THE CENTRAL NERVOUS SYSTEM OF *LOLIGO*

I. THE OPTIC LOBE

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CONTENTS

The optic nerve fibres project on to the optic lobe in a regular manner, being precisely re-assorted after passing through a chiasma. In the outer plexiform zone the optic nerve fibres end in contact with the dendrites of second-order visual cells. These presumably serve to classify the visual input and four types can be recognized anatomically: (1) The smallest have minute circular dendritic fields, in contact with one or few optic nerve fibres. (2) There are also larger circular fields. (3) Many cells have very elongated narrow dendritic fields each running straight in one direction and thus perhaps sensitive to edges. (4) The largest second-order visual cells have enormous oval dendritic fields, several millimetres long, orientated in the long axis of the lobe. Each type of field occupies a different level, producing the characteristic layering of the outer plexiform zone.

Numerous amacrine cell processes end in the outer plexiform layer, some are very small with restricted branches, others have wide trees with fibres passing first inwards then outwards several times. There are thus possibilities of establishing uniform conditions of excitation or inhibition over small or large areas of the visual field.

The dendrites of the centrifugal cells with axons passing to the retina spread in the various layers of the plexiform zone. They could serve to project information of the areas excited, or inhibited, out to the retina.

The axons of the second-order visual cells form radial columns in the outer part of the medulla of the optic lobe. Those with the smaller dendritic fields end more superficially, the largest ones about half-way through the lobe. Each column contains fibres and neuropil at its centre, surrounded by multipolar and bipolar amacrine cells, whose branches enter the neuropil among the endings of the second-order visual cells. Horizontal multipolar cells of various sizes link the columns. Third-order visual cells send dendrites into these columns and axons deeper into the lobe, some directly to the optic tract. The giant cells of the magnocellular lobe can thus be activated by a visual pathway involving only two previous synapses (as well as by a direct static pathway involving none).

Central to the zone of radial columns is a zone where many of the connexions are tangential. There is an increasing number of large cells passing centrally, many being presumably fourth-order visual neurons.

They send axons either elsewhere within the lobe or to the optic tract. Fibres reaching the lobe from the central brain or opposite lobe are distributed in this region and also reach out into the radial columns.

In many of the tracts leaving the optic lobes for other centres the fibres maintain precise topographical relations, as also do those of the optic commissure. This regularity is especially clear in the bundles that pass to the motor centres (peduncle lobes and anterior basal lobes) but may be present in others. There is thus a regular mapping of the visual field throughout much of the system. Other pathways show complex interweaving, for instance those for colour control, where the response pattern is not topographically related to the visual input.

General introduction

In spite of the great amount of detailed anatomical and physiological information about nervous systems we still lack clear views of how the many parts and channels cooperate to produce actual behaviour patterns. Surveys of the organization of a variety of animal brains provide some insight into the systems of organization that are involved (Bullock & Horridge 1965). Basic general features begin to appear when a wide range of types is compared, for example retinal mechanisms for analysis of visual information are in some ways similar in arthropods, cephalopods and vertebrates. Differences are of course likely to be as instructive as similarities.

The present is the first of a series of papers attempting to give a view of the organization of the nervous system of *Loligo*, for comparison with *Octopus* (Young 1971). After the optic lobe there will be papers on the suboesophageal (Young 1974*a*) and supraoesophageal regions and peduncle lobes. Light microscope studies with silver stained material are able to show the pattern of connexions of many thousands of neurons at once. This, combined with information about the details from electron microscopy, can enable us to see as it were a 'blue-print' of how the system is built to perform its functions. Of course such an analysis has also to take account of results of investigations by electrical recording, stimulation and biochemical studies. It can also precede and provoke such investigations. Above all the light microscope has the right degrees of magnification to show the relations of many units all at once, which is obviously of special value in trying to understand a multi-channel system where separate items of information are carried in distinct fibres.

The present study tries to follow pathways through from receptors and receptor analysers to the various types of higher and lower motor centres all the way to effectors. This is somewhat easier in cephalopods than in vertebrates because the system is based on a very definite set of lobes, whose pattern of organization remains rather constant. The variations depend of course on the different behavioural patterns of the animals. The present studies allow us to contrast the epipelagic *Loligo* with the benthic *Octopus*. At the same time we have under way an investigation of a large range of octopods and decapods from all depths of the ocean; each species can contribute information as to the means of operation of the particular part of the brain that is developed for its special mode of life (P. N. Dilly, M. Nixon & J. Z. Young, in preparation).

1. Introduction to the optic lobe

The only account of this lobe is by Kopsch (1899), though Cajal (1917) adds some details in his description of *Sepia*. Cajal comments that study of the retina and optic centres of cephalopods 'son temas anatómicos de la más ardua dificultad'. It is true that Golgi methods are as fickle with this as with other material, but fortunately Cajal's own silver methods can be made to succeed admirably. With these and some successful Golgi–Kopsch preparations it has been possible to discover much fresh information about the principles of the organization by which visual signals are analysed (Young 1973). It is hoped that a detailed light-microscopic study will open the way for work with the electron microscope and micro-electrode, as well as with biochemical and pharmacological techniques. The analysis that is now given is considerably more detailed than has been possible for *Octopus* (Young 1971), mainly because fibres are larger in squids and also we have more successful Golgi preparations. Some observations on the optic lobe of *Alloteuthis* and *Sepia* have also been included.

2. MATERIAL AND METHODS

A large number of sections has been accumulated over several years from three species of squid, *Loligo vulgaris* at Naples, *L. pealeii* Lesueur* at Woods Hole and *L. forbesi* and *Alloteuthis subulata* at Plymouth. For Cajal's staining they were fixed in 10 % neutral formalin in sea water (Stephens 1971). An important detail is that the fixative should be kept cool. At summer temperatures in Naples a reaction takes place that produces irregular silver deposits throughout the nervous system.

The most successful Golgi preparations were obtained by the Kopsch technique of fixation in formol-bichromate (Stephens 1971). It was indeed during his study of *Loligo* that Kopsch (1896), having failed with osmium bichromate fixation, introduced this technique. It was the rediscovery of the Kopsch method at the beginning of the present work that led to its successful re-introduction to neurologists, especially through the work of Colonnier (1964).

The counts in figure 113 were made on a Cajal-stained transverse section, 15 μm thick, of a young squid, photographed at a magnification of 500. Measurements were made on a strip proceeding from the surface to the peduncle lobe (excluded). The medulla was divided arbitrarily into four parts. Totals were obtained by measuring the area of the section and the number of sections in the lobe, with allowance for the ends. Corrections were made so far as possible for thickness of the section. The estimates are therefore only approximate. The total is reasonable in comparison with that found for *Octopus* (Young 1962). Glial nuclei are not included, they can generally be recognized by their irregular outline (p. 270). There are also numerous nuclei of the subpedunculate tissue, especially at the centre of the lobe. They are small and easily recognized and were not included in the count.

* The name of this animal is often mis-spelled. *Loligo pealeii* was so named after R. Peale of the Philadelphia Museum by C. A. Lesueur in 1821, in his 'Descriptions of several new species of Cuttle-fish' published in the *Journal of the Academy of Natural Sciences of Philadelphia*, **2**, 86–101.

All figures are of preparations by the Cajal silver or Golgi–Kopsch methods. Except where stated they are all of *Loligo*, and are orientated so that the surface of the lobe is to the left. A few photographs have been re-touched where stated to show features out of focus.

DESCRIPTION OF PLATE 8

FIGURE 1. Transverse section of the optic lobe of a young *Loligo*. Cajal.

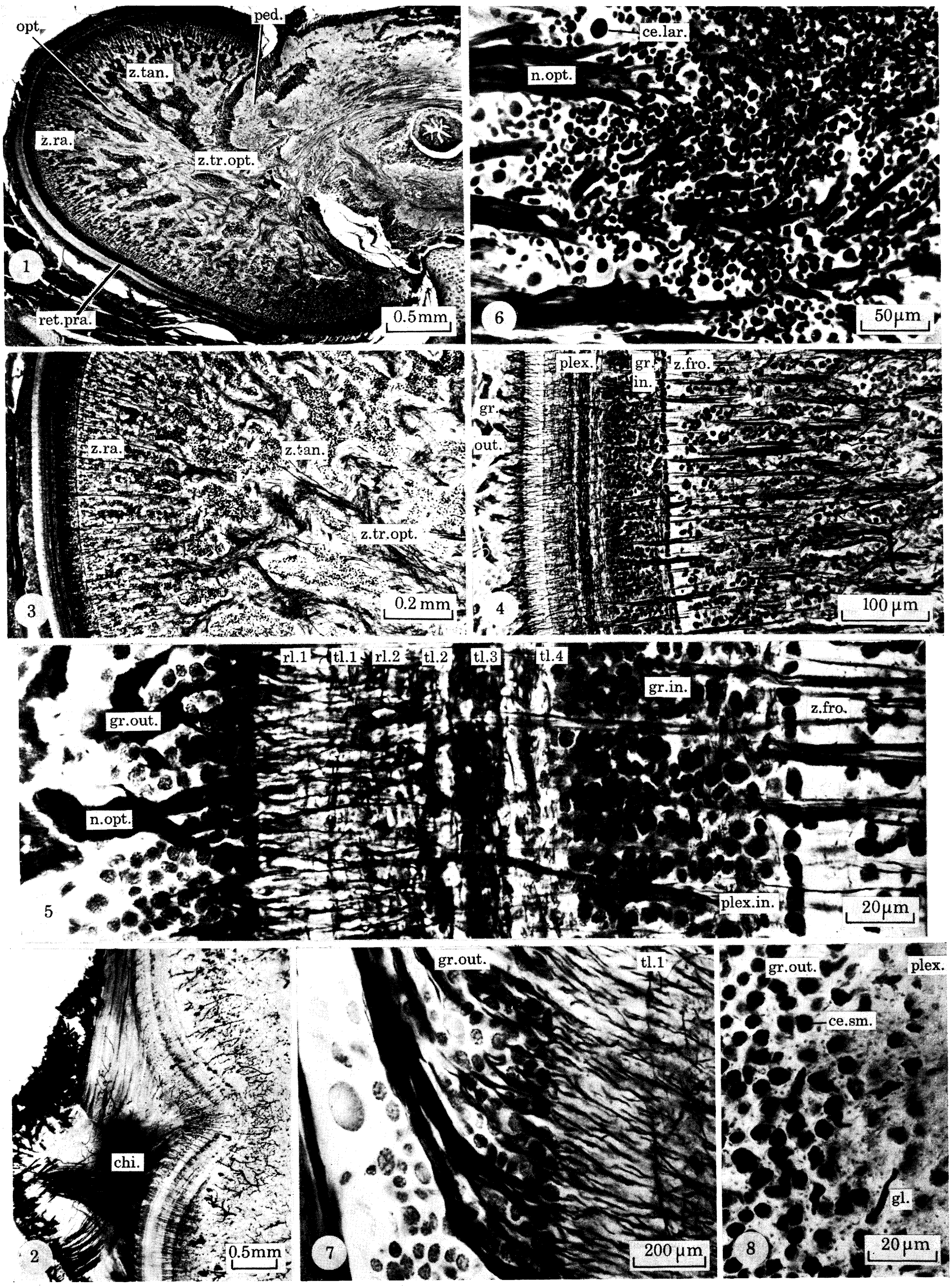
FIGURE 2. Transverse section at centre of the lobe, showing the chiasma and depression of the surface. Golgi.

FIGURES 3–5. Transverse sections at increasing magnification to show the organization of the lobe. Cajal.

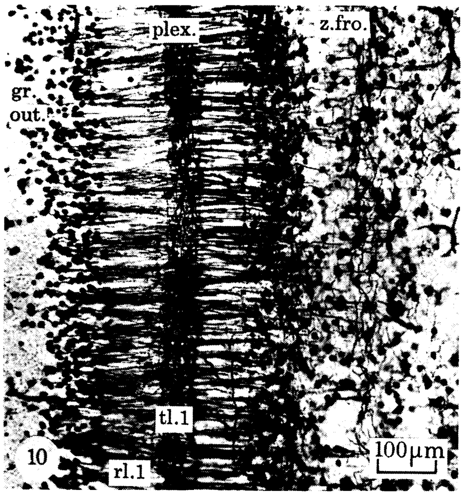
FIGURE 6. Section tangential to the surface to show the entering bundles of optic nerve fibres and large and small cells of the outer granular layer. Cajal.

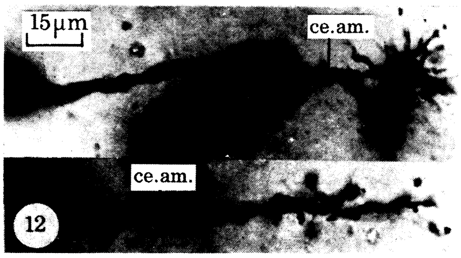
FIGURE 7. Outer granular layer to show nerve fibres entering the surface in bundles and entering the plexiform zone singly. Sagittal section. Cajal.

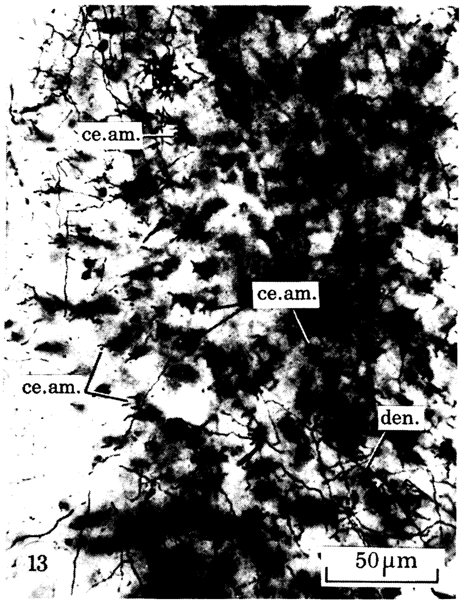
FIGURE 8. Oblique sagittal section at inner border of outer granular layer to show nerve fibres and neuronal and glial nuclei. Cajal.

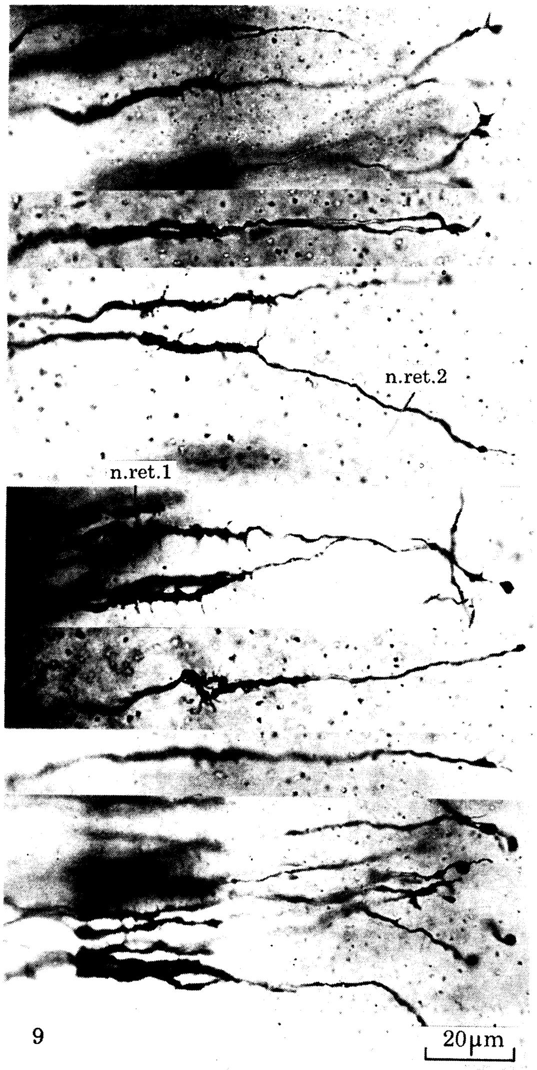


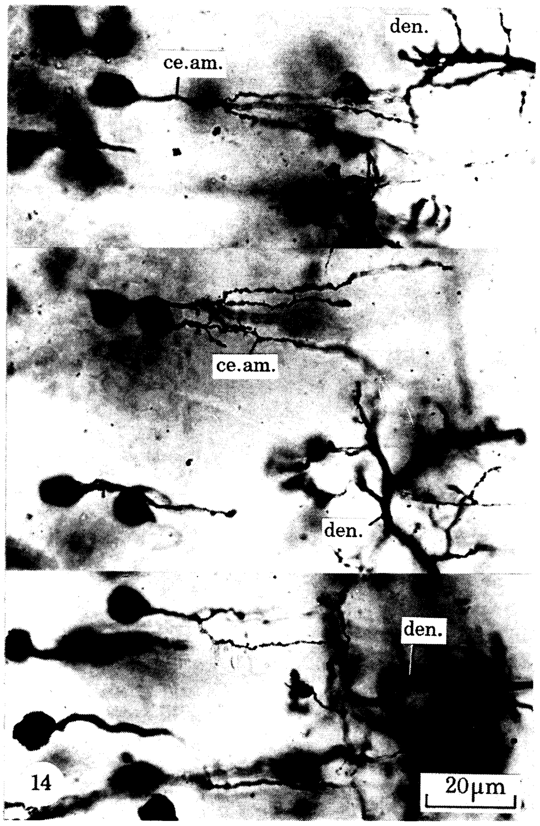
FIGURES 1–8. For description see opposite

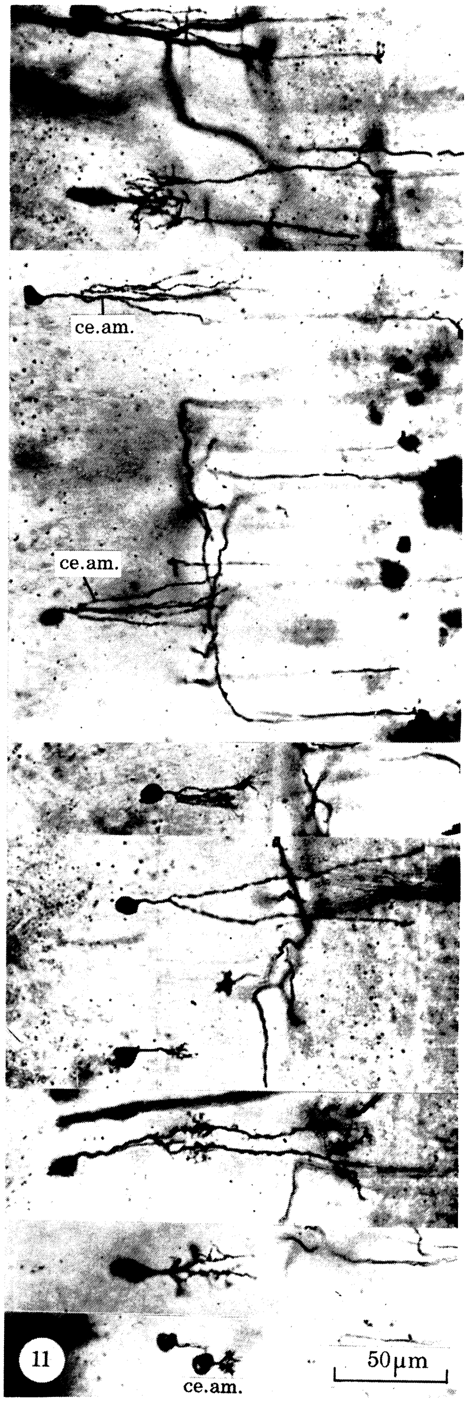


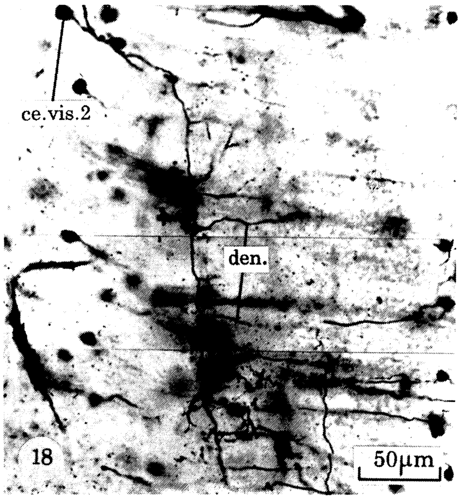










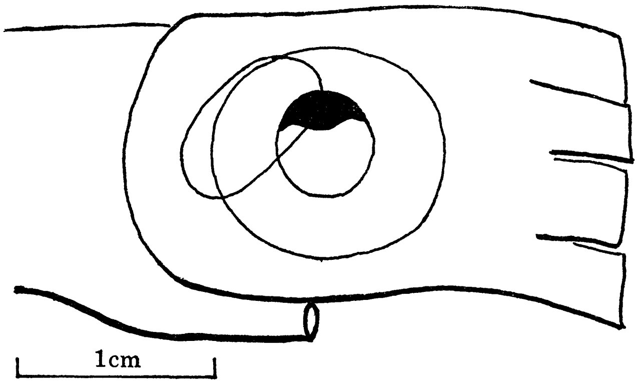


FIGURES 9–15 AND 18. For description see opposite

3. FORM AND DIVISIONS OF THE LOBE

The optic lobe of *Loligo* is oval in outline as seen from the lateral side. It is slightly concave on its lateral and more so on its medial side and therefore has an irregular dumb-bell shape (figure 1†). The long axis lies obliquely in the orbit, at an angle of about 60° with respect to the horizontal plane of the body, with the anterior end more dorsal (figure 111†). The optic lobe is thus elongated along an axis oblique to that of the eye as determined by the margin of the iris. There may be some significance in these relations since the dendritic fields of many of the cells of the optic lobe are regularly orientated with respect to the optic lobe. The optic nerve fibres enter over the lateral surface and make a chiasma along a line that follows the long axis of the lobe. The chiasma lies slightly anterior to the middle of the lateral surface. Where the fibres cross there is a slight depression in the surface of the lobe (figure 2) (Kopsch 1899).

The optic nerve fibres spread out over the lobe and pass through an outer layer of granule



JRE 111. Diagram to show the position of the optic lobe. Figure prepared by cutting in half a head of *Loligo vulgaris*, removing the eye on one side to make a photograph of the optic lobe. A tracing from this was then projected on to a photograph of the other side.

DESCRIPTION OF PLATE 9

FIGURE 9. Optic nerve endings in the plexiform zone after staining with Golgi. Some end in the 1st radial layer (n.ret.1) but most have a fibre continuing to the deeper layers (n.ret.2). Sagittal section.

FIGURE 10. Low-power view of outer part of optic lobe stained by the Golgi method. Shows the numerous branches of amacrine cells in the first radial layer and fibres in the first tangential layer. Sagittal section.

FIGURE 11. Amacrine cells of the outer granule cell layer, with branches of various lengths. Sagittal section. Golgi.

FIGURE 12. Two very short amacrine cells of the outer granule cell layer, one with numerous fine twigs, the other with blunt granular processes. Sagittal section. Golgi.

FIGURE 13. Section tangential to the surface of the lobe showing the branches of the outer amacrine cells occupying small circular fields. Also some long straight dendrites of second-order visual cells (at bottom of picture). Sagittal section. Golgi.

FIGURE 14. Amacrines of the outer granule cell layer showing how the branches of some of them reach to the region of the tops of the dendrites of second-order visual cells with round fields (den.). Sagittal section. Golgi.

FIGURE 15. Low-power view to show large amacrine cell of outer granule cell layer (ce.am.lar.). Sagittal section. Golgi.

FIGURE 18. Second-order visual cell of outer granule cell layer (ce.vis.2), showing a single main trunk with numerous dendritic branches in deeper plexiform layers (den.). Sagittal section. Golgi.

† Figures 1–110 appear on plates 8–18; figures 111–122 appear in the text.

cells to a plexiform zone, where the majority of them end. The thickness of the layers at the surface of the lobe is probably constant over the surface, but on account of the curvature small differences would be hard to detect. The retina of *Loligo* has longer rhabdomes round the edges than at the centre (Young 1963), but these differences in the retina seem not to be associated with any marked differentiation of the deep retina of the optic lobe, though it may be that the outer layers are slightly thicker at the centre (figure 2).

The hilum of the lobe contains the peduncle lobe, which is also elongated along an oblique dorso-ventral axis (figure 1). The optic tract is short, making it easy to study the connexions with the central brain.

The organization of the optic lobe can be considered in two parts (figure 1). An outer cortex or deep retina, where the incoming optic nerve fibres meet the tangential dendrites of the second-order visual neurons, and an inner medulla composed partly of radial columns based on the axons of these latter cells. The medulla contains third- and perhaps higher-order neurons, leading to the optic tract. Both deep retina and medulla contain many other types of neuron. In transverse section a series of layers can be recognized as follows (figures 3–5):

$$\left.\begin{array}{l}\text{outer granule cell layer}\\ \text{outer plexiform zone}\\ \text{inner granule cell layer}\\ \text{inner plexiform zone}\end{array}\right\}\ \text{deep retina (retina profunda)}$$

$$\left.\begin{array}{l}\text{palisade layer} = \text{1st medullary zone}\\ \text{frontier zone} = \text{2nd medullary zone}\\ \text{zone of radial columns} = \text{3rd medullary zone}\\ \text{zone of tangential bundles} = \text{4th medullary zone}\\ \text{zone of optic tract bundles} = \text{5th medullary zone}\end{array}\right\}\ \text{medulla}$$

These layers are based on those recognized by Cajal (1917), but he used the term optic ganglion for the region we are calling medulla. This is actually the largest part of the optic lobe and the most difficult to describe. The layers of the deep retina are clearly marked, but the medulla is a continuous system, without sharp divisions and the inner three zones can only be delimited approximately (see p. 287).

4. Functional organization of the lobe

In order to make the description useful and understandable it is necessary to provide first the interpretation that has been reached and used in the nomenclature. The arrangement suggests the hypothesis that the two main regions of the lobe have distinct functions. In the outer plexiform zone there are the receptive fields of second-order visual cells, providing sets with specific dendritic orientation and no doubt other characteristics, enabling them to detect particular features of the visual input. This can be regarded as a process of coding, by which information about events in the outside world is selected and passed on to the centre of the lobe. The medulla then serves to select from the repertoire available the responses that are appropriate to the information, and to pass the necessary commands to the motor centres of the central brain.

To perform these functions the organization of the plexiform zone is based upon a series of receptor dendritic fields displayed tangentially, while in the medulla there are radial columns linked by cells with dendrites spreading tangentially, some of them very widely, each connecting with several columns. Large efferent cells send axons to the optic tract. Many smaller cells (amacrines or microneurons) and multipolar cells are found in both parts. The cells with long axons that are presumed to carry visual signals onwards are named second- and third-order visual neurons to distinguish them from the amacrine cells and other interneurons of the lobe.

5. The outer plexiform zone. Second-order visual cells

The outer plexiform zone is the region in which the optic nerve fibres mostly end, passing signals on to the second-order visual neurons. These latter have receptive dendritic fields of various sizes and orientations. The cell bodies of some of them lie in the outer granule cell layer, but the majority in the inner granule layer. The trunks of the cells in either layer proceed to the plexiform zone and then after a short or longer course they pass to the medulla (figure 112). Those originating in cells of the inner granule layer therefore turn back and pass through that layer again on the way to the medulla. During their passage through the plexiform zone the fibres originating in either the inner or outer granule cell layer carry collateral receptive dendritic twigs. The arrangement of the resulting dendritic fields perhaps provides the basis for selection of patterns of stimulation. Many of these 'dendritic' trunks run straight for remarkably long distances tangentially in the plexiform zone. These dendritic fields are presumably stimulated only by visual contours of the appropriate orientation and length.

The outer plexiform zone contains numerous endings of other neuron types in addition to the optic nerve endings and second-order visual cell dendrites. The amacrine cells of both inner and outer granule layers send branching processes in to the plexiform zone but do not extend beyond it. The centrifugal fibres to the retina arise from cells of the inner granule cell layer. Their trunks give off dendritic branches in the plexiform layer and the axons proceed on into the optic nerve bundles. Fibres arising from cells in the medulla or in the central nervous system or perhaps the opposite optic lobe also reach to the outer plexiform zone.

6. The layers of the outer plexiform zone

The various components of the outer plexiform zone are organized into a highly regular system of layers. The zone has been divided in *Octopus* into four radial layers, separated by four tangential ones (Young 1971). This classification can usefully be applied to *Loligo*, but with some further subdivision and recognition that the layers are not all sharply distinct (figure 5). The layering represents an important functional differentiation between the dendrites of various second-order visual cells. In general the smaller receptive fields lie more superficially and the larger ones deeper. The first radial layer contains no second-order endings but is mainly composed of the swollen ends of the optic nerve fibres and the trunks and branches of the amacrine cells of the outer and inner granule layers.

At the inner border of the first radial layer lie the tops of those second-order recurrent neurons that have the smallest dendritic fields, whose axons turn immediately downwards through the inner granule layer to the medulla (p. 281). Just inside these lie the tangential dendritic trunks of those second-order visual neurons that have orientated dendritic fields of short or medium length, their axons turning back into the medulla after distances of up to a few hundred micrometres. These make a compact tangential layer, the major element of the first tangential layer (tl.1). At this level there are also the long tangential trunks of the second-order neurons that arise from external granule cells, but most of their dendritic collateral branches end deeper, in the third or fourth tangential layers (p. 278).

The second radial layer contains the continuing trunks of the optic nerve fibres and outer granule cells. It also contains many dendritic branches from the second tangential layer. In fact it is by no means a layer of wholly radial fibres (figure 5). The second tangential layer (tl.2) contains the dendritic branches of the largest second-order visual neurons, whose axons turn sharply back and carry signals deep into the lobe (p. 285). Branches of these dendrites also pass both up into radial layer 2 and down into radial layer 3, which is very thin. The third tangential layer (tl.3) is thick and contains the branches of many types of fibre, including receptive collaterals of the long, orientated dendrites of the second-order visual cells of the outer granule layer (figures 111 and 115), also dendrites of the efferent fibres to the retina and branches of the external and internal granule layer amacrines. The fourth radial layer (rl.4) is again very thin, but clearly separates the third and fourth tangential layers, which last is a thin tangential layer of mixed components, separated from the inner granule cell layer by a thin fifth radial layer (rl.5), not recognized in *Octopus*.

The outer plexiform zone thus undoubtedly contains clearly marked layers, but it must be recognized that the analysis and nomenclature are still incomplete and arbitrary. Lenhossék (1896) and Cajal (1917) used a somewhat different system. The present analysis has the advantage that it suggests functional components for some of the layers. It remains for future work to show why the layers are so clearly separated.

7. Outer granule cell layer

The surface of the optic lobe is not bounded by any thick membrane. The optic nerve fibres enter over its surface, passing through a thin layer of flattened epithelial cells. Immediately beneath this lie a number of large cell bodies forming a subdivision of the outer granule cell layer, which Cajal (1917) called the 'piso externo de las amacrinas gigantes' (figure 7). Actually these large cells are of at least two sorts. Some are second-order visual cells, sending axons to the medulla (p. 278), others are amacrines with processes spreading widely within the outer plexiform zone (p. 277). The largest cells have nuclei up to 15 μm and cell bodies 30 μm or more in diameter (figures quoted are for full-grown *Loligo vulgaris* of 18 cm mantle length). These are spaced rather irregularly over the surface, about 100 μm apart (figure 6). Some have round nuclei but others are often elongated and extended tangentially among the incoming optic nerve fibres (figure 7). A little deeper there are medium-sized cells, of about half the size of the giant ones, and with round cell bodies and nuclei.

It is probable that the largest cells send axons to the medulla (p. 279), while the somewhat smaller ones are the giant amacrines, with spreading branches in the outer plexiform layer (p. 277), but it may be that both types of cell are of various sizes. The rest of the outer granule cell layer is occupied by a population of smaller cells, with nuclei between 4 and 8 μm (figures 5, 7 and 8). The larger ones are more frequent towards the outside, but there are differences in size throughout the layer. These cells are mainly or wholly amacrines, sending their fibres to the plexiform layer, but not beyond it (p. 277). There are some glial nuclei throughout the outer granule layer and they are especially conspicuous at the inner border, where the plexiform zone begins. They have a less rounded form than the neuronal nuclei and are often very elongated, with irregular lobes (gl., figure 8).

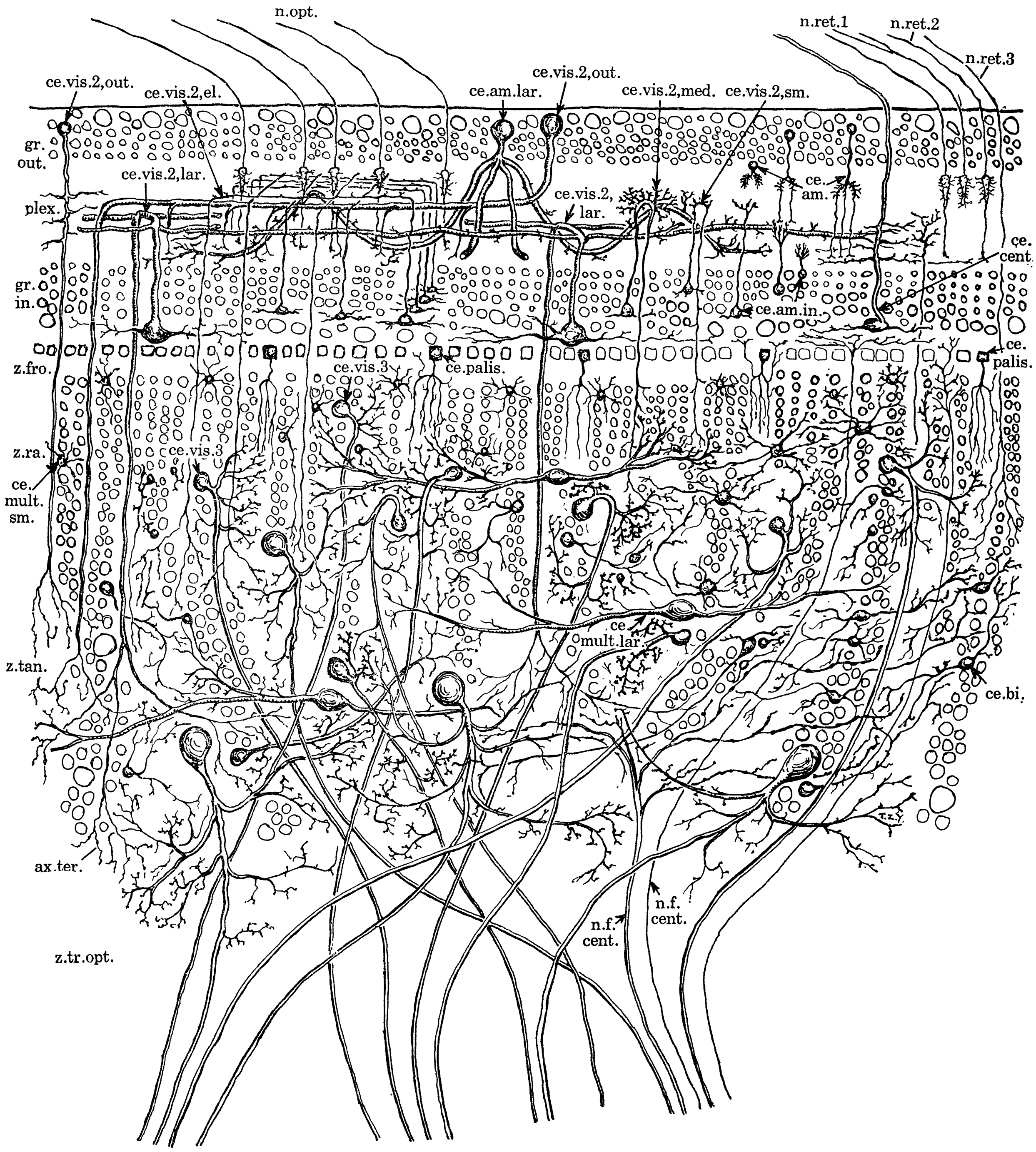


Figure 112. Diagram of some of the cell types found in the optic lobe of *Loligo* as seen in a transverse section. The long axis of the lobe therefore runs across the page.

Counts made on a small squid showed a total of over ten million neurons in the outer granule layer, and this is probably an under-estimate (figure 113). The great majority have nuclei less than 5 μm in diameter and are probably amacrine cells. It is not possible to say for certain how many outer granule cells send axons to the medulla, but one million may be a useful estimate, namely all those with nuclei of 6 μm and over in this specimen. The diameters in this small squid are of course less than those quoted above for larger animals.

