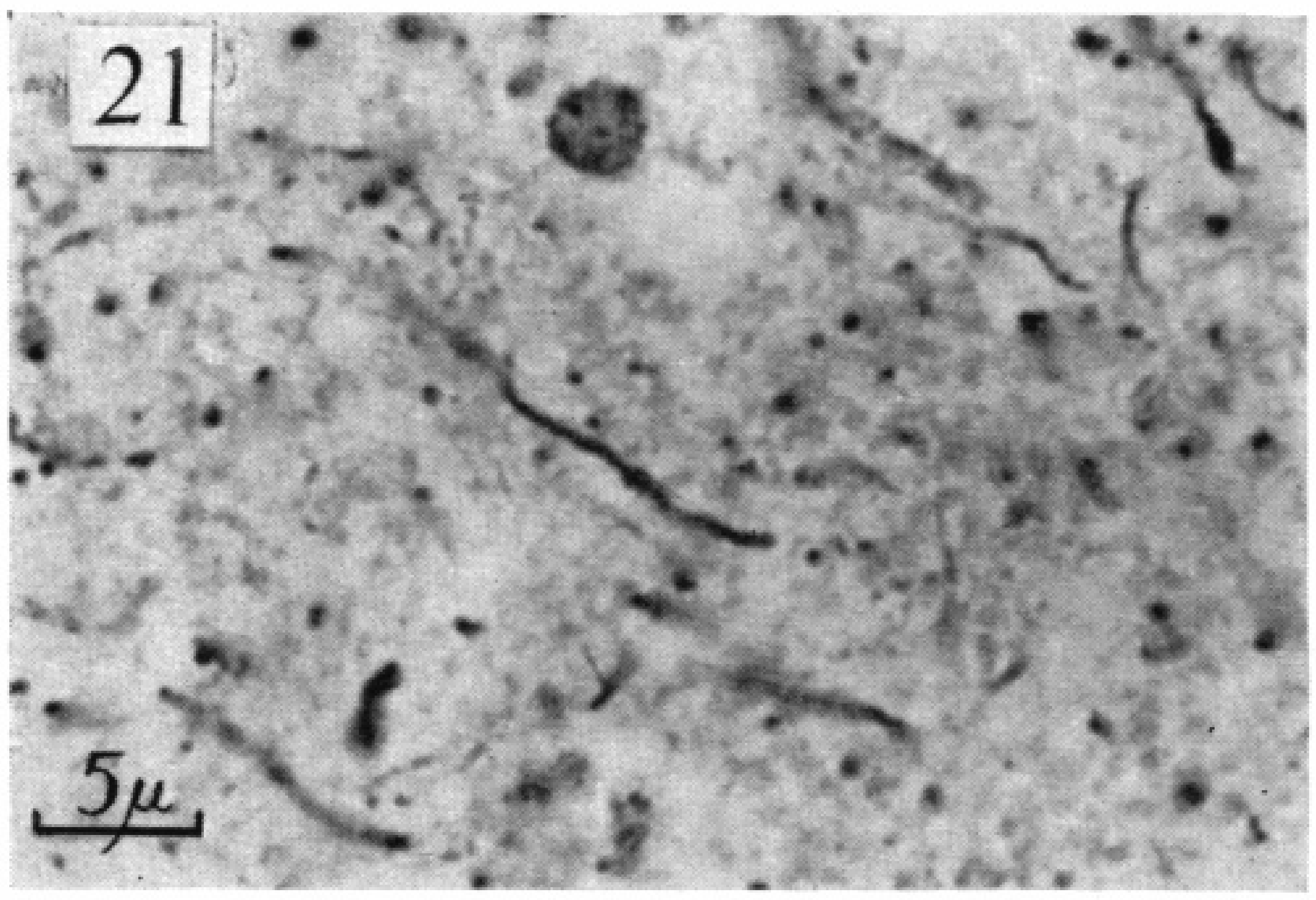

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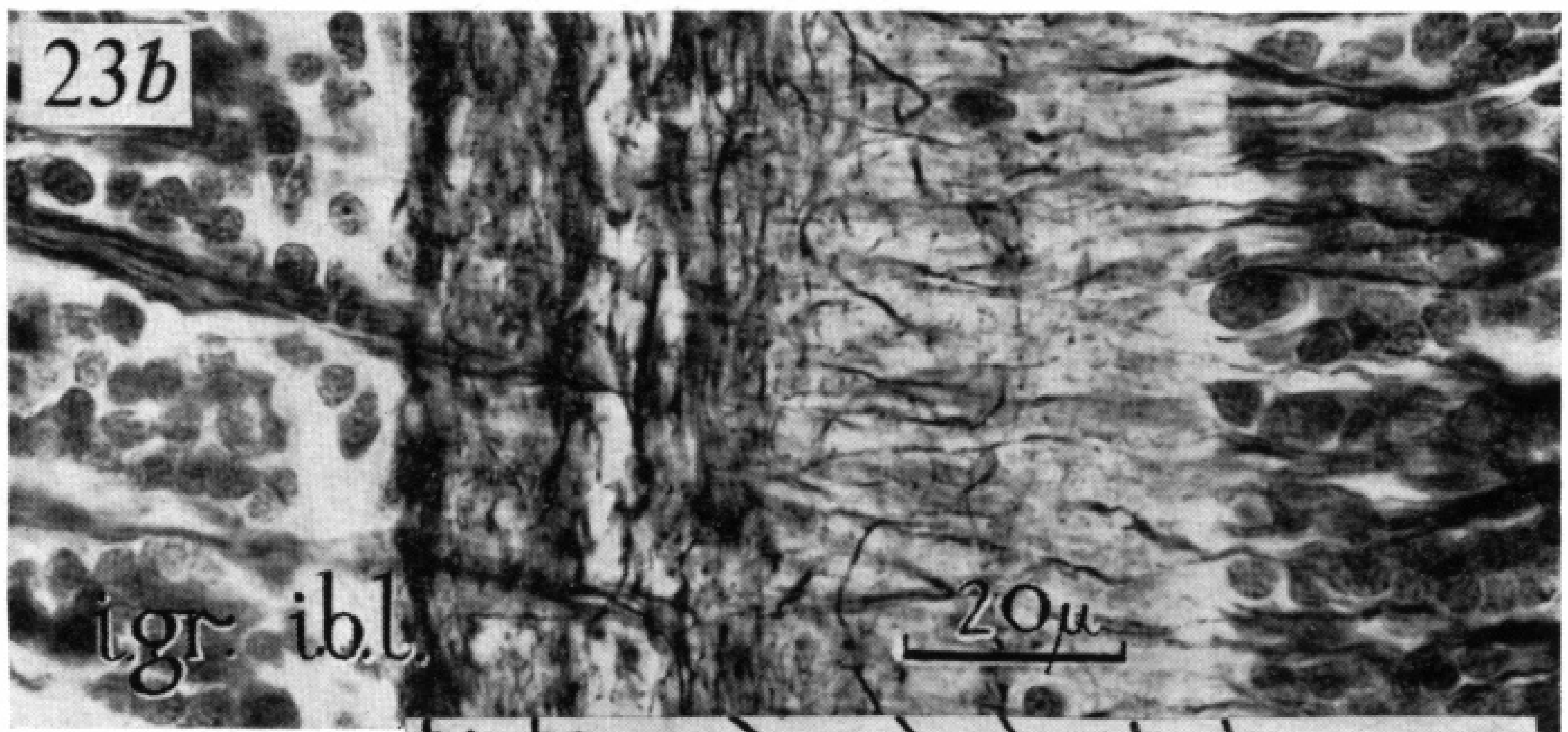

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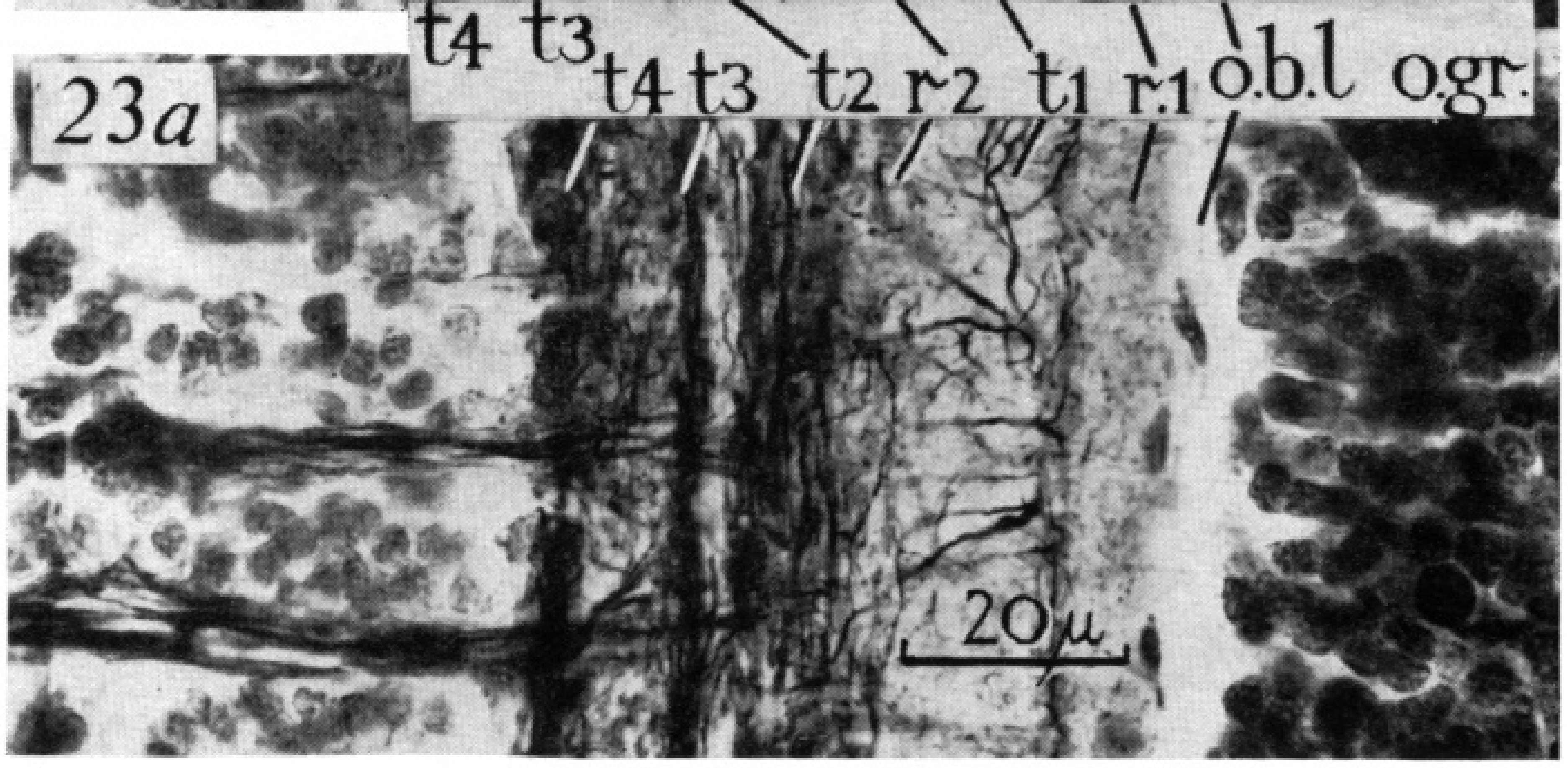

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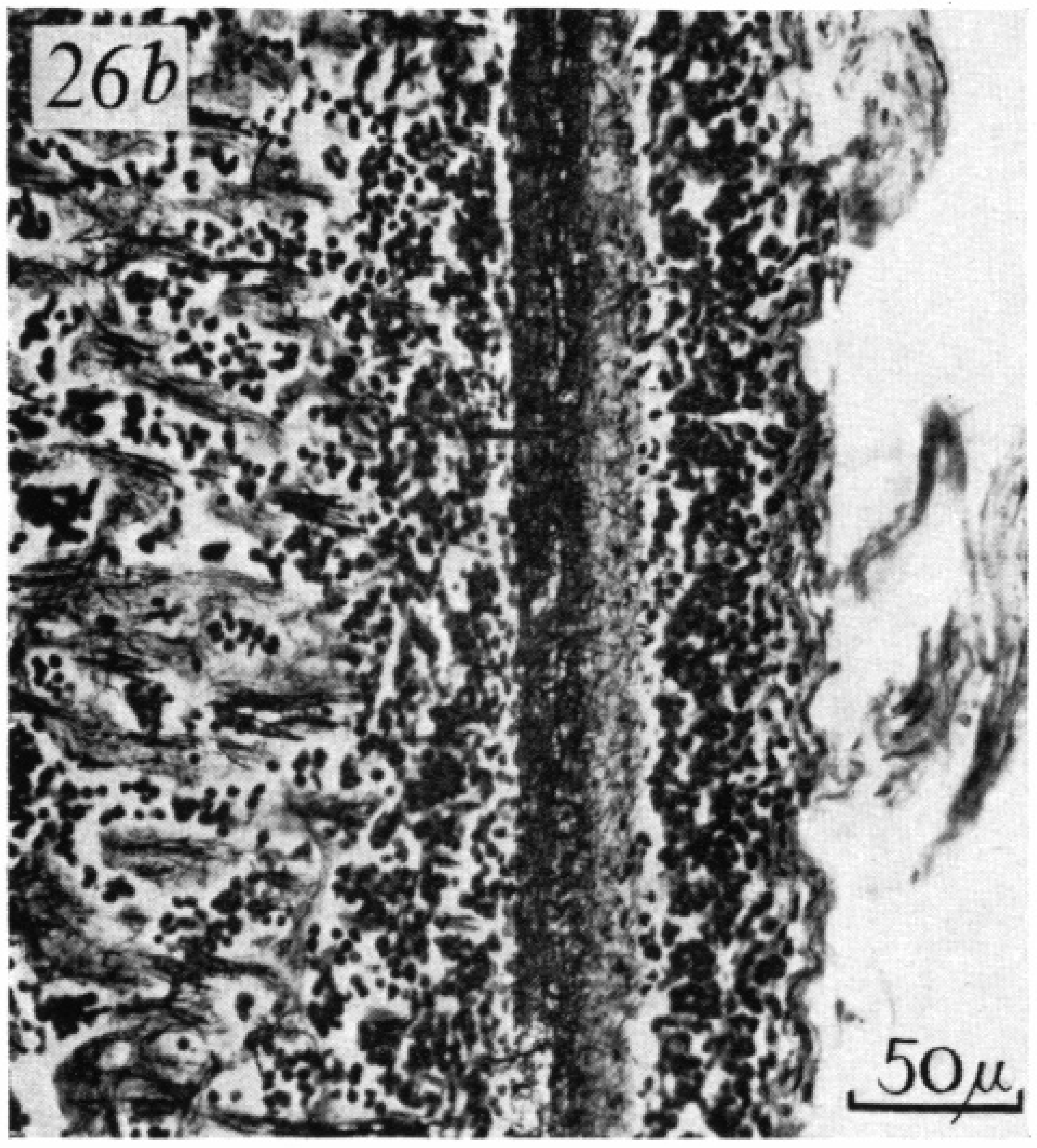