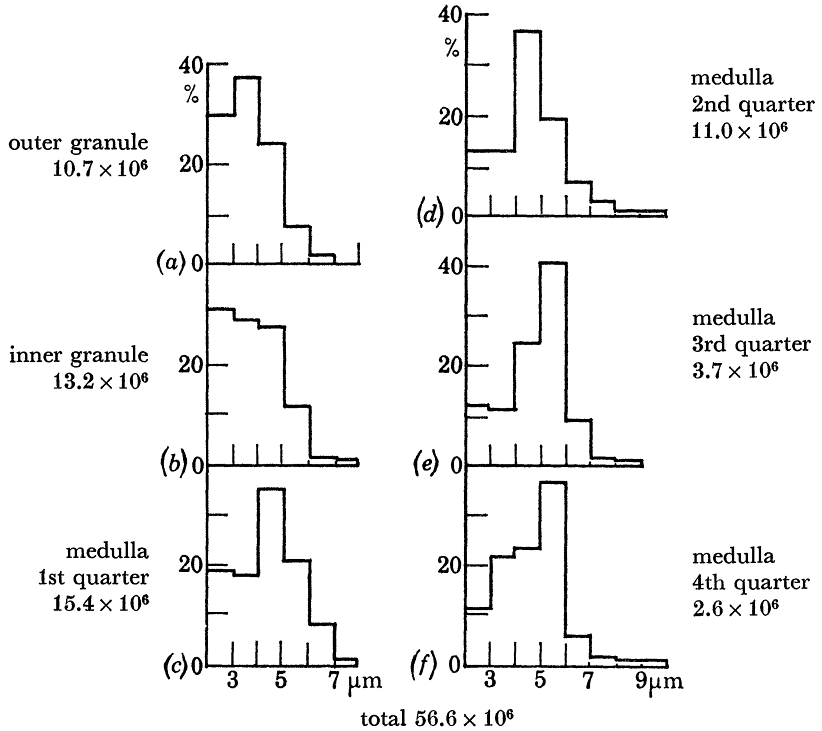


FIGURE 113. Numbers and nuclear diameters of neurons in the optic lobe of a small *Loligo vulgaris* (mantle length 7 cm).

8. OPTIC NERVE FIBRES AND THEIR ENDINGS

The optic nerve fibres enter the lobe in bundles (figures 5 to 7), which divide up as they pass through the outer granule layer. As in *Octopus* there is a progressive twisting leading to re-assortment of the fibres as the bundles divide (figure 114). This preserves the original relationships of the fibres after passing through the chiasma (Young 1971). This very accurate registration of connexions recalls the condition revealed in the eye of the fly by Horridge & Meinertzhagen (1970). Passing through the outer granule cell layer the fibres form smaller and smaller bundles and finally enter the plexiform zone singly (figure 7).

The majority of the optic nerve endings have the typical conical or carrot shape seen in *Octopus* (Case, Gray & Young 1972) (figures 9 and 114 to 117). Immediately on entering the plexiform zone the fibre shows an expansion, smoothly rounded at the edges. Proceeding in through the first radial layer of the zone it gradually tapers, carrying numerous very short lateral twigs. These twigs are in relation to the collaterals of the external amacrine cells and also to fibres entering from below, including inner amacrine cells and possibly fibres from the optic lobe or beyond (though these last have not been identified for certain (Dilly, Gray & Young 1963)).

The twigs on the 'carrots' cease abruptly at the first tangential zone, but it may be that the lower of these twigs make synaptic contact with the various bulbous formations on the smaller second-order visual cells, both those with circular and with short orientated fields (p. 281). Many of the optic nerve fibres then continue as fine smooth threads to the second or third tangential layer. Here each begins to become beaded again and finally swells into a small bulb (figures 116, 117 and 9). From this bulb proceeds a final hook, or a few very fine terminal threads. These endings are at the level of various components of the inner tangential layers. It has not been possible to determine with which types of dendrite they make synaptic contact, but probably with the very long dendrites of the large second-order visual cells, also with the dendritic collaterals of the efferent fibres to the retina and with both large and small amacrines.

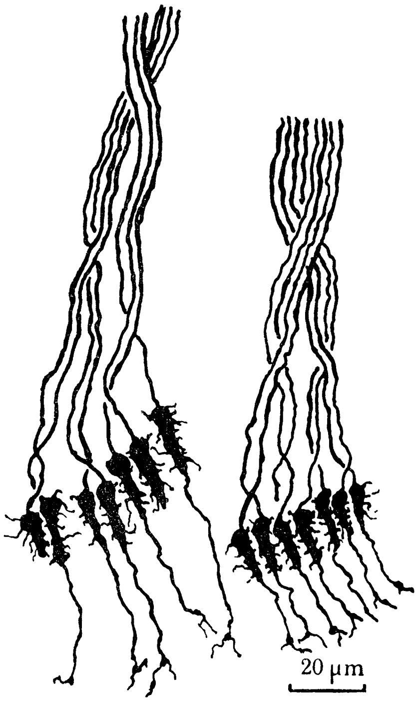


FIGURE 114. Endings of optic nerve fibres within the optic lobe. The fibre bundles cross over at each division point down to the very last, restoring the order of their origin in the retina. Golgi–Kopsch method used for sections illustrated in figures 114–120 inclusive.

The final bulbs and twigs mostly lie just deep to the second tangential layer as if largely in the third radial layer. The limited extent of these final terminations is a striking contrast to the great area presented by the numerous branches at the outer end of each optic nerve fibre in the first radial layer. It is significant that it is the few inner terminals that make contact with the second-order dendrites, so that each primary nerve fibre can influence only a very small extent of the surface of a second-order neuron. At present nothing can be said about the possible effects of the amacrines on the 'carrot' endings, but they certainly present a large surface to them.

It is a question whether any optic nerve fibres end in the first radial layer, without continuing further. Some of them seem to terminate at the first tangential layer (figure 9), but it is hard to be sure that this is not due to the plane of section, or failure to stain. However, fibres ending here have been seen in *Octopus* (Young 1971) and by Cajal (1917) in *Sepia*, so it will be assumed that they exist also in *Loligo*.

A further question is whether any optic fibres run through the plexiform zone to the medulla. Such fibres were found in *Octopus* (Young 1971) and by Kopsch (1899) in *Loligo*. As Cajal emphasized, the difficulty is to distinguish them from processes of cells of the outer granular layer (p. 278). It will be assumed that such optic nerve fibres do exist in *Loligo*, and terminate in the outer part of the medulla (?n.ret.3, figure 116). The fibres in question probably run

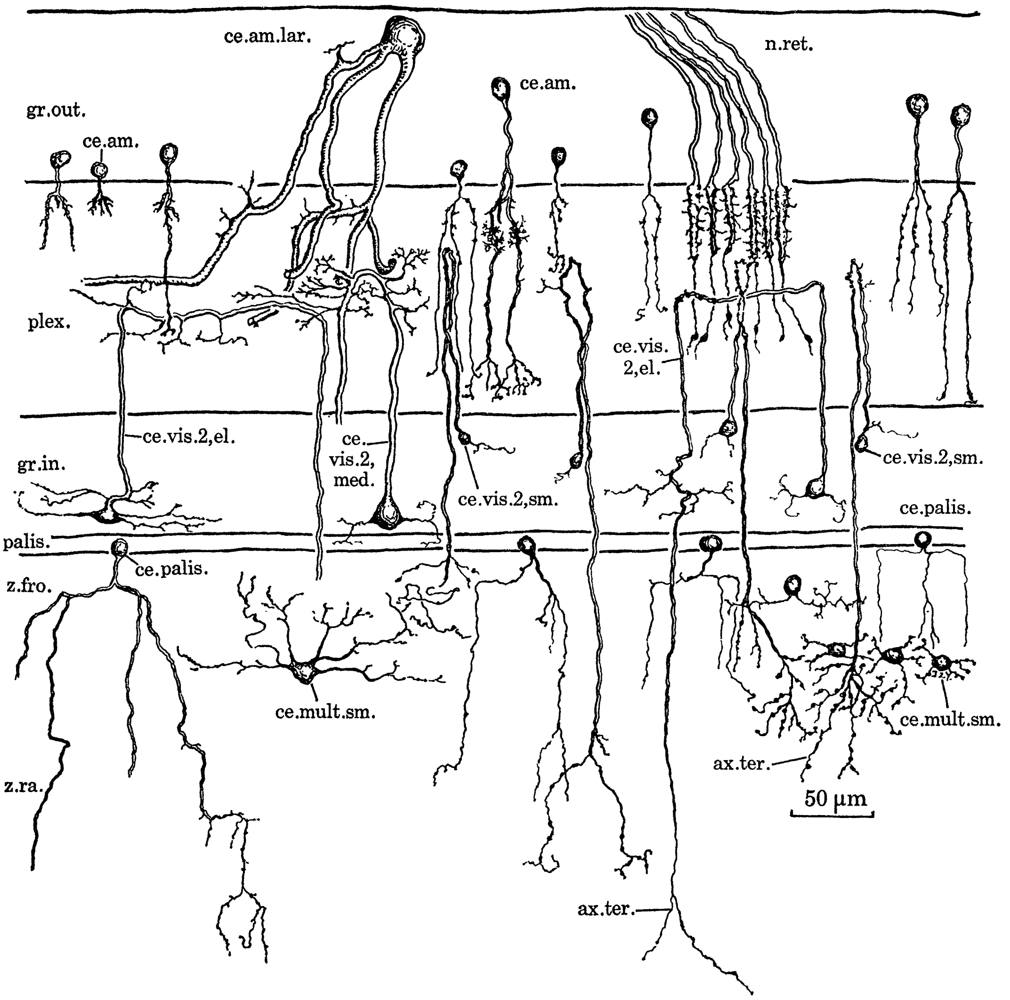


FIGURE 115. Drawing of optic nerve fibres and other constituents of the deep retina seen in sagittal section. This and figures 116 and 117 are composites made from tracings of cells seen in different parts of the same preparation.

through the first radial zone without a swelling (as they also do in *Octopus*). Within the medulla they soon begin to show swellings, also small collateral twigs and a few larger branches. They then taper away to a fine varicose terminal at a short distance from the surface.

The optic nerve endings of *Loligo* are thus considered to include three classes: (1) those with a swelling in the first radial layer but not proceeding beyond; (2) those with a swelling in the first radial layer and continuing as a fine thread to end in the second and third tangential layers; (3) those proceeding to the medulla. The majority seem to belong to the second category.

9. CELLS OF THE OUTER GRANULE CELL LAYER

These are a rather heterogeneous population ranging from very large cells at the outer side to tiny ones within (figures 5–8). Cajal (1917) supposed that all these cells were amacrines, but it is now shown that this is true only of the small ones and some of the largest. We can therefore recognize two main types: (1) Those with trunks restricted to the plexiform layer. These have

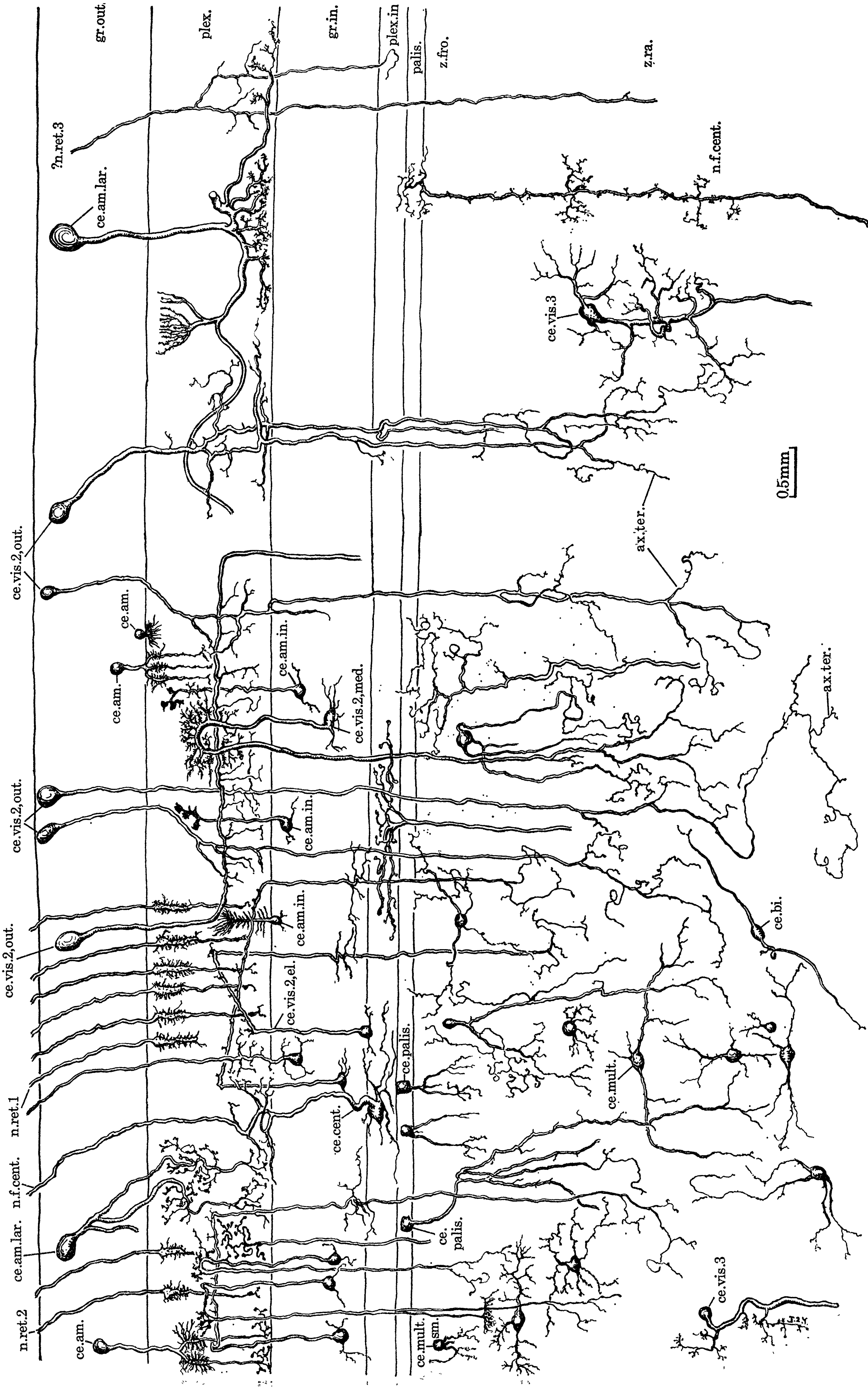


FIGURE 116. Drawing of further cells seen in sagittal section.

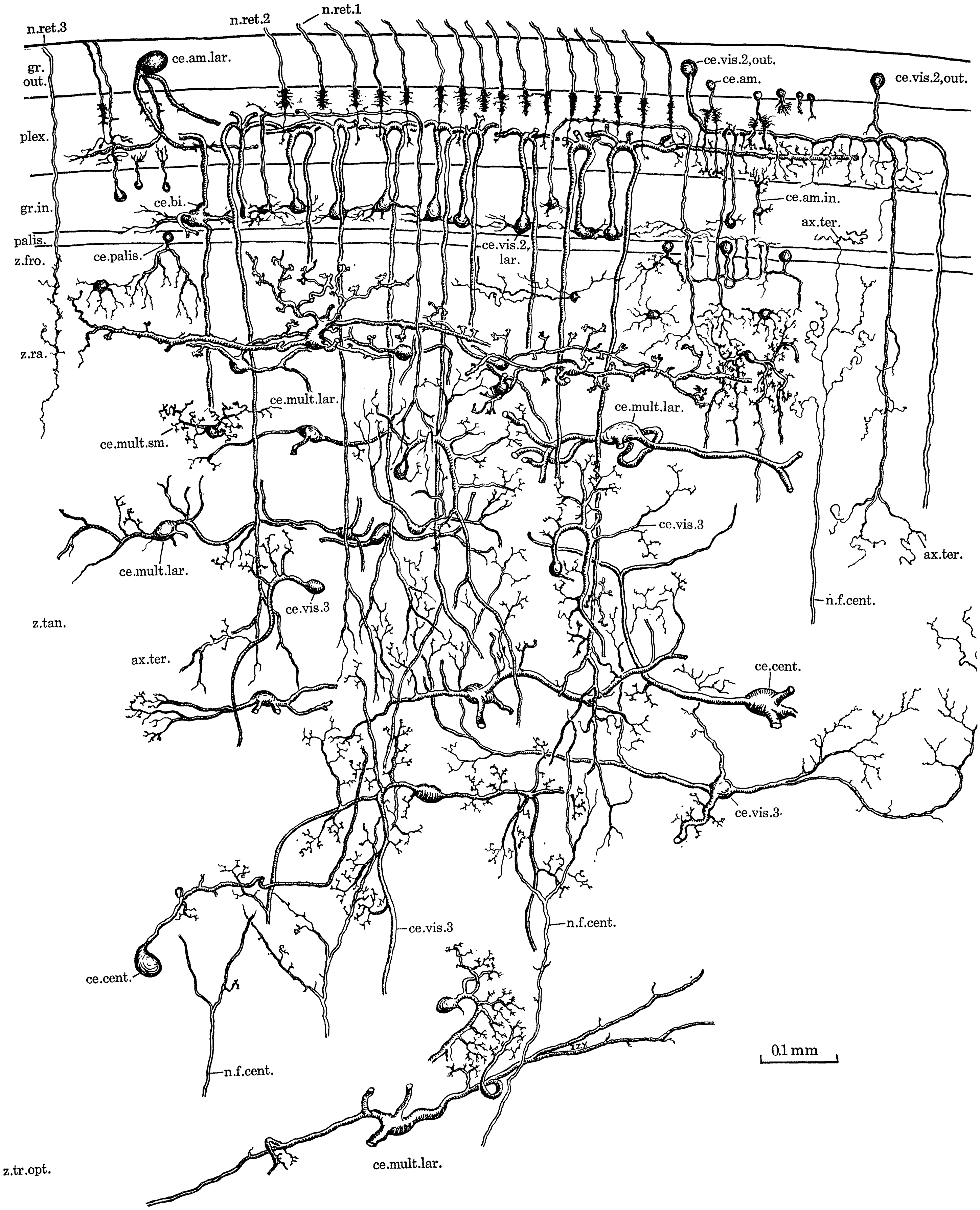


FIGURE 117. Drawing of cells in sagittal section showing especially the axons of the largest second-order visual cells, the large multipolar cells of the medulla and the third-order (efferent) cells of the lobe.

no single axon and can thus be called amacrine cells (though not all are small). (2) Second-order visual cells with axons proceeding to the medulla after giving dendritic branches in the plexiform zone.

9.1. *Amacrines of the outer granule cell layer*

These are of various sizes. The smallest of them, in the innermost layers, have numerous very short bushes in the first radial layer (ce.am., figures 115–117, 11, 12). The larger ones have branches proceeding to the deeper parts of the plexiform zone and the largest of all spread for great distances.

The trunks of the medium-sized ones usually divide into two or more branches as they enter the plexiform zone, but occasionally a single main trunk runs straight through without division. The trunks show numerous very fine branches as they pass through radial layer 1 probably all have these branches, though they show more clearly on some than others. A few amacrines have a single trunk running to tangential layer 1 and turning there to the tangential plane. Many end in fine bulbs among the trunks of the small recurrent second-order visual fibres of the first tangential layer. Others run deeper to give branches in either of the tangential layers 2, 3, or 4, or in several of these and in the radial layers between. The branches of each of these small amacrines occupy a cylindrical space, that is they diverge only slightly as they pass through the plexiform zone (ce.am., figure 13). Each thus produces its effect only in a cylinder of small radius.

These amacrine trunks sometimes show coarse knobs at the level of the first tangential layer, (figure 5). These knobs are in relation to the somewhat similar knobs on the tops of the smaller recurrent axons and are often difficult to distinguish from them (p. 281). They make quite elaborate grape-like endings. Amacrines of the inner granular layer have similar but even larger endings at this level (p. 280).

The main terminal branches of any one medium amacrine cell usually end at the same level (figures 115, 116). The terminal branches may be few or quite abundant. They diverge slightly, but usually only for less than 100 μm and mostly all end quite close together. Many come into relation with the dendritic collaterals of the second-order visual cells with small fields (figure 14). When they proceed deeper they diverge rather more widely and may branch a few times before ending. The fibres are beaded along their length, it may be that they make synapse all along and not only at their ends.

The largest amacrines have very widely spreading processes. (ce.am.lar., figures 115, 116 and 15). They arise from cells in the outermost granule layers and divide into massive branches within the outer granule layer and these into numerous short ones in the plexiform zone (figures 115–117). It is difficult to distinguish them from the large second-order visual cells, which also have branches in the same regions and in addition have an axon proceeding to the medulla (p. 279). The large amacrines have such wide-spreading branches that it has been very difficult to show their whole extent. They sometimes send a branch down to tangential layer 3, where it gives numerous collaterals and then proceeds back again to give further branches in radial layer 1 (figure 6). Single branches of these cells may go several times down to the deeper plexiform layers and then out again to radial layer 1, giving collateral twigs at various levels (figures 16 and 112). It is assumed that these large cells are amacrines in the sense of having no single axon. However, they are by no means microneurons, since their processes spread very widely in all directions. It may well be that they are functionally similar to horizontal cells in the vertebrate retina (see Discussion, p. 299).

Cajal (1917) described some external amacrines as sending branches to the inner plexiform zone. These have not been seen in the present material. It is obviously hard to distinguish them from cells that have branches in the inner plexiform zone and then send axons in to the medulla (p. 278). It will be assumed that they are all in that category (i.e. are not amacrines).

Cajal (1917) also described multipolar cells in the outer granule layer (of *Sepia*), some with branches spreading widely near the surface. These also may function as horizontal cells.

The outer amacrines are thus in a position to serve either to produce some influence within radial layer 1 alone (e.g. between neighbouring optic nerve endings) or to carry signals from radial layer 1 to the tangential layers and perhaps also in the reverse direction. The larger ones could serve to even out the level of excitation or inhibition over large areas of the plexiform zone (p. 299).

9.2. *Second order visual cells of the outer granule cell layer*

These are all large neurons with cell bodies in the outer part of the layer. They are of two sorts: (1) those running directly through to the medulla, with restricted dendrites in the plexiform zone; and (2) those turning to run for a long distance in the tangential plane before proceeding to the medulla.

The first class have dendritic twigs in the first radial zone and then several rather larger ones as they pass through the deeper outer plexiform layers ce.vis.2,out., figures 116, 117). These cells have been very difficult to follow. The axons may give branches as they pass through the inner granule or inner plexiform layers and then proceed on to divide up into terminal branches in the medulla. It is clear that these are axons and that they come from trunks that run right through the outer plexiform and outer granule layers. Because of the dark staining of the Golgi preparations in which they occur it is seldom possible to trace them to cell bodies in the outer granule layer. It has been suspected that they might really be optic nerve fibres running through (see p. 273). The branches in the deeper outer plexiform layers, however, suggest that these are indeed the trunks of outer granule layer cells acting as second-order visual neurons collecting influences from optic nerve fibres in a limited area of the outer plexiform zone.

DESCRIPTION OF PLATE 10

FIGURE 16. Branch of a large amacrine cell of the outer granule cell layer to show how it proceeds several times from the deeper plexiform layers to the more superficial and back again. Transverse section. Golgi. Re-touched.

FIGURES 17, 19. As figure 18 (see p. 267), to show second-order visual cells of the outer granule cell layer (ce.vis. 2 out). Sagittal section. Golgi. Figure 17 is re-touched.

FIGURE 20. Oblique tangential section through the inner granule cell layer, showing the cells grouped around the radial fibre bundles. The inner plexiform layer appears on the right Sagittal section. Cajal.

FIGURE 21. Oblique tangential section through the inner granule cell layer showing the larger cells in the deeper parts and the inner plexiform layer. Sagittal section. Cajal.

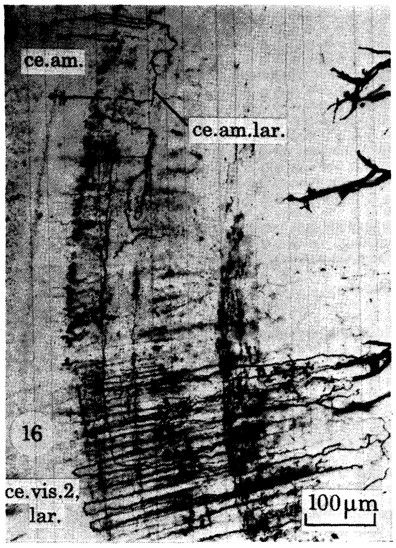
FIGURE 22. Tangential section through base of inner granule cell layer, showing large cells and some very long fibres of the inner plexiform layer. Sagittal section. Cajal.

FIGURE 23. Amacrine cells of the inner granule cell layer. Sagittal section. Golgi.

FIGURE 24. Short amacrine cell of inner granular layer with numerous fine processes. The photograph also shows the blunt granular knobs in the second radial layer which may also be the endings of amacrine cells (ce.am.in.?). Sagittal section. Golgi.

FIGURE 25. Blunt granular knobs presumed to be of inner amacrine cells, showing their relationships to outer amacrine processes. The photo also shows a tangential amacrine fibre (ce.am.tan.). Transverse section. Golgi photograph has been re-touched.

FIGURE 26. Three cells sending centrifugal fibres to the retina. Sagittal section. Golgi.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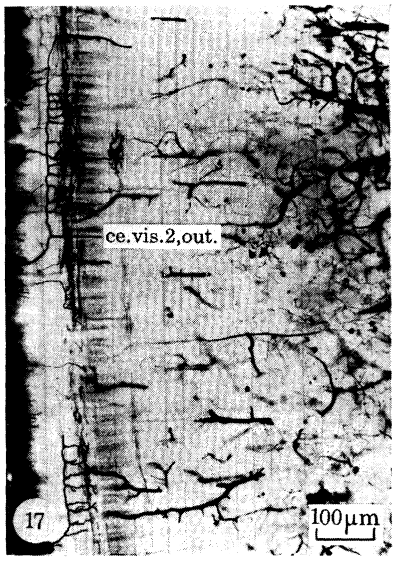
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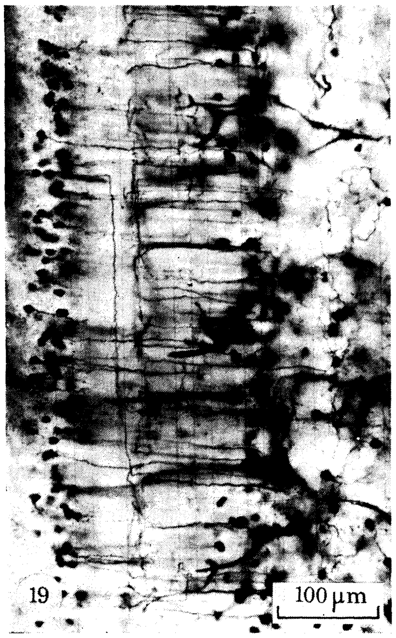
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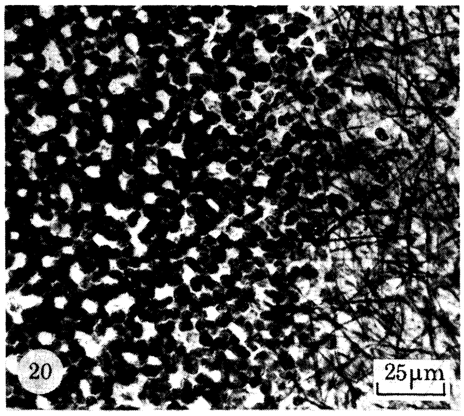
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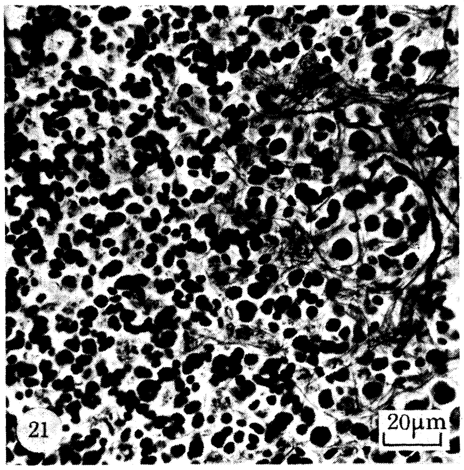
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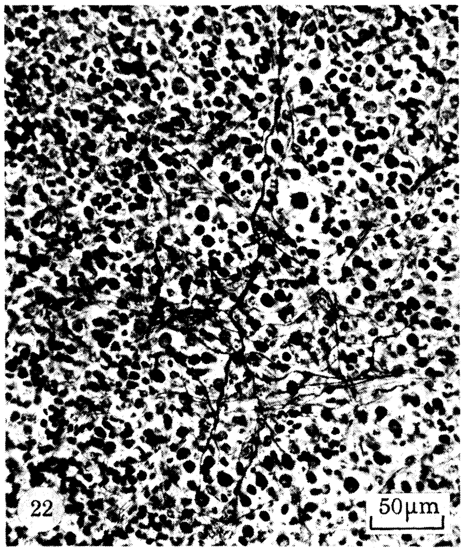
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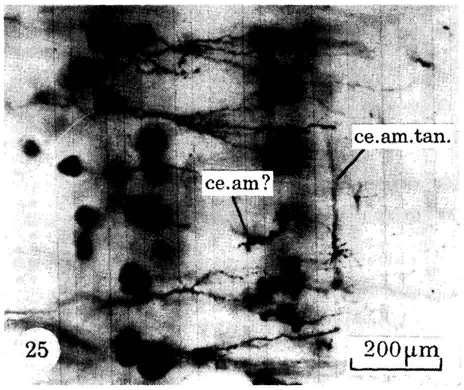
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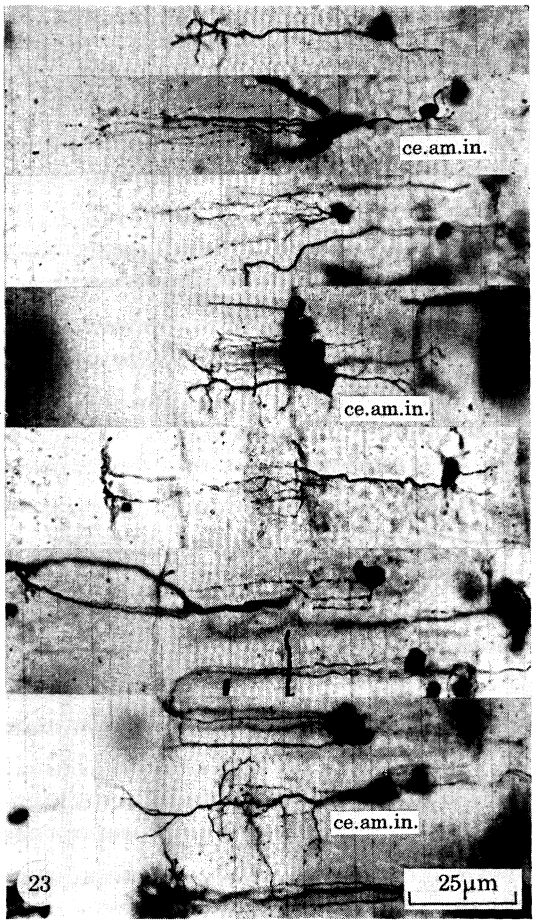
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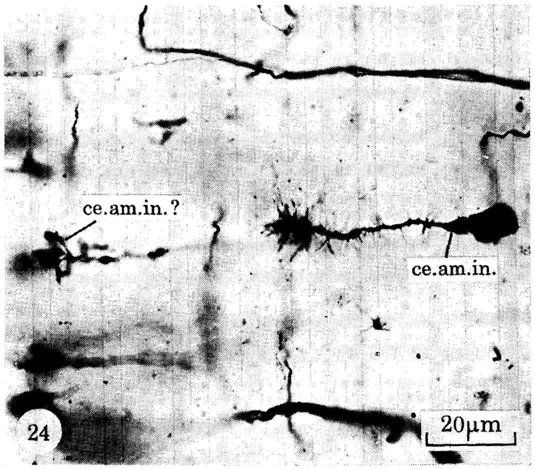
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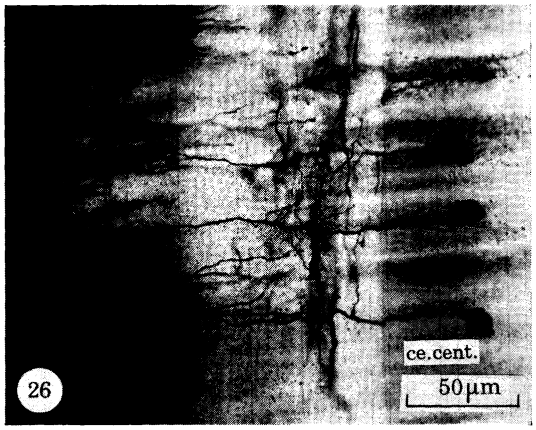
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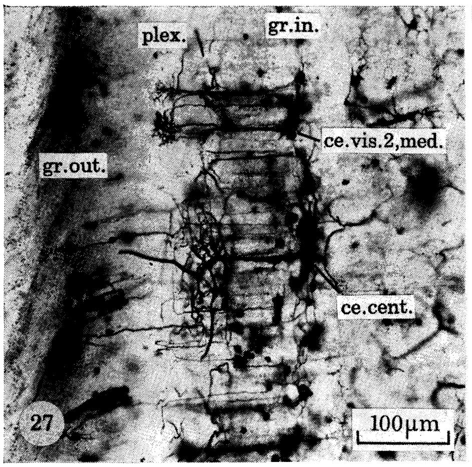
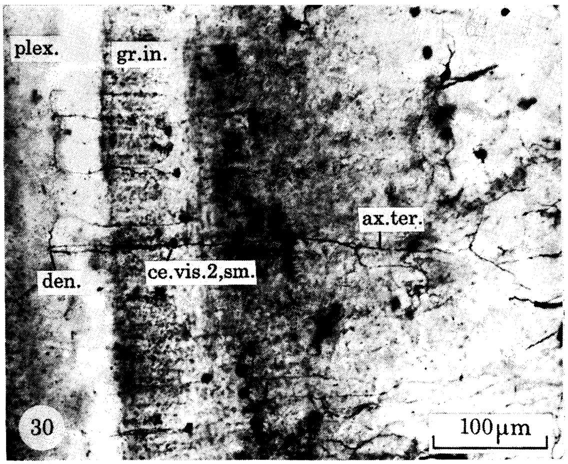
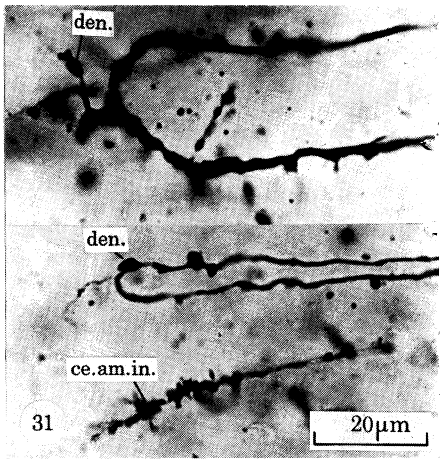
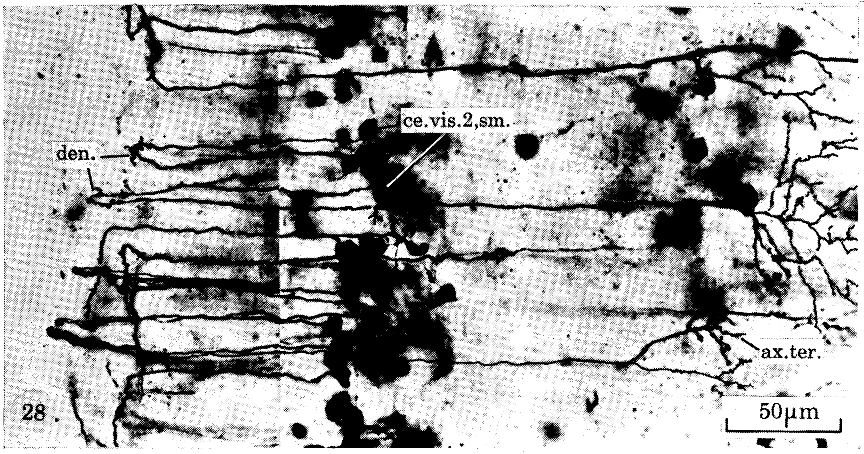
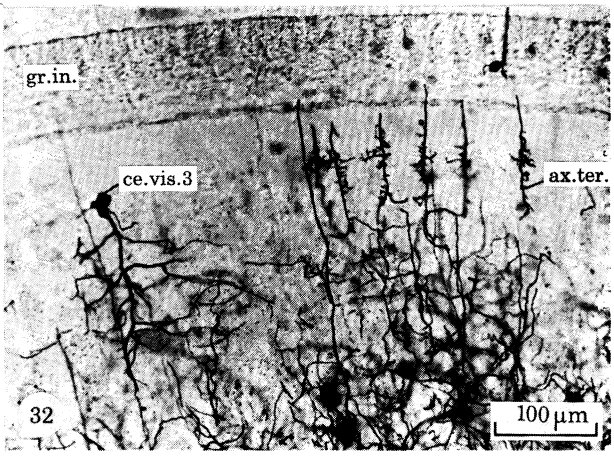
FIGURES 16, 17, 19–26. For description see opposite

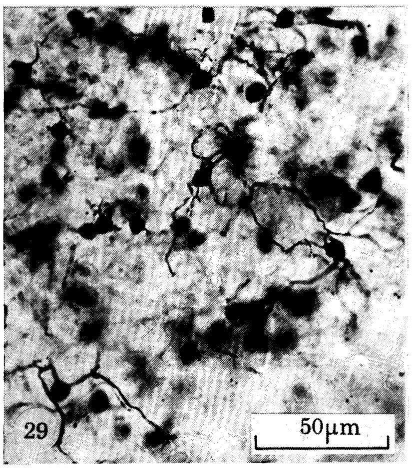


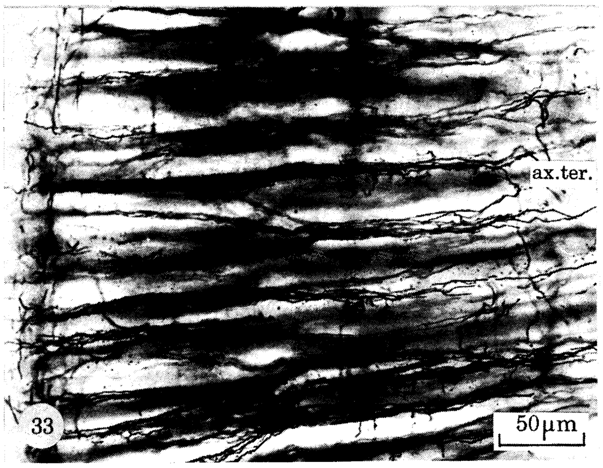


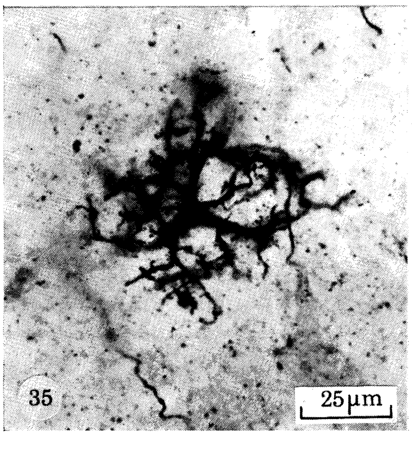


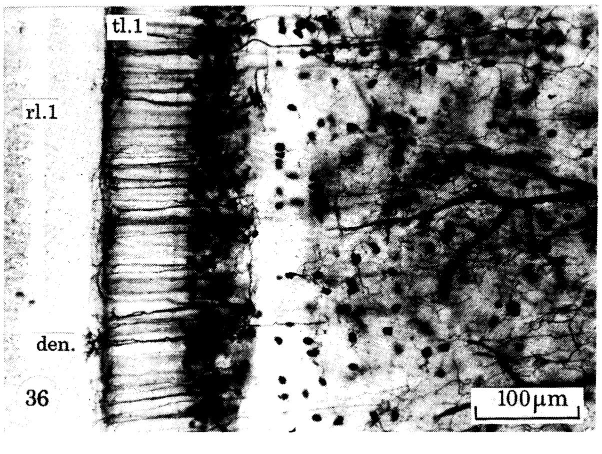












FIGURES 27–36. For description see opposite

The other class of second-order visual outer granule cells has been seen very clearly. Their trunks proceed tangentially for long distances in the plexiform zone. Many have only a single process running straight in the first tangential layer (ce.vis.2,out., figures 116, 117, 17–19). These trunks give numerous dendritic collaterals; some are quite short, but most reach down into the deeper plexiform layers. The fibre finally turns down through the inner granular layer. It becomes narrow at this point but then increases again as it runs into the medulla (figures 117, 17). No fibre has been followed all the way from the cell body to final termination in the medulla, so it is not known how deeply they run.

10. Inner granule cell layer

10.1 *Cell types and sizes*

The inner granule layer includes at least four types of cell. The thickness and actual number of cells is greater than in the outer granule layer (figure 113). There is a progression from smaller cells close to the outer plexiform zone to the largest ones, which are the deepest (figure 5). But cells of several sizes and types occur at each level. In its outer part the inner granule layer includes cells of two sorts, with nuclei of about 3 and 6 μm diameter (figure 20). They are grouped around the regular bundles of large fibres that pass through this layer. This arrangement contrasts with the fine fibre bundles passing through the outer granular layer (figure 8). These more superficial inner granule cells include the inner amacrine cells and the smaller centripetal (second-order visual) cells with recurrent axons. Deeper in the layer are larger cells, with nuclei of up to 8 μm, often oval in tangential section (figure 21). These include some second-order visual cells and also cells with centrifugal fibres proceeding to the retina.

Finally, at the inner side of the inner granular layer are very large cells with nuclei up to 20 μm and cell bodies 30 μm or more in diameter. These are centripetal second-order visual

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Description of plate 11

Figure 27. Large cell sending centrifugal fibre to the retina, showing its basal dendrites and dendrites in the deep plexiform layers. Sagittal section. Golgi.

Figure 28. Second-order visual cells with very small dendritic fields (den.) and axon terminals near the surface of the medulla (ax.ter.). Some longer straight second-order dendrites are also shown. Note that they lie deeper than the very small dendrites. Re-touched photograph. Sagittal section. Golgi.

Figure 29. Section tangential to the inner granule cell layer to show the basal dendrites of smaller second-order visual cells. Sagittal section. Golgi.

Figure 30. Single complete second-order visual cell with very small dendritic field and recurrent axon terminating near the surface of the medulla. Sagittal section. Golgi. Photograph re-touched.

Figure 31. Tops of two second-order visual neurons with very small fields, showing short branches and characteristic swellings. Sagittal section. Golgi.

Figure 32. Axons and their endings in the outer part of the medulla, presumably of small second-order visual cells. Also a third-order visual cell. The surface of the lobe is above. Horizontal section. Golgi.

Figure 33. Radial bundles of axons entering the medulla and many ending there. Transverse section. Golgi.

Figure 34. Second-order visual cells with medium-sized round dendritic fields in the centre of the plexiform layer, seen laterally. Sagittal section. Golgi.

Figure 35. Single circular dendritic field of medium-sized second-order visual cell, seen in tangential view. Sagittal section. Golgi.

Figure 36. Low-power view of Golgi preparation to show a round dendritic field (den.) slightly superficial to the layer of long straight dendritic fields (tl.1). Sagittal section. Golgi.

cells with large dendritic fields in the second tangential layer and recurrent axons reaching deep into the lobe. These large cells lie very close to the inner plexiform layer to which they send enormous spreading dendritic fields (figure 22). Deep to this again lies the palisade zone, where the nuclei are about 5 to 8 μm in diameter (p. 288).

10.2. *Reversed amacrine cells of the inner granule cell layer*

This is a convenient name for cells of the inner granule layer whose branches proceed to the outer plexiform zone but do not leave it again. These cells often have several basal dendrites (ce.am.in., figure 23) or several short processes arising close to the cell body. There are then one or several branches proceeding to the inner tangential layers and sometimes one or several passing right up to the first radial layer (figure 116). These branches are granular and may show very numerous fine lateral twigs (figure 24). Some of the cells close to the outer plexiform zone give simply a bunch of fine branches, similar to those of the smallest outer amacrines (figure 117).

The tips of the reversed amacrines often carry rather large swellings at the level of the inner edge of radial layer 1 (figures 116, 24, 25 and 31). These lumps are very conspicuous in some Golgi preparations, but are often stained without showing their connexion with the cell body. Indeed it has been hard to decide which of them belong to inner amacrines and which to outer amacrines or the tops of second-order visual neurons (p. 282). Fibres running tangentially in radial layer 2 and ending in tufts of fine twigs also probably belong to reversed amacrines (ce.am.tan., figure 25).

10.3. *Efferent fibres to the retina*

The cell bodies of the efferent (centrifugal) cells lie in the inner granule layer (ce.cent., figures 116, 26 and 27). They are of various sizes, the largest lying in the deepest layer. Most of them have basal dendrites, which are especially conspicuous on the larger ones, spreading in all directions in the inner plexiform zone. Probably these basal dendritic fields are circular. Their final twigs carry bushes of collaterals.

The main trunk of the centrifugal cell runs unbranched through the inner granule cell layer. Immediately on entering the outer plexiform zone it gives lateral branches in tangential layer 4 and then others in tangential layers 3 and 2. There is thus some sign of lamination, but the branches do not keep strictly to any one layer (figure 27). In particular, they tend to turn downwards into the radial layers between the tangentials. The branches divide dichotomously five or more times and the terminal ones carry numerous fine twigs.

The main trunk then runs on, through radial layers 2 and 1. Here it may show a few further short branches. Possibly all the fibres have lateral twigs here too fine to be seen, but many of them seem smooth as they pass through the first radial layer.

10.4. *Second-order visual cells of the inner granular layer*

10.4.1. *Recurrent centripetal cells*

The inner granule cell layer contains numerous cells whose trunks proceed to the outer plexiform zone, give dendritic collaterals there, and then turn back as axons proceeding to the medulla. These vary in size from minute cells with restricted dendritic fields and short axons to very large ones whose dendrites might be influenced by thousands or tens of thousands of optic nerve fibres and whose axons proceed far into the medulla. All these presumably serve as second-order visual neurons and the particular forms of their dendritic trees may in part specify the configurations of visual stimuli to which they respond. In this way they would serve to classify and encode the visual input.

This possible classifying function can be used to divide them into four types (figure 112): (1) Cells with a restricted circular field of dendrites and short axons (ce.vis.2,sm.). (2) Cells with a larger circular dendritic field and longer axons (ce.vis.2,med.). (3) Cells with very narrow elongated dendritic fields (ce.vis.2, el.). (4) Cells with very large, oval dendritic fields (ce.vis.2,lar.).

Each of the last two classes includes cells with fields of different orientation and length. It may be that in all of the classes there are cells with other specific properties.

10.4.2. *Recurrent cells with very small fields and short axons*

These are cells of the inner granular layer whose fibres proceed to tangential layer 1 and then give dendritic collaterals and turn sharply back. Their recurrent axons may give a few branches within the inner granular layer or inner plexiform layer but they mainly end in the outer layers of the medulla (ce.vis.2,sm., figures 28, 30, 112 and 115). The cell bodies are about 3 μm in diameter and carry a few short basal dendrites all round, or sometimes mainly in one direction (figure 29). These dendrites are varicose and branch two or three times in the neighbourhood of the cell. A trunk of about 2 μm or less in diameter proceeds through the plexiform zone, to a level slightly above (distal to) tangential layer 1 and then turns very sharply down. It carries a few conspicuous dendritic swellings and short branches near the point of the turn (den., figures 28, 31). These swellings are probably postsynaptic to the first-order visual fibre endings. This is of course also a region containing branches of both outer and inner amacrines, including the large swellings of the latter (ce.am.in., figure 31). Presumably each of these smallest second-order visual fibres samples only a very small visual field, perhaps making contact with only one or few optic nerve endings.

The axons of these sharply recurrent fibres run to the outer levels of the medulla (ax.ter., figures 115, 116, 119, 28 and 32). They may give collaterals in the inner plexiform layer, similar to those of the larger recurrent axons (see below). They give branches in the frontier zone, which proceed at right angles to the main trunk for a short distance (25 μm) and carry swellings (figure 32). The main trunk continues in the central direction and tapers away to a few fine endings limited to the outer 200 μm of the medulla. Since these and the larger axons enter in bundles this arrangement provides for cylinders of endings of the smallest second-order visual fibres within and around each bundle (figure 33). Each cylinder has a diameter of about 50 μm. The endings of its axons are mingled with branches of the multipolar cells of the frontier zone and third medullary zone (p. 291) and also with fibres ascending from the centre of the lobe.

10.4.3. *Recurrent fibres with larger circular dendritic fields*

These are very conspicuous in the region of the first tangential layer (den., and ce.vis.2,med., figures 34, 35 and 116). Their cell bodies lie deep in the inner granule layer and are of medium size (10 μm diameter), with basal dendrites. The trunk is stout, about 4 μm in diameter and turns over sharply in the outer part of the first tangential layer. As it turns it gives off numerous short stout collaterals, which divide after a short distance into numerous fine terminals. These dendritic branches arise all round the arching trunk and probably sample a circular field of optic nerve endings (figure 35). They may lie at a level just below the first tangential layer as well as above it. The visual field sampled is thus larger than that of the cells mentioned last, but smaller than the next classes. The axon proceeds immediately back, close to its ascending parent, and enters the medulla. The final branches are somewhat deeper than those of the first class of cells (figure 116).

10.4.4. *Second-order visual cells with narrow, orientated dendritic fields*

These form a striking mesh of receptive fields in the first tangential layer, of which they are a main component (figures 36 and 38). Each arises from a cell body of medium size (10 to 20 μm) lying rather deep in the inner granule layer and carrying basal dendrites spreading for a short distance (figures 112, 115–117 and 119). The trunk proceeds straight to the level of tangential layer 1 and then turns sharply into the tangential plane and runs for a variable distance before turning back into the centre of the lobe (den., figure 37). As they run through the first tangential layer the fibres are often orientated in sets, parallel to each other and at right angles to other nearby sets (den., figure 38). The second turn may take place after a course of at least 400 μm, but most are much shorter (150 μm) (figure 39). The tangential portion in the plexiform zone carries swellings and gives off short lateral branches (ce.vis.2.el., figures 115 and 116, and den., figure 37). Probably there are many other branches too fine to be seen. However, these trunks give fewer large branches or large knobs than the previous type. The endings of the two types can be compared in figure 28.

At the level where they run tangentially these fibres are of course in the region of the lower ends of the 'carrots' of the optic nerve fibres and of branches of the amacrines of the outer and inner granular layers. Their dendritic fields form a network of straight fibres, which appear in sections taken sagittally to the surface of the lobe. They run in various directions (figure 41), but the greatest number run along the long axis of the lobe (figure 46). Since the trunk of each

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DESCRIPTION OF PLATE 12

FIGURE 37. Complete single second-order visual cell showing basal dendrites, short, narrow dendritic field in the first tangential layer and axon with branches in the superficial part of the medulla. Re-touched photograph. Sagittal section. Golgi.

FIGURES 38, 39. Long narrow dendritic fields of second-order visual neurons in the first tangential layer. Sagittal sections. Golgi.

FIGURE 40. Sagittal section to show several large second-order visual cells with branches spreading in the second tangential layer. Sagittal section. Cajal.

FIGURE 41. Section tangential to surface of optic lobe showing dendrites of second-order visual cells running in all directions, but with many in the long axis of the lobe, which is that of the page, or at right angles to this. Sagittal section. Cajal.

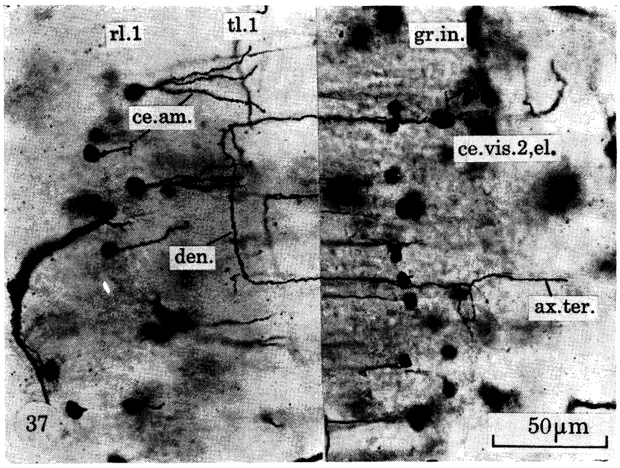
FIGURE 42 (*a*) Golgi preparation showing terminations of large second-order visual cells. Sagittal section.

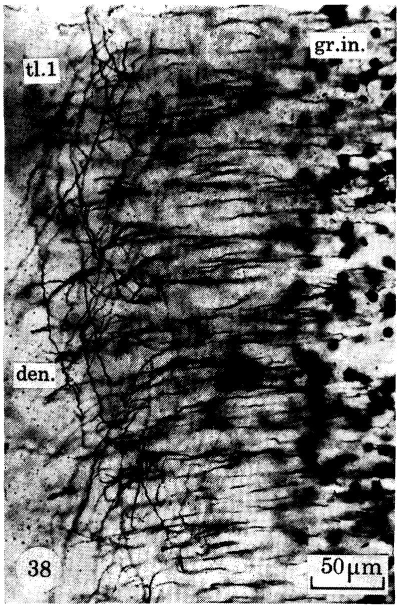
FIGURE 42 (*b*) An oblique sagittal section of *Alloteuthis* to show the course and terminations of the large second-order visual cells. Golgi preparation. This figure has not been re-touched.

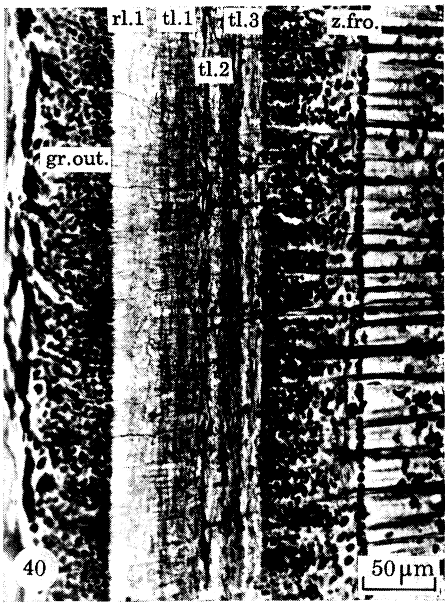
FIGURE 43. Section tangential to surface of the optic lobe, showing the various layers and the branches of one large second-order visual cell in the second tangential layer. Sagittal section. Cajal, re-touched.

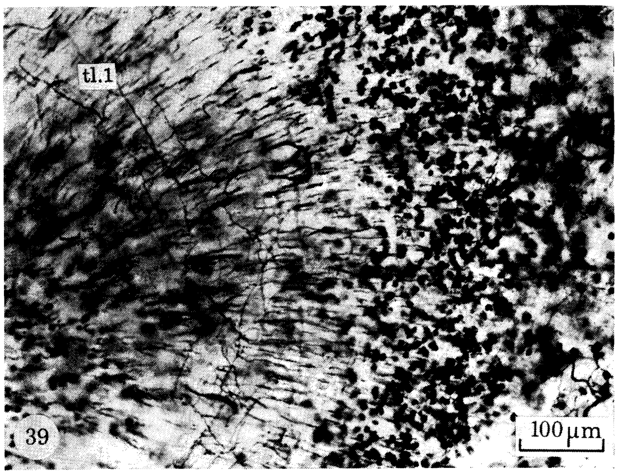
FIGURE 44. As figure 43, at higher magnification to show the large cell, but not re-touched. Sagittal section. Cajal.

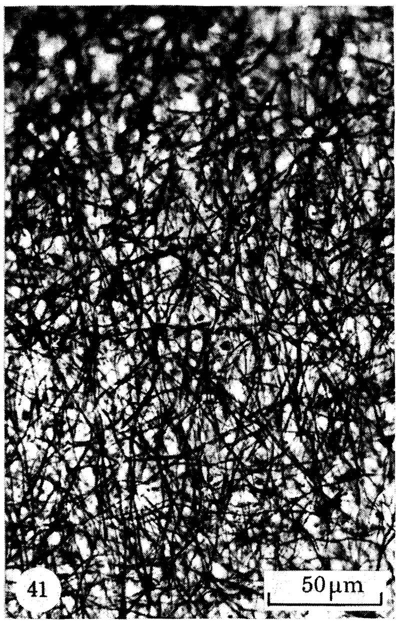
FIGURE 45. Section through the second tangential layer to show the tops of several large second-order visual cells, all orientated transverse to the long axis of the lobe, re-touched. Sagittal section. Cajal.

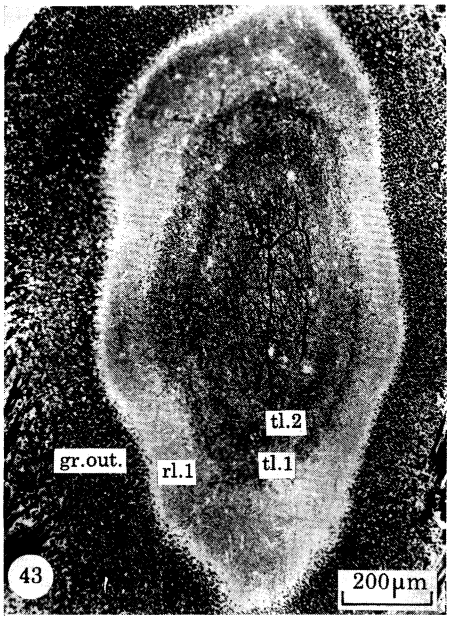


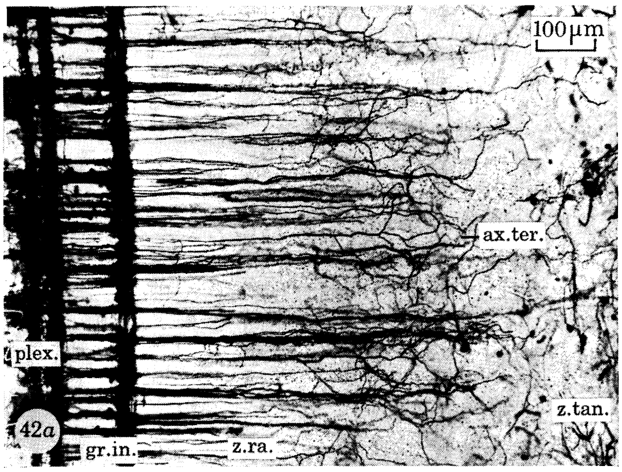


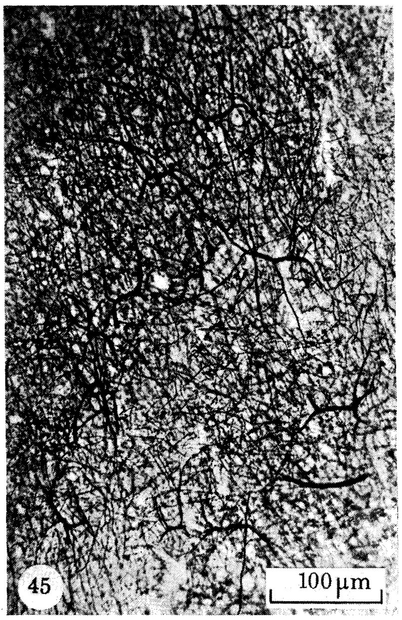


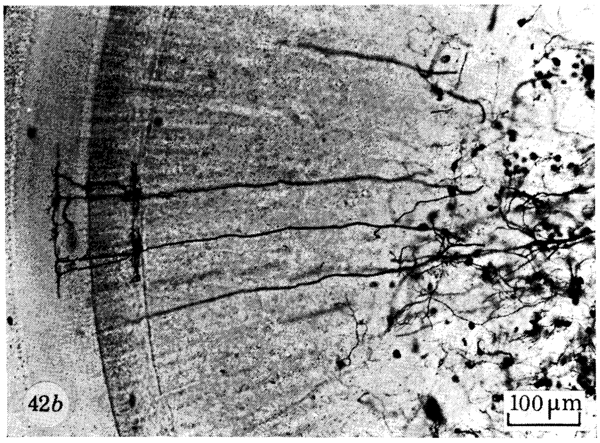


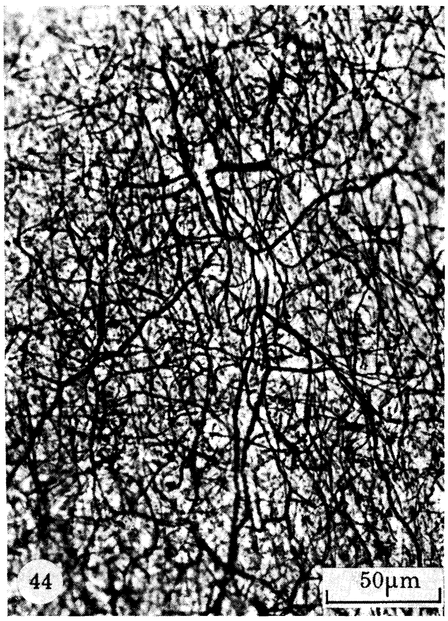






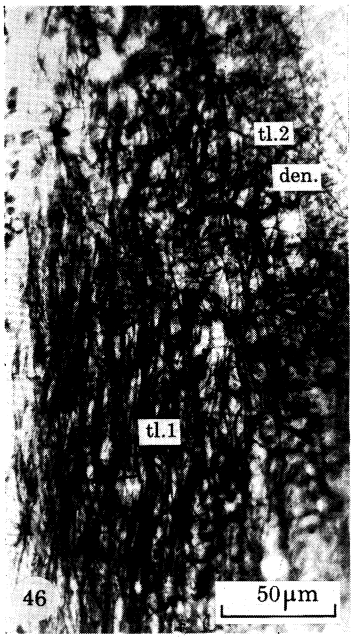


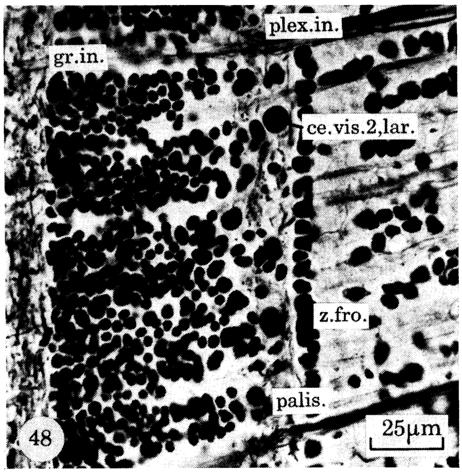


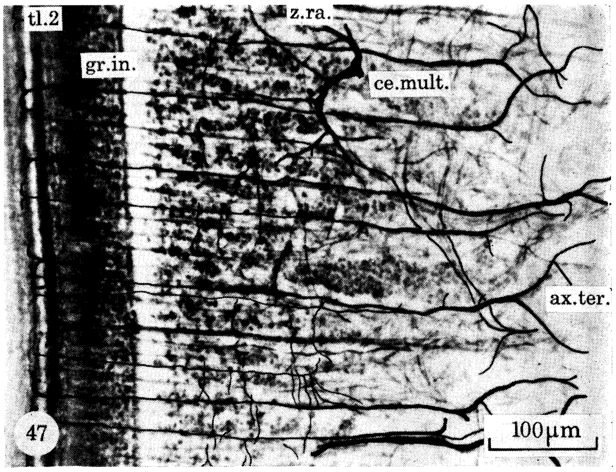


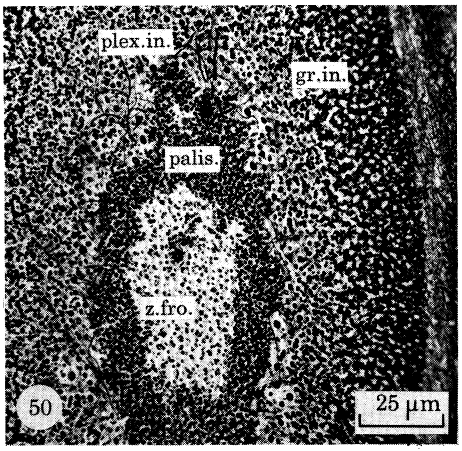
FIGURES 37–45. For description see opposite

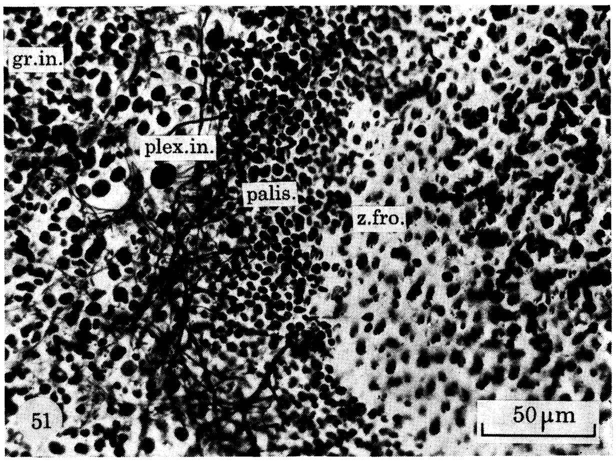
(Facing p. 282)

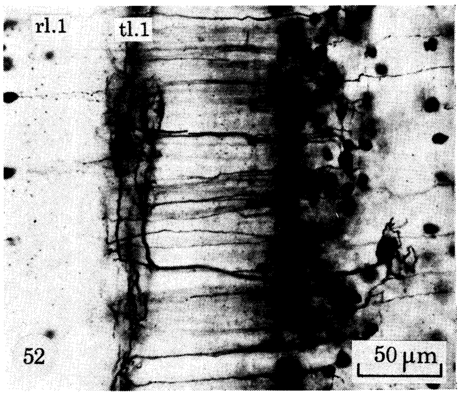


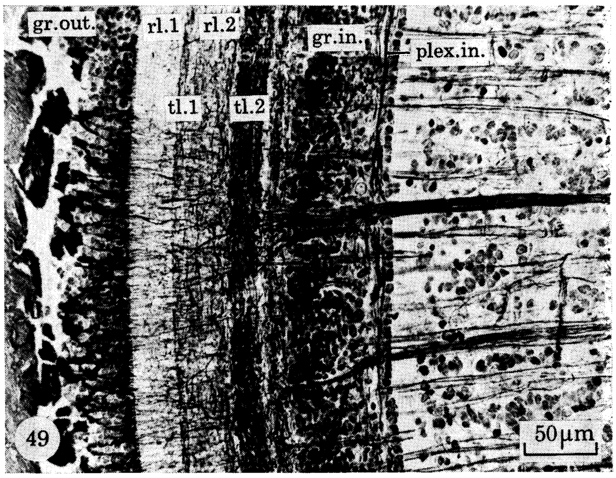


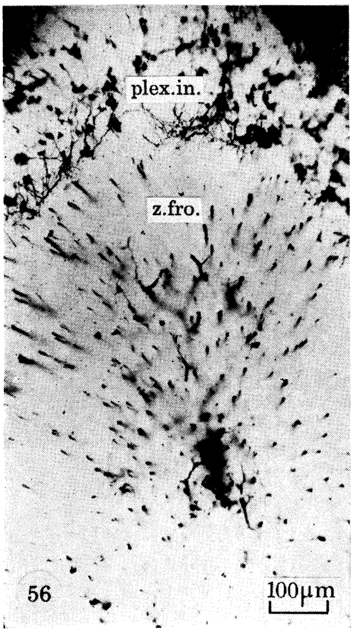


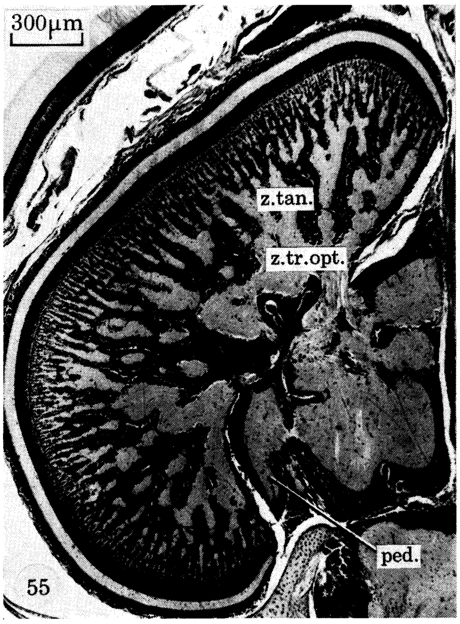


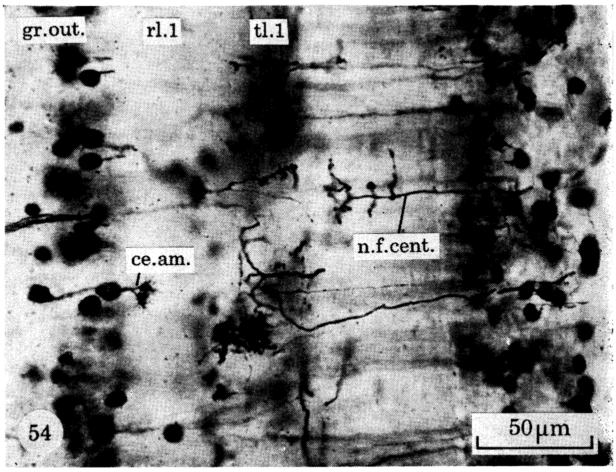












FIGURES 46–56. For description see opposite

cell runs only in one direction it is presumably maximally excited by a contour moving across parallel to it and so activating all its dendritic twigs at once.

The recurrent axons of these cells give branches within the inner granular layer or just below it in the inner plexiform zone (ax.ter., figures 37, 115 and 116). Here they are of course in the neighbourhood of the basal dendrites of their own and other recurrent cells, thus establishing short closed loops. The axons then proceed to the frontier zone of the outer part of the medulla and divide there or deeper to form fine varicose terminal twigs (ax.ter., figures 42*a* and *b*). Most of them probably proceed further than the axons of the smaller second-order neurons, but it is hard to separate the two sorts at this level.

10.4.5. *The giant second-order visual cells*

The full extents of these remarkable cells are very hard to see in any one section since their processes reach out for great distances in two opposite directions: the dendrites spread for millimetres tangentially in the outer plexiform zone and the axon proceeds for millimetres in to the centre of the medulla. The large cell bodies lie at the base of the inner plexiform layer (ce.vis.2,la., figures 112, 117 and 48). They carry numerous basal dendrites, with extensive spread in the inner plexiform layer (see p. 286).

The main fibre proceeds from the cell body towards the plexiform zone and is 3 μm or more in diameter. Reaching tangential layer 2 the trunk divides to give a flat spreading tree of branches and then arches over and turns back as an axon to proceed deep within the medulla (figures 117, 42*b* and 47).

The cells are spaced at regular intervals along the base of the inner granular layer. The dendritic trees therefore form regular series within the plexiform zone (figures 40, 45). Each tree is orientated in the same direction. The main arch between the ascending and descending

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DESCRIPTION OF PLATE 13

FIGURE 46. Section tangential to surface of the lobe, showing the top of a single large second-order visual cell in the second tangential layer (den.) and numerous straight dendrites of smaller cells in the first tangential layer. Sagittal section. Cajal.

FIGURE 47. Sagittal section showing large second-order visual cells branching in the second tangential layer, turning into the medulla and dividing deep within it. Also shows a large multipolar tangential neuron. Re-touched photograph. Cajal.

FIGURE 48. Inner granule cell layer to show the large nuclei of the largest second-order visual cells, lying partly in the inner plexiform zone (plex.in.). Sagittal section. Cajal.

FIGURE 49. Bundles of fibres running between the medulla and the outer and inner plexiform zones. Transverse section. Cajal.

FIGURE 50. Section tangential to the surface to show the cell types of the inner granule cell and palisade layers and the columns of fibres in the frontier zone. Sagittal section. Cajal.

FIGURE 51. Section similar to figure 50 to show the inner plexiform zone. Sagittal section. Cajal.

FIGURE 52. Single medium cell of the inner granule cell layer to show basal dendrites in inner plexiform layer. Sagittal section. Golgi.

FIGURE 53. Tangential section of inner plexiform layer, showing branching multipolar dendrites. Sagittal section. Golgi.

FIGURE 54. Centrifugal fibres (n.f.cent.) running from the medulla to end in the outer plexiform zone. Sagittal section. Golgi.

FIGURE 55. Horizontal section of optic lobe of a young squid to show the arrangement of columns of fibres and cells. Haematoxylin and eosin.

FIGURE 56. Section tangential to surface of the lobe to show inner plexiform layer and frontier zone traversed by columns of fibres. Sagittal section. Golgi.

trunks lies in the plane transverse to the long axis of the lobe, that is approximately horizontal in relation to gravity (figures 118, 43, 45 and 46). From the main arch up to ten branches proceed, each of which divides and runs mainly in the long axis of the lobe, that is in an approximately vertical direction (figure 118). They divide repeatedly towards the tips and taper to fine terminations. The whole dendritic tree thus covers a huge oval field, with its long axis lying in the long axis of the lobe. The longest of these dendrites has been traced for half a millimetre and the spread of a whole dendritic tree must therefore be at least a millimetre, that is one tenth or more of the whole length of the optic lobe. The branches are not strictly limited to tangential layer 2, but spread up into radial layer 2. The whole spread therefore functions as a dendritic tree, receiving impulses from enormous numbers of optic nerve fibres and presumably also from other endings in the outer plexiform zone.

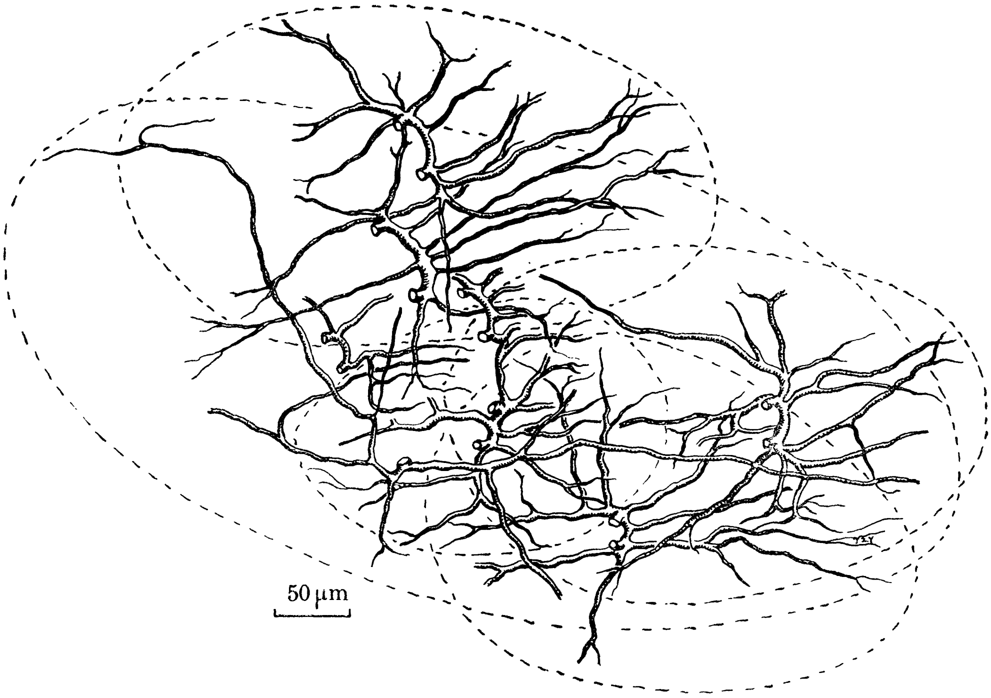

FIGURE 118. Drawing of the dendritic branches of four large second-order visual cells. Seen in a sagittal section tangential to the surface of the lobe. The dendritic fields are thus ovals, indicated by dotted lines. The long axis of each corresponds to the long axis of the optic lobe.