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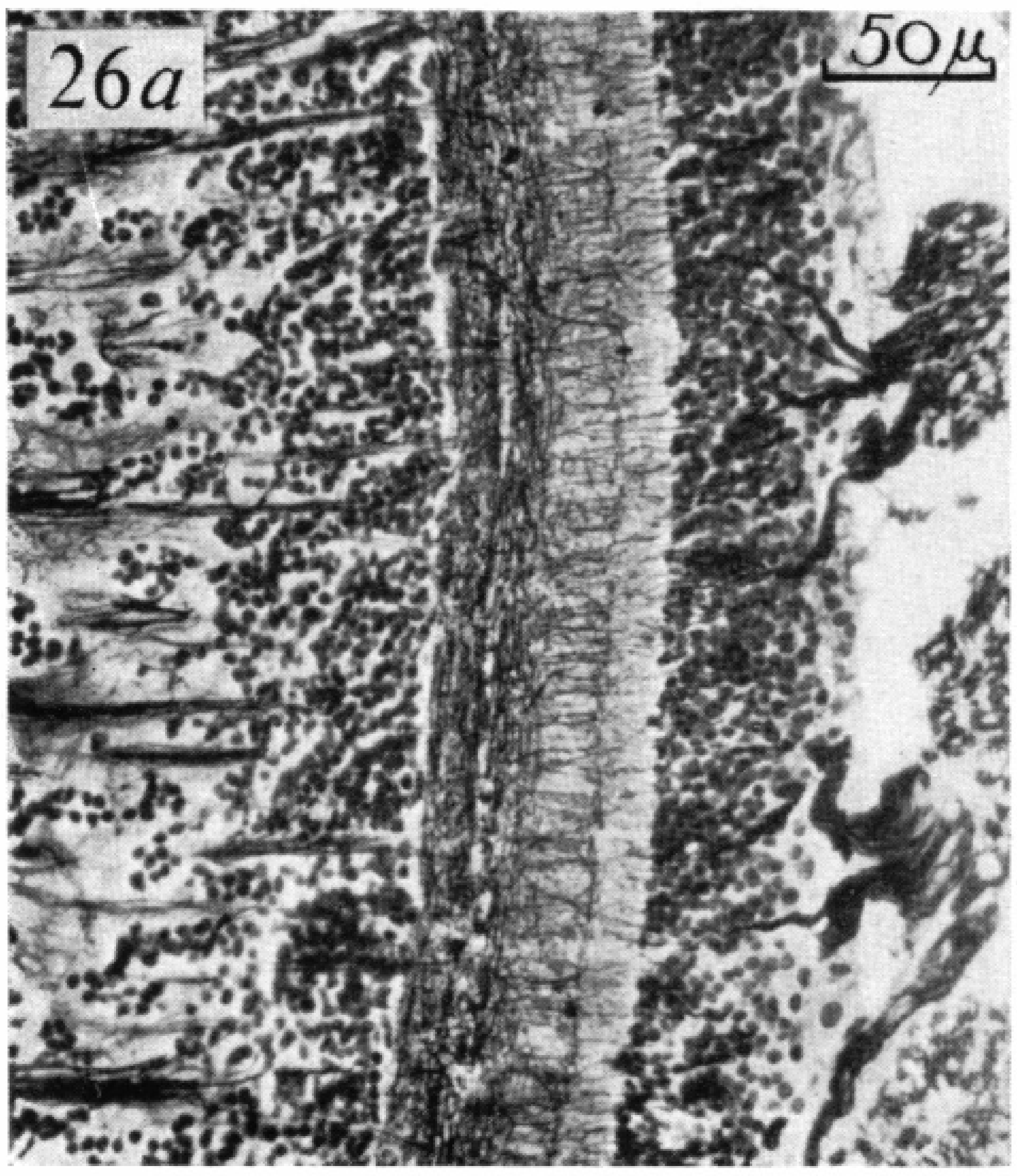

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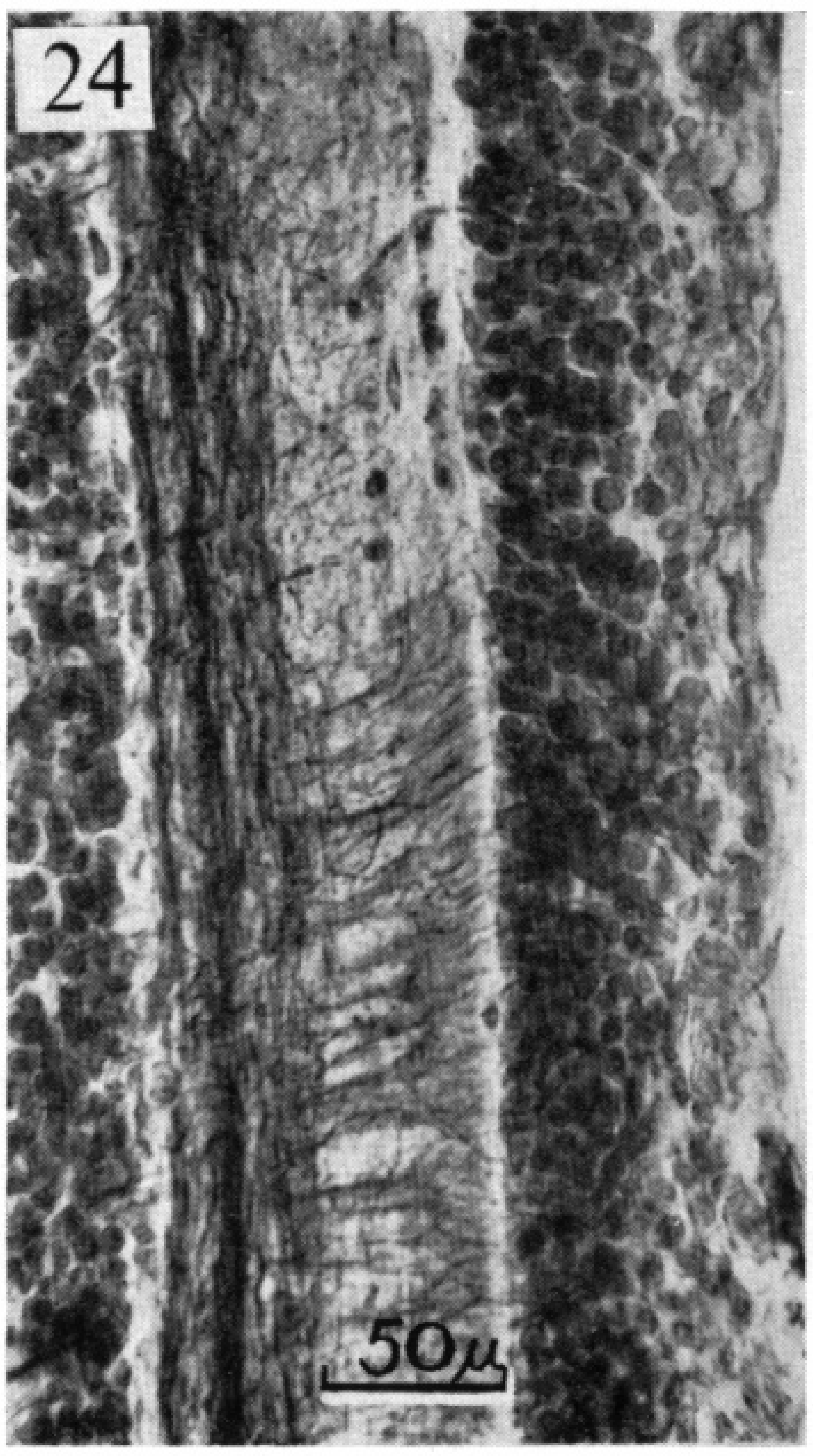

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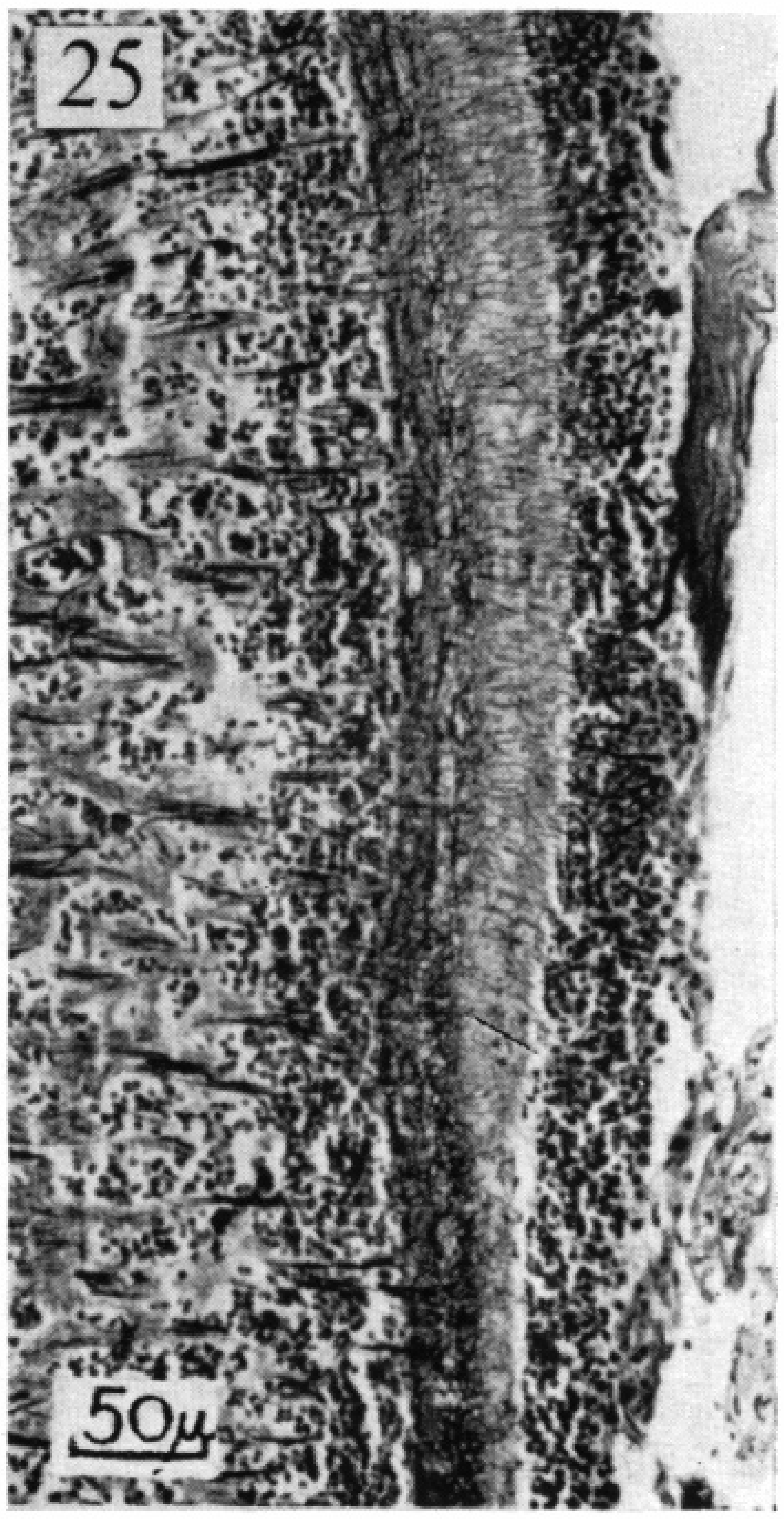

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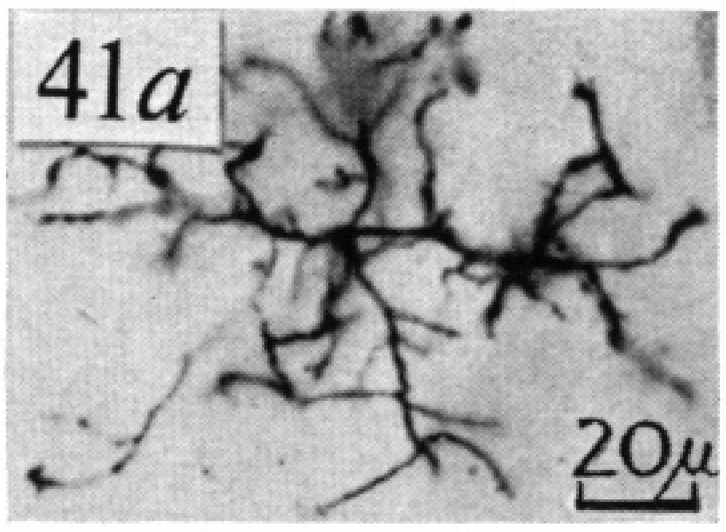

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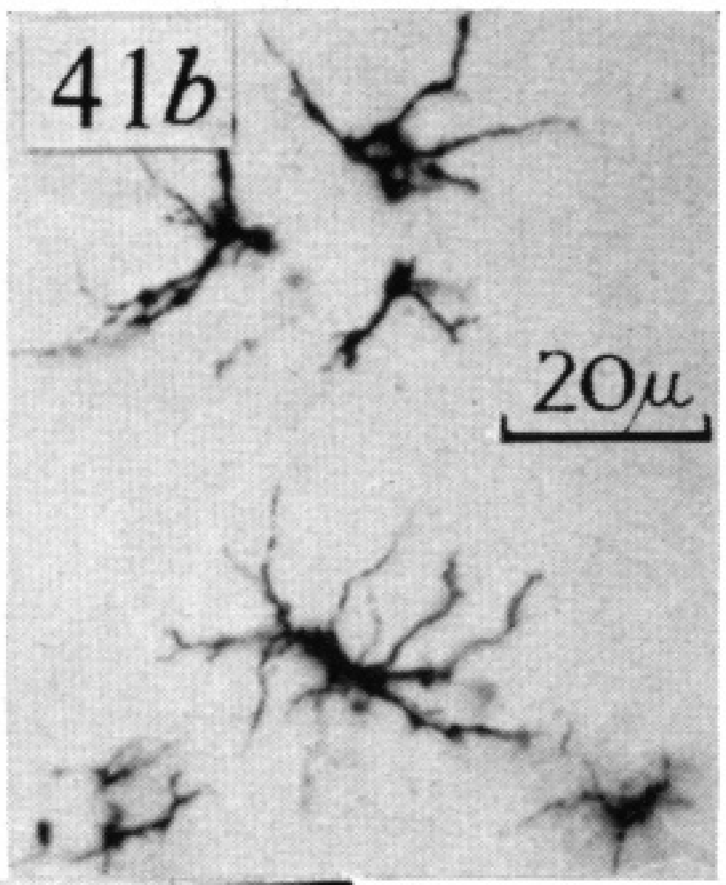

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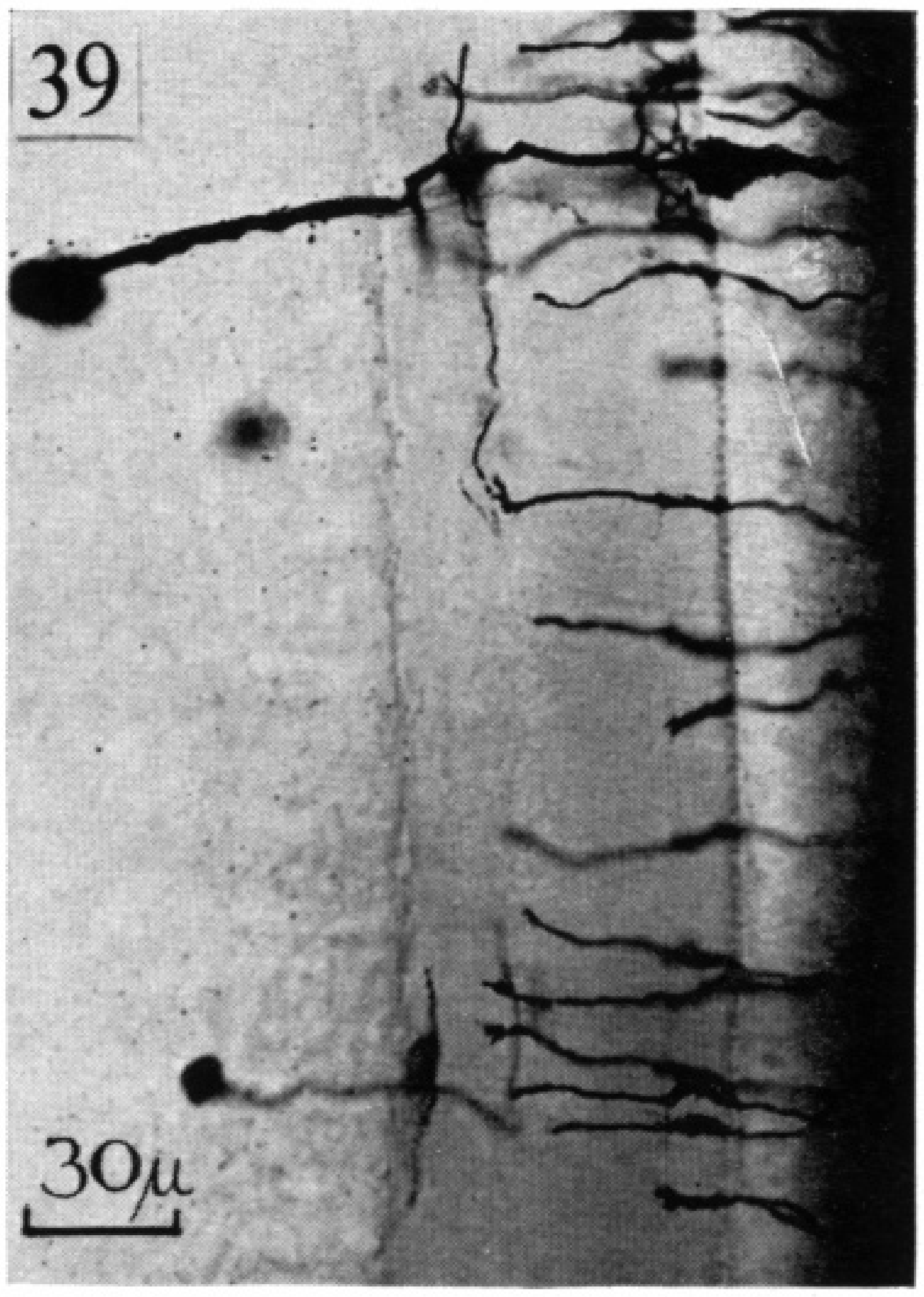

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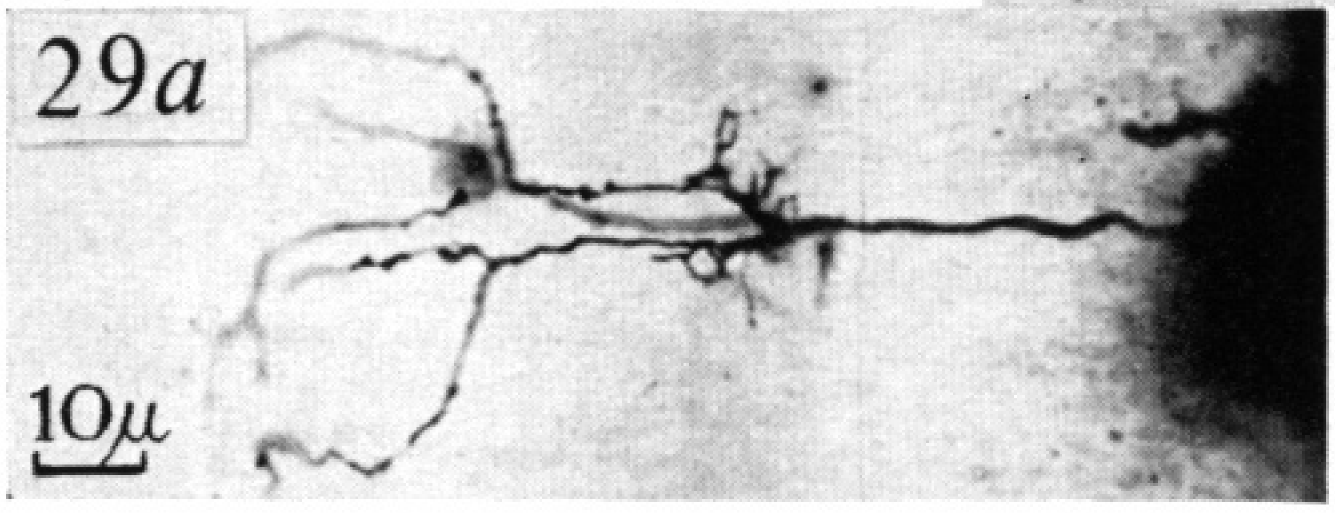

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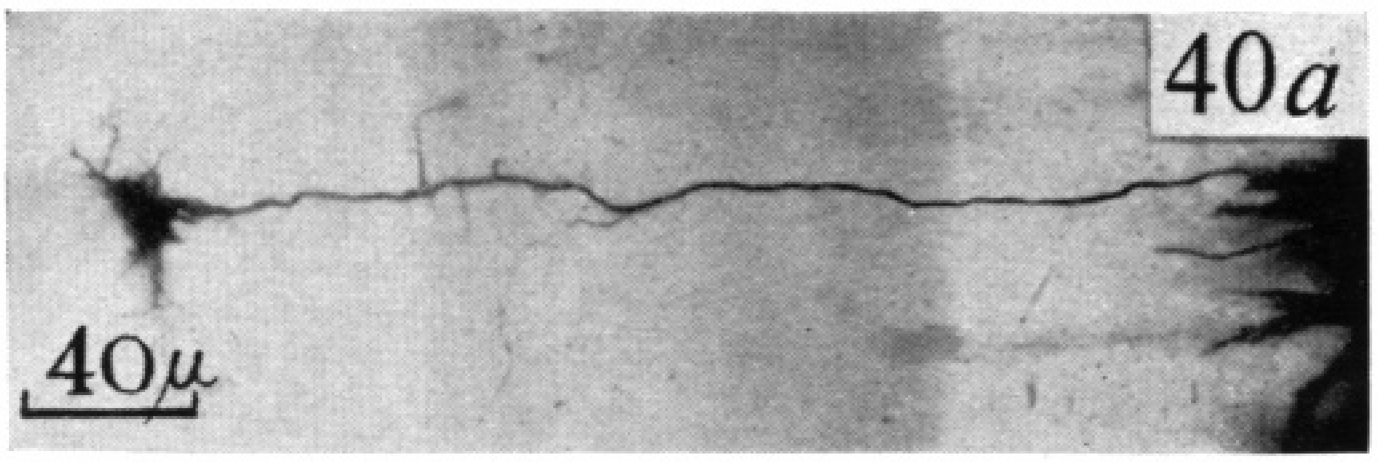

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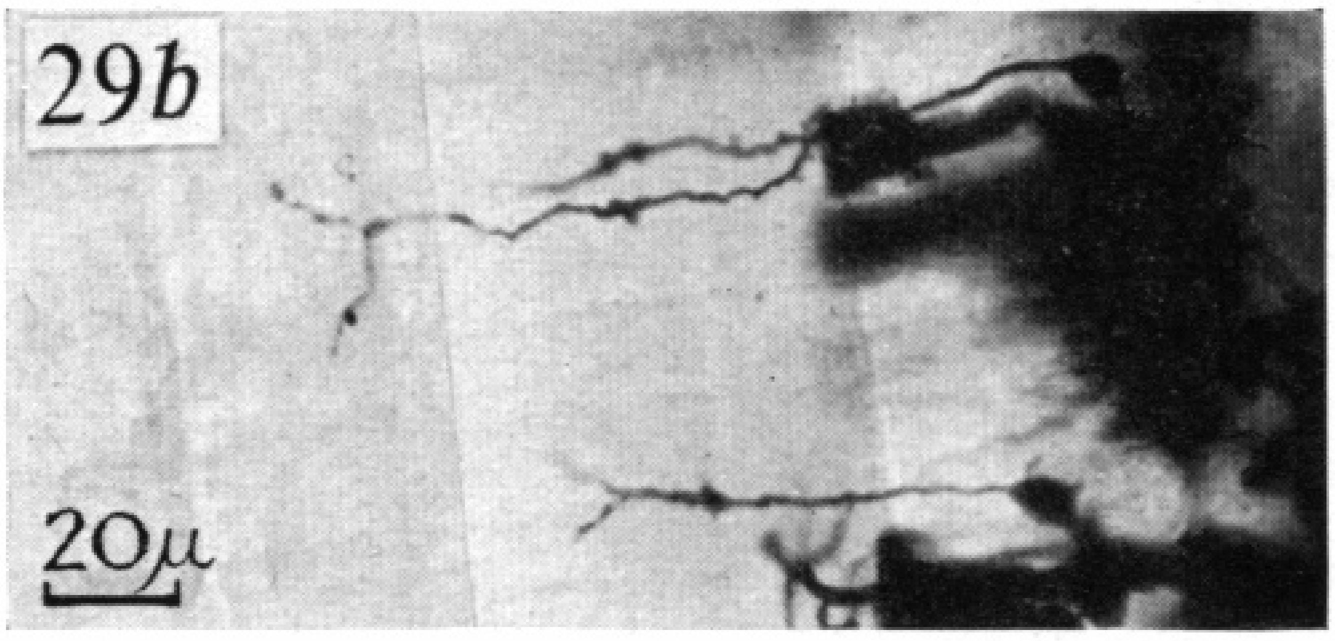

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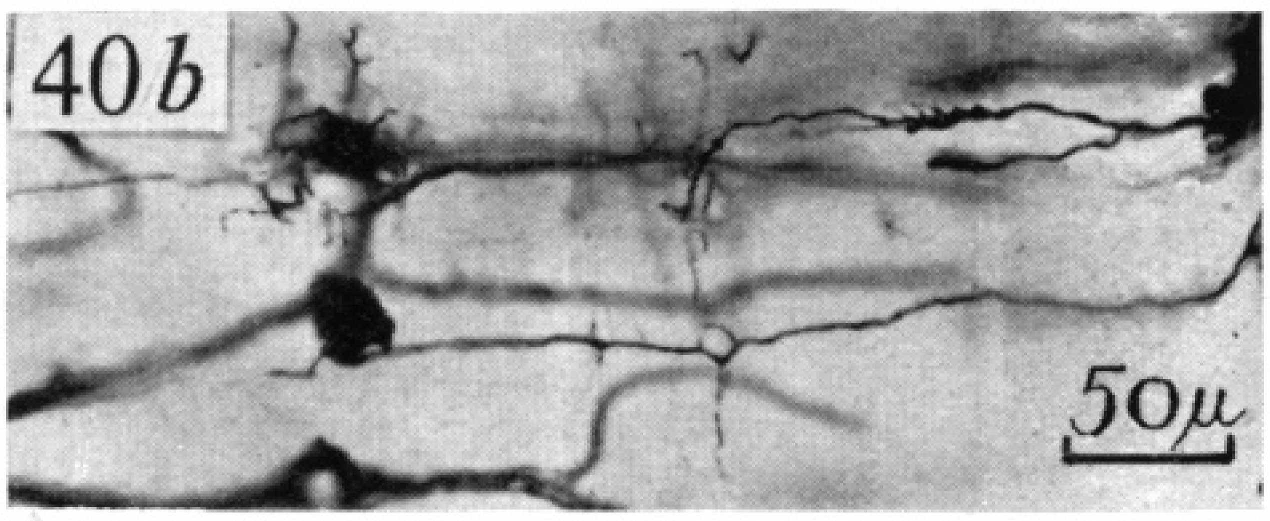

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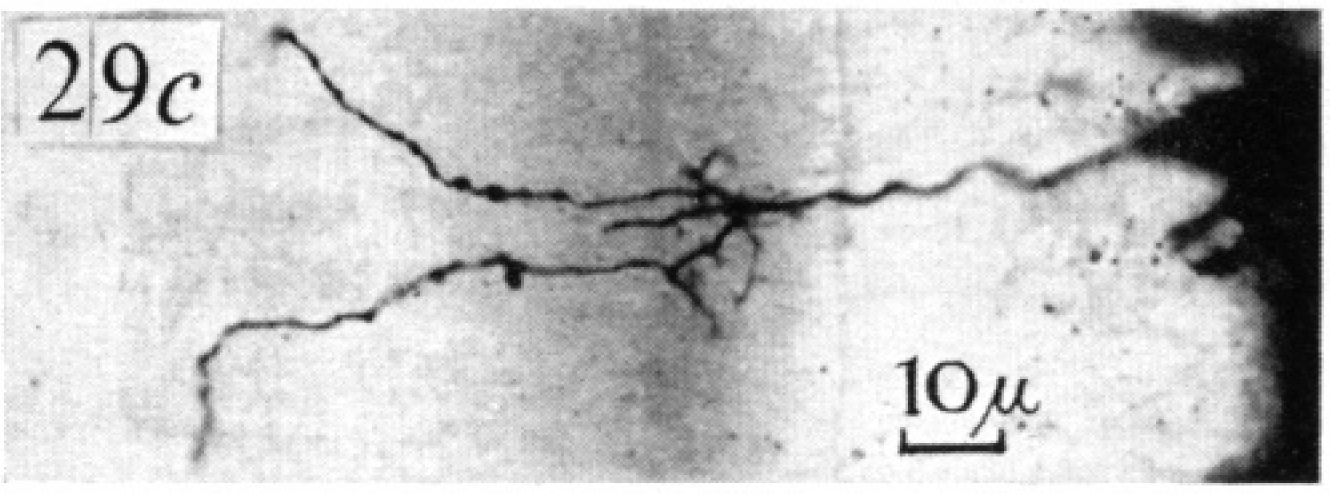