The recurrent axons of these large cells run through the inner granular and inner plexiform layers without branching, nor do they divide in the outer part of the medulla. Their fibres end deeper in the lobe, 1 mm or more from the surface (ax.ter., figures 47, 59). Here they divide dichotomously, providing endings occupying cylinders (or cones) of several hundred micrometres in depth and width. Signals can therefore reach to essentially any part of the lobe with only one synapse from the retina (figures 112, 117 and 119).

Occasionally bipolar cells have been seen, with one trunk (dendrite) proceeding to the outer plexiform zone and another (?axon) to the medulla (ce.bi., figure 117). Bipolar cells approximately of this form were seen by Lenhossék (1896) in *Eledone* and certainly occur in *Octopus* (Young 1962). It is not possible to say whether the rarity of their appearance in *Loligo* is a freak of Golgi staining.

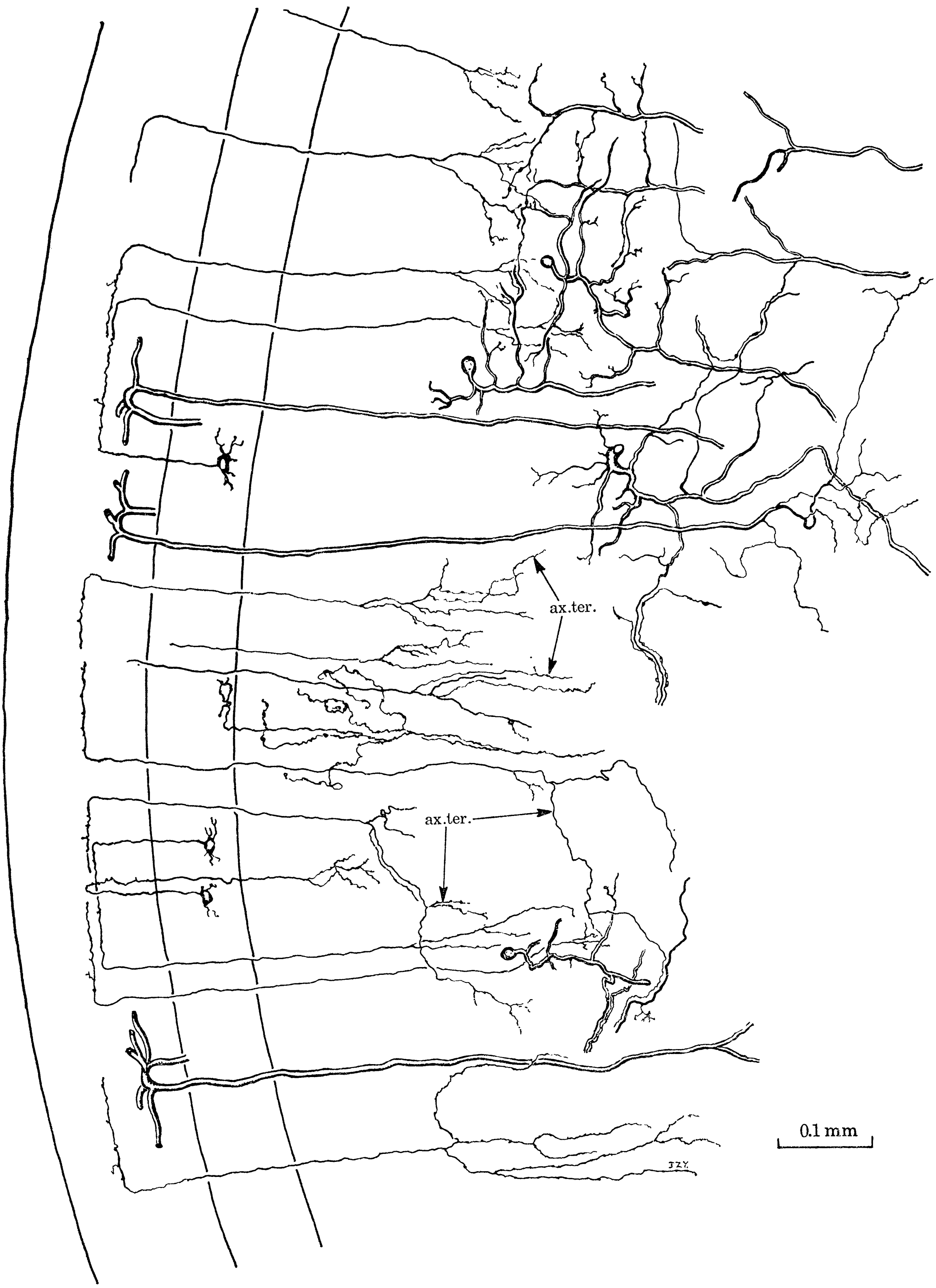

Figure 119. Drawings of second- and third-order visual cells of various sizes as seen in approximately transverse section. Some fibres coming from deeper in the lobe (or from other centres) are also shown.

10.4.6. *Inner plexiform zone*

This zone, characteristic of decapods, lies between the inner granular layer and the palisade layer (which is also absent from octopods) (plex.in., figures 48 to 51). It contains the cell bodies of the largest second-order visual neurons and their basal dendrites. Also the basal dendrites of many of the smaller second-order cells and of the cells with centrifugal fibres to the retina. The basal dendrites of the large cells have broad major trunks, tapering rapidly to fine points with many fine collateral twigs (figure 53). They are displayed all around the base of the cell to form an oval or circular field in which some of the branches run for hundreds of micrometres. The branches of neighbouring cells are intertwined to make an open network, very different in appearance from the dendrites in the outer plexiform zone. Parts of the plexus are characteristically joined together by some form of glial material in these Golgi preparations.

This plexus receives branches from the axons of second-order visual cells (p. 282). Some of the shorter ones may end here, others give collateral branches as they pass through on the way to the medulla (figures 115–117).

11. Fibres entering the plexiform zones from the medulla

Numerous fibres run outwards from the medulla and spread in both the outer and inner plexiform zones (figure 49). These centrifugal fibres probably include fibres arising from the cells of the medulla, the peduncle and basal lobes, subvertical lobe and the opposite optic lobe. Without degeneration experiments their origin remains uncertain. They spread out for 100 μm or more in the inner plexiform zone (figure 116). In the outer plexiform zone they end mostly in the deeper layers (n.f.cent., figure 54). They have not been seen reaching to the first radial layer.

12. The medulla of the optic lobe

12.1. *General arrangement*

The whole region central to the palisade layer is organized very differently from the layers of the retina profunda. It is the region that receives the axons of the second-order visual (classi-

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Description of plate 14

Figure 57. Low-power view of sagittal section of Golgi preparation to show division of the medulla into an outer region of radial columns and an inner one with mainly tangential layers. Transverse section.

Figure 58. Sagittal section to show outer region of radial columns and inner with tangential bundles. Cajal.

Figure 59. Sagittal section to show endings of second-order visual fibres at various levels in the radial columns. Also shows, on the right, a fibre arriving at the lobe from the optic tract. Re-touched photograph. Transverse section. Golgi.

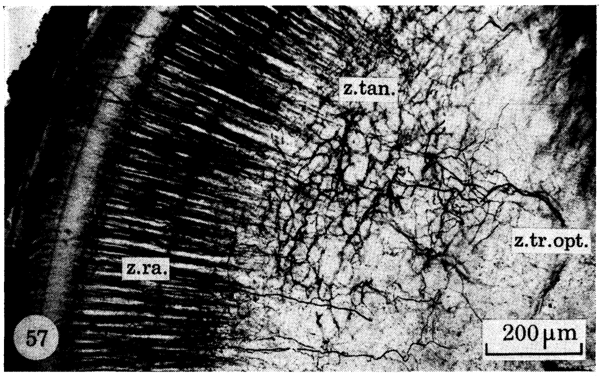
Figure 60. Tangential section through frontier zone showing columns of fibres of various sizes and a few scattered neuronal nuclei. Sagittal section. Cajal.

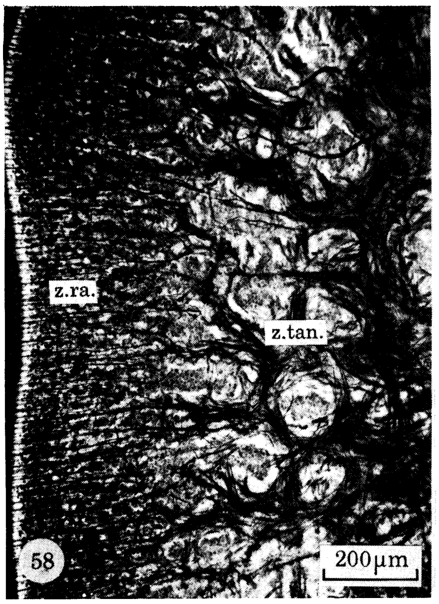
Figures 61 to 65. Tangential sections at increasing depths. Superficially there are radial bundles of fibres with cells between. Proceeding deeper the bundles increasingly run tangentially and the cells become larger. Sagittal sections. Cajal.

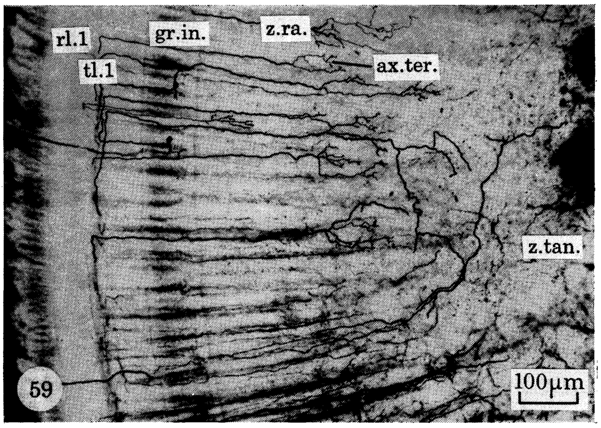
Figure 66. Tangential section through palisade layer, showing nuclei of small cells with a range of sizes and one large cell belonging to the inner granule cell layer. Sagittal section. Cajal.

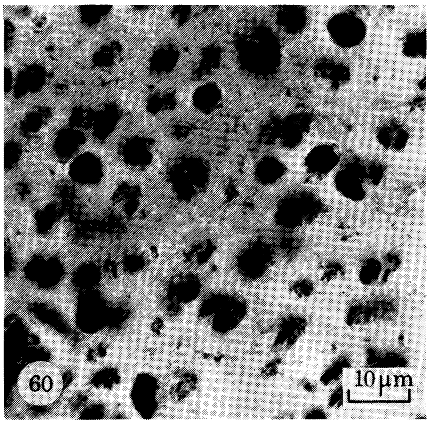
Figure 67. Sagittal section to show cells of the palisade layer. Golgi.

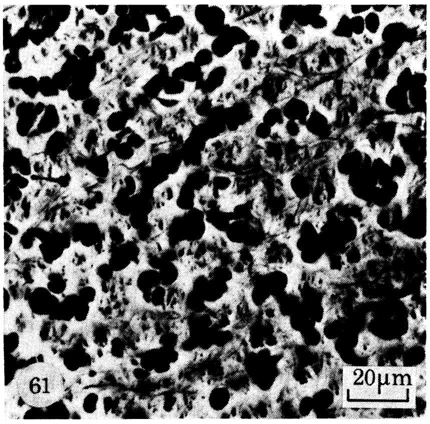
Figures 68, 69. Single cells of the palisade layer, showing numerous long branches. Figure 69 has been re-touched. Horizontal sections. Golgi.

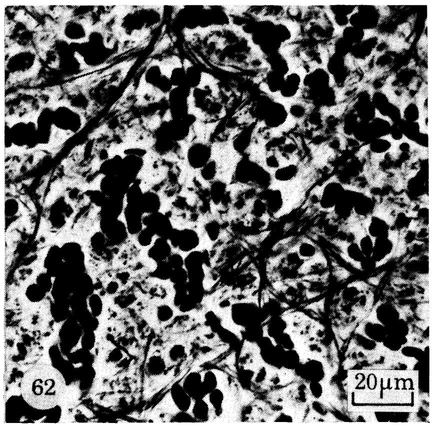


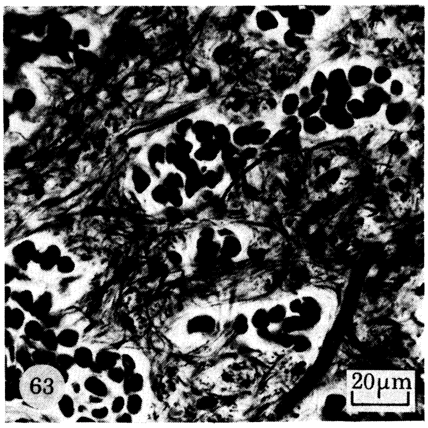


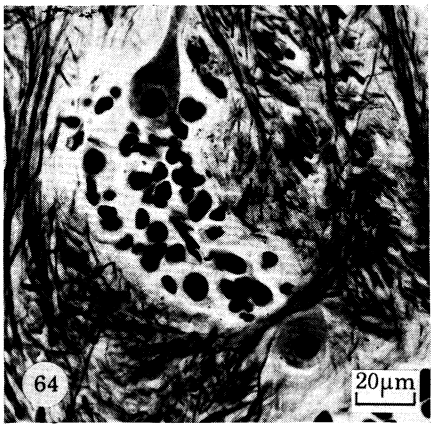


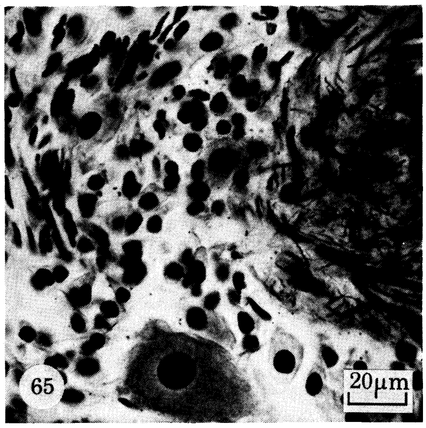


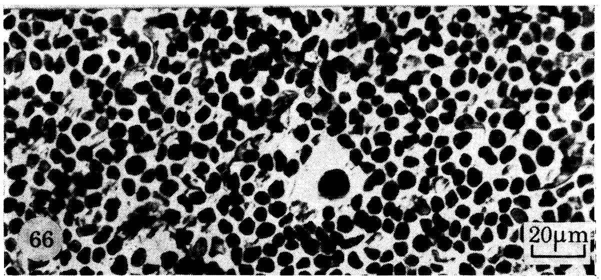


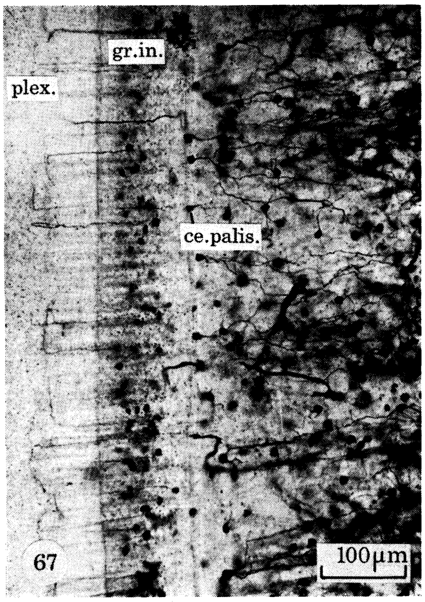


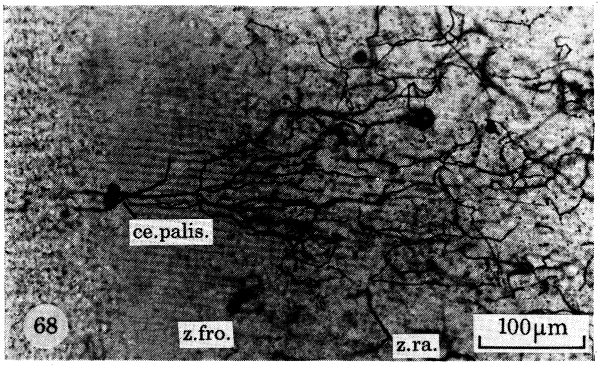


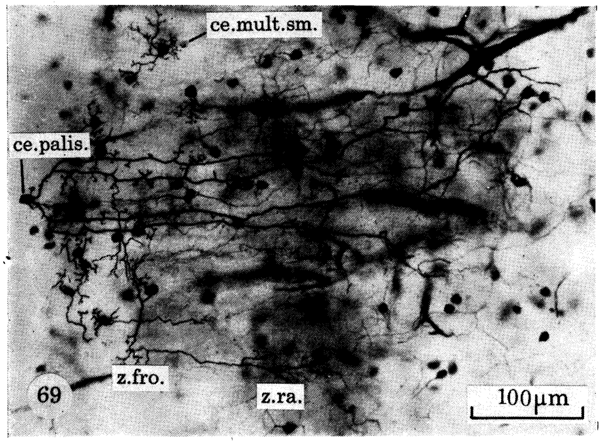




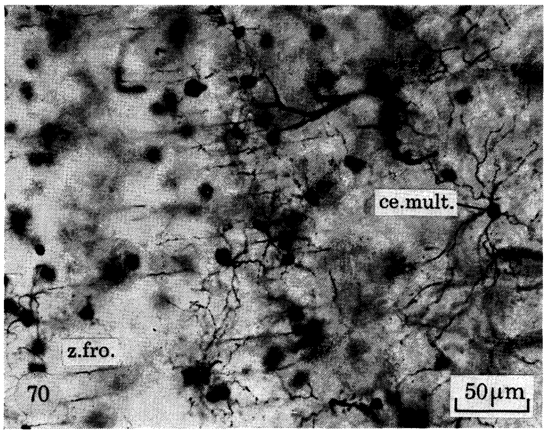








FIGURES 57–69. For description see opposite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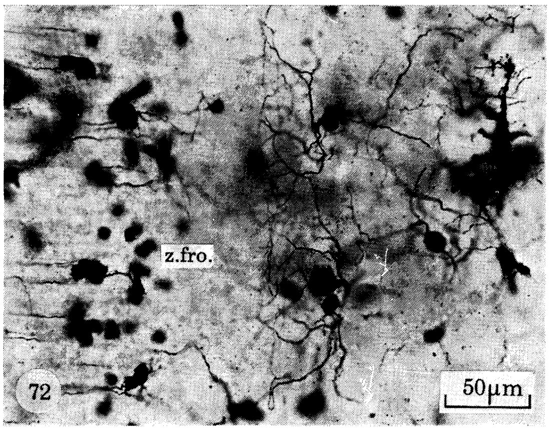
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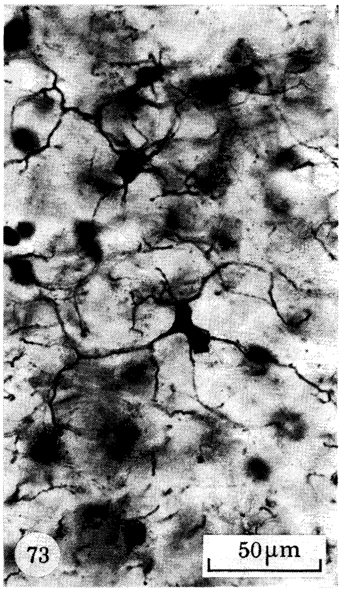
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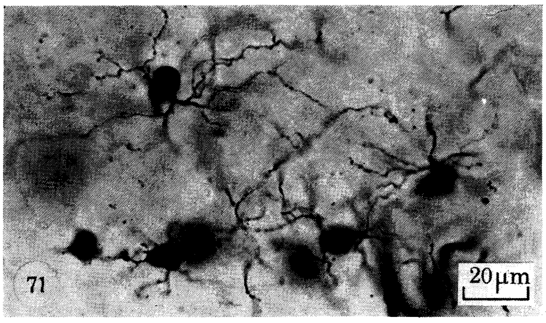
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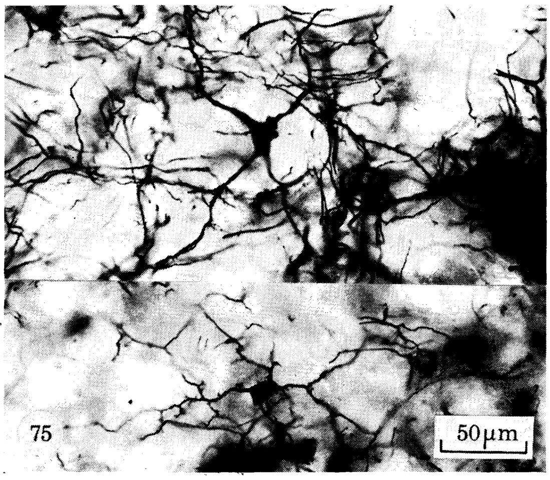
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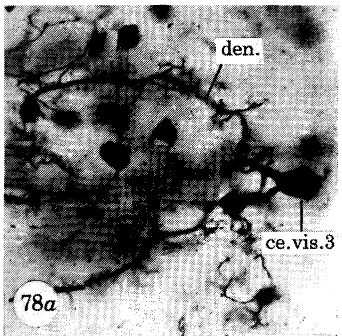
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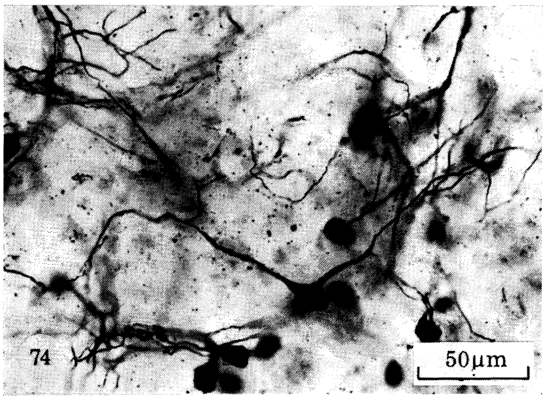
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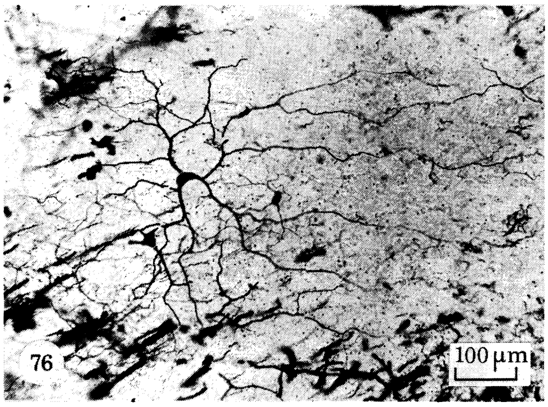
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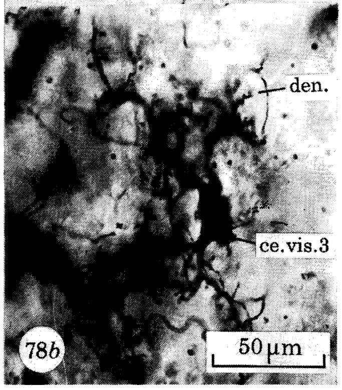
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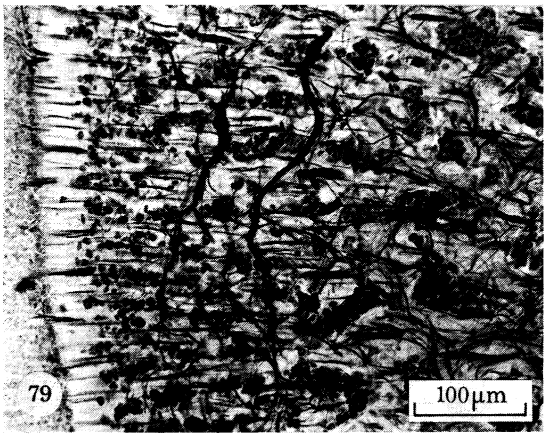
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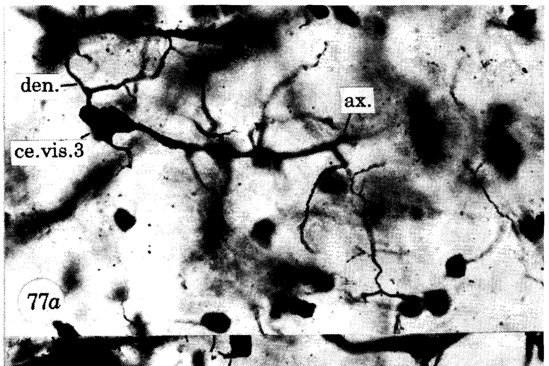
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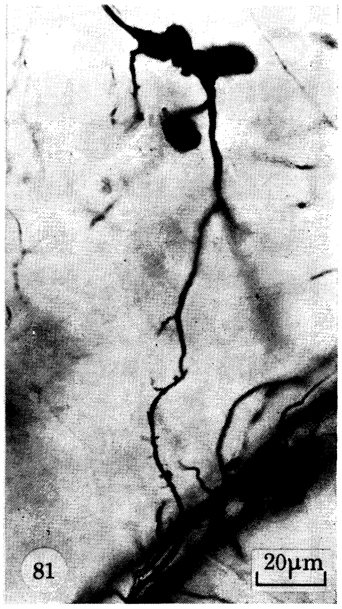
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77*b*

Figures 70–81. For description see opposite

fying) cells, and presumably allows the formation of appropriate combinations of their information, and then sends efferent fibres to the motor centres. For these purposes it is organized as a system of radial columns converging towards the centre, which are crossed by the horizontal dendrites of large cells, forming a series of tangential layers (ce.mult.lar., figures 112, 117). The general arrangement of cells and fibres is well seen in a horizontal section across the middle of the lobe (figure 55). Immediately within the palisade cell layer is a 'frontier zone' with few cells, where the columns consist only of the bundles of fibres coming through from the plexiform zone (z.fro., figures 48, 56 and 60). Then the bundles become accompanied by a few cells, but are still largely separated (figure 61). Proceeding centrally cross-connexions are made so that the columns of neuropil continually join, as do the cell layers. Thus, the strands of both neuropil and cells become thicker and thicker (figures 55, 62 to 65).

There are no sharp divisions as one proceeds centrally through the medulla. The organization changes progressively. The small cells become fewer and the large cells larger. The areas of neuropil and fibres become greater and the cell columns fewer but thicker, until they are almost absent at the hilum, which is filled with fibres of the optic tract.

Proceeding centrally the second-order visual fibres in the radial columns gradually terminate, first the smallest, then larger and larger ones. The endings diverge little near the surface, but more and more widely passing deeper (figures 115–117, 59). As they diverge these endings come into contact with the dendritic branches of third-order visual neurons and with large multipolar cells, which spread very widely, forming cross connexions between the columns. The effect is to produce wider and wider columns of neuropil proceeding towards the hilum (figures 55, 58). There are also very many small multipolar and bipolar neurons, especially near the surface. Some of these no doubt act upon the synapses between second- and third-order neurons. Others form further links within the lobe. The effect of the arrangement is that the fibres reaching the optic tract arise from a series of third-order visual cells activated by the second-order neurons, with extensive modulation by interneurons of various sizes. Elaborate plexuses at the centre sort the third-order axons into the various efferent bundles (p. 292).

It is difficult to decide whether to divide the medulla for descriptive purposes and if so how. Cajal (1917) recognized, besides the palisade and frontier zones, two others, a 'zone of delicate

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Description of plate 15

Figure 70. Small stellate cells near the surface of the medulla. Sagittal section. Golgi.

Figure 71. As figure 70 but section is here tangential to surface. Sagittal section. Golgi.

Figure 72. Cells of outer region of the medulla with numerous branches reaching towards the frontier zone. Sagittal section. Golgi.

Figure 73. Small multipolar cells of region of radial columns seen in tangential section near surface of the medulla. Sagittal section. Golgi.

Figure 74. Bipolar cell from same region as figure 73. Sagittal section. Golgi.

Figure 75. Tangential sections rather deeper than figures 73 and 74. Multipolar cells. Sagittal section. Golgi.

Figure 76. A horizontal section of *Alloteuthis* to show a large multipolar cell with branches reaching out among the radial columns. Golgi.

Figure 77*a*, *b*. Outer region of medulla. Third-order visual neurons with axons proceeding centrally. Sagittal section. Golgi.

Figure 78*a*, *b*. Cells similar to figure 77, cut tangential to surface, showing numerous branched dendrites. Sagittal section. Golgi.

Figures 79, 80. Giant horizontal cells. Transverse section. Cajal.

Figure 81. Dendrite of giant horizontal cell showing lateral spiny processes. Sagittal section. Golgi.

cellular cartridges' and a 'zone of voluminous cellular cores'. The cartridges are clearly the radial columns of our description, and they are very evident in a heavily stained Golgi preparation (z.ra., figure 57). I have preferred to call the inner zone one of tangential bundles. Although tangential fibres are present throughout, they are especially conspicuous towards the centre (z.tan., figures 57, 58). It is further convenient to recognize a central zone where the optic tract bundles are formed and where there are very few neurons.

We may thus use the following terminology:

(1) The palisade layer, first medullary zone.
(2) The frontier zone, second medullary zone.
(3) The zone of radial columns, third medullary zone.
(4) The zone of tangential bundles, fourth medullary zone.
(5) The zone of optic tract bundles, fifth medullary zone.

12.2. *First medullary zone = palisade layer*

This is a very conspicuous row of regularly arranged cells (palis., figures 48–51, 66). Cajal (1917) divided them into giant and small cells, and indeed large ones may appear in the sheet but probably really belong to the layer more peripherally (large second-order visual cells). The true palisade cells are all rather small, but they are not an entirely homogeneous population. They all send several branches inwards into the medulla (ce.palis. figures 67–69). These branches often arise from a single main trunk (ce.palis. figures 115–117). Some end immediately in the 'frontier' zone, others proceed for considerable distances. Some branches turn back and end in the inner plexiform zone.

The significance of this very well-marked layer is obscure. Neither Kopsch (1899) nor Cajal (1917) could find axons on these cells and none have been seen here. Cajal called them 'deep amacrine cells', or 'amacrines of the optic ganglion' (by which he meant what we are calling the medulla). But of course they are not the only cells in this region that lack axons. Indeed it may possibly be that all the branches should be regarded as axons as well as dendrites. They show tiny collateral twigs in the parts near the cell body but taper away to fine axon-like terminals deeper in the lobe (figure 69).

Description of plate 16

Figure 82. Giant horizontal cell in horizontal section of the lobe. Golgi.

Figure 83. Multipolar cell deep in the medulla, with long branches radiating in all directions. Transverse section. Golgi.

Figure 84. Sagittal section showing cell at base of radial columns, sending branches outwards into them. Several fibres entering the optic lobe are also seen at right. *Sepia*. Golgi. Photograph re-touched.

Figure 85. Tangential section across the radial columns showing the small cells that accompany them. Sagittal section. Golgi.

Figure 86. Cell of the medulla with main trunk dividing into long branches (axons?) running tangentially. *Sepia*. Horizontal section. Golgi.

Figures 87, 88. Third-order visual cells with a main trunk giving off dendritic collaterals and proceeding as an axon towards the optic tract. Horizontal section. Golgi.

Figure 89. Details of the dendritic twigs of a cell similar to figures 87 and 88. Horizontal section. Golgi.

Figure 90. Transverse section showing the bases of the radial columns meeting the tangential bundles containing beaded fibres coming from the optic tract. Golgi.

Figure 91. Fibre running from the optic tract (above) towards the surface (below in this figure). Horizontal section. Golgi.

Figure 92. Large cell of the medulla with axon proceeding towards the optic tract. Transverse section. Golgi.