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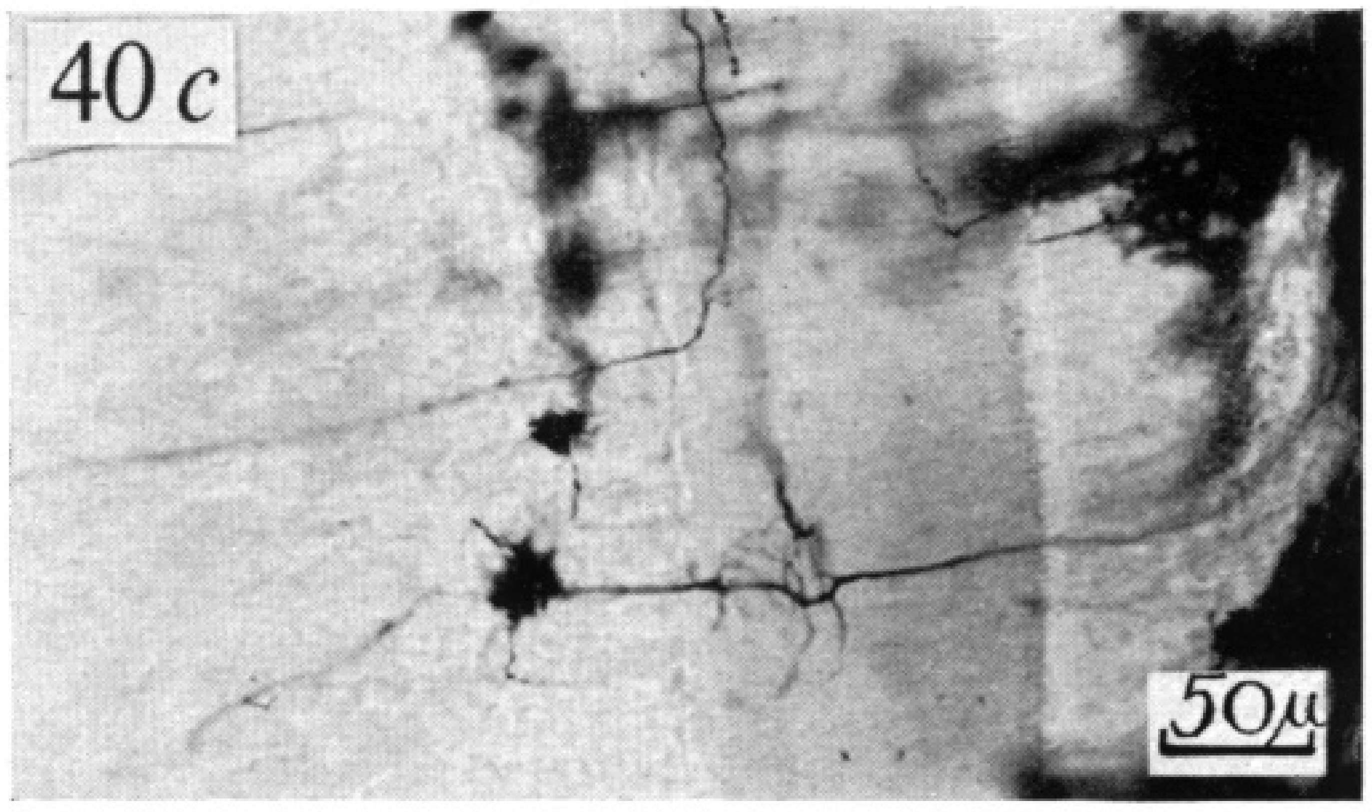

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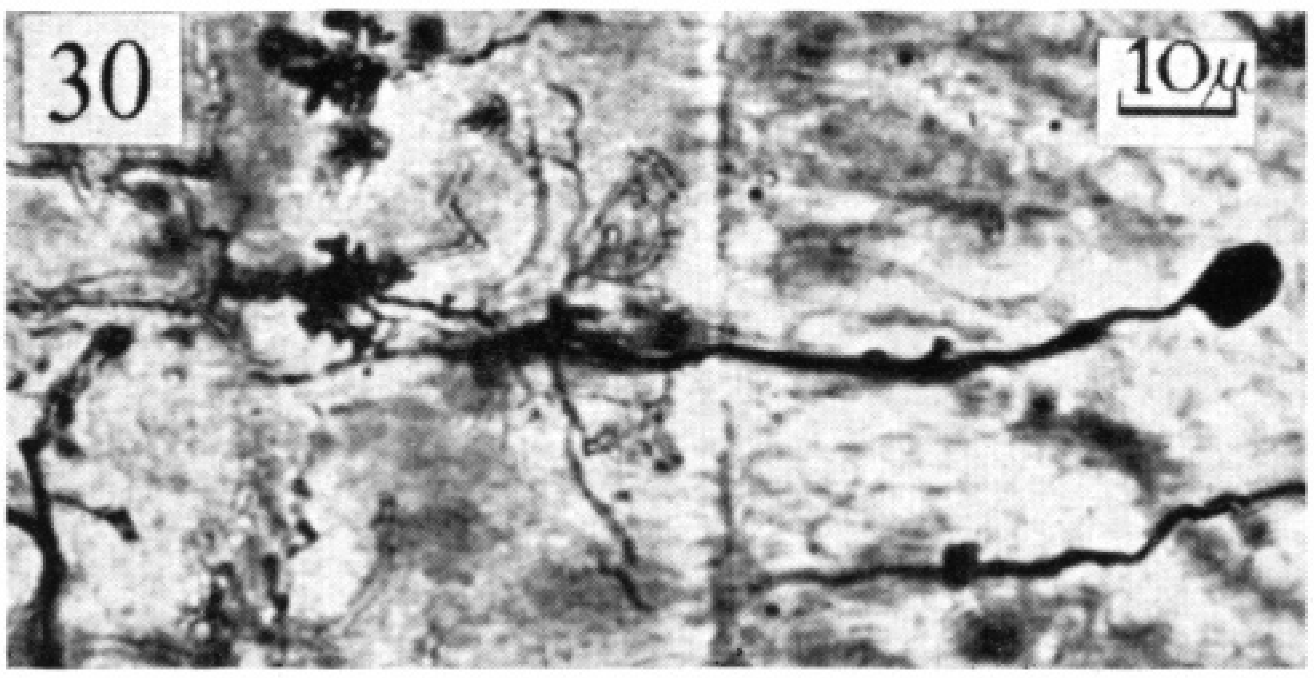

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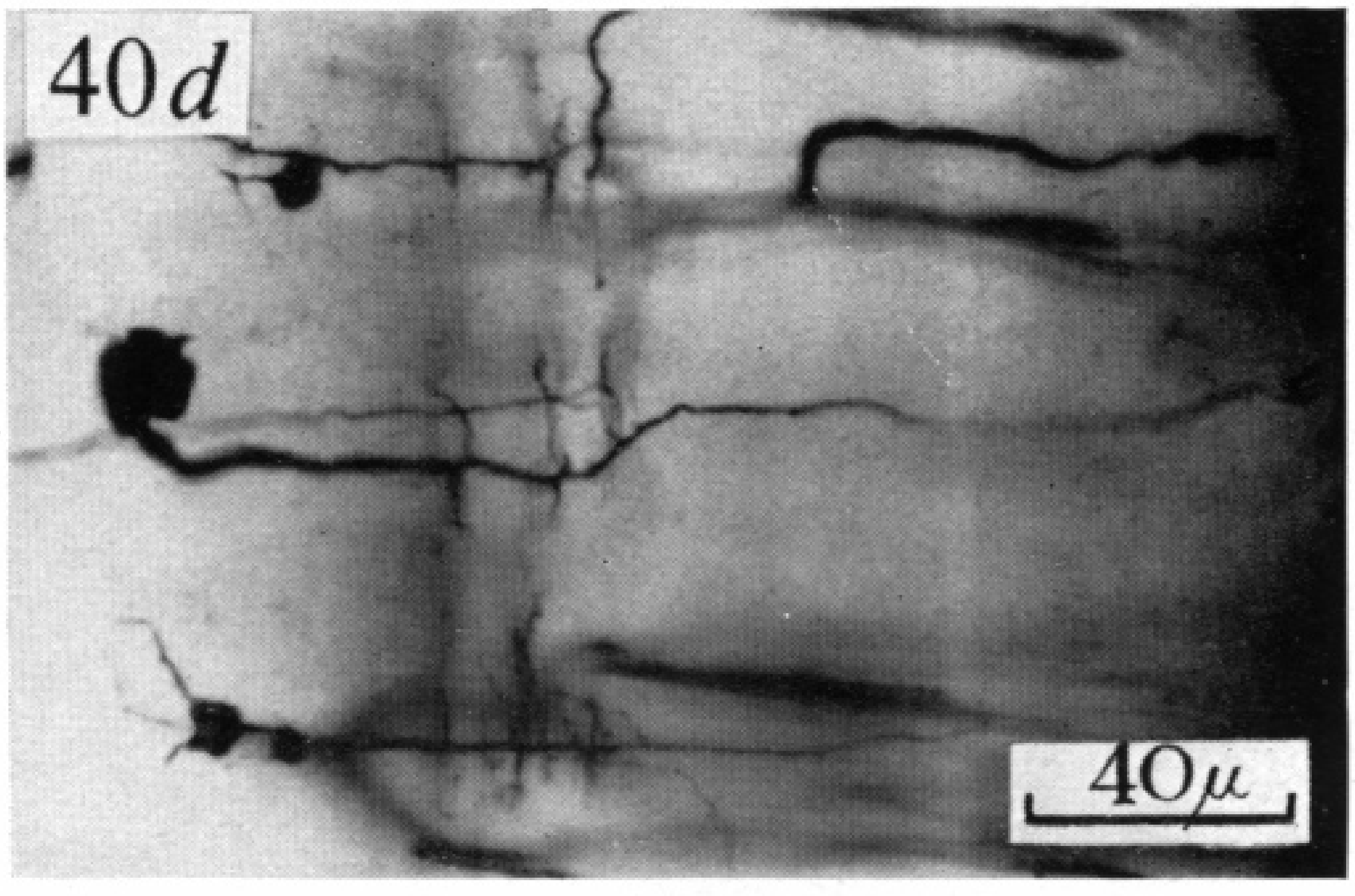

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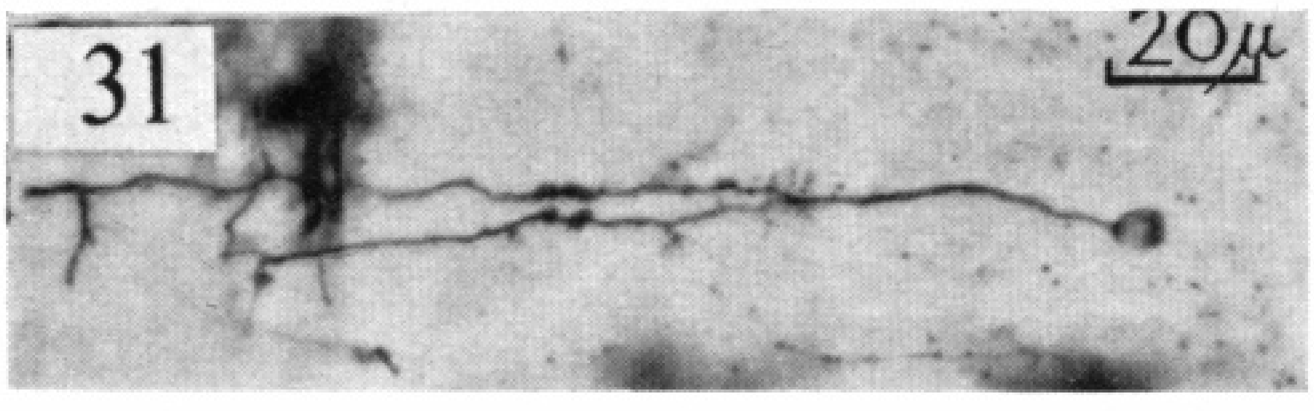

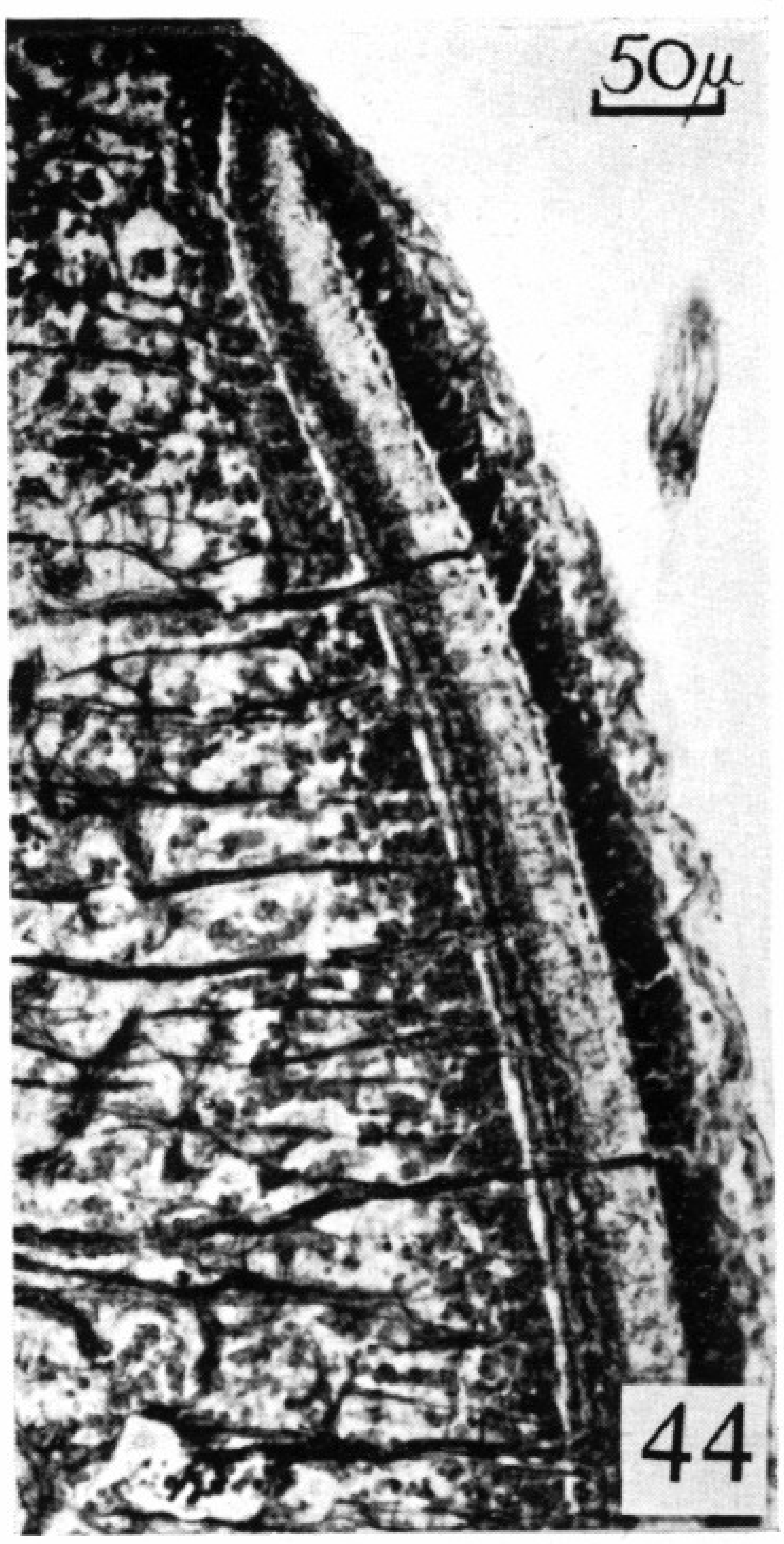
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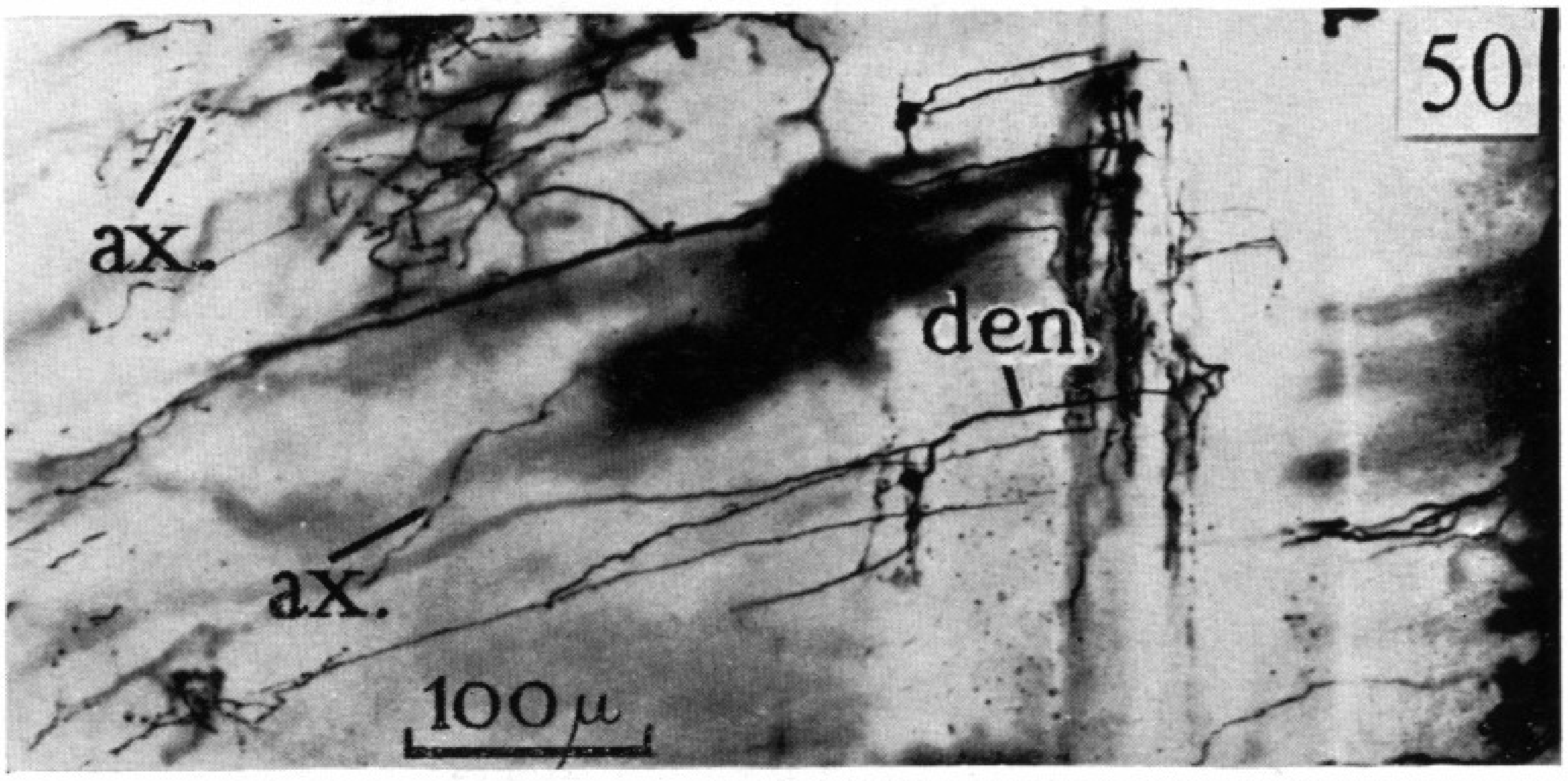
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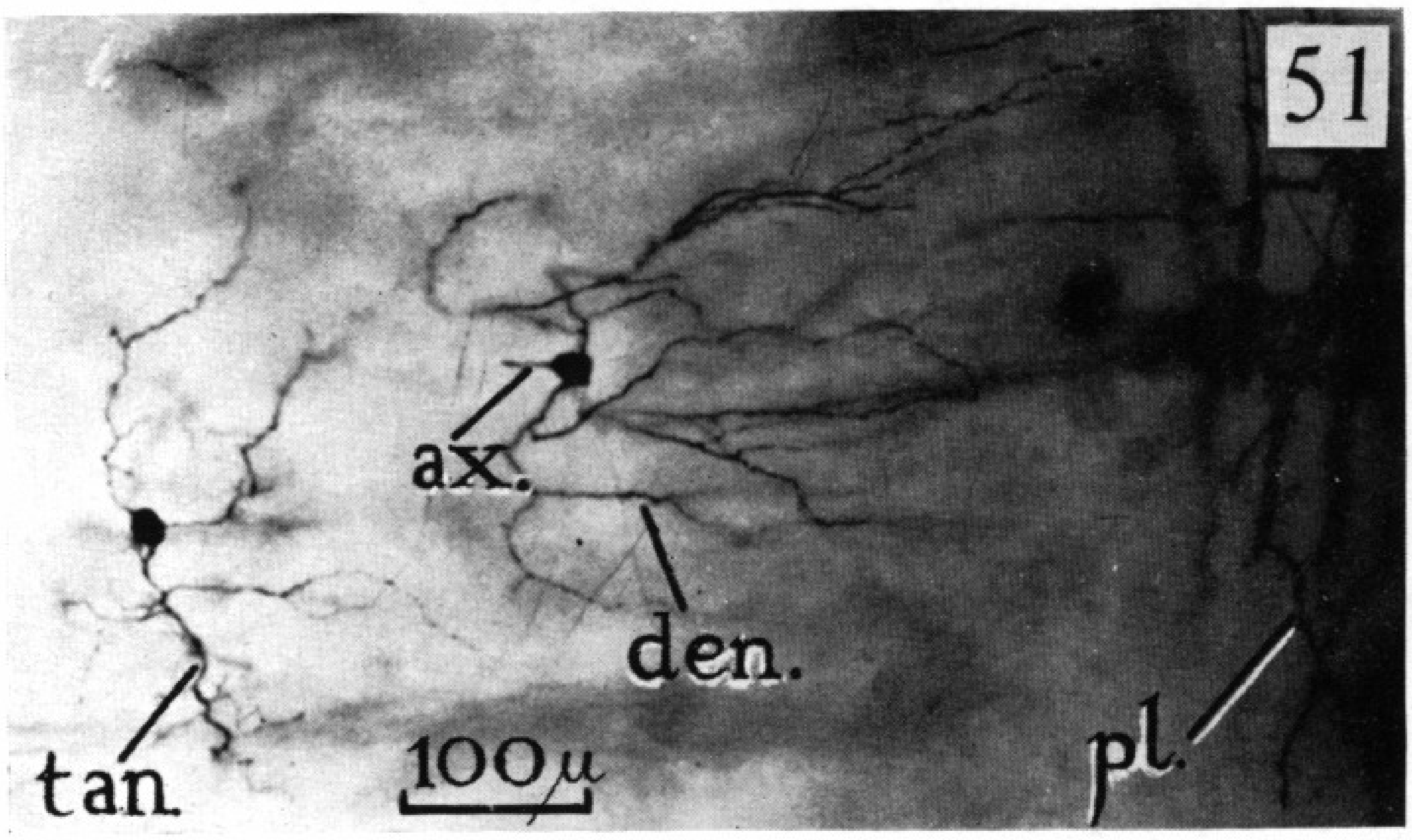
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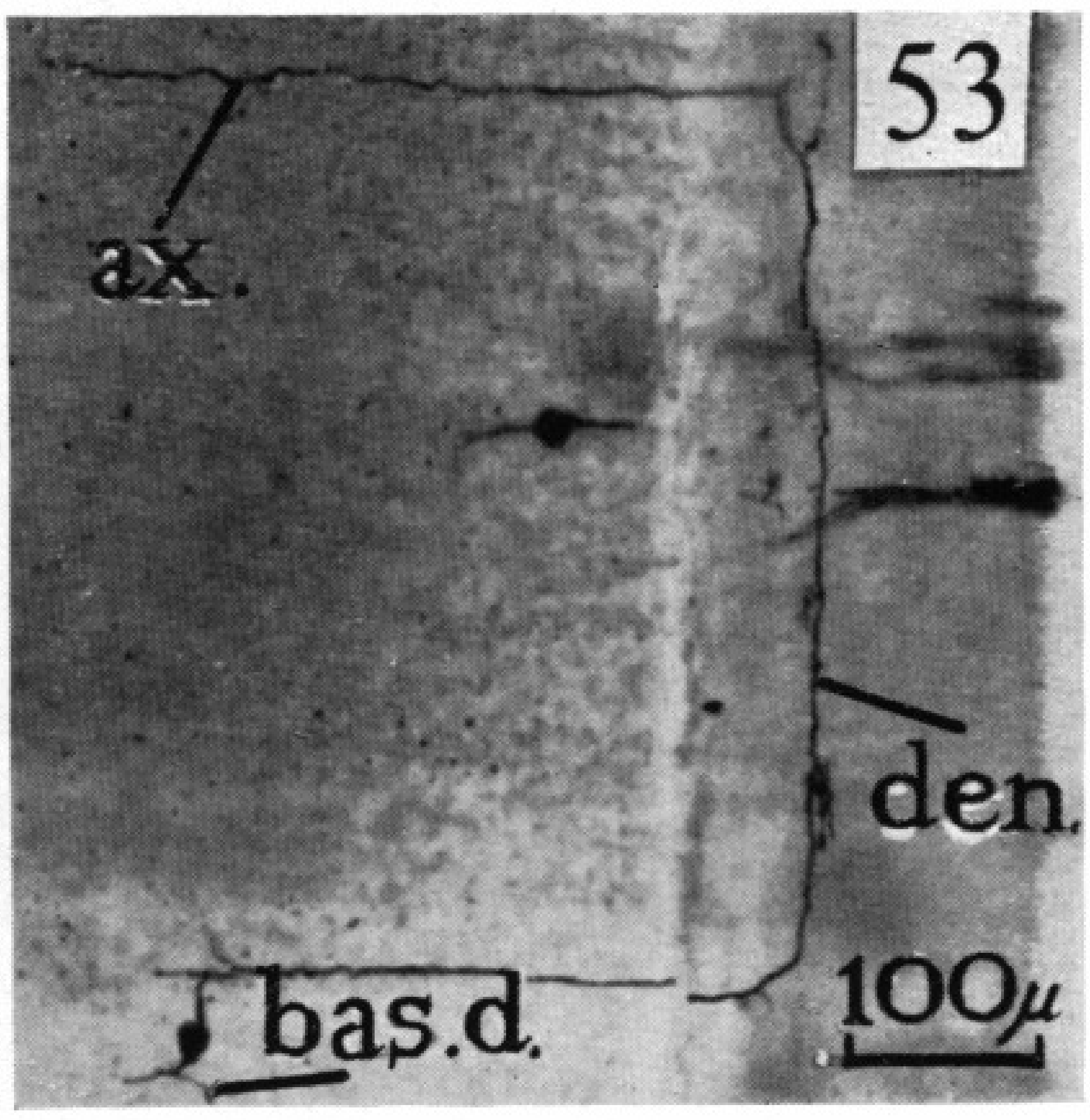
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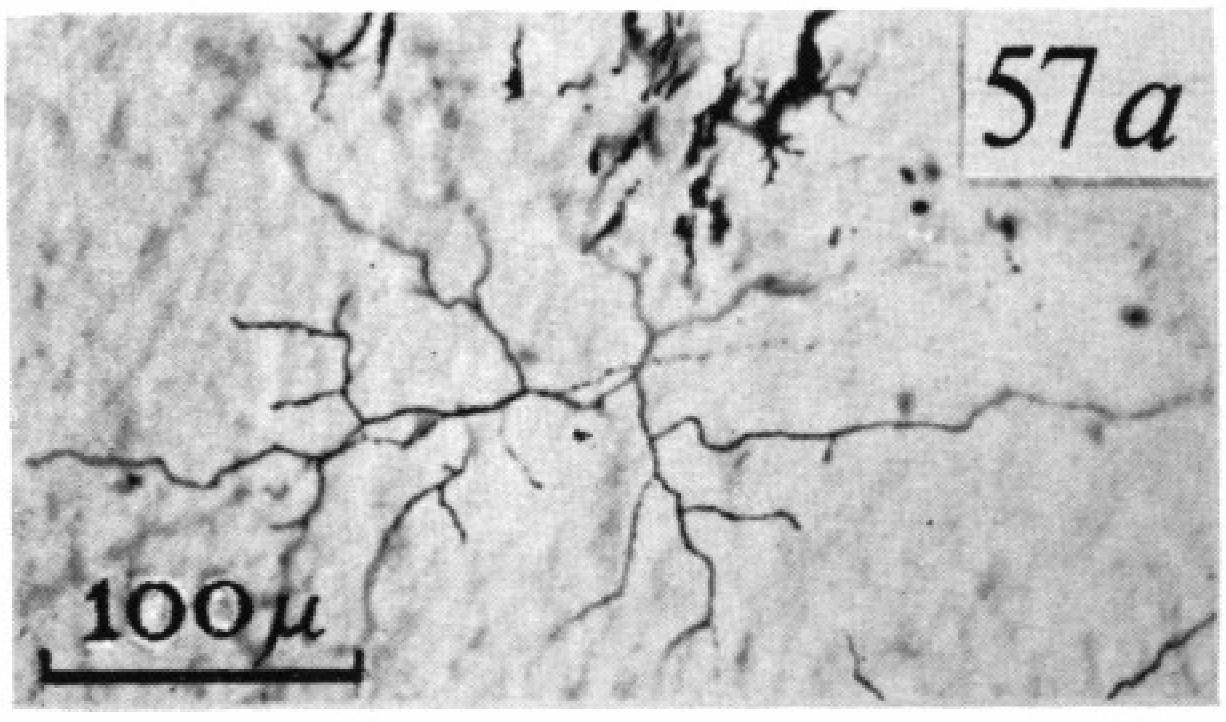
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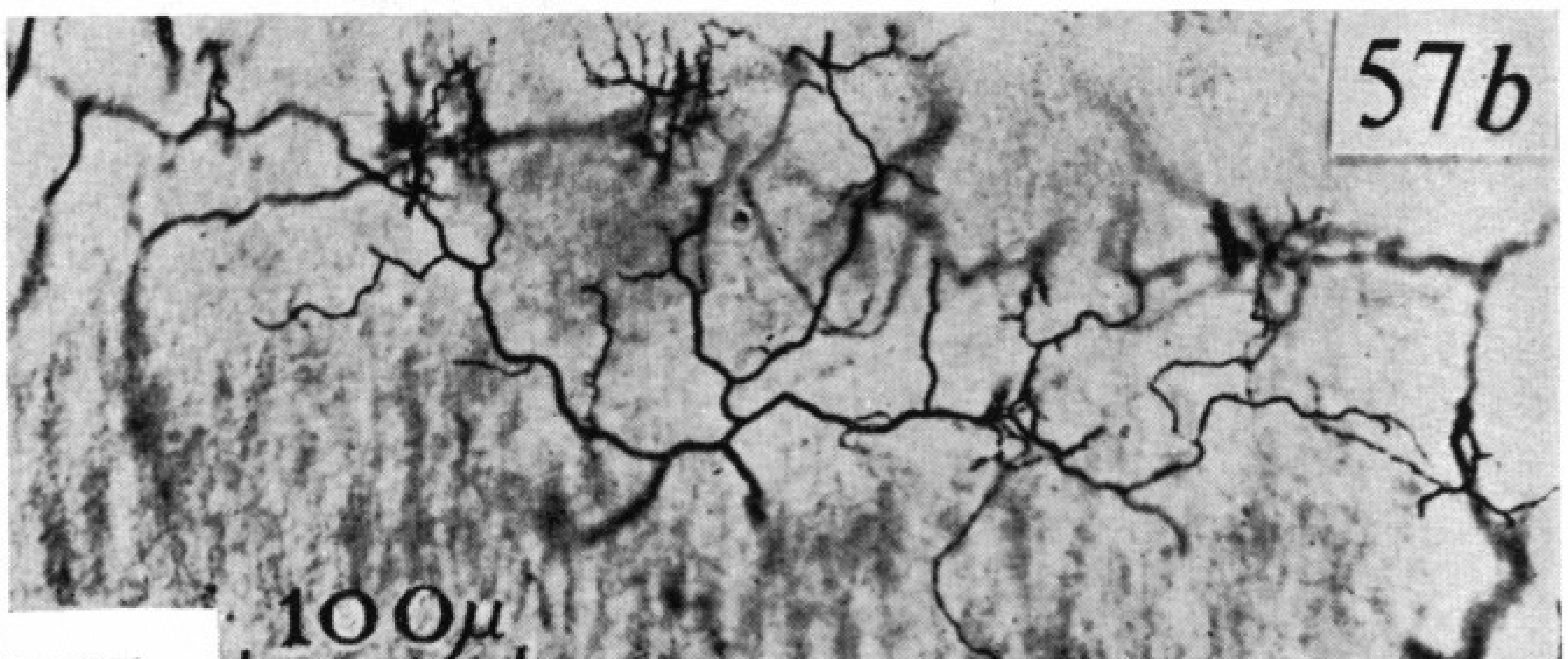
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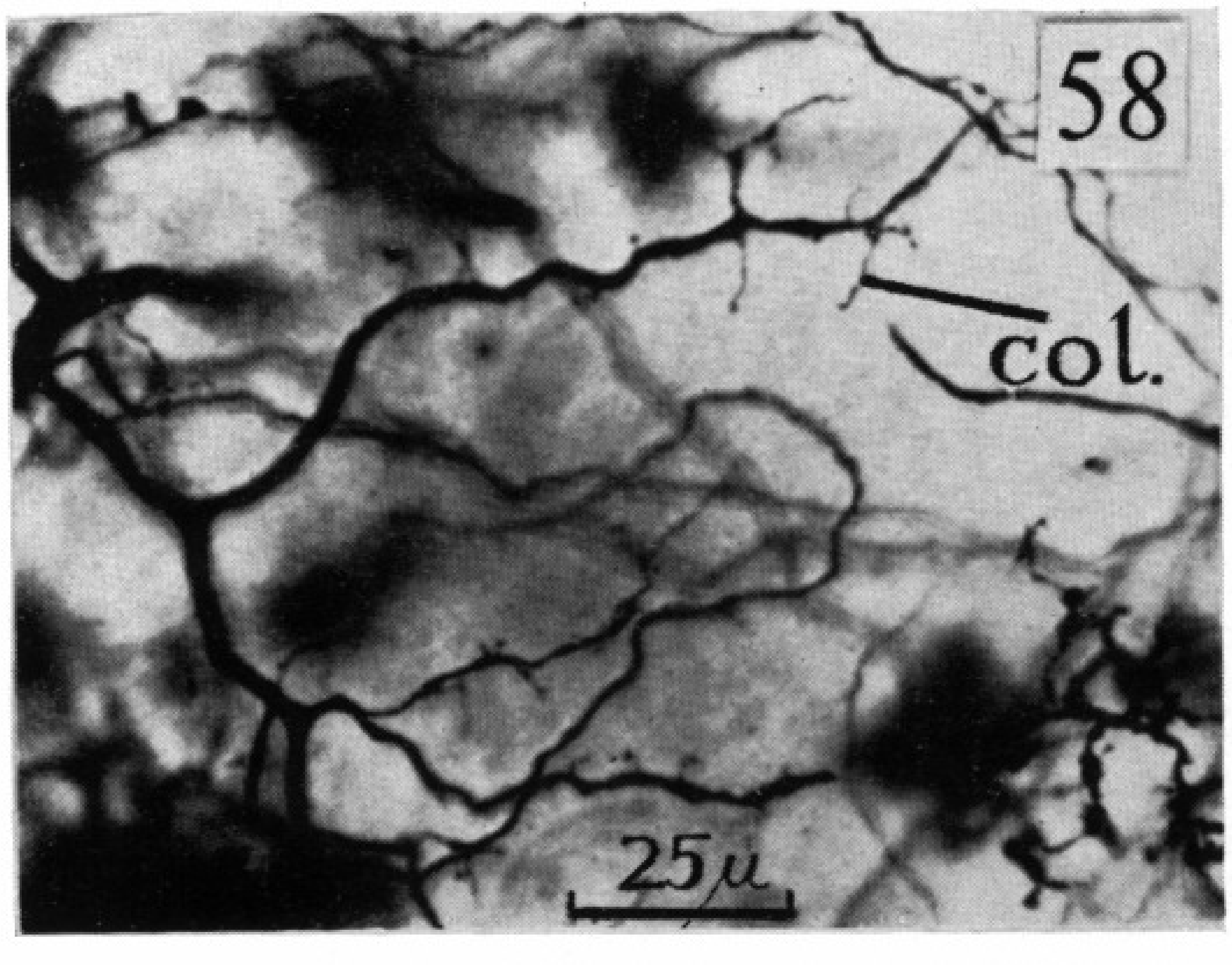
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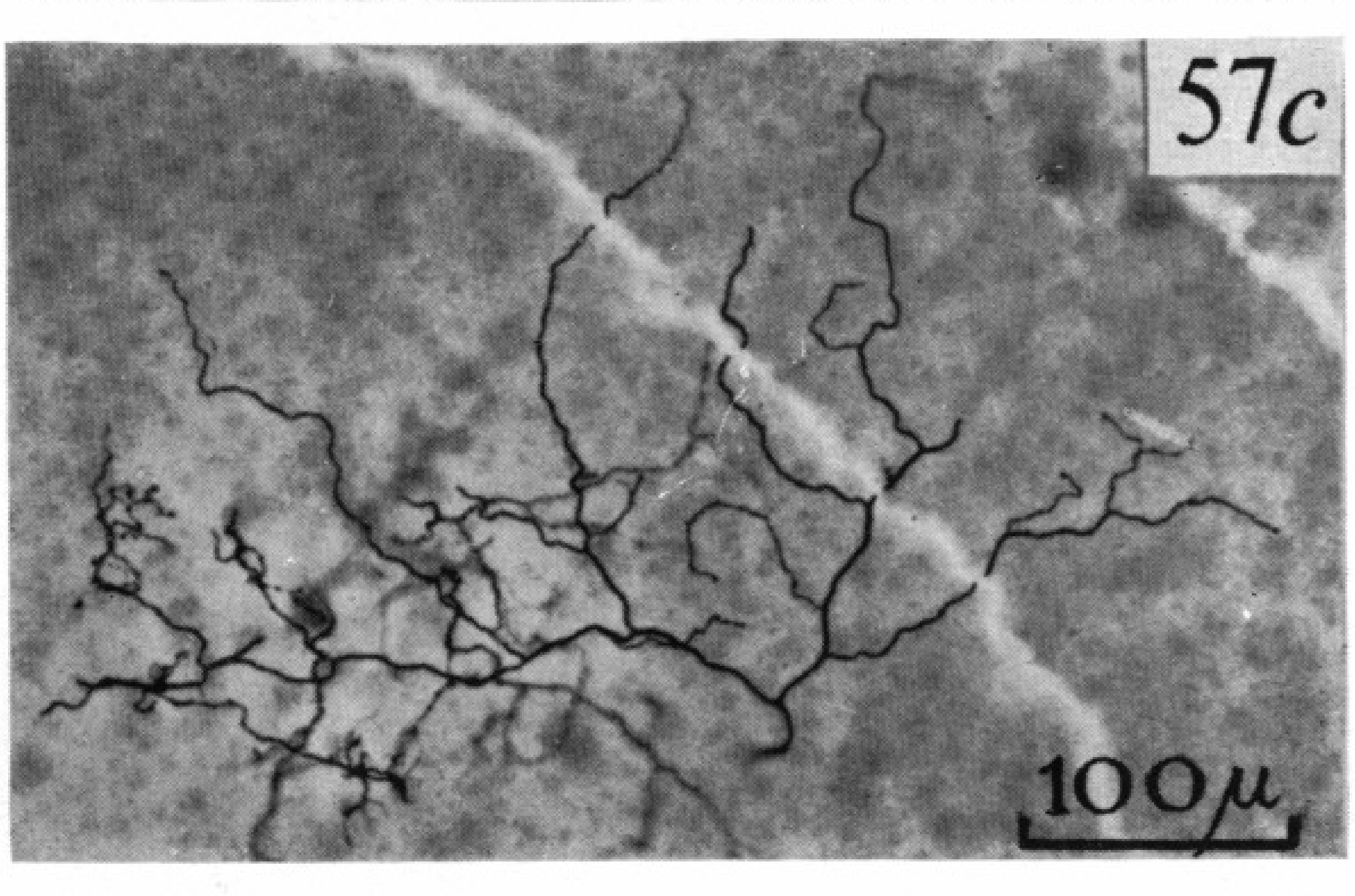
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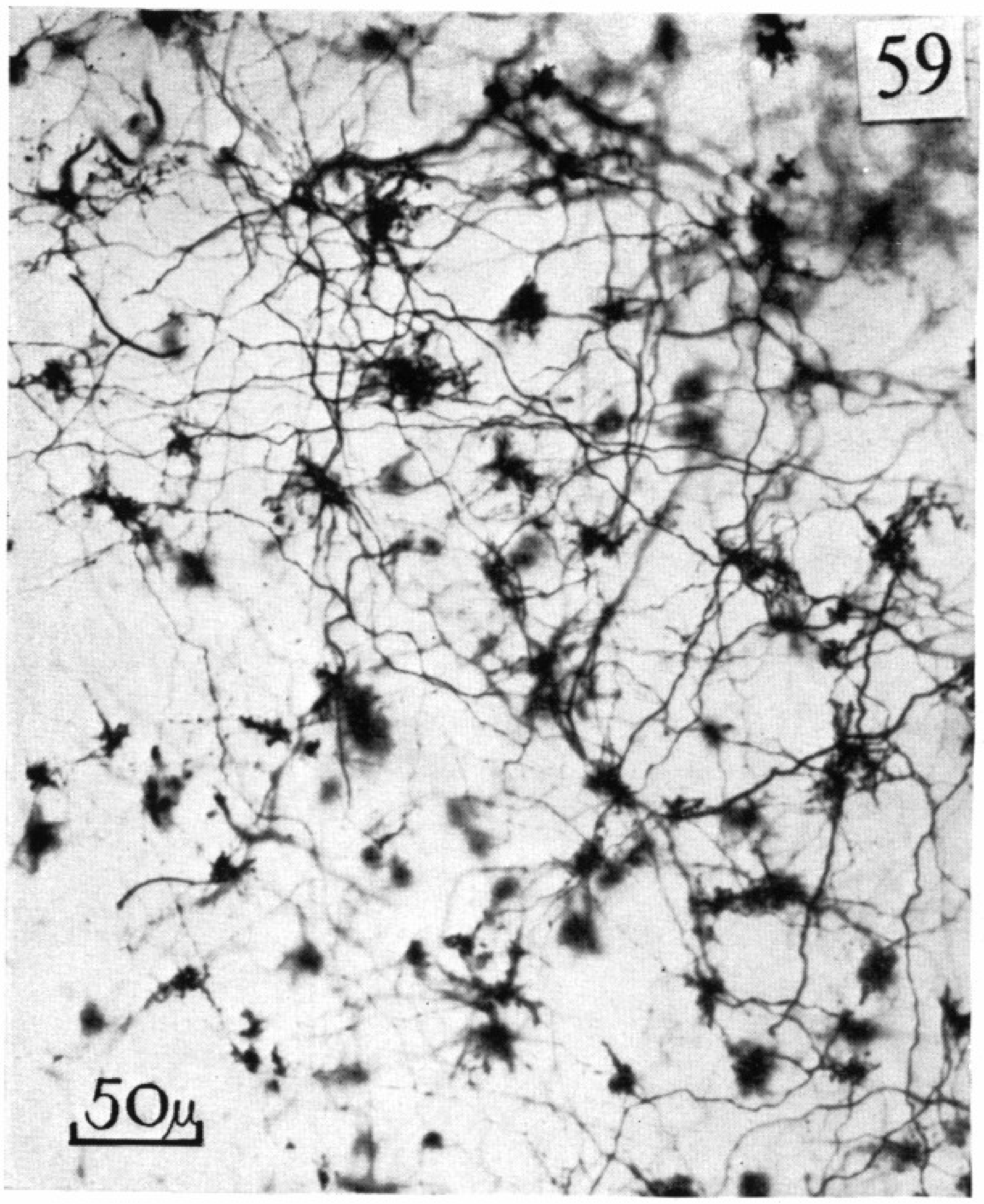