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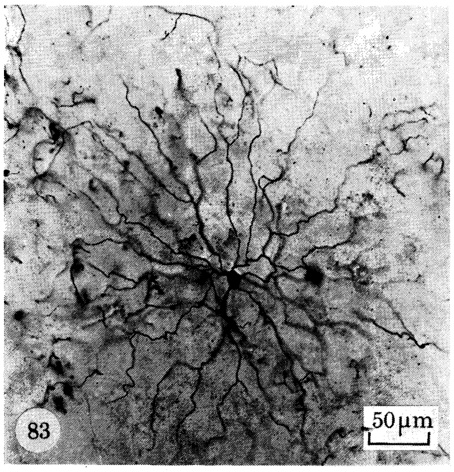
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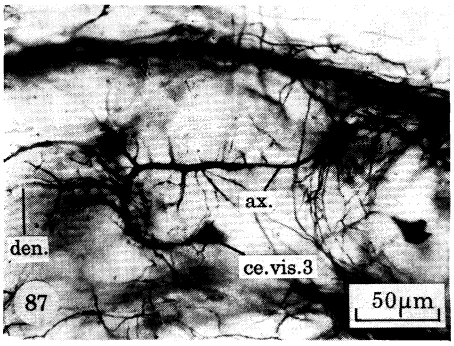
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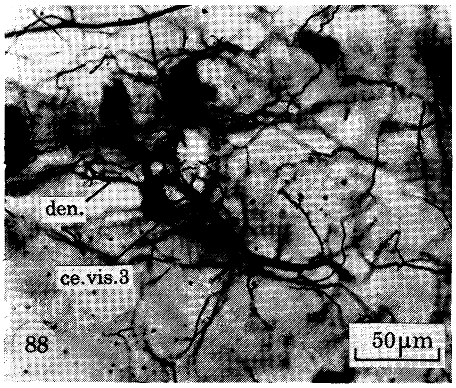
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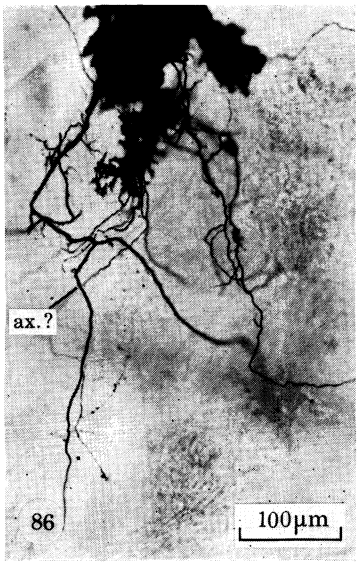
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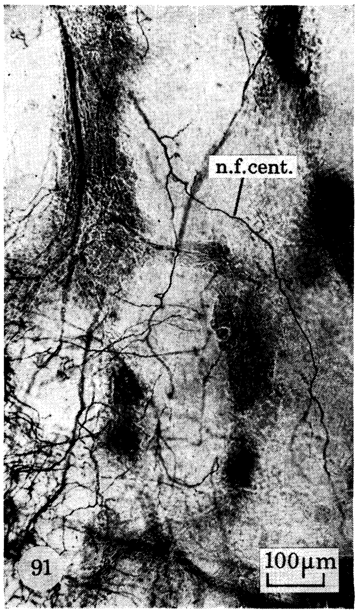
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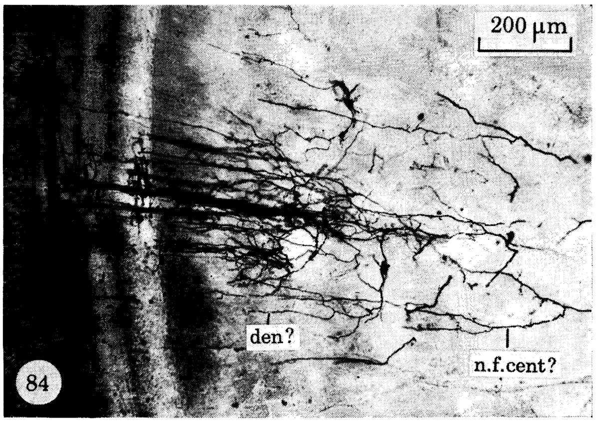
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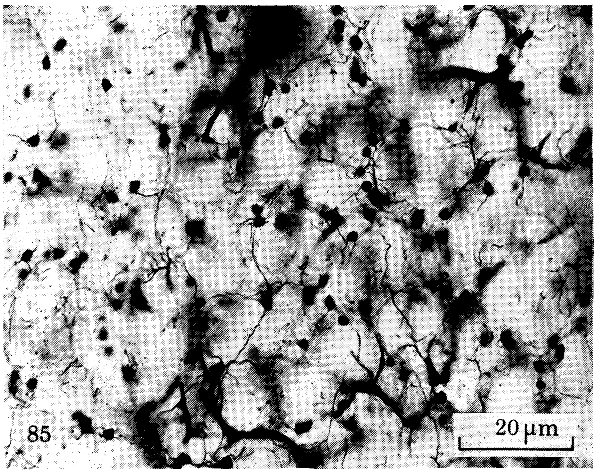
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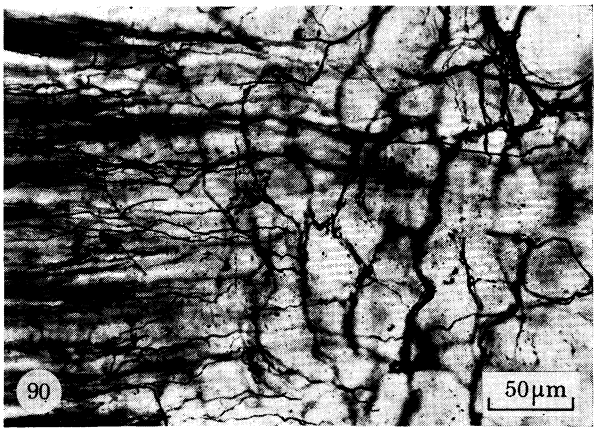
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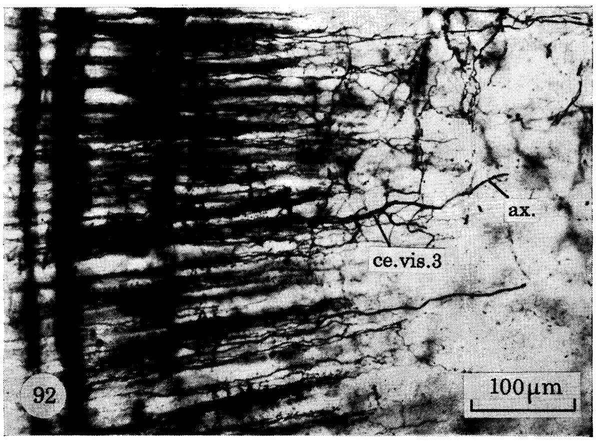
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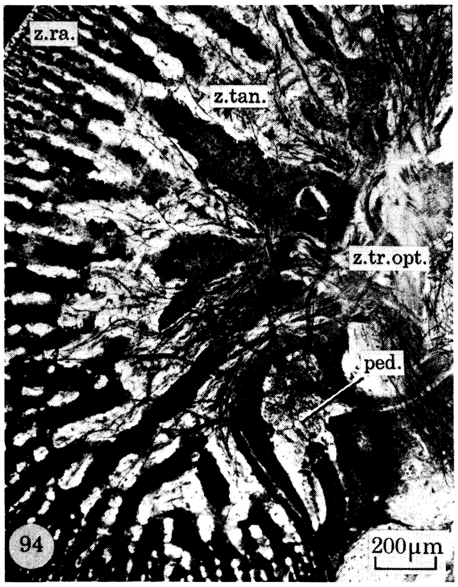
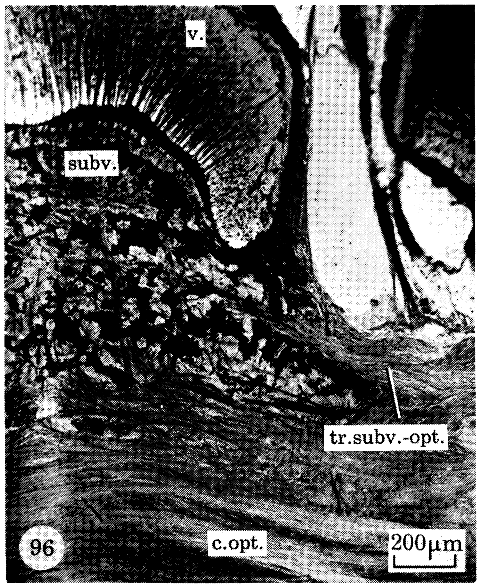
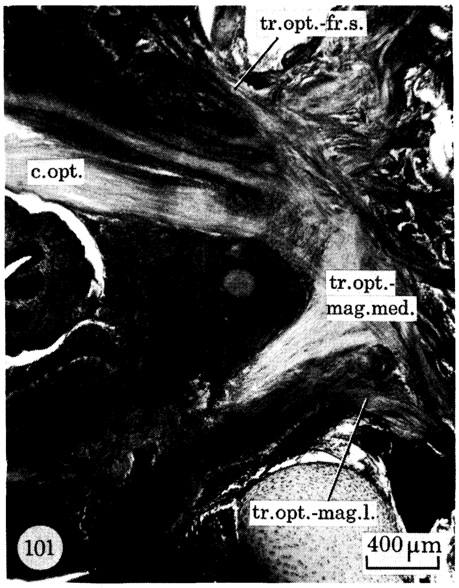
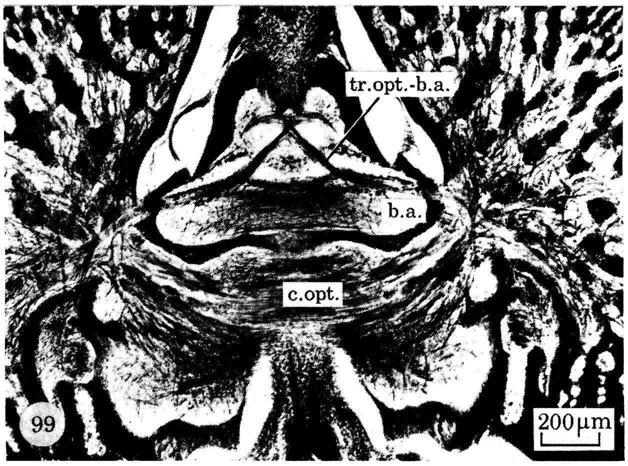
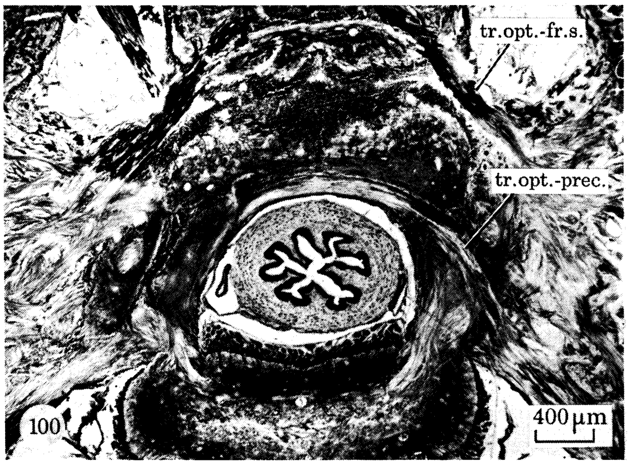
FIGURES 82–92. For description see opposite











Figures 93–101. For description see opposite

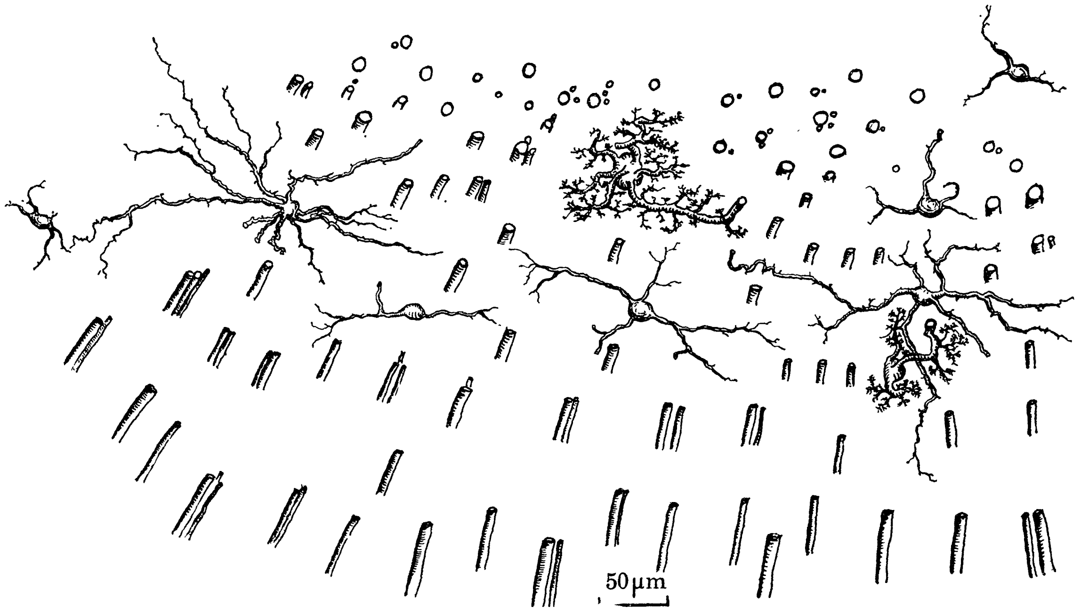


FIGURE 120. Drawing of section obliquely tangential to the surface of the optic lobe. The surface is below and bundles of fibres are there seen passing obliquely through the frontier zone. Above the section can be seen deeper structures. The bundles are there cut transversely and multipolar cells and the third-order visual cells are seen.

12.3. *Second medullary zone = frontier plexiform zone*

The region immediately within the palisade layer differs from the rest of the medulla. Cajal called it the 'plexiform, tangential or frontier region' of the medulla. It has only a few nerve cells, with round nuclei about 5–6 μm in diameter. The bundles of fibres entering through the palisade zone are here very distinct and separate from each other (figures 56 and 120). Most of them pass through to deeper levels, but some give branches in this zone (ax.ter., figure 32).

This second medullary zone is primarily fibrous: including branches both of neurons of the palisade layer, entering from the outside and those of the medulla proper, entering from within (figure 116). Its cells include the 'cells of Kopsch' as described by Cajal (1917). Their branches often run tangentially. Some branches reach up through the palisade layer into the inner plexiform and inner granular layers, and these 'ascending' branches may carry numerous tufts oi fine collaterals immediately within the palisade layer and then proceed on into the inner granular layer. These may be axons conducting outwards.

DESCRIPTION OF PLATE 17

FIGURE 93. Medulla in sagittal section showing large second-order visual fibres in the radial columns and a third-order cell, sending dendrites to the bases of several columns. Cajal. Re-touched photograph.

FIGURE 94. Sagittal section showing optic to peduncle lobe tracts.

FIGURE 95. Transverse section of optic to superior frontal lobe tract.

FIGURE 96. Transverse section of subvertical to optic lobe tract and optic commissure.

FIGURE 97. Transverse section of optic to anterior basal lobe tract.

FIGURE 98. Transverse section to show regular arrangement of the optic to anterior basal lobe tract.

FIGURE 99. Horizontal section of optic to anterior basal lobe tract.

FIGURE 100. Transverse section of optic to precommissural lobe tract.

FIGURE 101. Transverse section of the optic to magnocellular lobe tracts.

12.4. *Zone of radial columns, the third medullary zone*

This is arbitrarily defined as the region within the frontier zone extending to the level where most of the radial columns end (z.ra., figures 57–59). It is arranged on a definite radial plan. There are bundles of fibres passing inwards and outwards, surrounded by irregular cylinders of small cells (figure 61). Neighbouring cylinders are richly interconnected, and there are also very large cells with tangentially spreading dendrites. Many second-order visual fibres end here, spreading out over one or a few neighbouring columns (ax.ter., figure 59). Dendrites of third-order neurons make synapse with these endings and send axons deeper into the lobe, some reaching to the optic tract or peduncle lobe. There is a system of small irregular tangential bundles between the radial columns (figure 62).

The zone is populated by multipolar and bipolar cells of various sizes. The outermost part contains very small multipolar cells each spreading its branches through a small spherical volume of tissue (ce.mult., figures 70, 71). They thus appear multipolar in both the radial and tangential planes. The branches are all equally fine and varicose, with numerous minute collateral spines (ce.mult., figures 115–117). These very small cells have never been seen to have an axon and may be defined as amacrine cells. A little more deeply the cells are slightly larger (figure 72). Some of them have numerous branches proceeding outwards into the layer of smallest cells, but no clear axon. Others have a fibre proceeding for a short distance centrally, which might be an axon.

Passing still more deeply the cells come to have rather fewer, longer and smoother branches (figures 73, 74). Many of them are bipolar, with branches reaching out in opposite directions. There are also many larger multipolar cells (figures 75, 76). They have not been seen with axons, but it is hard to be sure that they do not have them. Their processes may reach out for several tenths of a millimetre, probably equally in all directions. They are covered with fine spines.

Impulses are carried on from this region by a different type of cell. These have a thick central trunk, which turns in towards the centre of the lobe. From this trunk arise numerous lateral branches, dividing rapidly into short, rather coarse terminals (ce.vis.3, figures 112, 116, 117, 77 and 78). These dendrites receive from approximately cylindrical volumes in the inner part of this zone. A single main fibre proceeds centrally and is presumably the axon, carrying signals inwards. The destination of these has not been traced in detail, but some probably reach the optic tract (p. 294). These are obviously the cells that Cajal (1917) called 'neurons with descending axon', including his 'inverted pyramids' and 'mitral neurons'.

This zone therefore consists of a series of radial columns of fibres and neuropil, separated by cylinders of cells, including multipolar cells of various sizes whose dendritic processes radiate in all directions, but which have no axon and are therefore amacrine cells. Signals enter from the endings of the second-order visual neurons, which permeate this zone, and signals leave by the third-order visual neurons proceeding centrally and constituting some at least of the efferent fibres of the lobe.

12.5. *Giant horizontal cells*

These are very striking cells recurring at all levels of the medulla except the most superficial. They were described by Cajal (1917) as 'corpúsculos horizontales gigantes'. They have branches proceeding for distances up to 500 μm in all directions tangentially and some up towards the surface (ce.mult.lar., figures 117, 79 and 80). These dendrites carry numerous characteristic short collateral branches ending in bushy terminals often of somewhat blunt form. These give the dendrites an appearance quite different from that of the smaller multipolar cells so far considered. In addition, these dendrites run an undulating course, as noticed by Cajal (1917) (figures 79, 82). It is especially hard to determine whether the cells have axons. Fibres that might perhaps be axons proceed from them towards the centre of the lobe, but it is not certain how far they go, nor do they appear different from other branches, Cajal was also unable to decide on this point. These giant cells have cell bodies that are small in relation to the spread of the dendrites (figures 79 and 80).

The outermost layer of giant tangential cells is more regular than the others and can be followed all round the lobe at a depth of about 100 μm within the palisade layer. The apparent irregularity of the other layers may be an artefact of the plane of section. The cells of the outer layer occur regularly at intervals round the lobe. This layer of cells thus serves to provide interaction within the whole of the more superficial part of the medulla, the region in which the axons of the smallest second-order visual cells end. The deeper large multipolar cells provide tangential influences between large areas at all levels throughout the lobe, including the deepest (figures 112, 117).

12.6. *Zone of tangential bundles*

As already explained this cannot be separated sharply from the zone of radial columns. An obvious functional demarcation is at the level where the axons of the largest second-order neurons end (figures 117, 59). Central to this level large bundles run tangentially as well as radially (z.tan., figures 57, 58). These bundles contain numerous axons entering from the optic tract as well as many running to it. These latter are efferents arising from cells whose size increases passing centrally (figures 64, 65). Many of them are third-order visual cells. It is not certain whether some of their axons end within the lobe. It may be that some of the largest cells represent a fourth or higher order from the retina. In addition, there are numerous small cells at all levels, though relatively fewer as one passes centrally. Some of the cells at the bases of the columns send conspicuous branches outwards into the columns (den?, figure 84). These are presumably dendrites, but it is not known whether these cells have axons. They may be third-order visual cells influenced from a wide area.

12.7. *Smaller cells of the medulla*

The smaller cells of the medulla are similar in the deeper and more superficial parts. Some are multipolar and send their spreading dendrites for long distances in all directions (figure 83). It is not easy to distinguish which, if any, of their processes are axons and which dendrites, but some that terminate in fine varicose branches may be axons. There is a whole series of sizes of cell with varying number and extent of branches. These processes form an elaborate web of fibres uniting the bases of the columns of axons that proceed inwards from the classifying cells (figure 85). Many of the smaller cells are unipolar. The trunk proceeds into the neuropil, gives off lateral dendritic branches there and continues as an axon to break up some distance away radially or tangentially (figure 121). The axons may run in any direction, towards the centre, or outwards or tangentially.

The trunks often carry lateral spines, more especially in the parts near to the cell body. These spines have sometimes been seen making contact with other fibres. There is then often a region with few or no spines and finally a set of terminal branches, which often show small swellings and short collateral spines (figure 121). Contacts of these terminals with other fibres have also been seen. Assuming that some of these fibres are axons these cells serve to produce interaction between the influences of the second-order (classifying) cells. They may run for quite long distances (ax?, figure 86). But other cells here are small and without obvious axon.

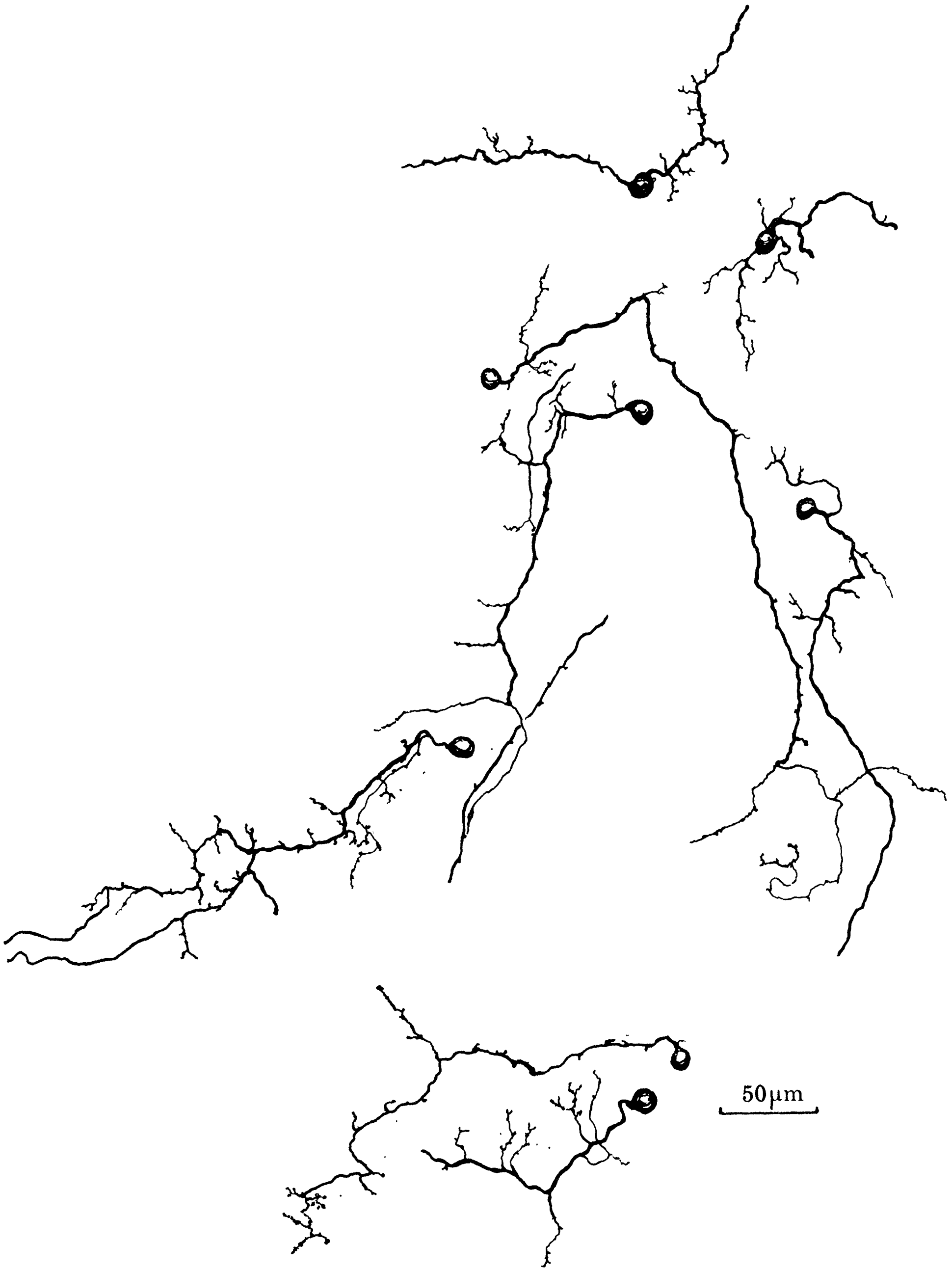


FIGURE 121. Drawings of small cells from the medulla. They may be uni-, bi- or multipolar. Their trunks carry collaterals, presumably dendritic. Some of them end in terminations that may be 'axonal'.

12.8 *Efferent cells of the medulla*

Throughout the medulla there are efferent cells that collect their influences from the radial columns. They have a single main trunk turning towards the optic tract, and giving off numerous dendritic collaterals (den.) before becoming an axon (ax., figures 87–89). The dendrites come off at right angles to the main trunk and themselves give off branches at right-angles, with third- and fourth-order branches (ce.vis.3, figure 92). The final terminations of the dendrites are delicate twigs, sometimes carrying swellings of various forms (figure 89). The resulting dendritic systems collect from a larger and larger area proceeding centrally (ce.vis. 3., figure 93), and the largest receive from the bases of many primary columns (figure 117). Many of these cells are third-order visual neurons, but it is not certain whether others are activated only after further synapses.

12.9. *Fibres entering the optic lobe medially*

The optic tract includes many fibres running to the optic lobe from the peduncle lobe, supraoesophageal lobes and opposite optic lobe. Some at least of these fibres branch widely as they proceed outwards, joining the tangential bundles (n.f.cent?, figures 84, 91). Their terminal branches make beaded threads accompanying other members of these bundles (figure 90). Experimental studies in *Octopus* have shown degeneration granules in all parts of the medulla after bisection of the supraoesophageal lobe. They have not been seen in the plexiform layers.

The material available does not allow a decision whether all these fibres spread widely or whether there are some with more restricted distribution. The question is obviously of interest for consideration of the detailed specification of functions in the lobes.

13. THE OPTIC TRACT

13.1. *Parts of the optic tract*

The fibres leaving and arriving at the lobe from other centres can be grouped into nine tracts:

(1) optic to peduncle lobe tract;
(2) optic to superior frontal lobe tract;
(3) subvertical to optic lobe tract;
(4) optic to anterior basal lobe tract;
(5) optic to precommissural lobe tract;
(6) optic to median and dorsal basal lobe tracts;
(7) optic to lateral basal lobe tract;
(8) optic to magnocellular lobe tracts;
(9) optic commissure.

Some of these conduct in one direction only, others in both. The optic tract is much shorter in a squid than in an octopus. This has made it possible to follow the major bundles in thick sections stained with Cajal's method and to show some details of the arrangement of their fibres.

13.2. *Optic to peduncle lobe tracts*

These consist of about 100 bundles entering the latero-dorsal (large-celled) region of the peduncle lobe (ped., figure 94). This is the most posterior and the shortest efferent pathway from the optic lobe and its fibres can be traced all the way from the bases of the major fibre columns far out in the optic lobe. This shows that efferent fibres do not all arise from the largest cells near the centre of the lobe. However, the exact cells of origin of these bundles have not been determined. It is probable that some or all of the fibres are axons of third-order neurons from the retina. The fibres of these bundles are arranged regularly and do not pass through a plexus (Messenger 1971). The bundles contain fibres running in both directions, in *Octopus* degeneration experiments have shown numerous fibres passing from the peduncle to the optic lobe (unpublished results).

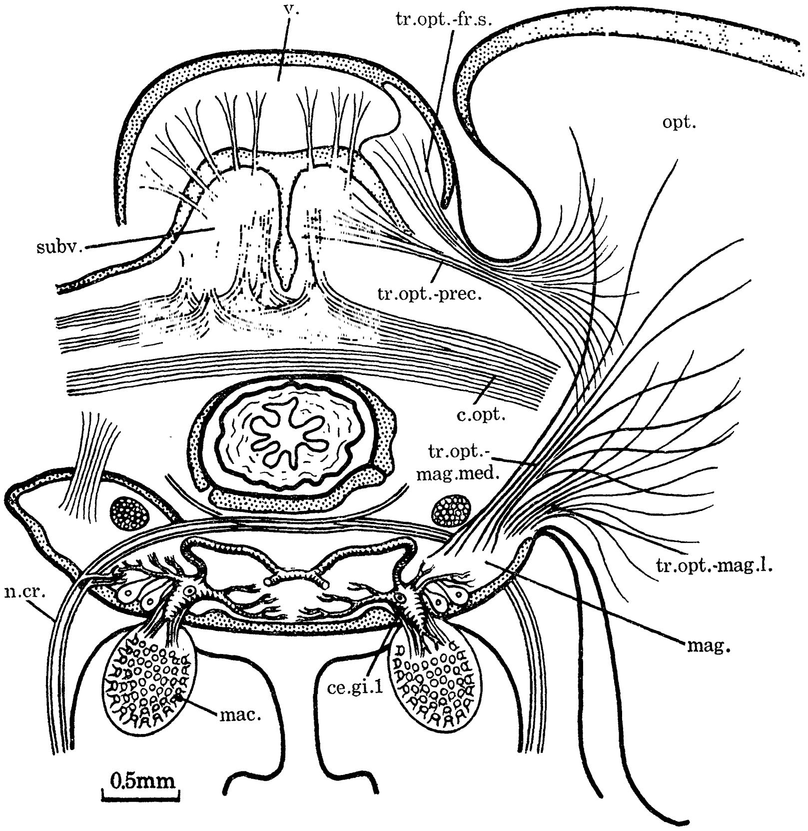


FIGURE 122. Diagram made from a transverse section to show some of the bundles of the optic tract.

13.3. *Other parts of the optic tract*

All the other bundles of the tract arise from the network of fibres in the hilum, around the very large venous sinuses there. Each pathway receives fibres from all parts of the lobes, so that together they make a web that looks very complex. It is probable, however, that the fibres of some of the separate tracts maintain a regular topographical order between the optic lobe and

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DESCRIPTION OF PLATE 18

FIGURE 102. Horizontal section of optic commissure.

FIGURE 103. Transverse section of optic to median basal lobe tract.

FIGURE 104. Horizontal section of optic to median basal lobe tract.

FIGURE 105. Sagittal section of optic to lateral basal lobe tract.

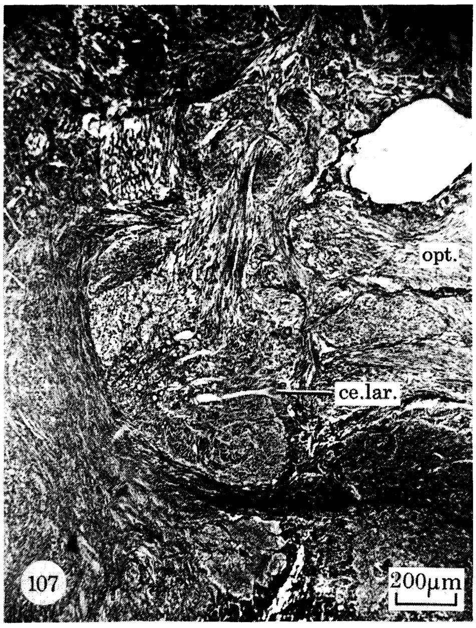
FIGURE 106. Sagittal section of optic to magnocellular lobe tract.

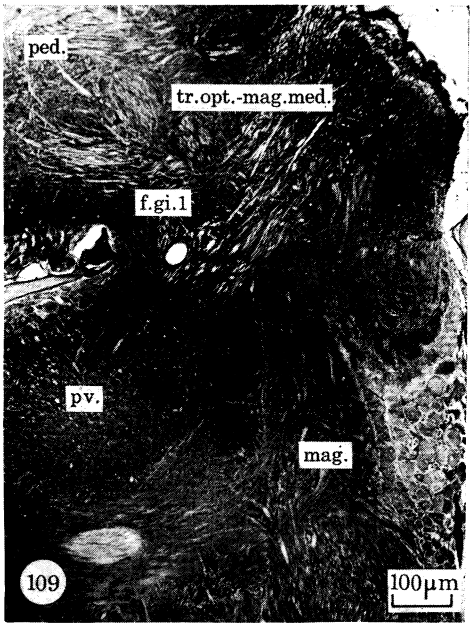
FIGURE 107. Horizontal section showing large cells at top of magnocellular lobe.

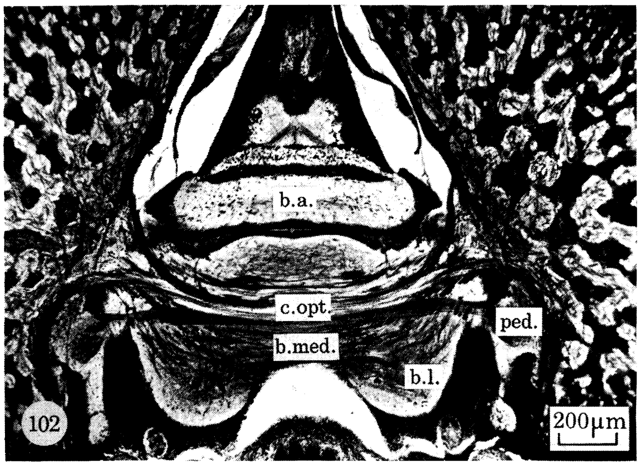
FIGURE 108. Transverse section showing median optic to magnocellular lobe tract reaching to region of dendrites of first-order giant cell.

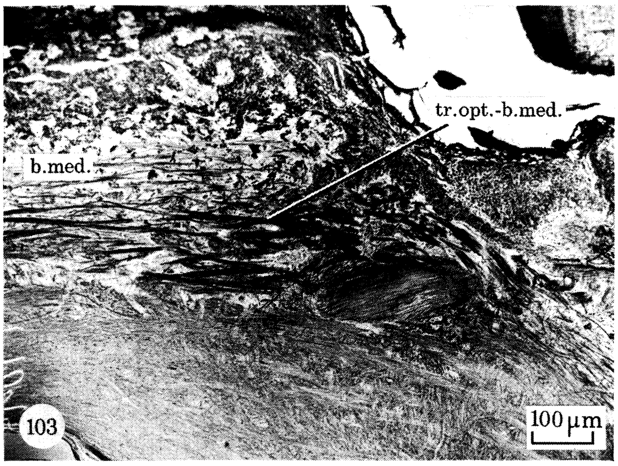
FIGURE 109. Horizontal section (oblique) showing fibres of the median optic to magnocellular lobe tract.

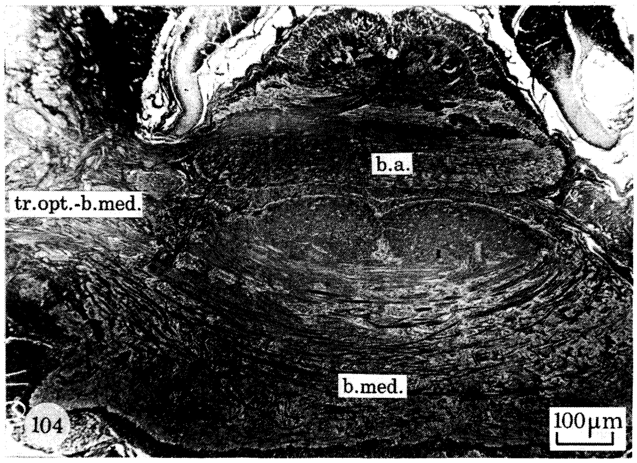
FIGURE 110. Branching formation in plexiform zone, probably vascular, but previously considered to be glial.

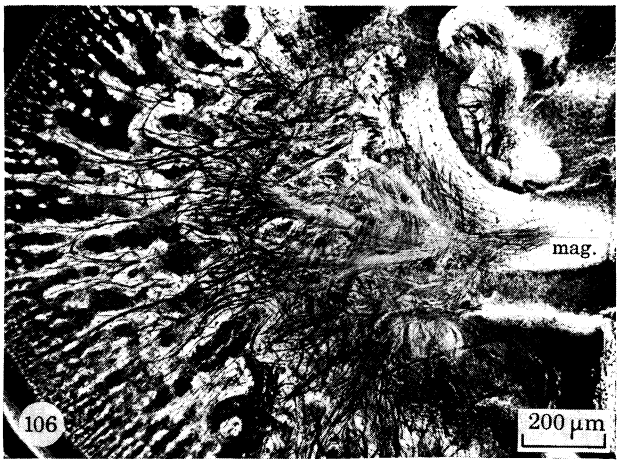


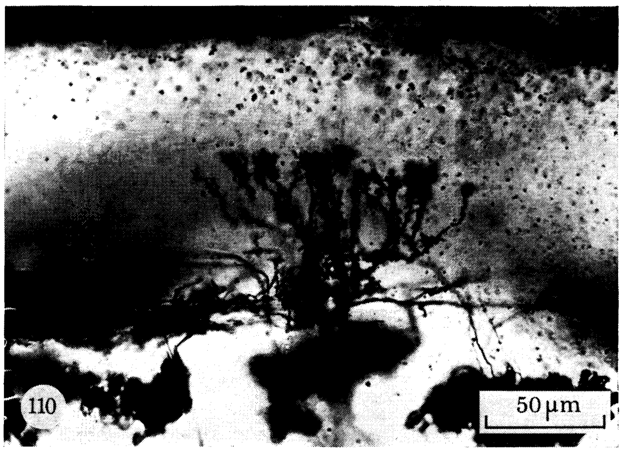












FIGURES 102–110. For description see opposite

(Facing p. 294)

their destination. Certainly many of the bundles do not involve interweaving and anastomosis by which fibres from the various regions are mingled. Obviously the question how far topographical relations are maintained is important. The courses of the fibres in the bundles show best in thick sections, but these are hard to photograph.

The most anterior part of the optic tract is occupied by the optic to superior frontal lobe tract, probably containing only fibres running from the optic lobe (tr.opt.–fr.s., figure 95). The fibres maintain their relations in the tract, at least in the dorsoventral plane. They may become involved in anastomosis within the superior frontal lobe itself. If the vertical lobe circuit is concerned with the setting up of stores of visual representations it is especially interesting to know whether its fibres maintain fixed spatial relations.

The output from the vertical lobe system, the subvertical to optic lobe tract, lies behind the optic to superior frontal tract. It consists of a complicated series of bundles (tr.subv.–opt., figure 96). Some of them run directly laterally, others run first ventrally and then turn sharply into the horizontal plane to reach the same or the opposite optic lobe. It is not possible to follow the relations of these fibres throughout their course, but there is certainly some regularity in the arrangement. There are some anastomoses but these are not randomly interweaving bundles interchanging fibres in all directions.

Below the optic to anterior basal lobe tracts lie the optic to precommissural lobe tracts, occupying the ventral part of the middle of the optic tract (opt.–prec., figure 100). These contain some very large fibres, whose origin and destination are uncertain. They probably come mainly from the ventral part of the optic lobe and run to the lowest part of the precommissural lobe. Some of them cross the mid-line above the oesophagus.

The massive optic and peduncle commissures lie below the subvertical to optic tracts, and they cross immediately above the oesophagus (c.opt., figures 99, 101). The optic commissure proper consists of fibres from all parts of the lobes. They maintain at least approximately a regular order, so that the front of each lobe is connected to the front of the other and so on (figure 102). The peduncle lobe commissure forms a separate bundle. Its fibres also keep a regular arrangement.

The question of the orientation of the bundles that join the optic lobes to the basal lobes is of especial importance in view of the regular orientations of these lobes, which was realized only after the present study had been completed (p. 399). It has not been possible to trace the origins of all these fibres fully. The tract from the optic lobe to the anterior part of the anterior basal lobe clearly contains fibres maintaining their relative positions in the dorso-ventral plane (tr.opt.–b.a., figures 97, 98). These bundles proceed to the mid-line and cross to enter the antero-median lobe of the opposite side (figure 99). It will be shown in a subsequent paper of this series that the organization of this lobe is indeed orientated vertically, with the dendrites of its main cells spreading upwards across the series of incoming optic fibres. The more dorsal and posterior part of this anterior anterior basal lobe sends fine fibres back to the optic lobe of the same side (figure 97).

The posterior part of the anterior basal lobe is organized in a horizontal plane, but the source of its input fibres from the optic lobes has not been clearly seen in horizontal sections, as they are interwoven with the input to the anterior anterior lobe. There are indications that these optic tract fibres undergo a complex chiasma in the horizontal plane.

The median basal and dorsal basal lobes are also organized in a horizontal plane, constituting a single entity corresponding to each of the two parts of the anterior basal lobe. There are some signs that the fibres to them from the optic lobes are regularly arranged in the horizontal plane, but the details are not clear (tr.opt.–b.med., figures 103, 104). The fibres in the connexion with the dorsal basal lobe include many running towards the optic lobe.

The optic to lateral basal lobe tracts lie at the back of the optic tracts dorsally. They probably contain fibres only running from the optic lobes. They arise from all parts of the optic lobe and the bundles show some interweaving, as they enter the lateral basal lobe (tr.opt.–b.l., figure 105). They presumably control the operations of the chromatophore lobes of the suboesophageal ganglia.