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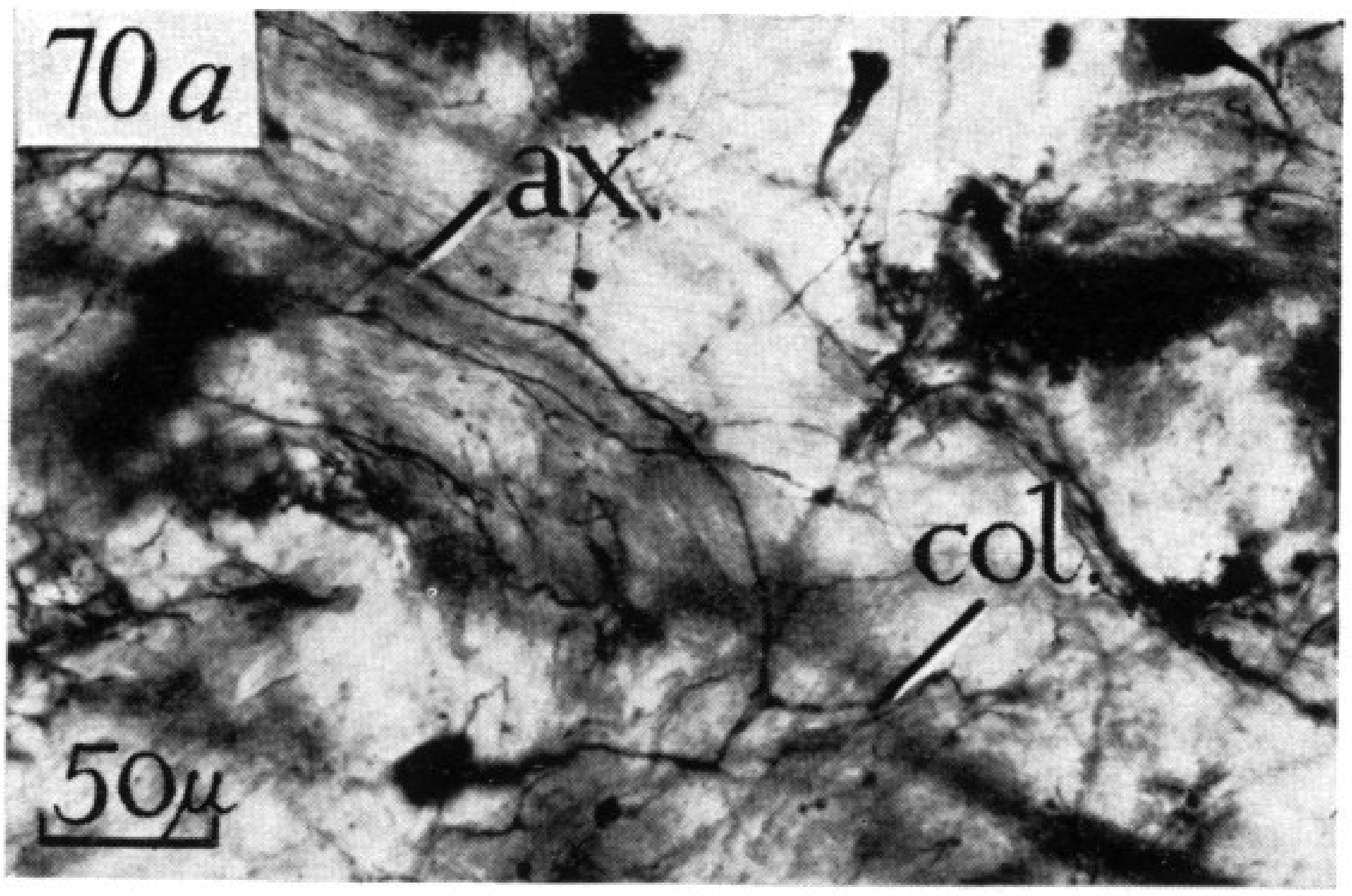

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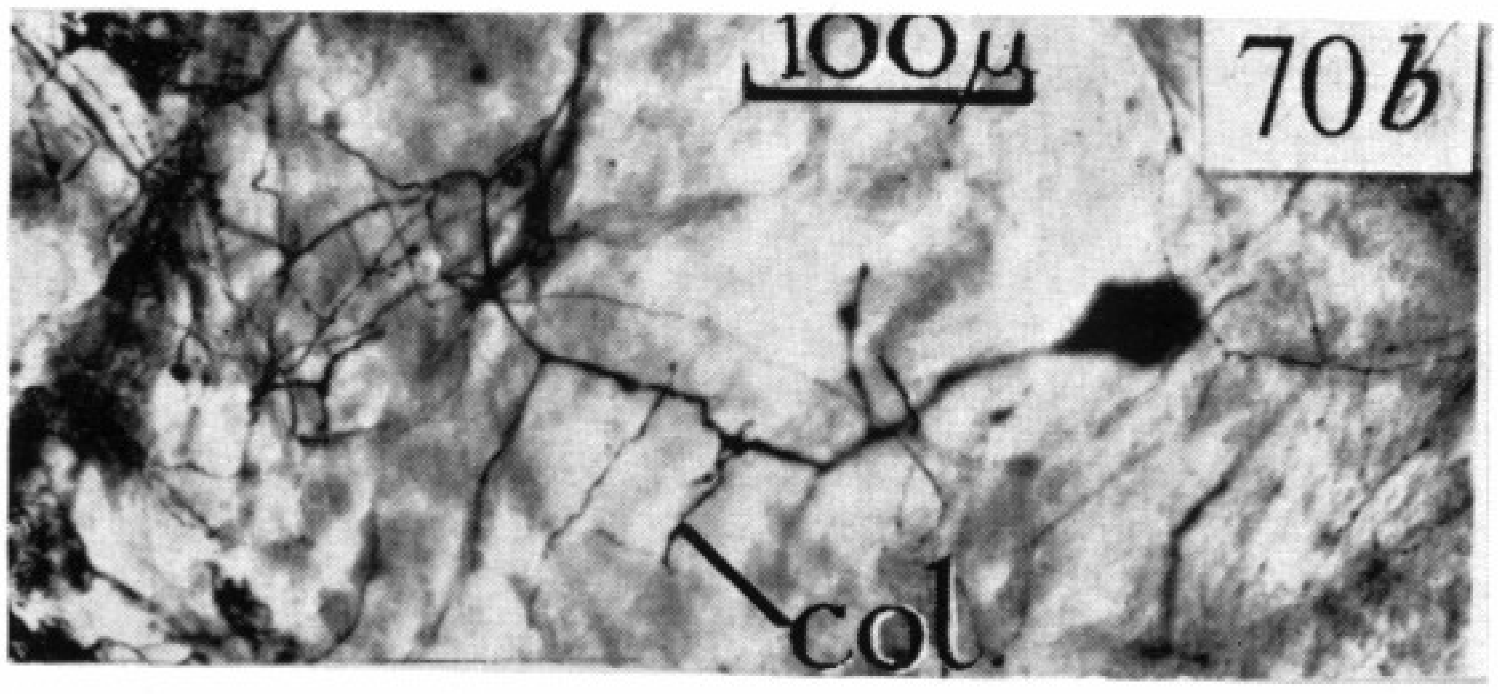

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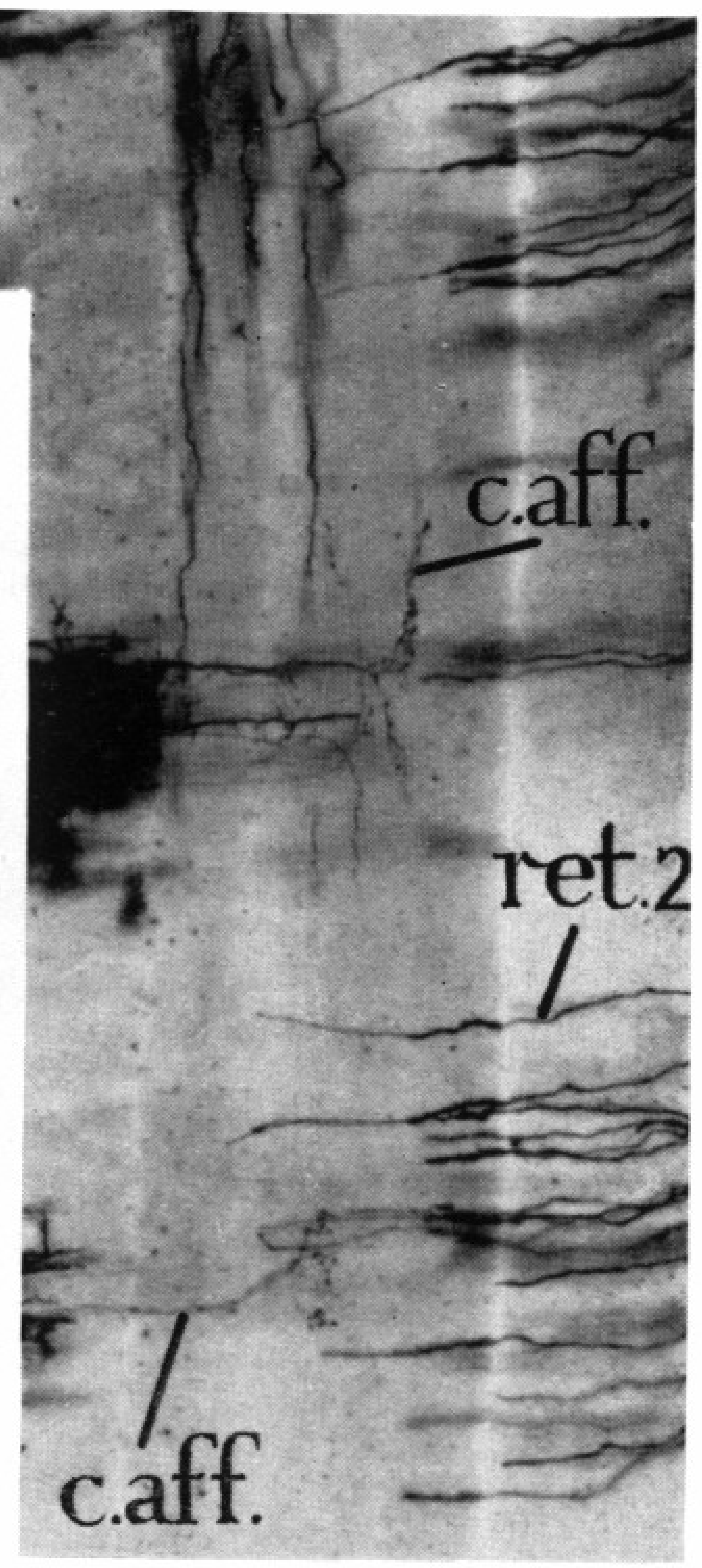

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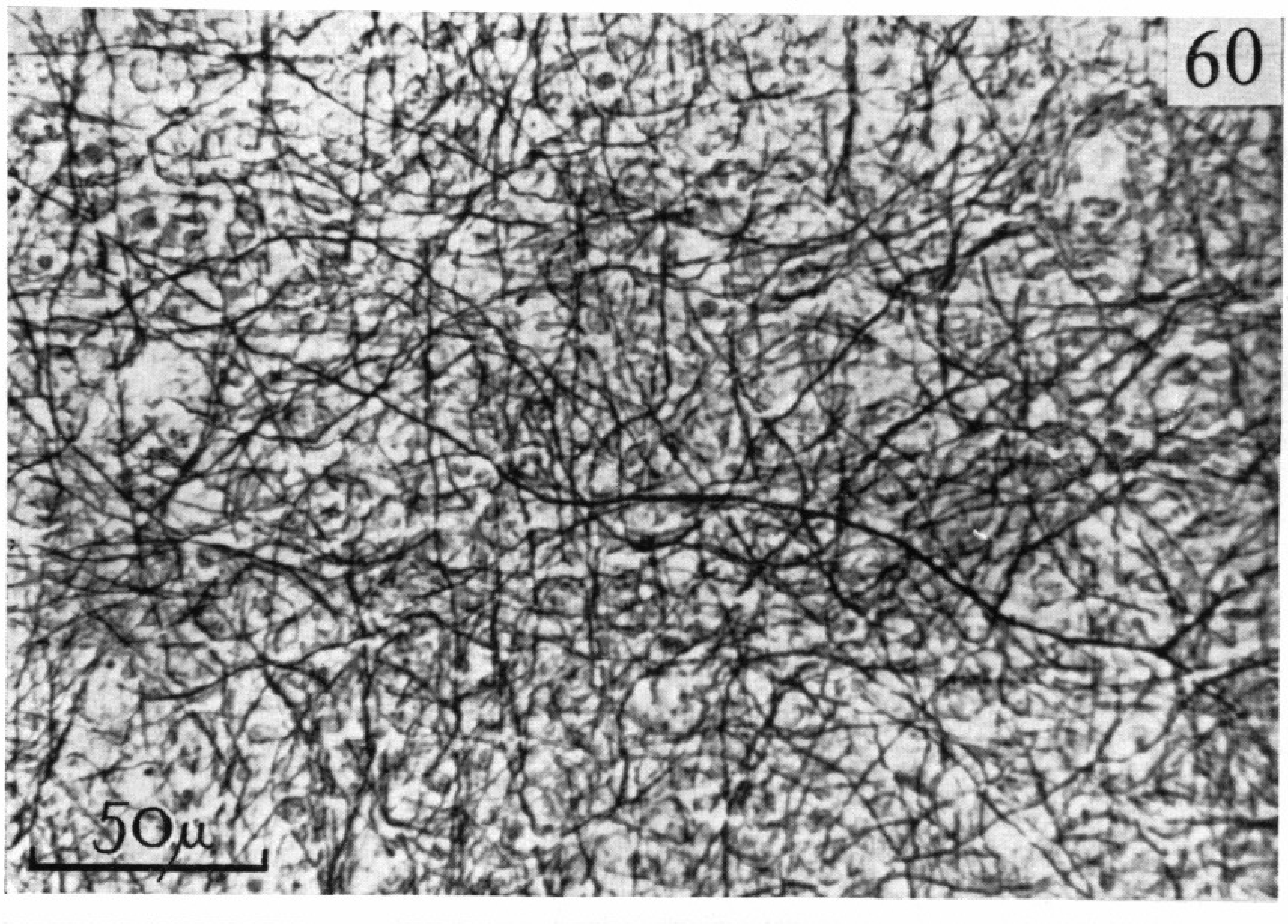