The most ventral part of the optic tract at the back is occupied by the optic to magnocellular lobe tracts. The lateral optic to magnocellular tract consists of fine fibres, staining deeply with Cajal's method (tr.opt.–mag.l., figure 101). This consists of fibres that run to the posterior magnocellular and latero-ventral palliovisceral lobe of the same side (see below). The medial optic to magnocellular tract consists of very large pale-staining fibres (tr.opt.–mag.med., figures 101, 106), which are probably the axons of the third-order visual neurons. They come from all parts of the optic lobe apparently without maintaining precise topographical order. They join to form bundles with axons arising from very large cells at the top of the magnocellular lobe (ce.lar., figure 107). Some of these bundles run to the ventral magnocellular lobe, to the region of the dendrites of the first-order giant cells (f.gi.1., figure 108). Some may cross in the ventral magnocellular commissure to the magnocellular lobe of the opposite side. Others (or perhaps branches of the same ones) turn back into the centre of the palliovisceral lobe (pv., figure 109). They run with the first-order giant axon and probably contribute to the synapses around the giant fibre bridge (Martin 1969). It is clear that this tract of large fibres is concerned with the elicitation of movements through the giant fibre system. Some of them also turn forwards to end in the pedal lobe (ped., figure 109). Yet another set run backwards into the posterior magnocellular lobe where they cross in the posterior magnocellular commissure and end in the latero-ventral palliovisceral lobe of the opposite side. This is a region from which fibres of the visceral nerves arise and the pathway may be concerned with ink ejection (Young 1974). Fibres from the pallial nerve join the posterior magnocellular lobe and run forwards. It may be that they reach to the optic lobe via the optic to magnocellular tracts.

14. Blood vessels and neuroglia of the optic lobe

These have not been especially studied in the present work but appear to be arranged essentially as in *Octopus* (Young 1971). A controversial question is the nature of the branching formations in the plexiform zone referred to as glial by Cajal (1917) and Young (1962), but later considered to be blood vessels (Young 1971). In *Loligo* they have been seen only moderately clearly, but the evidence suggests that they are indeed vascular channels (figure 110).

15. Discussion

15.1. *Dendritic receptive fields*

It has been possible in *Loligo* to extend our understanding of the organization of the optic lobe beyond that of *Octopus* (Young 1971). Optic nerve fibres end in the plexiform zone in contact with second-order visual neurons with various shapes of dendritic field. The four classes into which these have been divided suggest that they act as classifying cells (feature detectors), responding to at least these four distinct patterns of optic fibre input. There are great differences between the receptive dendritic fields of the smallest second-order cells, each contacted by few optic fibres (perhaps by only one) and the largest, which could be influenced by thousands. The smaller fields are round, the larger ones orientated, and some of them sharply restricted to straight lines. These could be cells especially sensitive to edges with particular orientation. The spread of the dendritic field does not of course necessarily correspond to a visual field as physiologically defined (see Dowling & Boycott 1966). Nevertheless, there is likely to be some correspondence between the size and shape of the receptive dendritic tree and the effective visual field. These fields of various sizes and shapes in the squid must have very different properties. Unfortunately far less is known about the physiology of vision in cephalopods than in insects or crustacea (Horridge 1966*a*, *b*). However, study of receptive fields in the optic lobe of cephalopods is possible (MacNichol & Love 1961; Daw & Pearlman 1969). They include circular fields of 20° to less than 3°, giving transient on-responses. Receptive visual fields are almost certainly determined by complicated interactions between distinct types of receptors and analysing cells. Cells with wide dendritic fields and numerous amacrines are found in arthropods as well as cephalopods but in neither case can we be sure how they operate (Horridge, Scholes, Shaw & Tunstall 1965; Strausfield & Blest 1970; Trujillo-Cenóz 1972).

15.2. *Layers of the plexiform zone*

The plexiform zone shows a division into layers similar to that in *Octopus* and the significance of the layers begins to be clear. The first radial layer contains mainly the swollen parts of the optic nerve endings, interwoven with numerous branches of the amacrine cells (Case *et al.* 1972; Cohen 1973). It is perhaps concerned chiefly with lateral interactions, establishing sharp contours for the input. It is striking that the largest part of each optic nerve ending is concerned with such lateral interaction through the amacrine cells and is not in contact with second-order dendrites. Only a narrow fibre proceeds inwards to make that contact.

The receptive dendrites of the various types of classifying cell end at different levels in the plexiform zone. Those with round fields are the most superficial. The narrow, highly orientated fields come next, making the dense network of the first tangential layer. The very large second-order dendrites occupy the second tangential layer and the parts of the radial layers lying above and below it. The two innermost tangential layers contain dendrites of the efferent cells and branches of the larger amacrines. They also receive the dendrites of the orientated second-order visual cells of the outer granular layer. The tangential layers are thus formed by the main dendritic branches of the various types of neuron.

15.3. *Distribution of synaptic transmitters in the optic lobe*

The optic lobes of decapods contain exceptionally high levels of substances known to be involved in chemical synaptic transmission. These include choline acetylase (Nachmansohn & Weiss 1948; Feldberg, Harris & Lin 1951), cholinesterase (Nachmansohn & Meyerhof 1941), acetylcholine (Florey & Florey 1954), and monoamines (Juorio & Killick 1972). In the medulla of the lobe cholinesterase occurs in the neuropil and is absent from the islets of cell bodies. The cholinesterase in the cortex is mostly localized in the plexiform zone in which radial layer 2, tangential layer 2 and radial layer 3 show bands of enzyme activity (Drukker & Schadé 1964; Turpaev *et al.* 1968). The decapod cholinesterase has a wider substrate specificity and some differences in distribution compared with the acetylcholinesterase of octopods. The acetylcholinesterase in *Octopus* shows additional bands of activity in the fourth tangential layer (Drukker & Schadé 1964) and in the first radial layers (Barlow 1974).

Application of the formaldehyde histochemical technique to octopus optic lobe (Matus 1973) has shown that monoamines also have a clearly layered distribution in the plexiform zone. Amine fluorescence is absent from the optic nerve fibres and their endings but present in the first tangential, and, the second, third and fourth radial layers. There are therefore clearly defined regions in the plexiform zone neuropil where acetylcholinesterase and monoamines are absent (optic nerve endings), where both are present (second radial layer) and where only acetylcholinesterase occurs (fourth tangential layer). The determination of the amine distribution in the decapod optic lobe would provide a fuller basis for a comparative study.

15.4. *Significance of amacrines and centrifugal cells*

The enormous number of these two classes of cell shows that they must be fundamental for the visual process. As suggested for the vertebrate retina the amacrines may provide a feedback arrangement with the ends of the retinal nerve fibres, serving for gain control or as an adaptation mechanism (Dowling & Boycott 1966). In the mud-puppy (*Necturus*) the interneurons have been shown to produce amplitude variant potential changes, which suggest gain controls, perhaps scaling the signals received up or down to an optimum working level (Werblin & Dowling 1969; Rushton 1972). This is obviously an important function, but the presence of amacrines with various spreads suggests that they may cooperate in the actual definition of the image. They may ensure that excitability is raised or lowered over particularly stimulated areas, say the outline of a fish or another squid. The centrifugal cells have dendrites in several plexiform layers and may serve to project the same patterns on to the retinal cells themselves. Thus if a fish enters the visual field the area within and just around its contour may come to levels of excitation different from the whole of the rest of the visual field.

15.5. *Organization in radial columns*

A striking finding has been that the axons of the second-order visual cells form columns of fibres and neuropil, radiating inwards. This is also so in *Octopus*, but its significance was not previously recognized. The result of this arrangement is to provide columns of third-order visual cells in which the successive levels receive the endings of classifying cells with fields of increasing size, some round and some highly orientated. The processes of many multipolar and bipolar amacrine cells enter the neuropil and mingle with the endings of the second-order and dendrites of the third-order cells. They may prove to be the cells by which the probability of activation of alternative pathways is altered during learning as suggested by the mnemon hypothesis (Young 1965). It is not yet possible to see the way in which these influences interact to allow responses to different configurations. But the forms of the small interneurons and the larger third-order visual cells have been described. Some of these third-order cells send axons to the optic tract. There are thus probably only two synapses on the paths from the retina to the giant cells or the peduncle lobes. These are perhaps the simplest outputs. The pathways for response to complex inputs no doubt involve influences passing in several directions within the optic lobe. The separate columns are of course progressively linked by cells with tangentially oriented dendrites and axons, allowing for interaction over short and long distances. There are also numerous fibres from the central brain and opposite optic lobe, ending at various levels in the optic lobe.

15.6. *Comparison of cephalopod and vertebrate visual systems*

The study has served to bring out further remarkable similarities between the pattern of organization of the visual system in cephalopods and vertebrates. The general resemblance between the retina profunda and the vertebrate retina is obvious enough, but the similarity extends even into details. The numerous amacrine cells are evidently a significant feature in both groups. The smaller of them allow interaction between the inputs of nearby optic nerve fibres, perhaps sharpening boundaries by inhibition. The larger amacrines may do the same over wider areas. Some of the multipolar cells in the outer part of the optic lobe are strikingly like vertebrate horizontal cells, e.g. figures 76 and 83.

The principle upon which the visual system operates seems to be similar not only in vertebrates and cephalopods but in arthropods too. A pattern of receptors is activated by the input. The edges of this pattern are sharpened by lateral inhibition and perhaps subjected to centrifugal influences. The pattern is then analysed by a system of classifying or encoding cells, each preset to respond to particular features (feature detectors). The output of these is combined to determine the appropriate response. This last is the stage of which we know least, indeed almost nothing. It may perhaps be significant that in cephalopods, as in vertebrates, the fibres carrying the signals from the feature detectors are arranged in columns. It is perhaps not fanciful to compare the radial columns of the outer part of the medulla of the cephalopod optic lobe with the columns of the cerebral cortex.

15.7. *Maintenance of topographical relations*

Another significant feature is that fibres recording from different parts of the visual fields maintain regular topographical relations. The chiasma between each retina and its optic lobe shows evidence that the inverted retinal image is re-inverted in the dorsoventral plane, down to the finest detail (p. 272). This emphasizes that the system functions by displaying the visual information in a map-like fashion on the optic lobe.

In the projections from the optic lobe to the motor centres of the peduncle and basal lobes the topographical regularity is probably preserved (p. 295). This suggests that the commands for steering are organized by the direction of movement of objects in the visual field (or of the squid in relation to them). The particular importance of these topographical relations has only been realized since the work for this study was finished. During further investigation it became clear that the peduncle lobes and basal lobes of the supraoesophageal brain constitute four structures with similar organization but different orientations (Young 1974*b*). They are connected to the suboesophageal centres that control the eye muscles and those concerned in steering with the funnel and fins. It is suggested that they provide a system for regulating the force and direction of muscular action, using similar principles to the vertebrate cerebellum (Hobbs & Young 1973).

The fact that these lobes are orientated in definite planes provides a further indication that the regularities seen in the optic lobes are a significant feature of the system. It has not yet been possible to discover the detailed topology of the connexions between the optic lobes and these higher motor centres.

The projections to the magnocellular lobe probably do not maintain topographical relations, perhaps because they are concerned in producing the movements of advance or retreat through the giant cell pathway, steering being by other centres. The magnocellular pathway may also be concerned with the emission of ink and other defensive measures.

The fibres between the optic and lateral basal lobes also show a complex interweaving. The colour patterns which they produce are presumably not topographically related to the visual input, in that the animal's coloration does not conform to the details of the surroundings.

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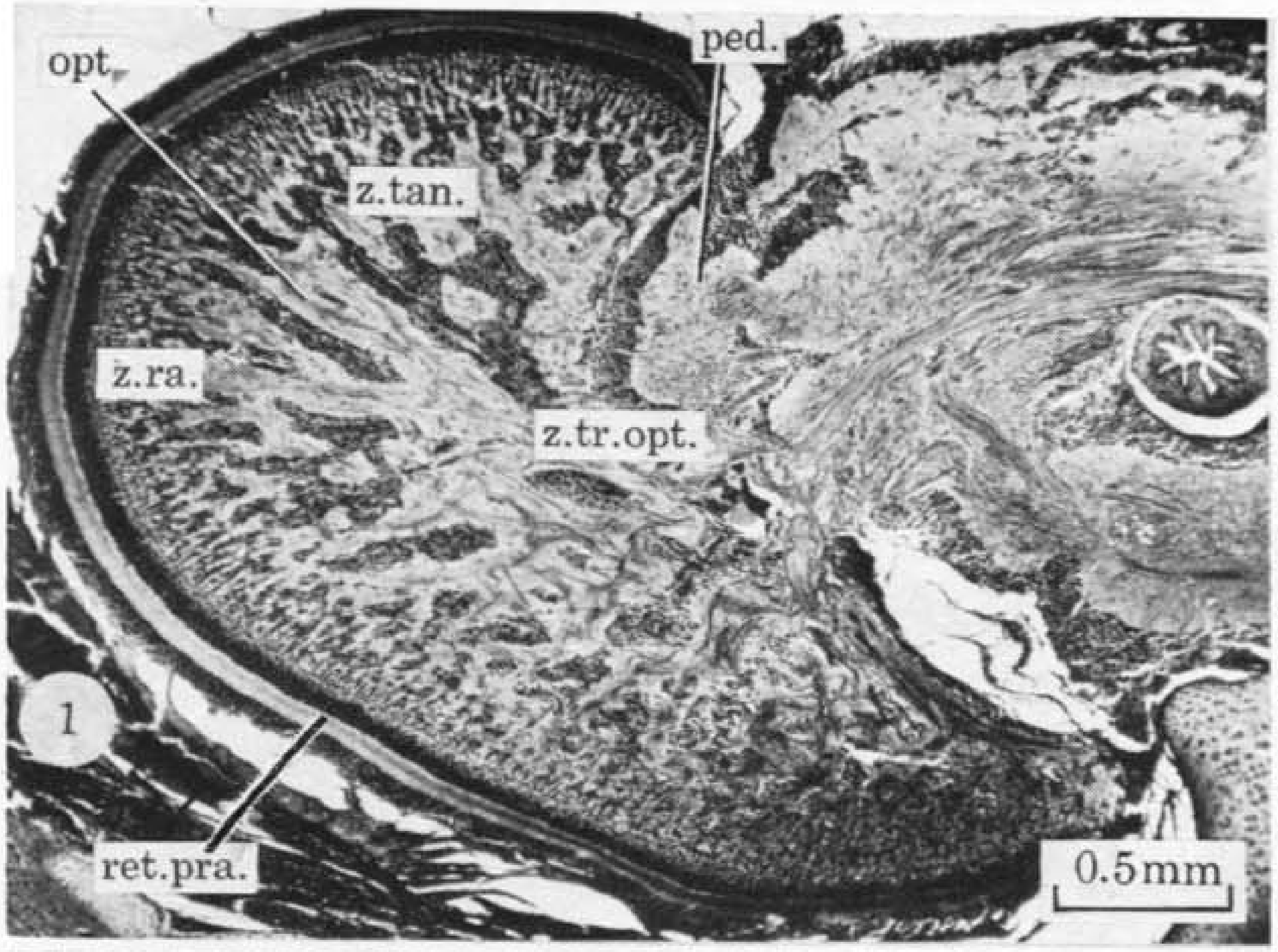
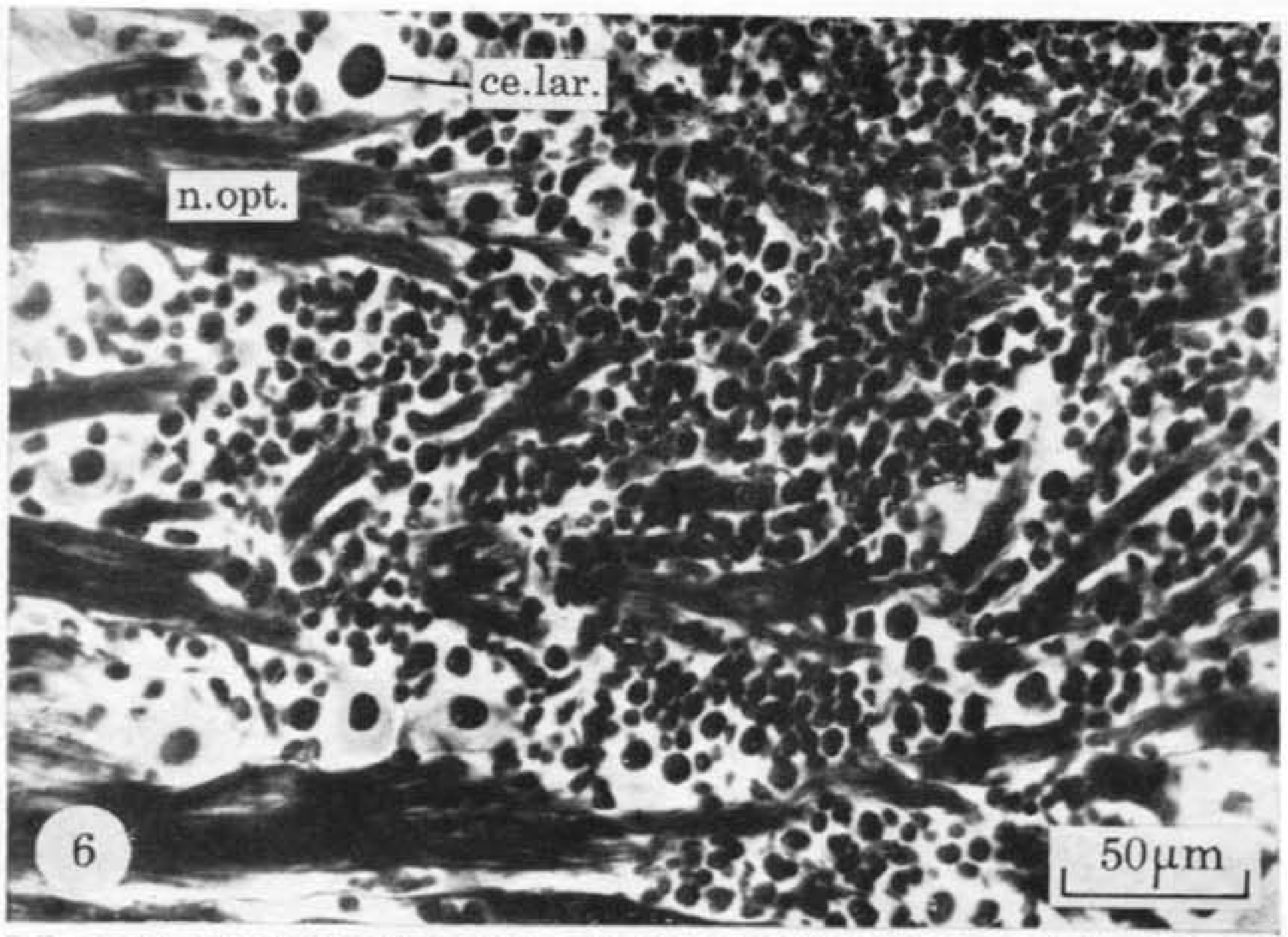
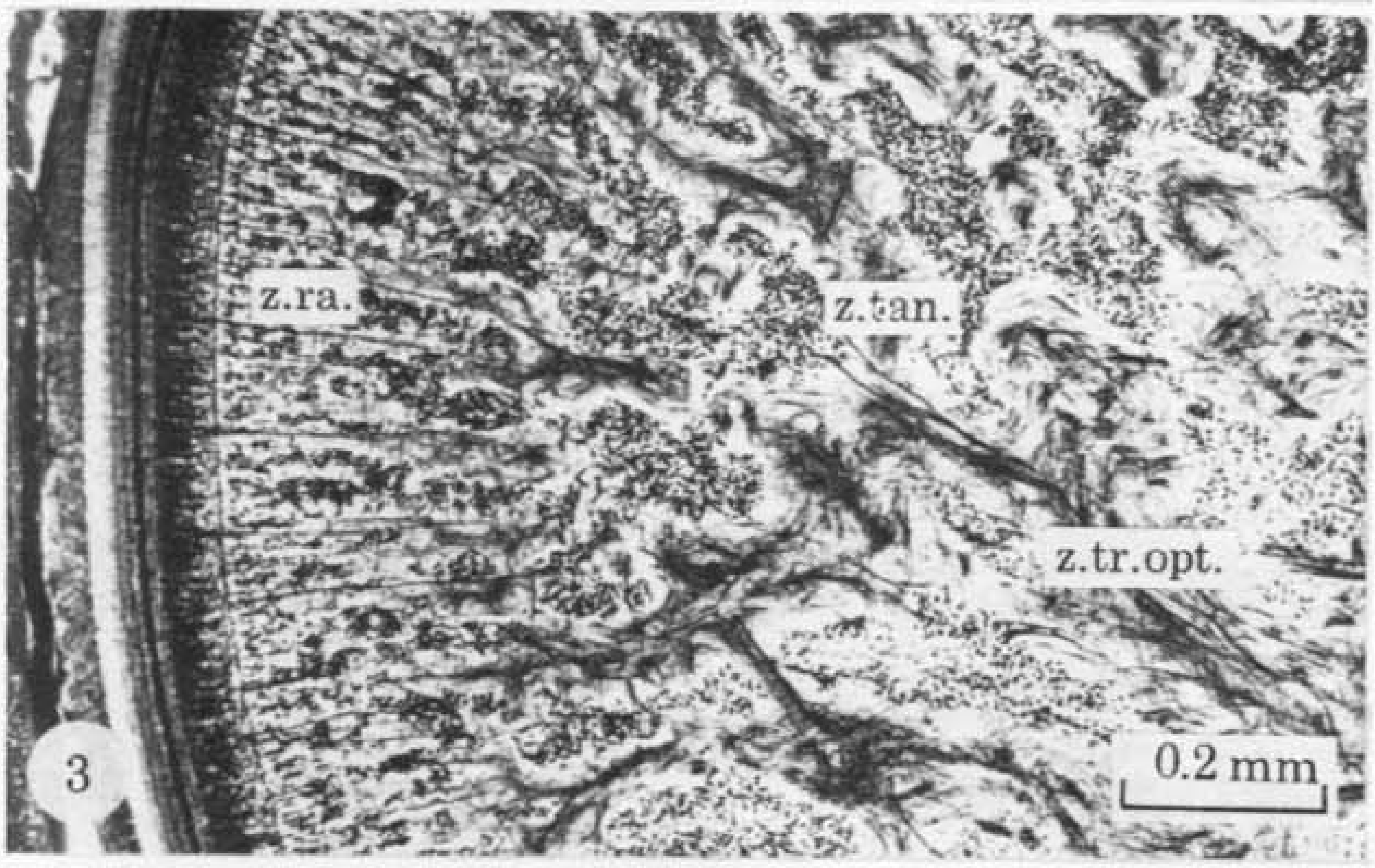
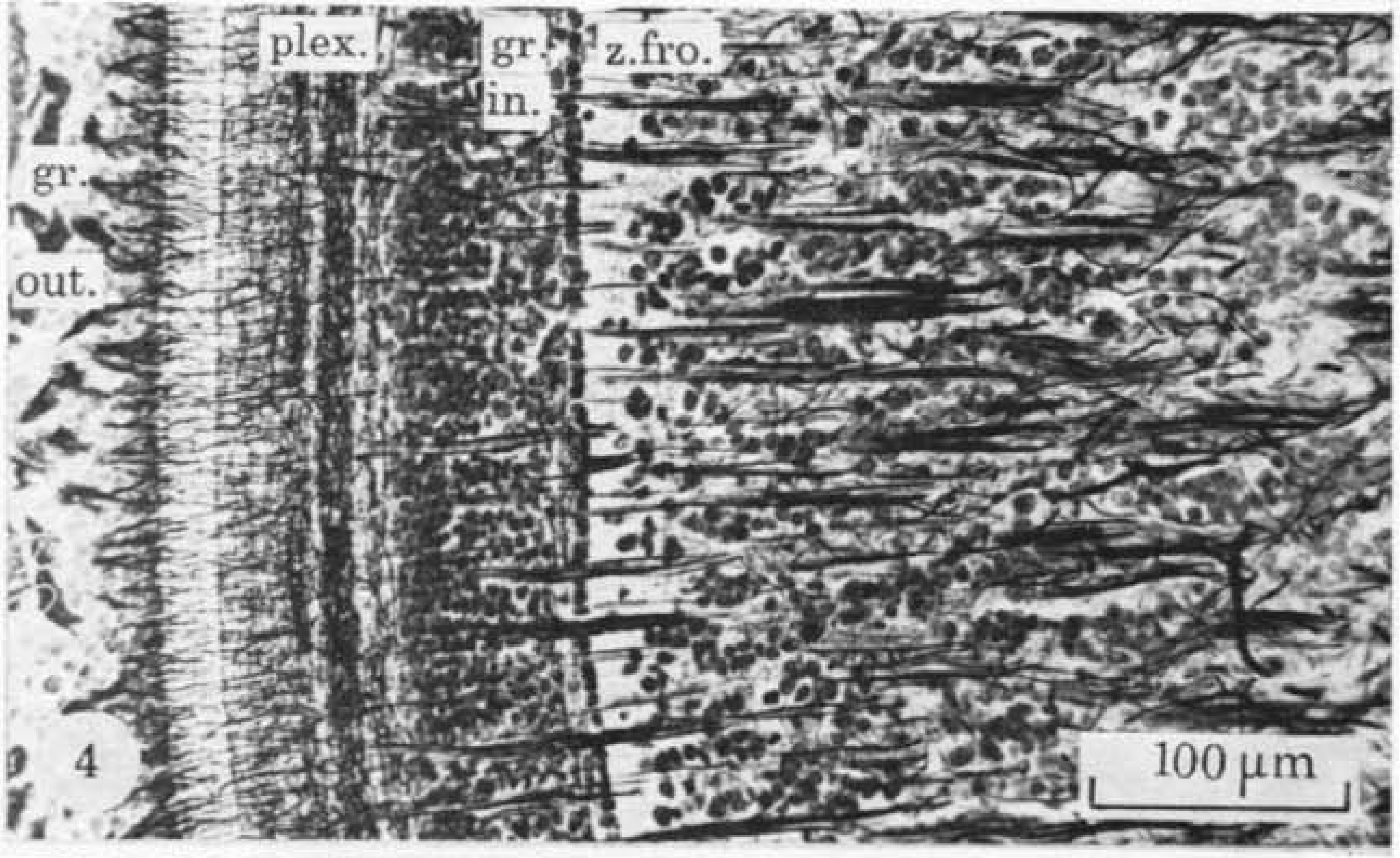
ABBREVIATIONS USED ON FIGURES

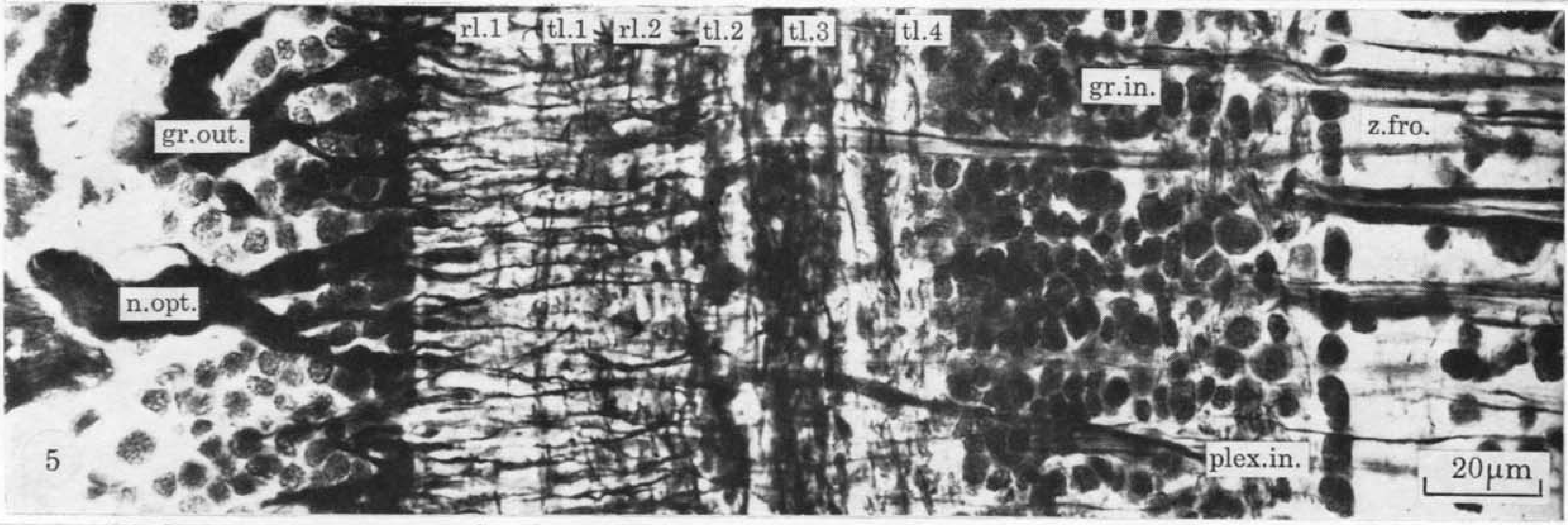
ax.	axon
ax?	possible axon
ax.ter.	axon terminal
b.a.	anterior basal lobe
b.l.	lateral basal lobe
b.med.	median basal lobe
c.mag.	magnocellular commissure
c.opt.	optic commissure
ce.am.	amacrine cell (microneuron)
ce.am?	probable amacrine cell (or fibre)
ce.am.in.	inner amacrine cell (or fibre)
ce.am.in?	probable inner amacrine cell (or fibre)
ce.am.lar.	large amacrine cell
ce.am.tan.	amacrine cell of tangential layer
ce.bi.	bipolar cell
ce.cent.	cell with centrifugal nerve fibres
ce.gi.1	first order giant cell
ce.lar.	large cell
ce.mult.	multipolar cell
ce.mult.lar.	large multipolar cell
ce.mult.sm.	small multipolar cell
ce.palis	cell of palisade layer
ce.sm.	small cell
ce.vis.2	second-order visual cell
ce.vis.2,el.	second-order visual cell with elongated receptive field
ce.vis.2,lar.	large second-order visual cell
ce.vis.2,med.	medium second-order visual cell
ce.vis.2,out.	second-order visual cell of outer granule cell layer
ce.vis.2.sm.	small second-order visual cell
ce.vis.3	third-order visual cell
chi.	chiasma
den.	dendrite
den?	dendritic branches of cell of medulla
f.gi.1	first-order giant fibre
gl.	glial cell
gr.in.	inner granule cell layer
gr.out.	outer granule cell layer
mac.	macula
mag.	magnocellular lobe
n.cr.	crista nerve
n.f.cent.	centrifugal nerve fibre
n.f.cent?	probable centrifugal nerve fibre
n.opt.	optic nerve
n.ret.1–3	retinal nerve fibre, types 1–3
?n.ret.3	? retinal nerve type 3
opt.	optic lobe
palis.	palisade layer
ped.	peduncle lobe
plex.	plexiform zone
plex.in.	inner plexiform zone
pv.	palliovisceral lobe
ret.pra.	retina profonda
rl.1–rl.2	radial layers of the plexiform zone
subv.	subvertical lobe
tl.1–tl.4	tangential layers of the plexiform zone
tr.opt.–b.a.	anterior basal to optic lobe tract
tr.opt.–b.l.	lateral basal to optic lobe tract
tr.opt.–b.med.	optic to median basal lobe tract
tr.opt.–fr.s.	optic to superior frontal lobe tract
tr.opt.–mag.l.	lateral magnocellular to optic lobe tract
tr.opt.–mag.med.	median magnocellular to optic lobe tract
tr.opt.–prec.	optic to pre-commissural lobe tract
tr.subv.–opt.	subvertical to optic lobe tract
v.	vertical lobe
z.fro.	frontier zone of optic lobe
z.ra.	zone of radial columns of medulla
z.tan.	zone of tangential bundles
z.tr.opt.	zone of optic tract bundles in optic lobe