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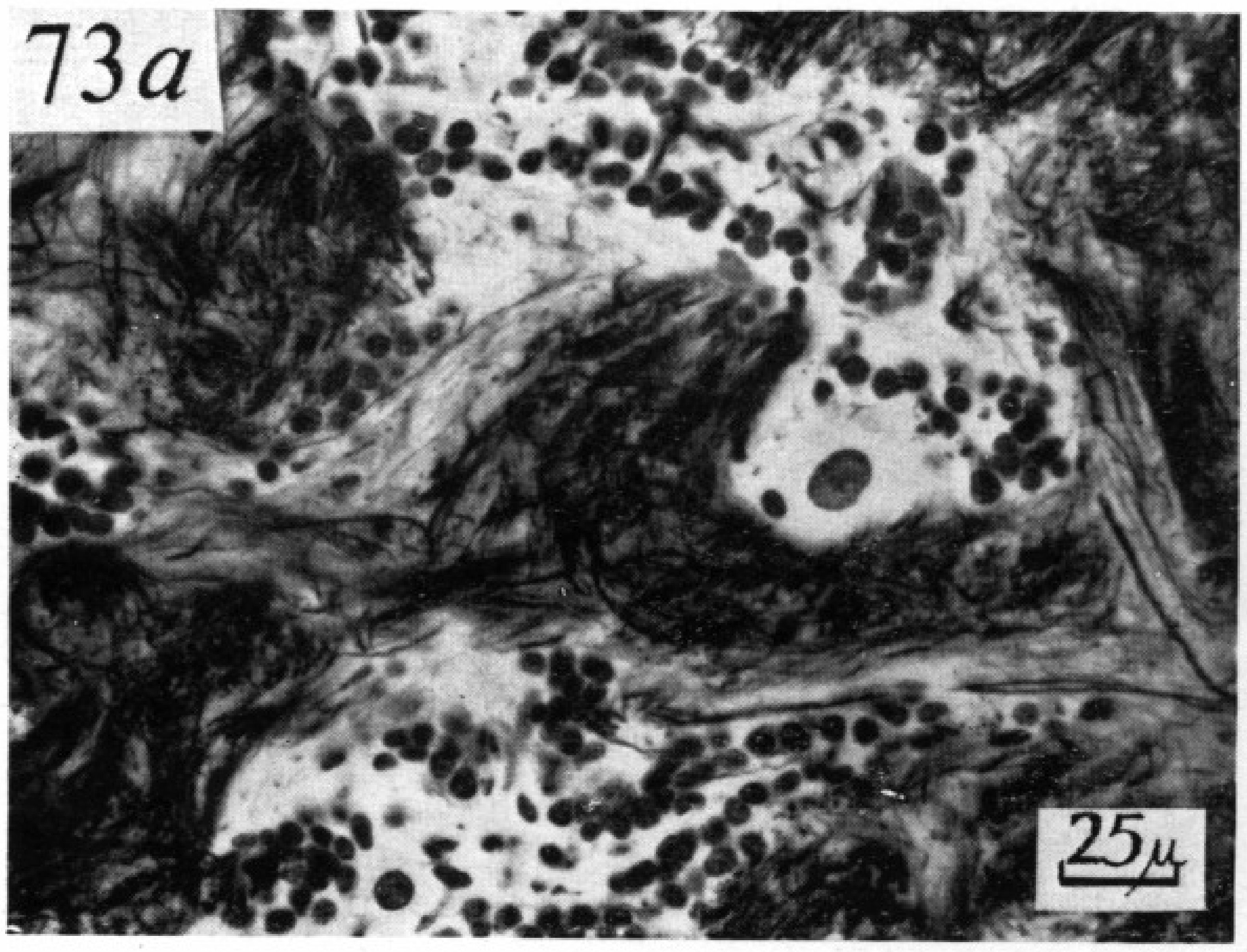

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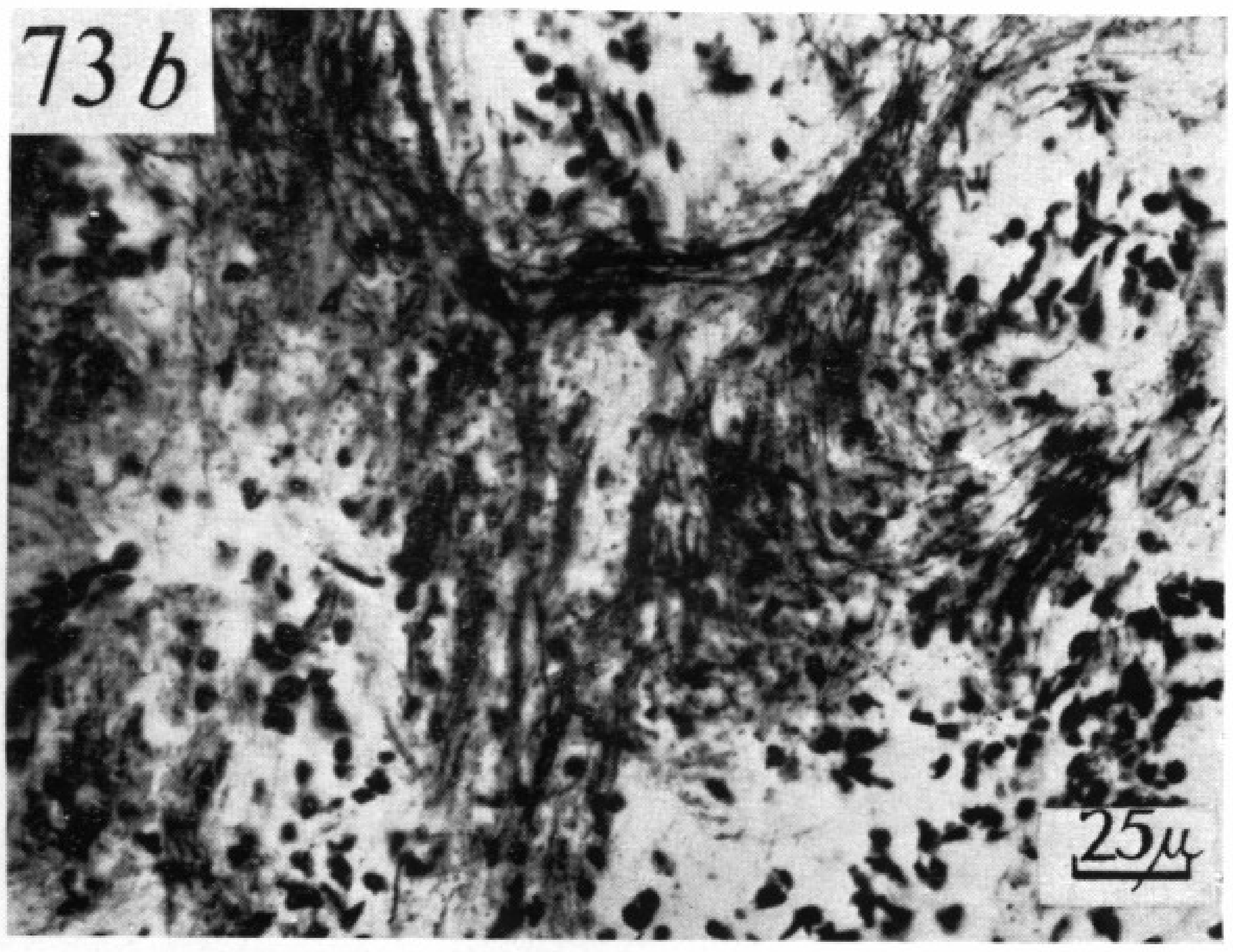

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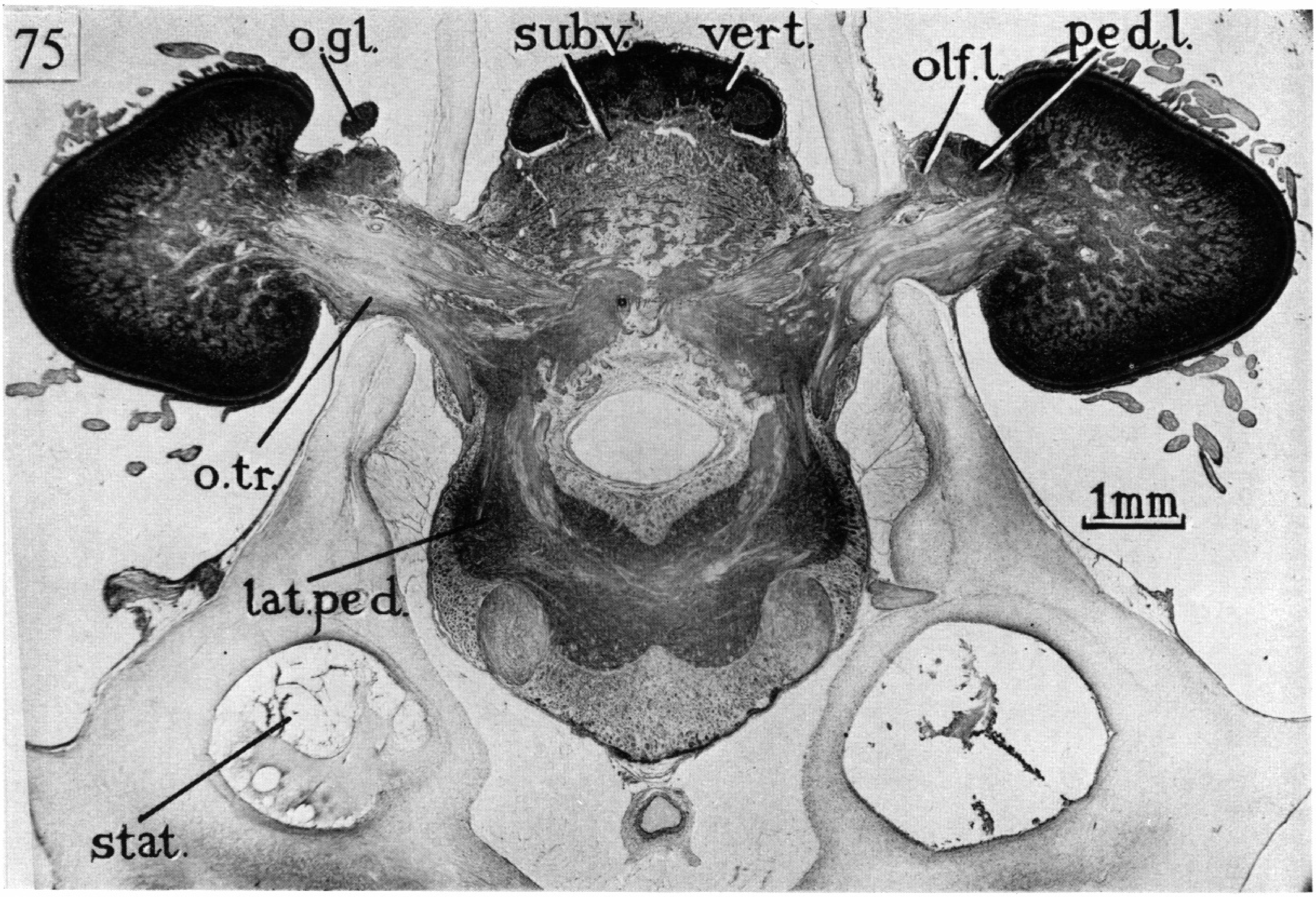
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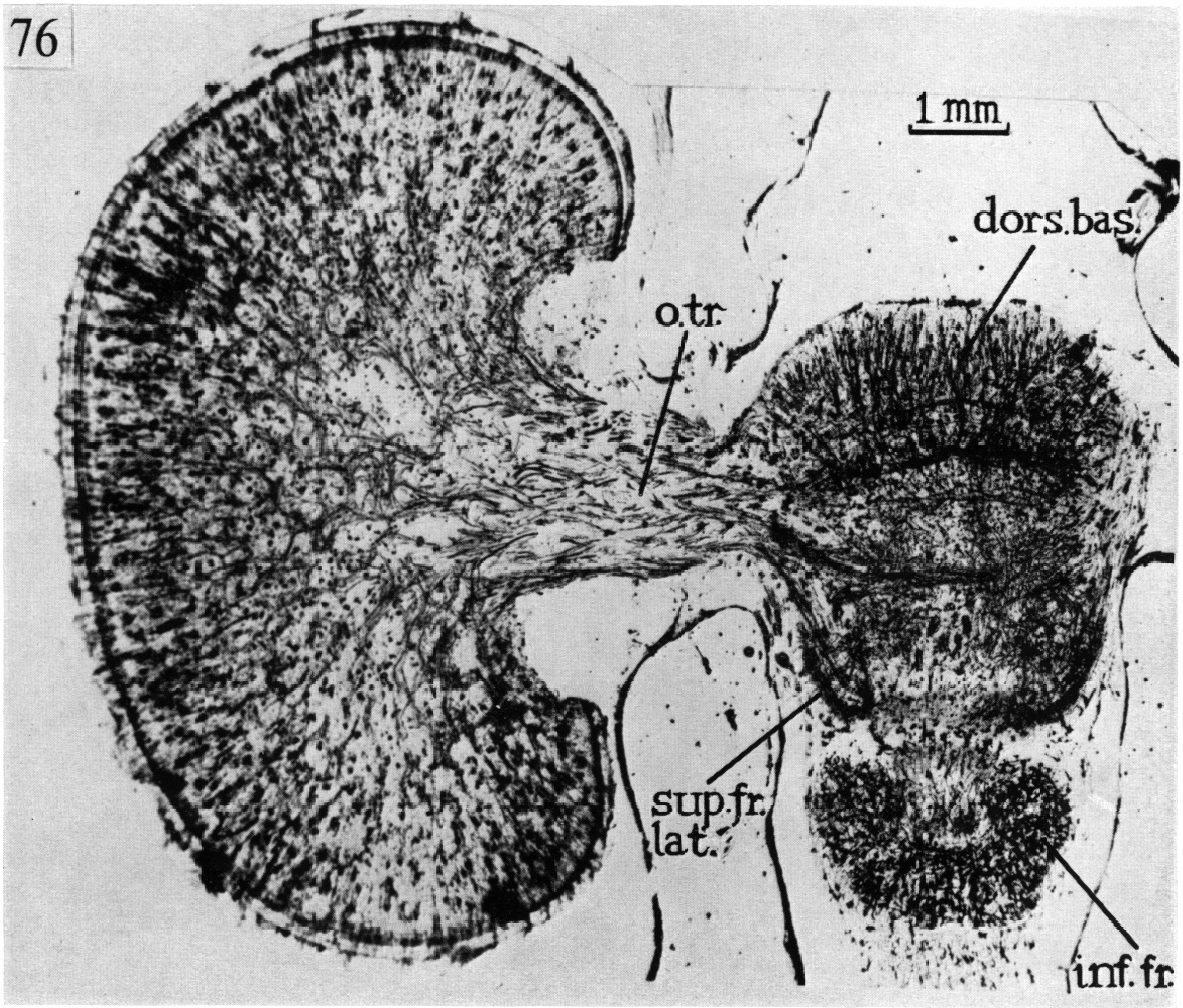
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