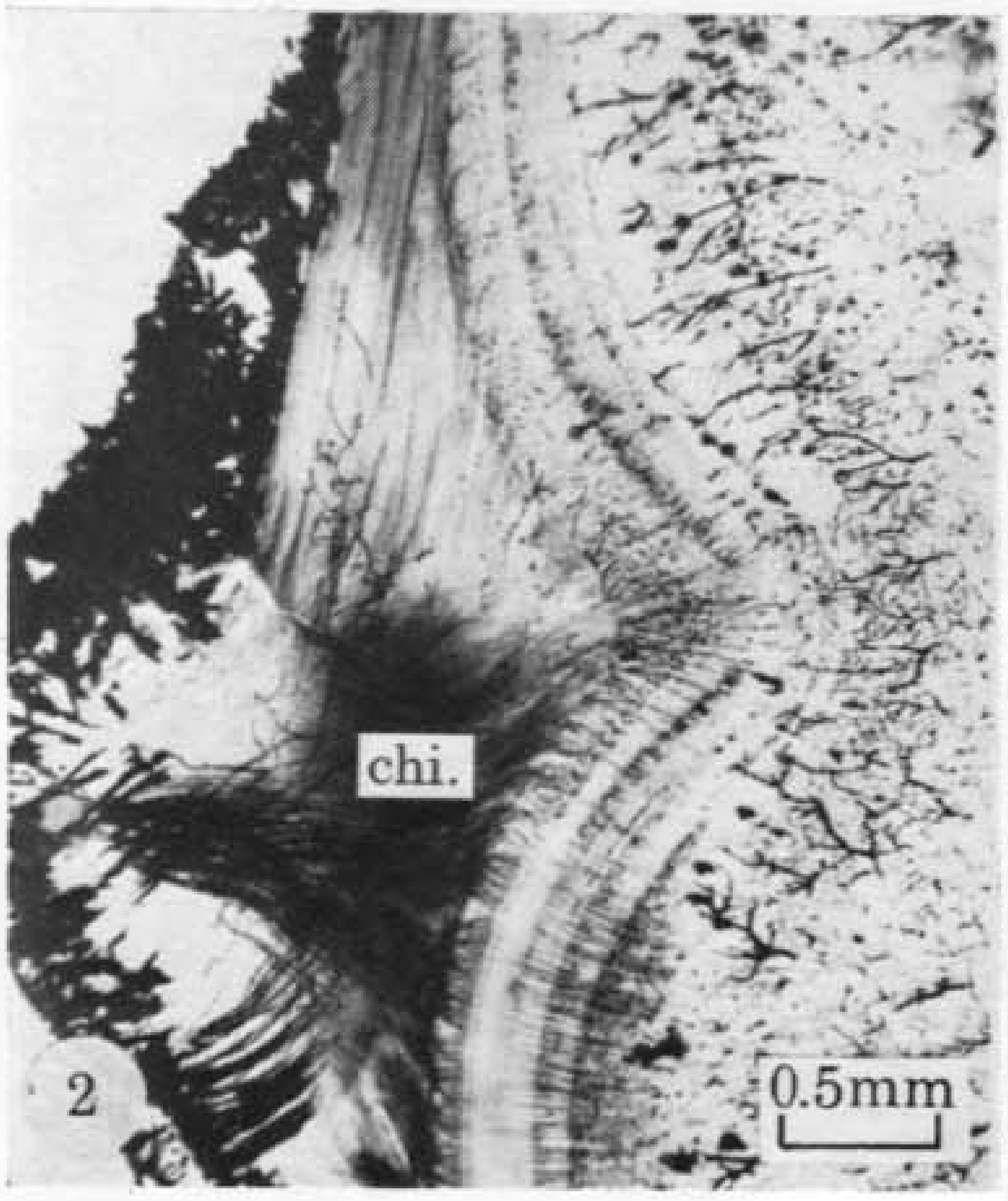


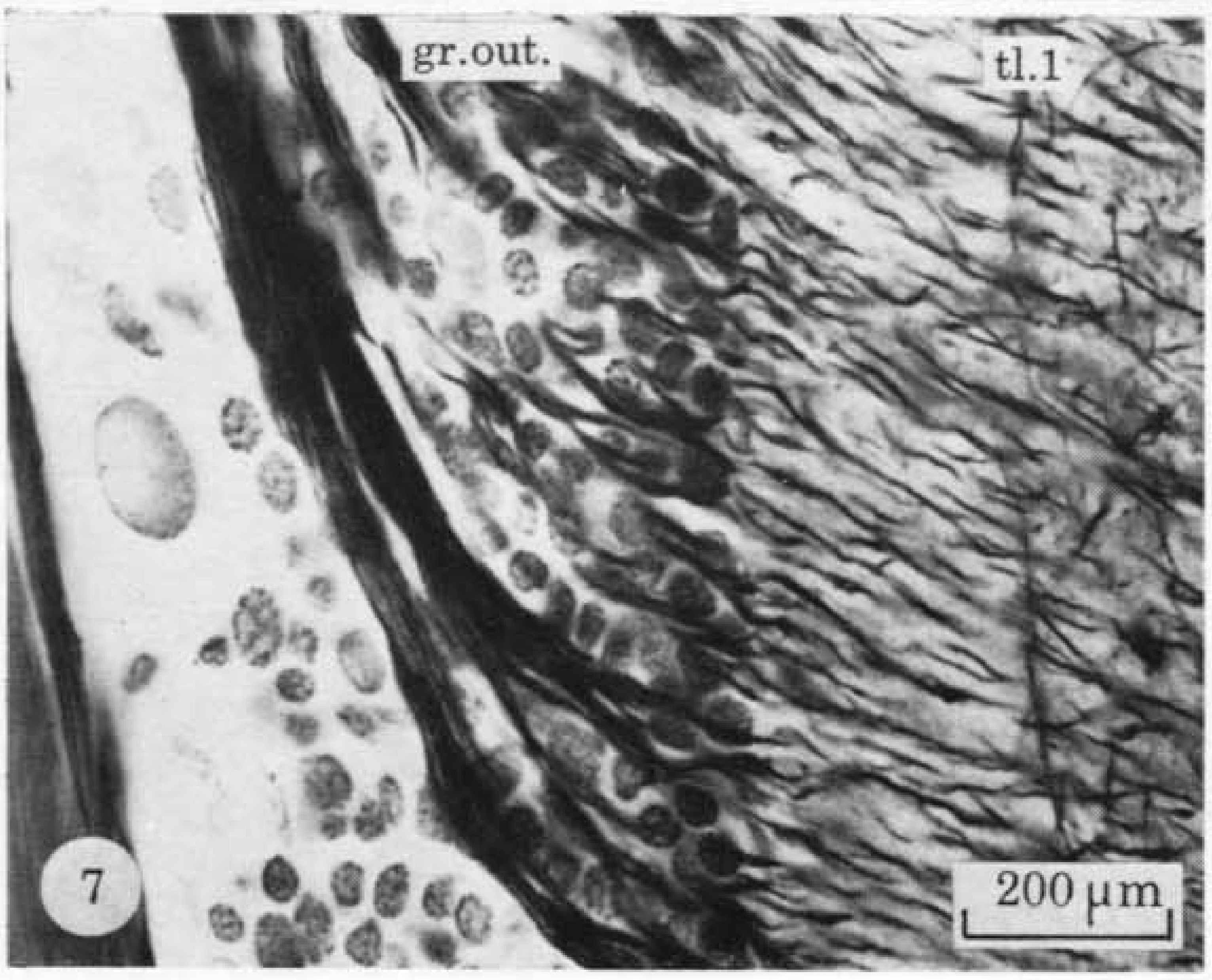


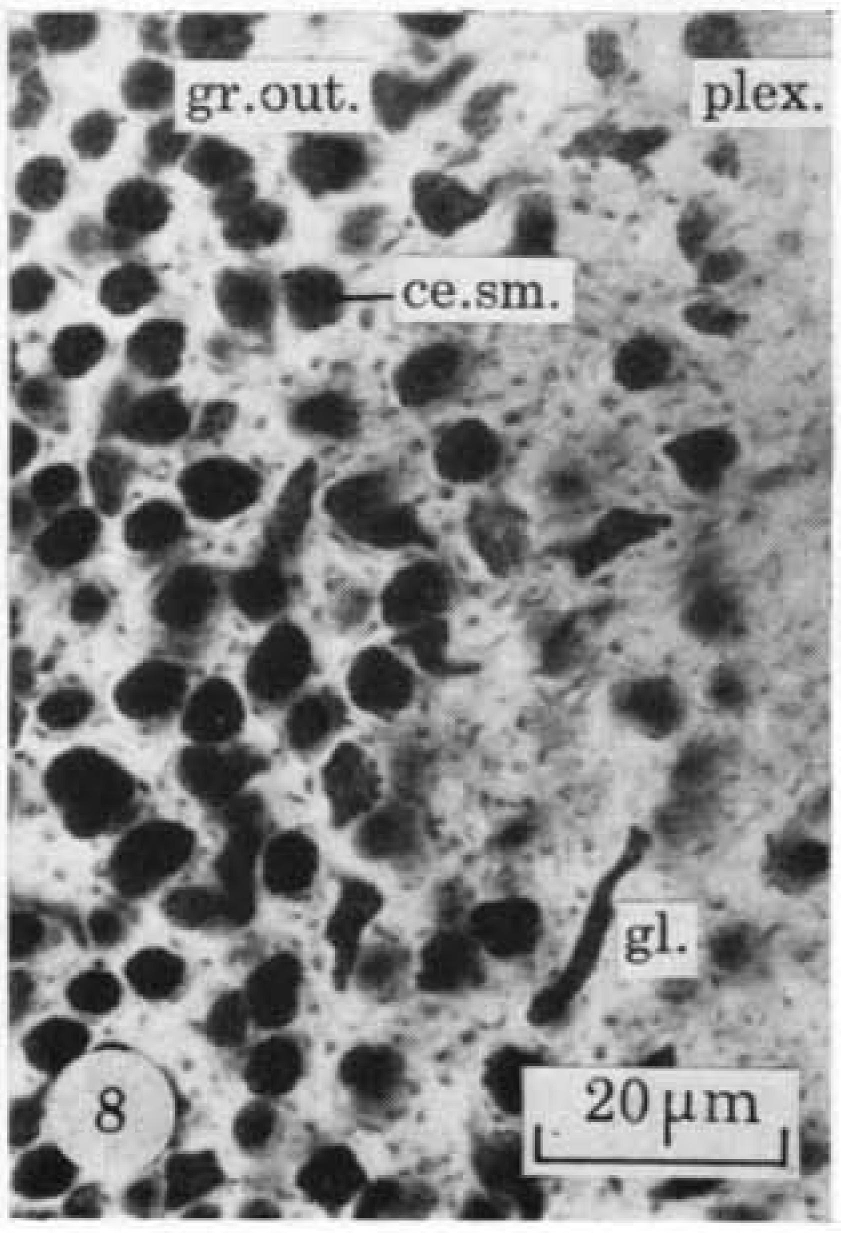




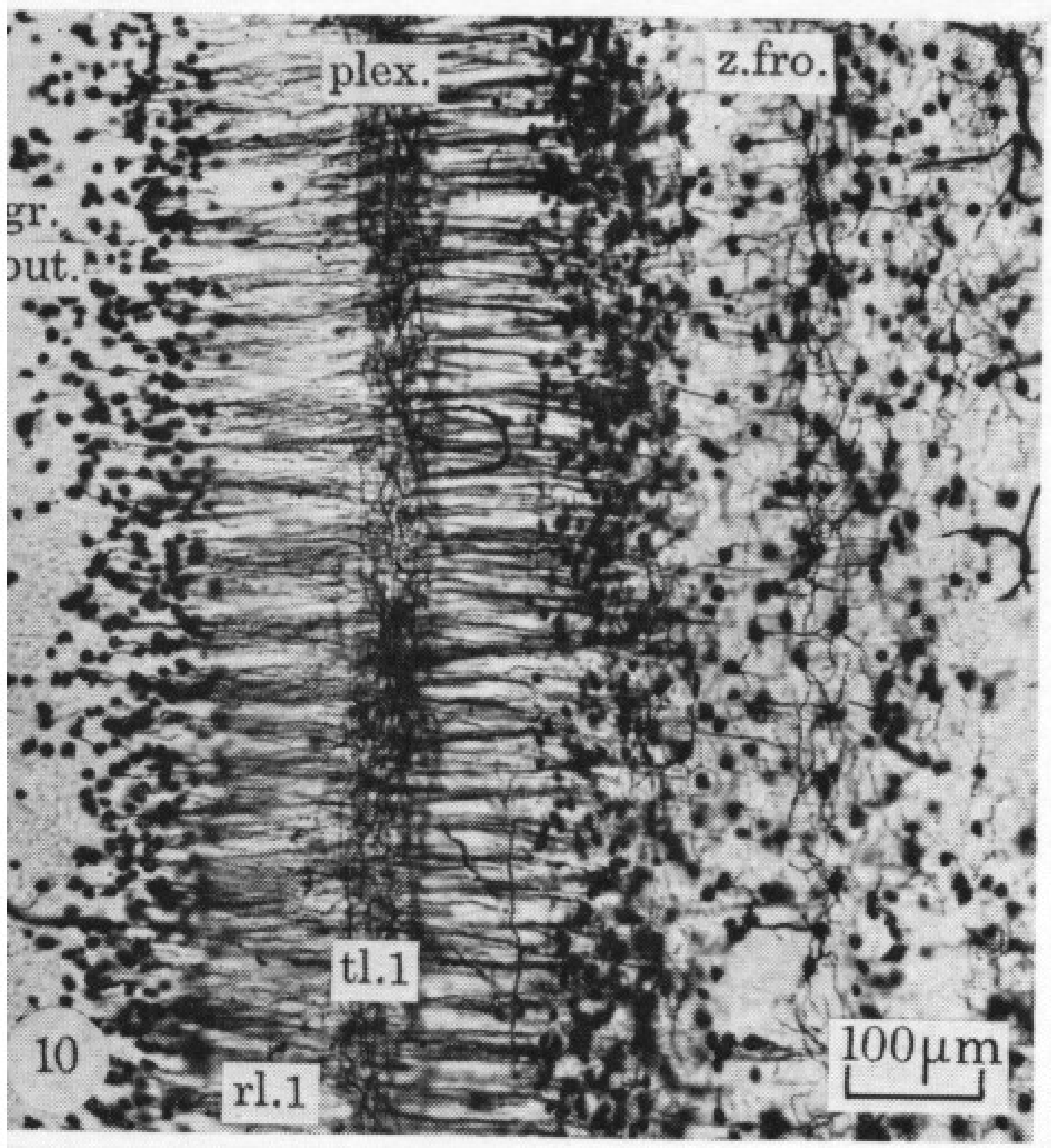


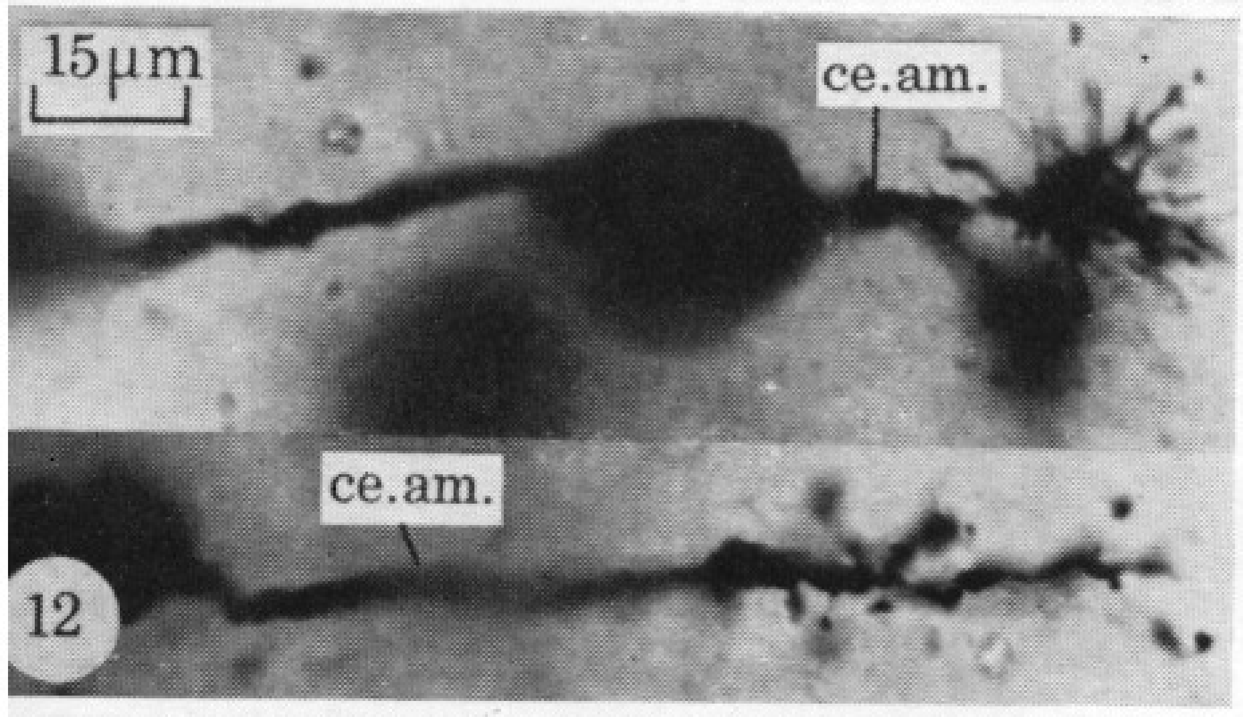


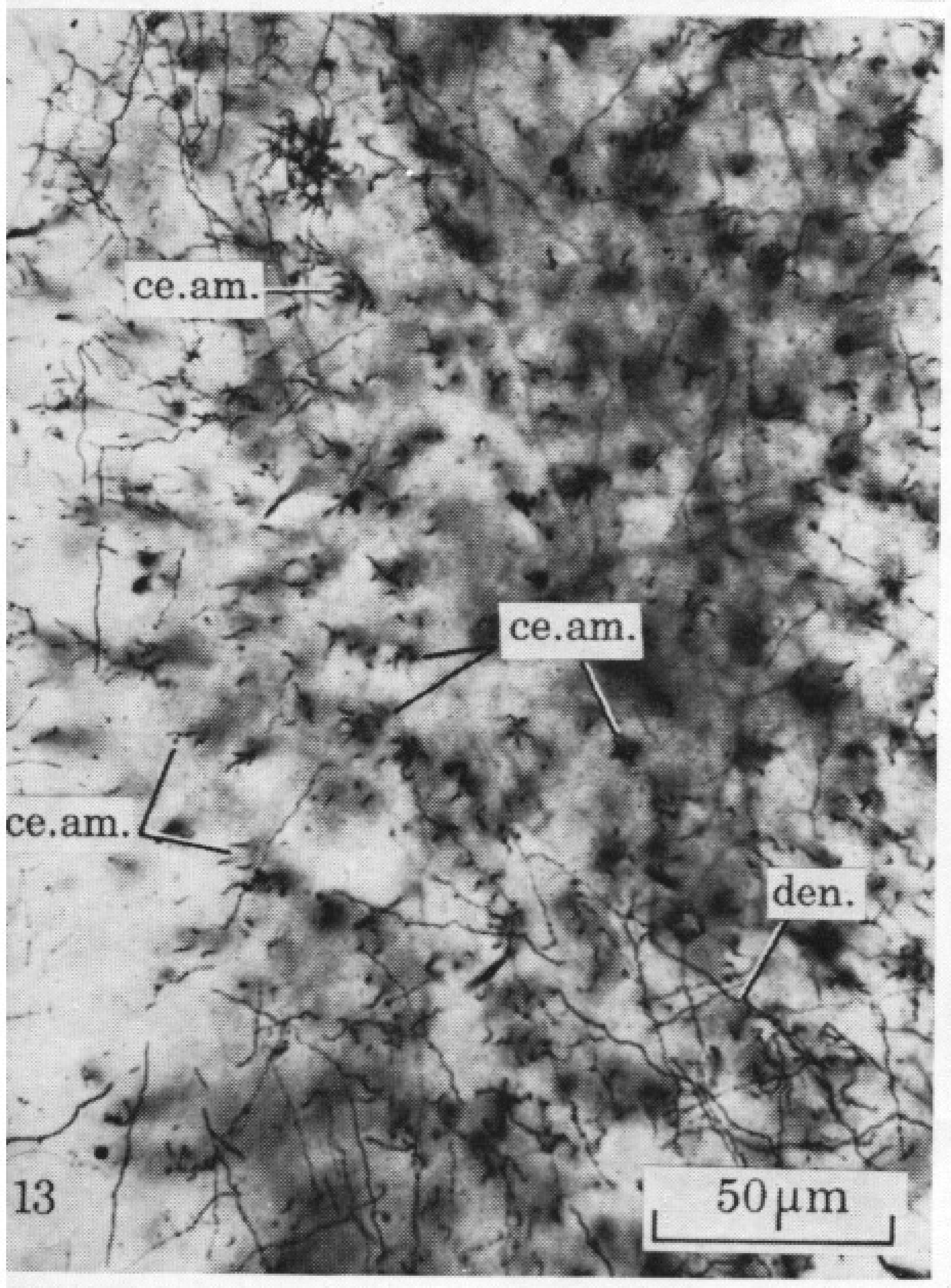


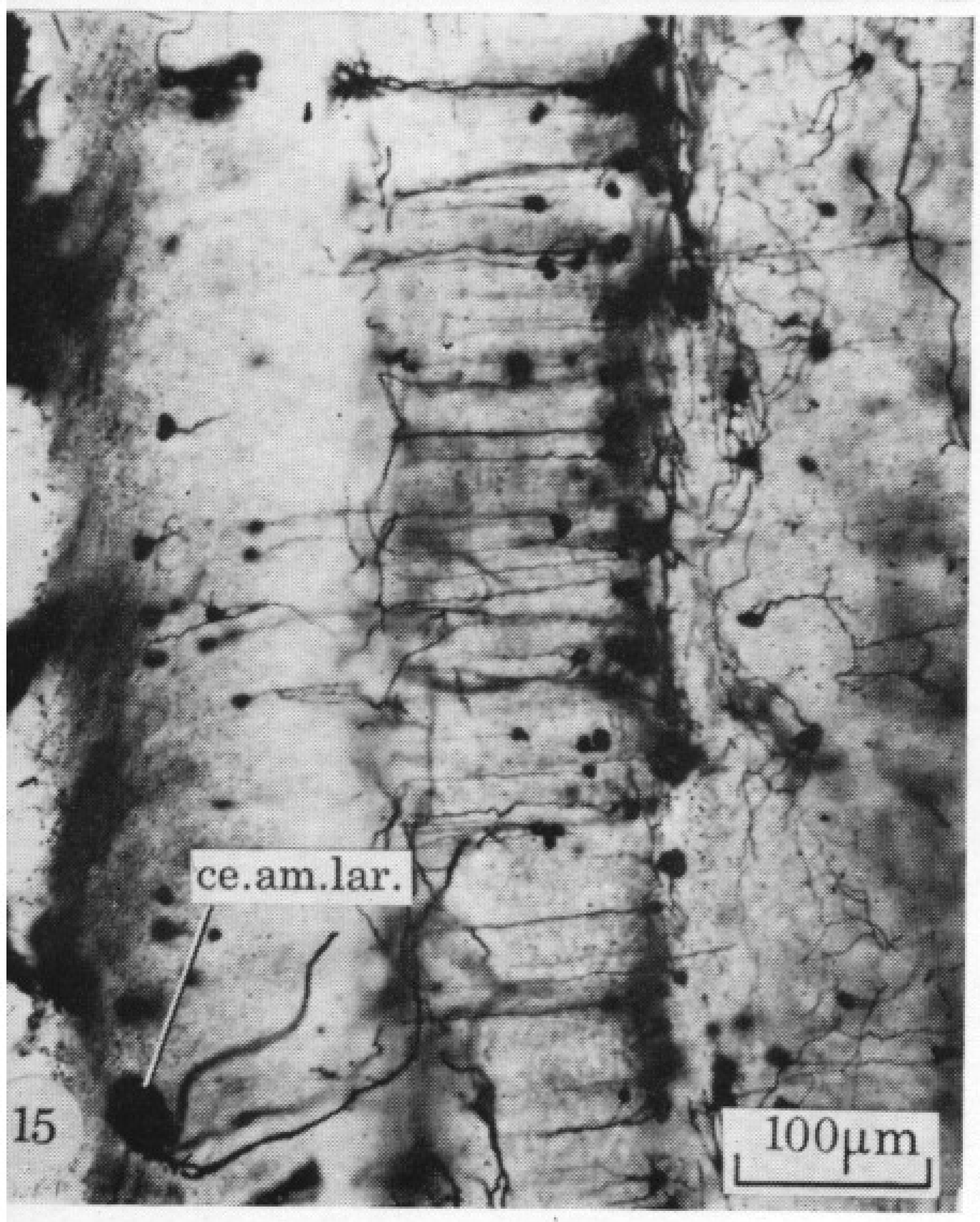


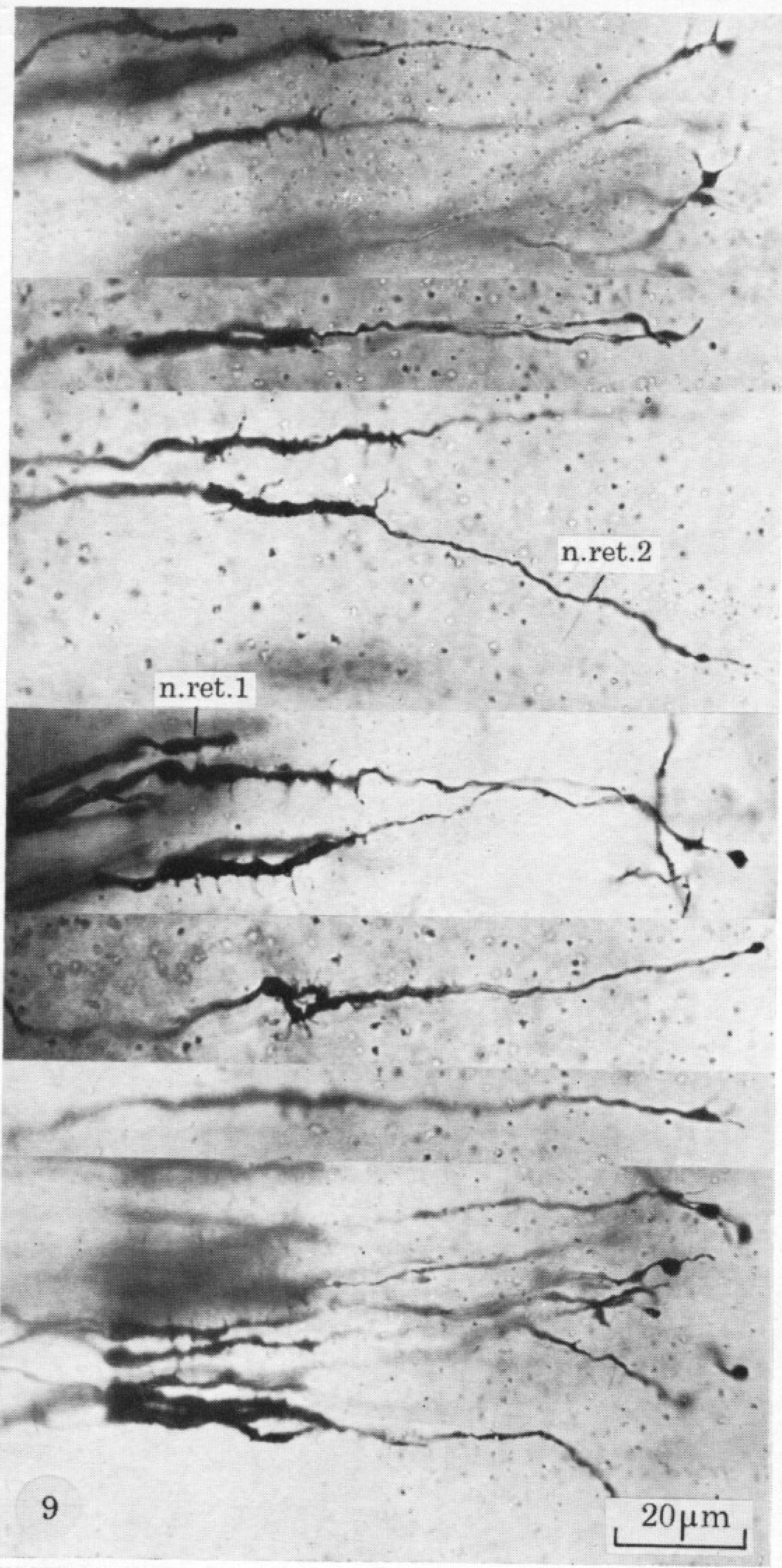
FIGURES 1–8. For description see opposite

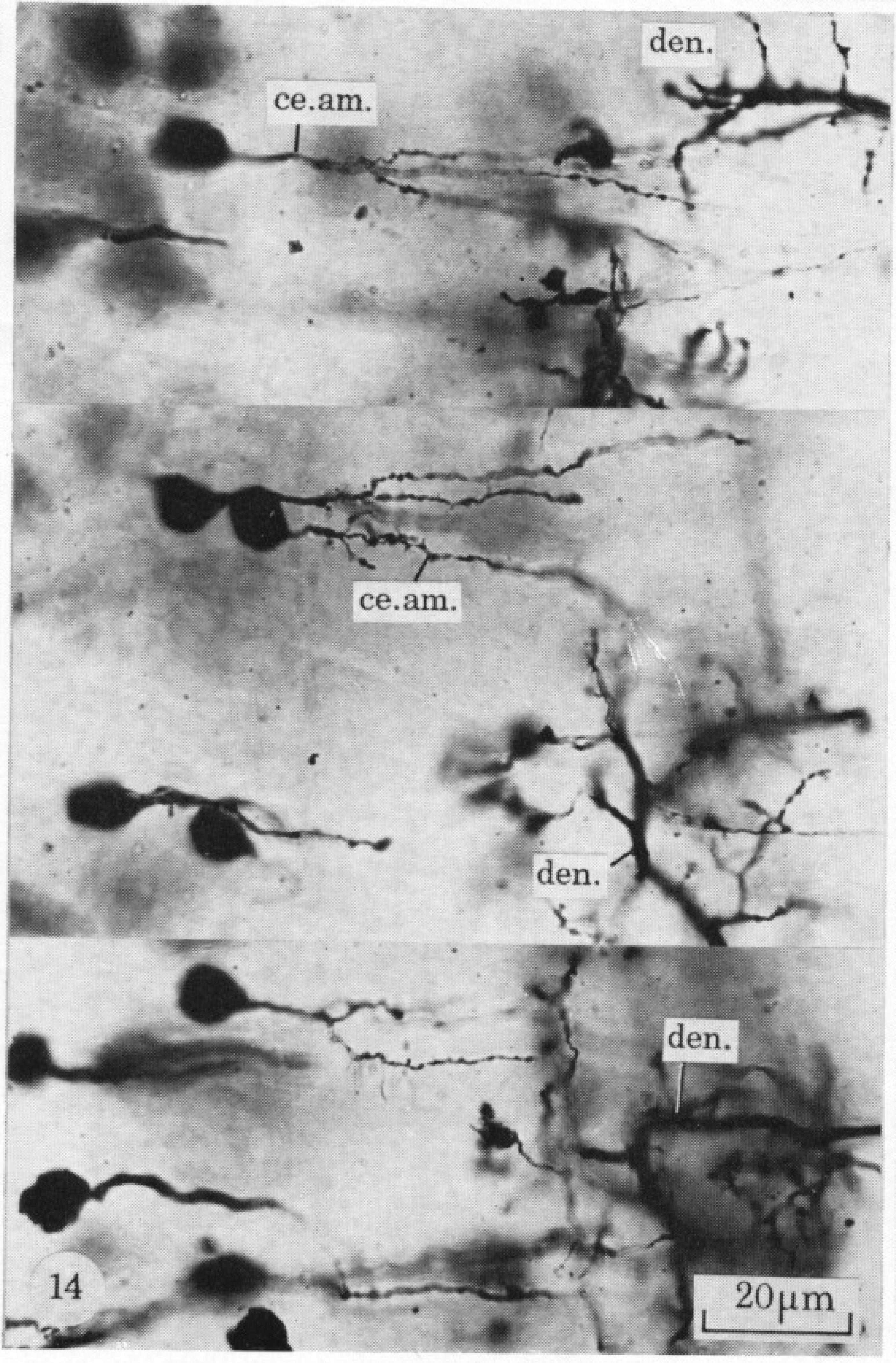


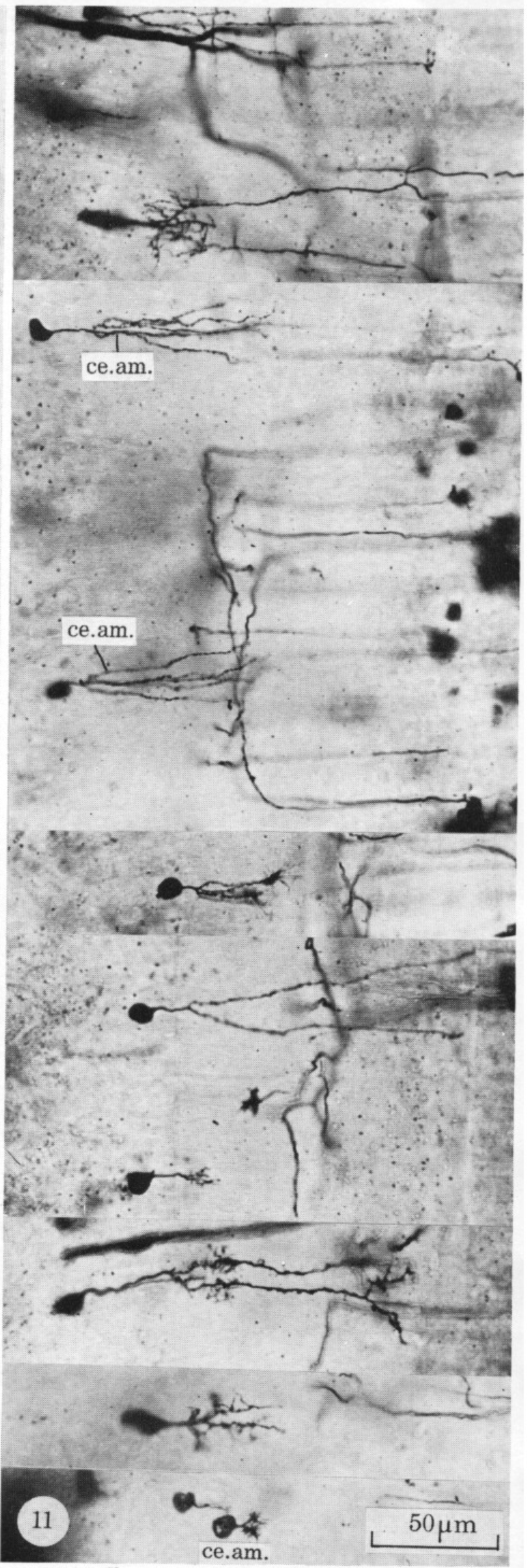


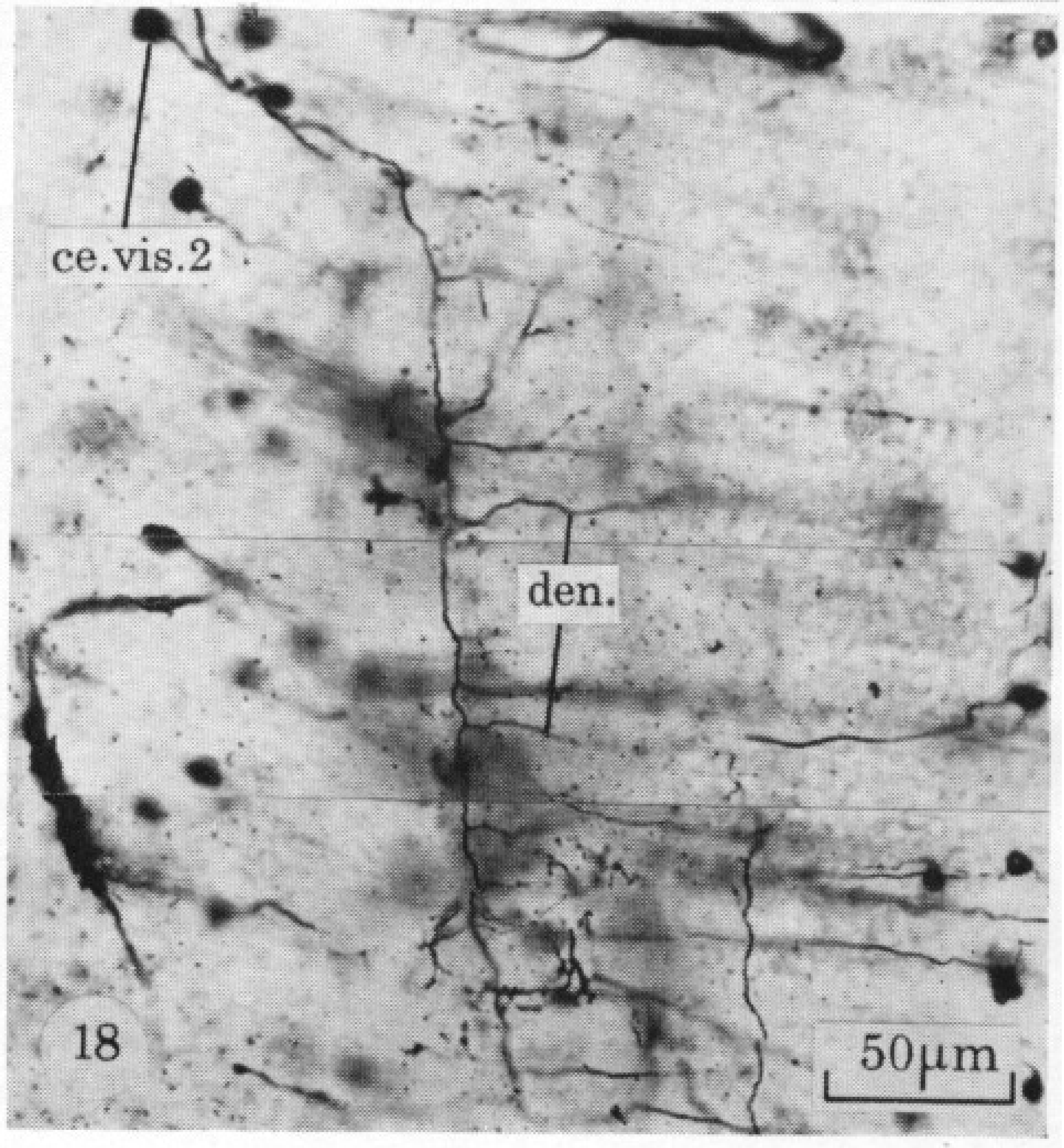




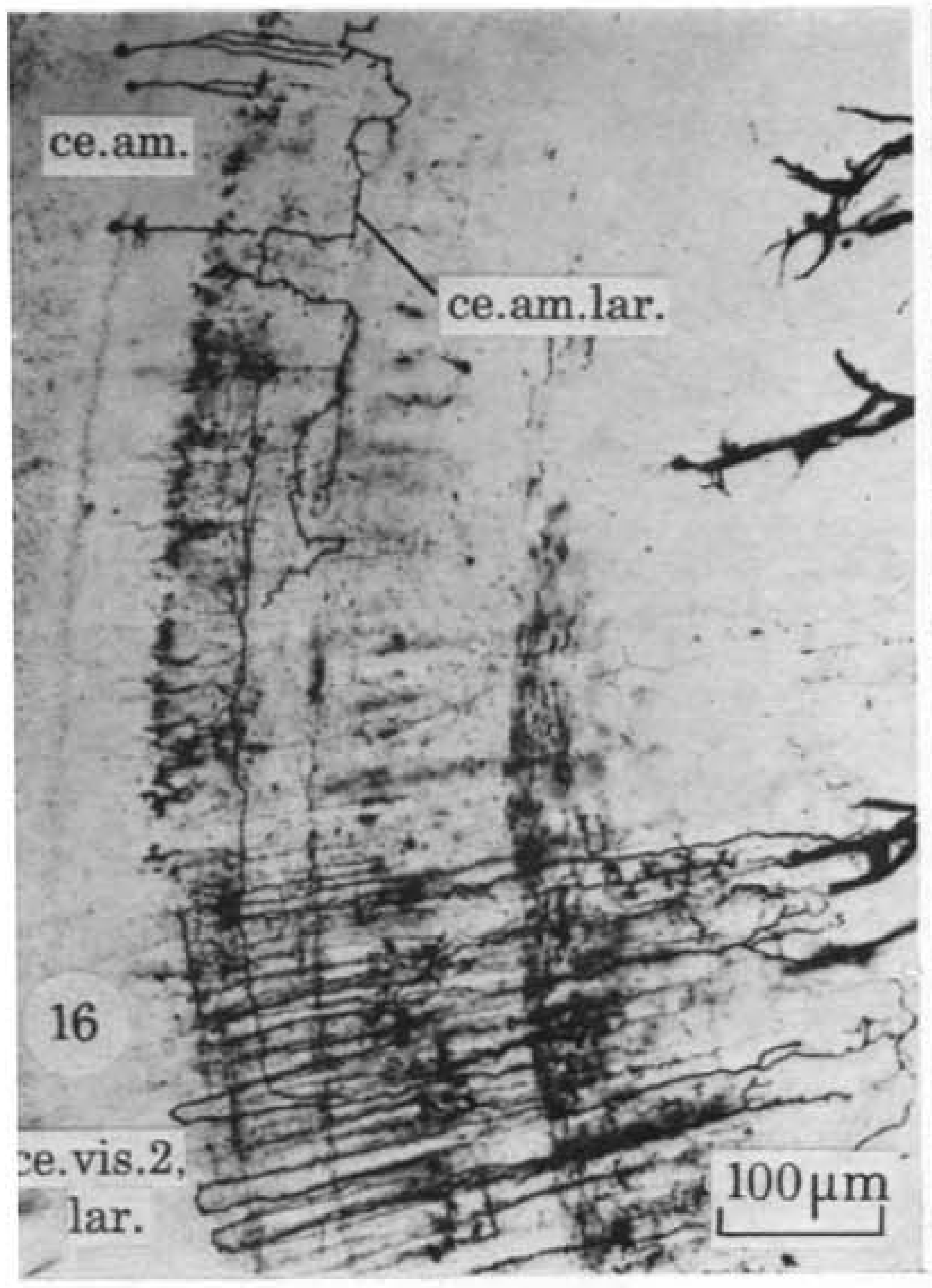


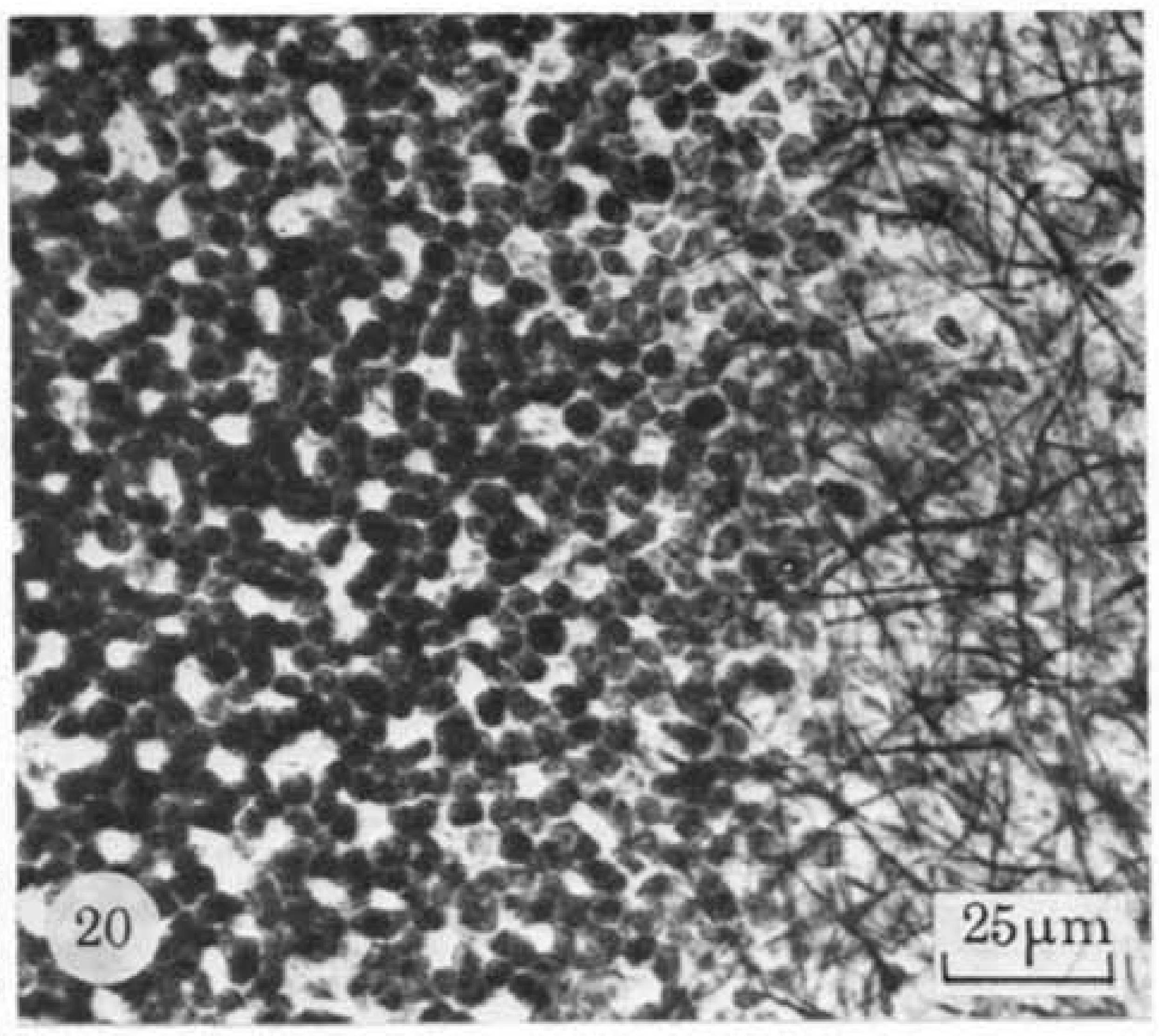


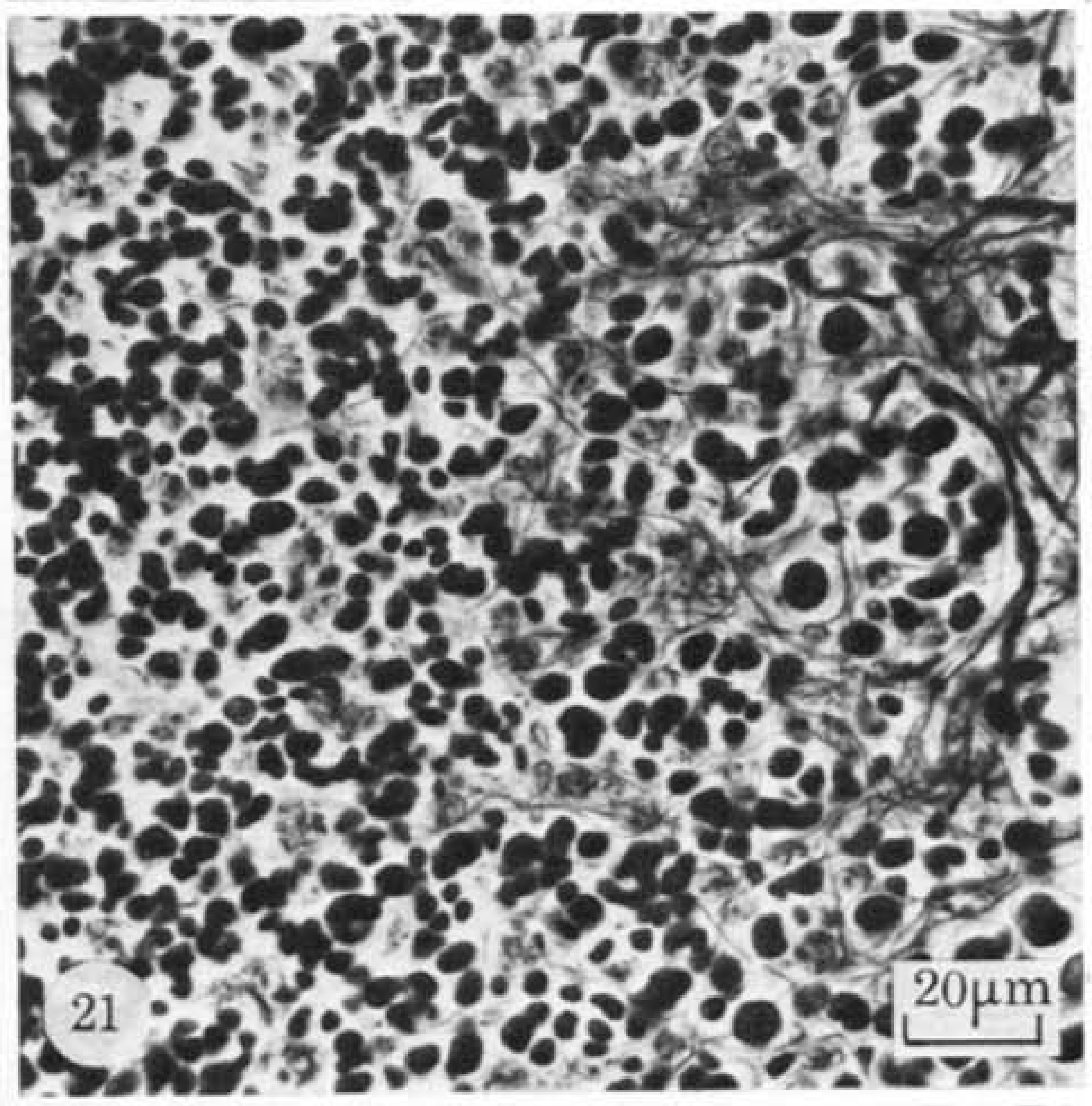


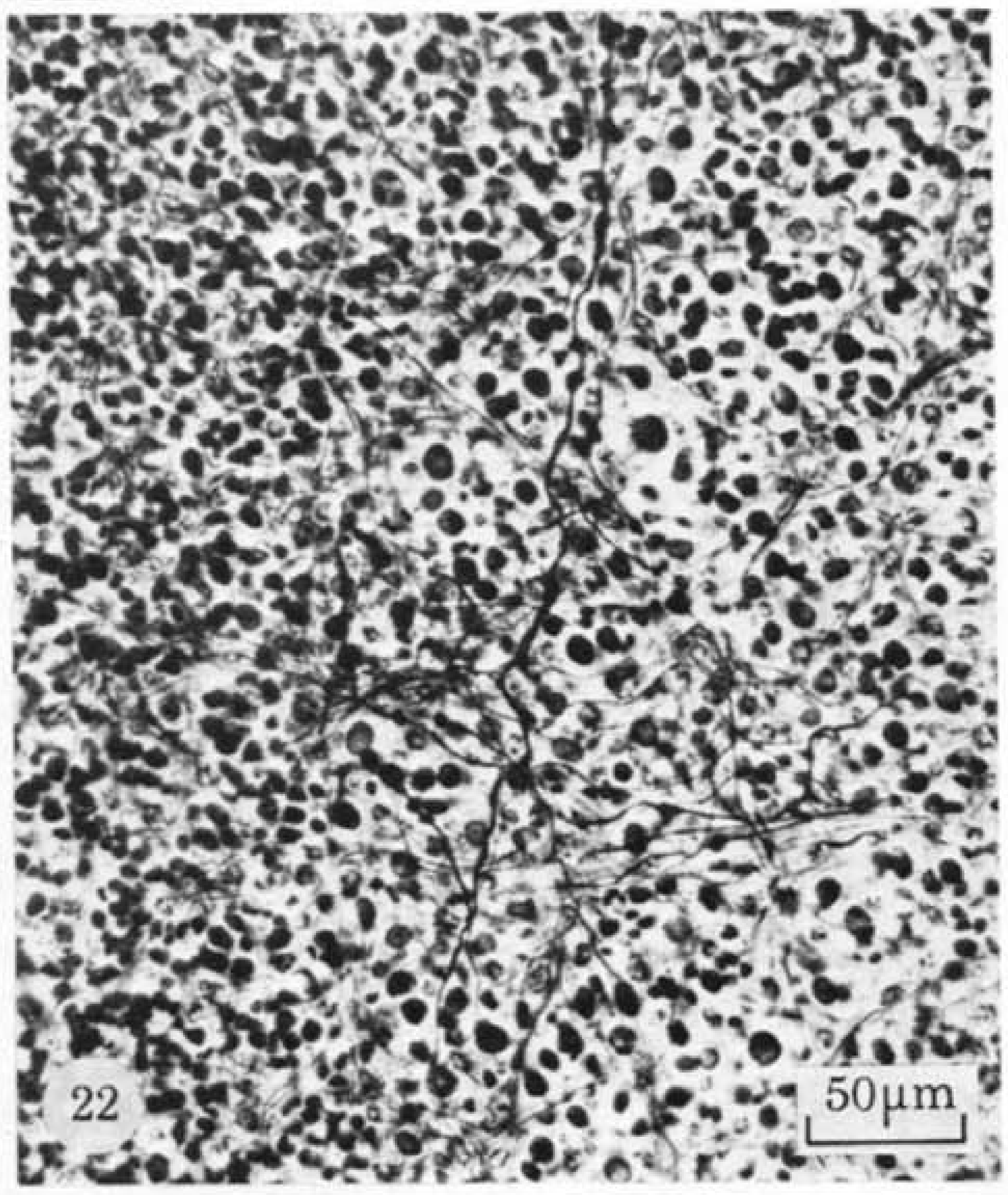


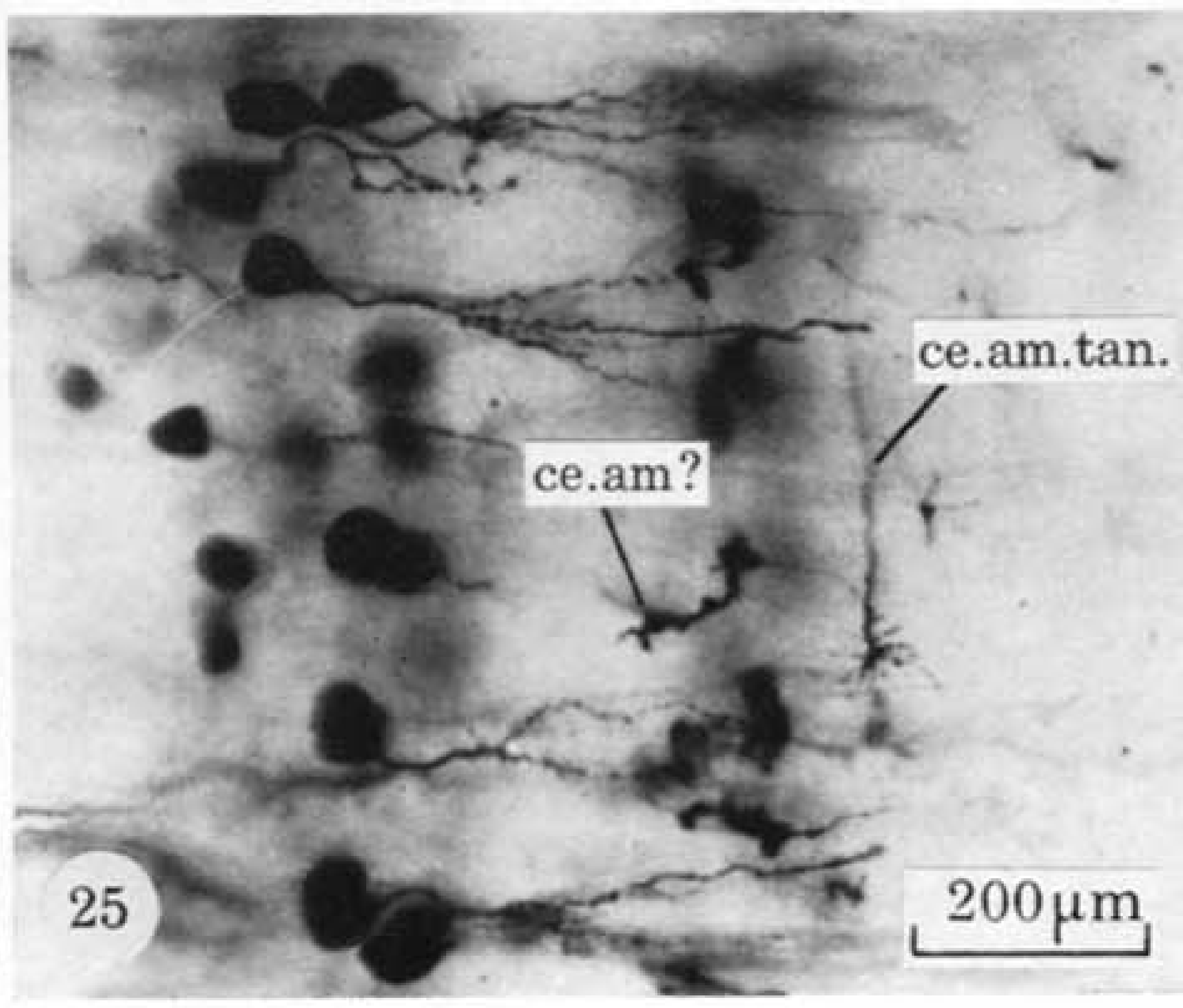
FIGURES 9–15 AND 18. For description see opposite

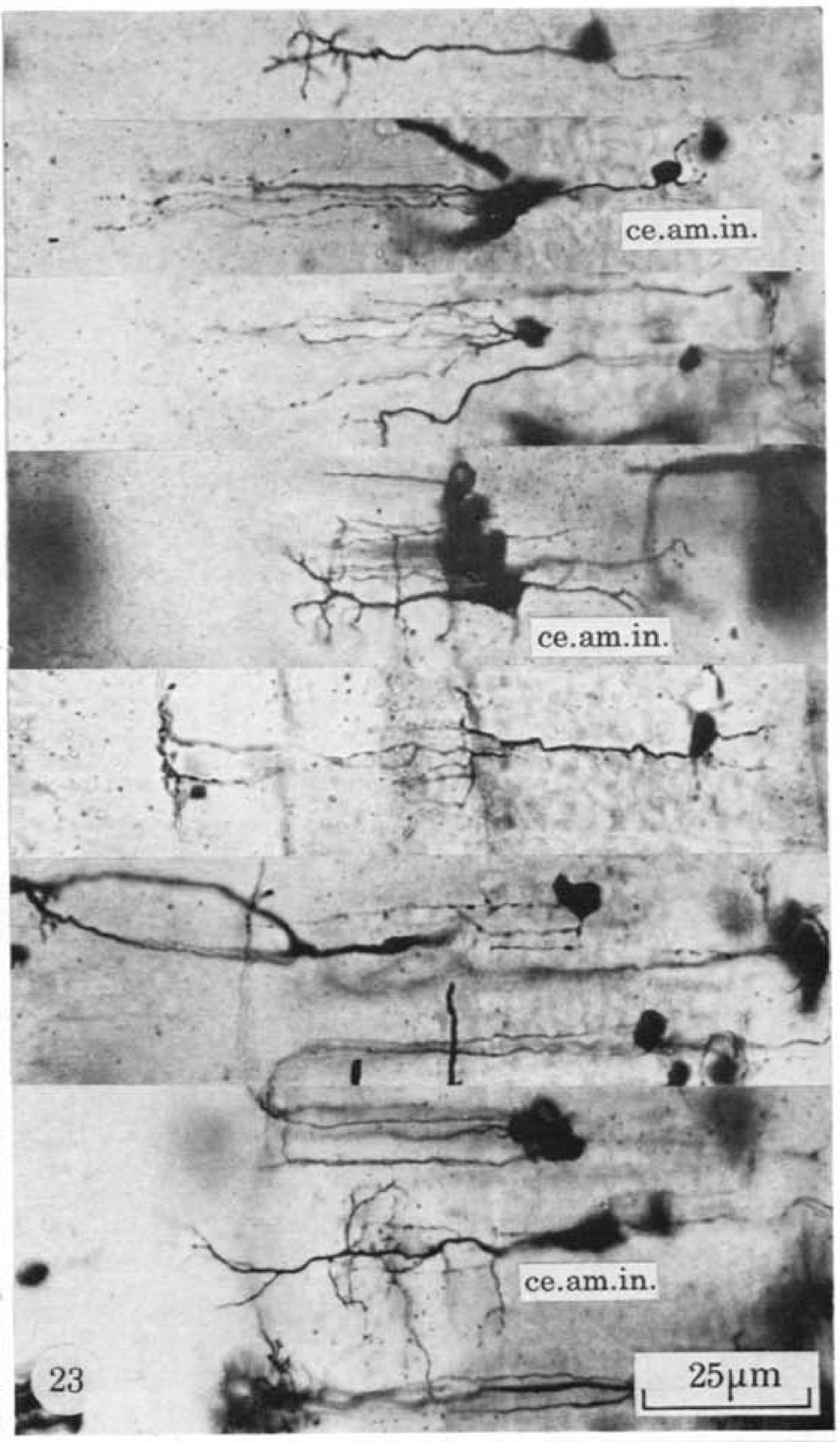


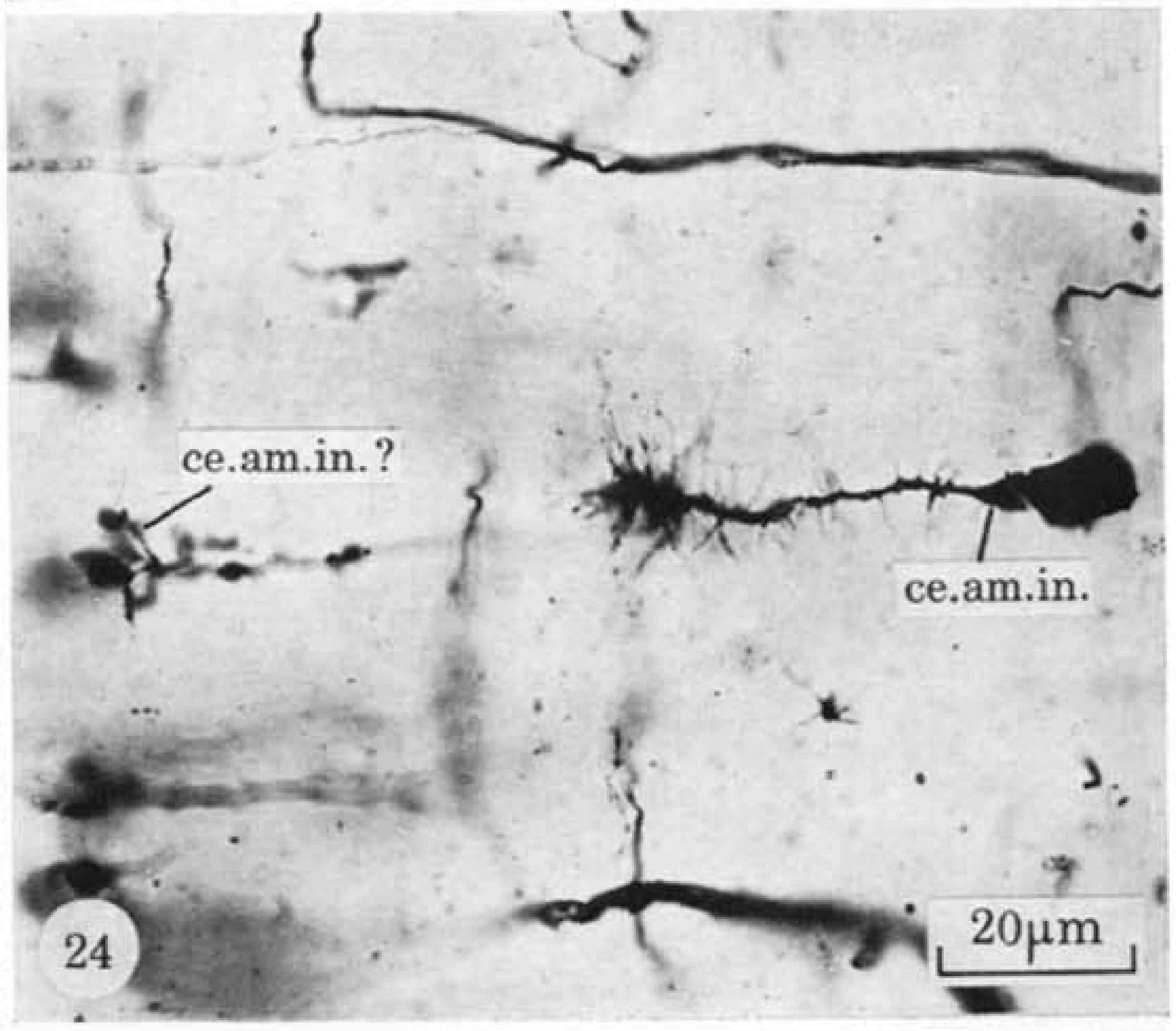


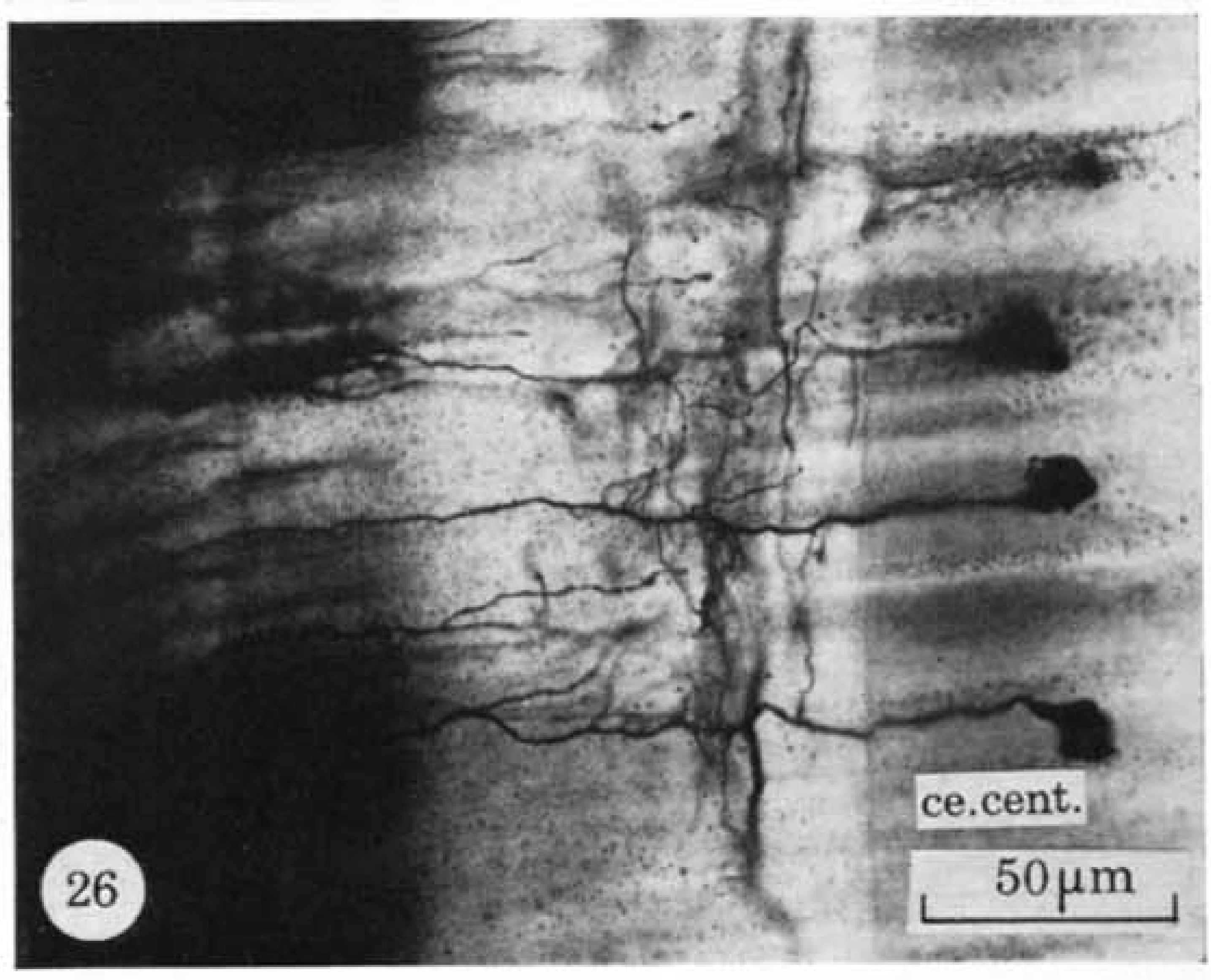




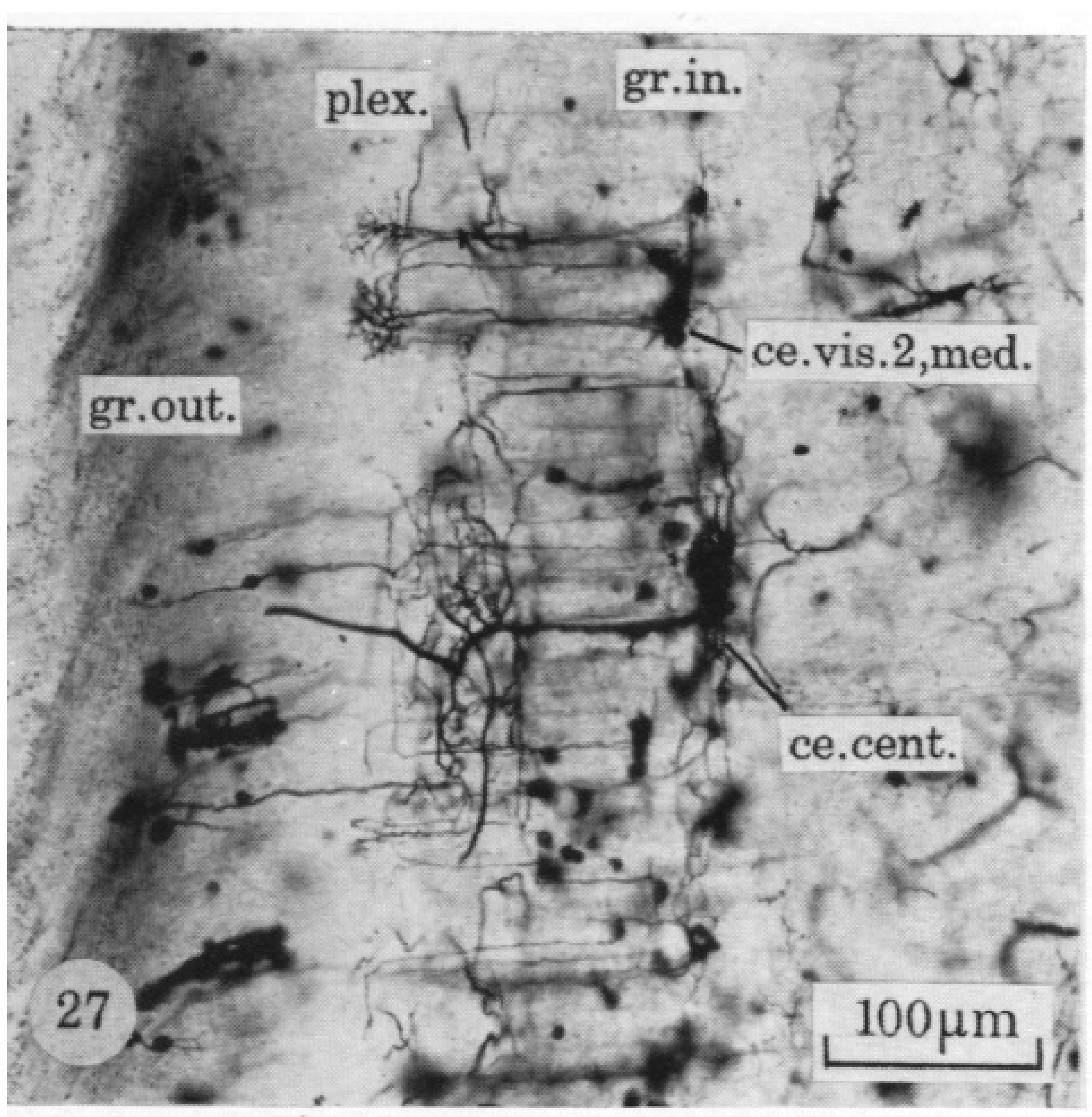


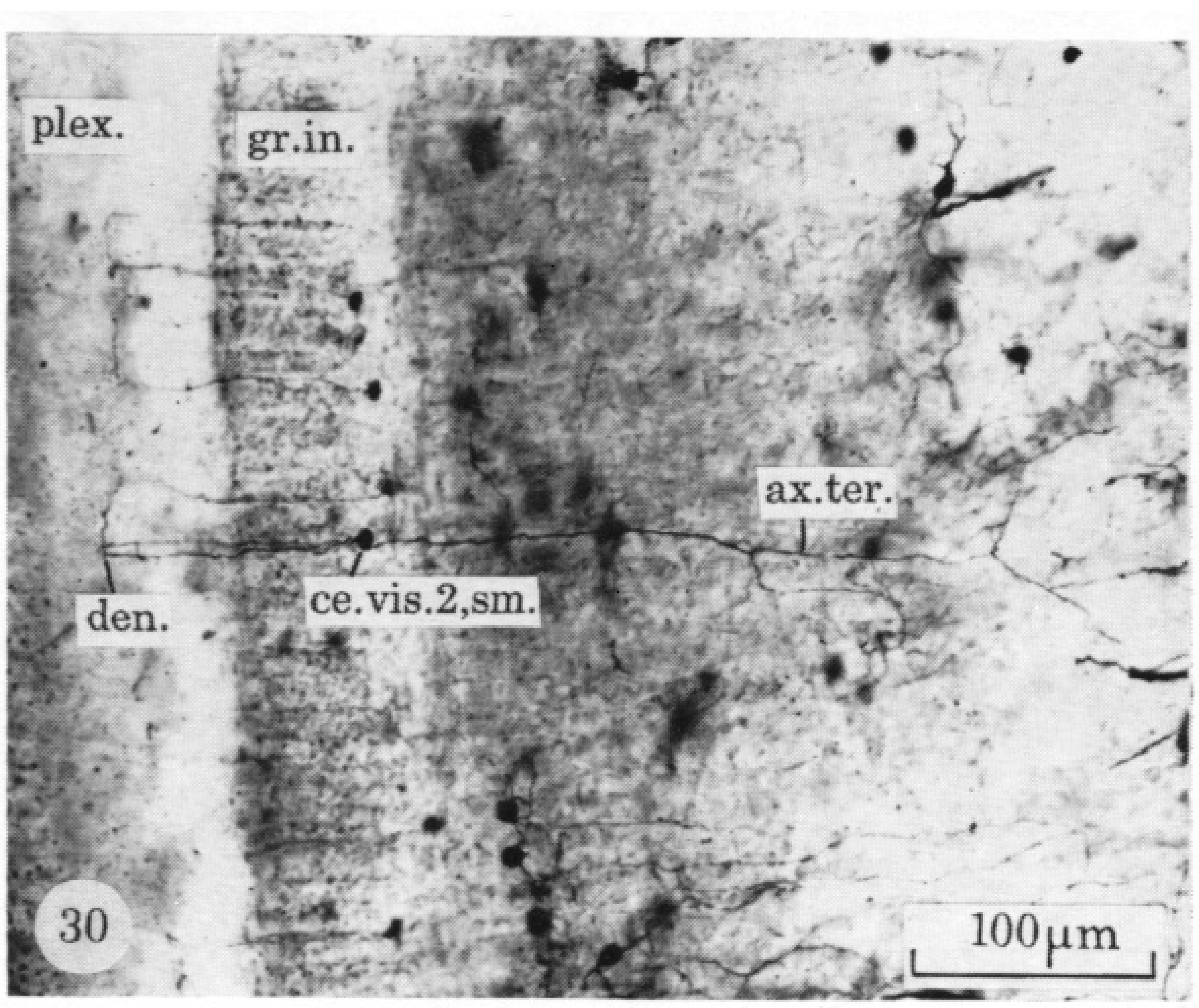






FIGURES 16, 17, 19–26. For description see opposite


27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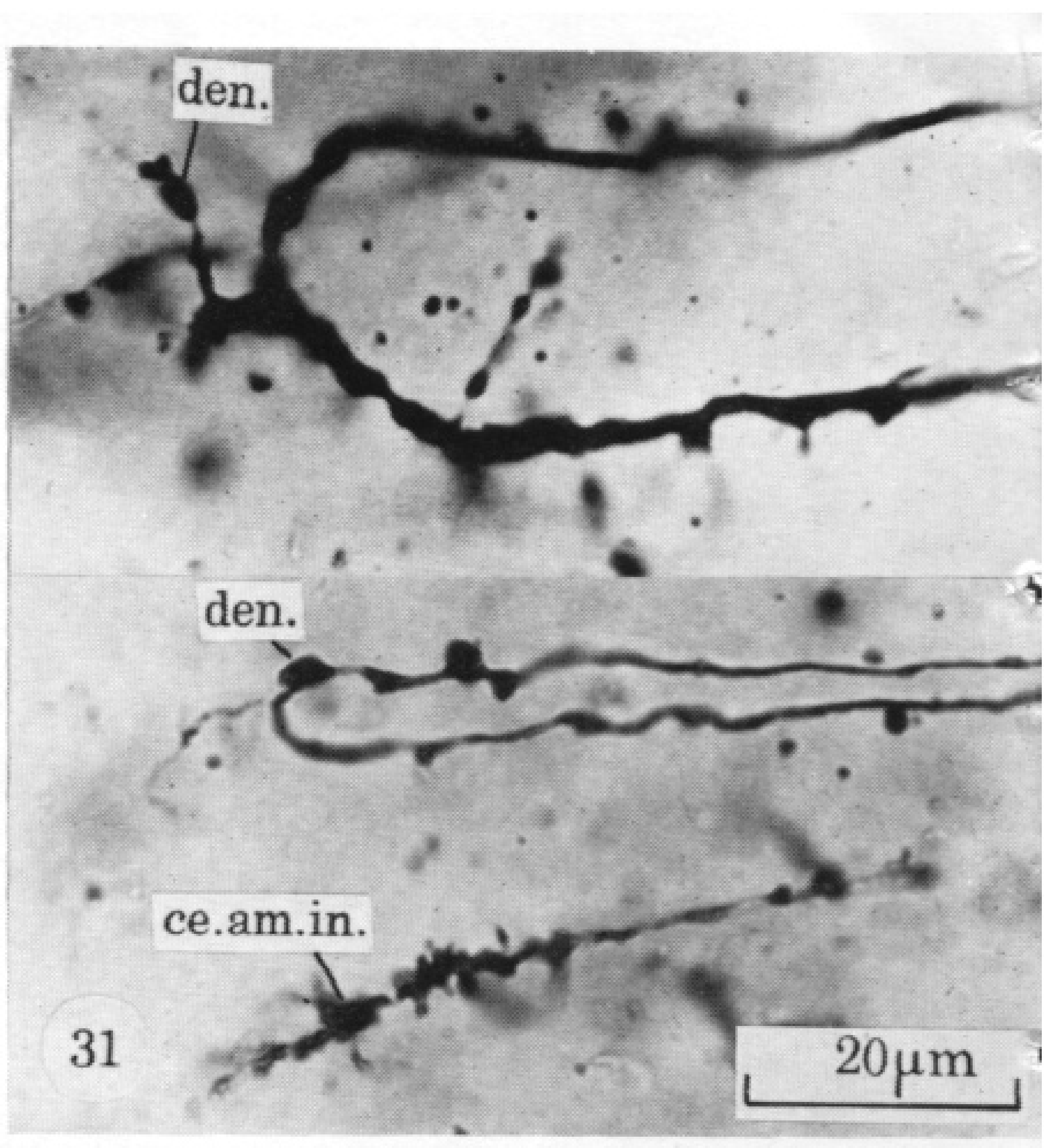
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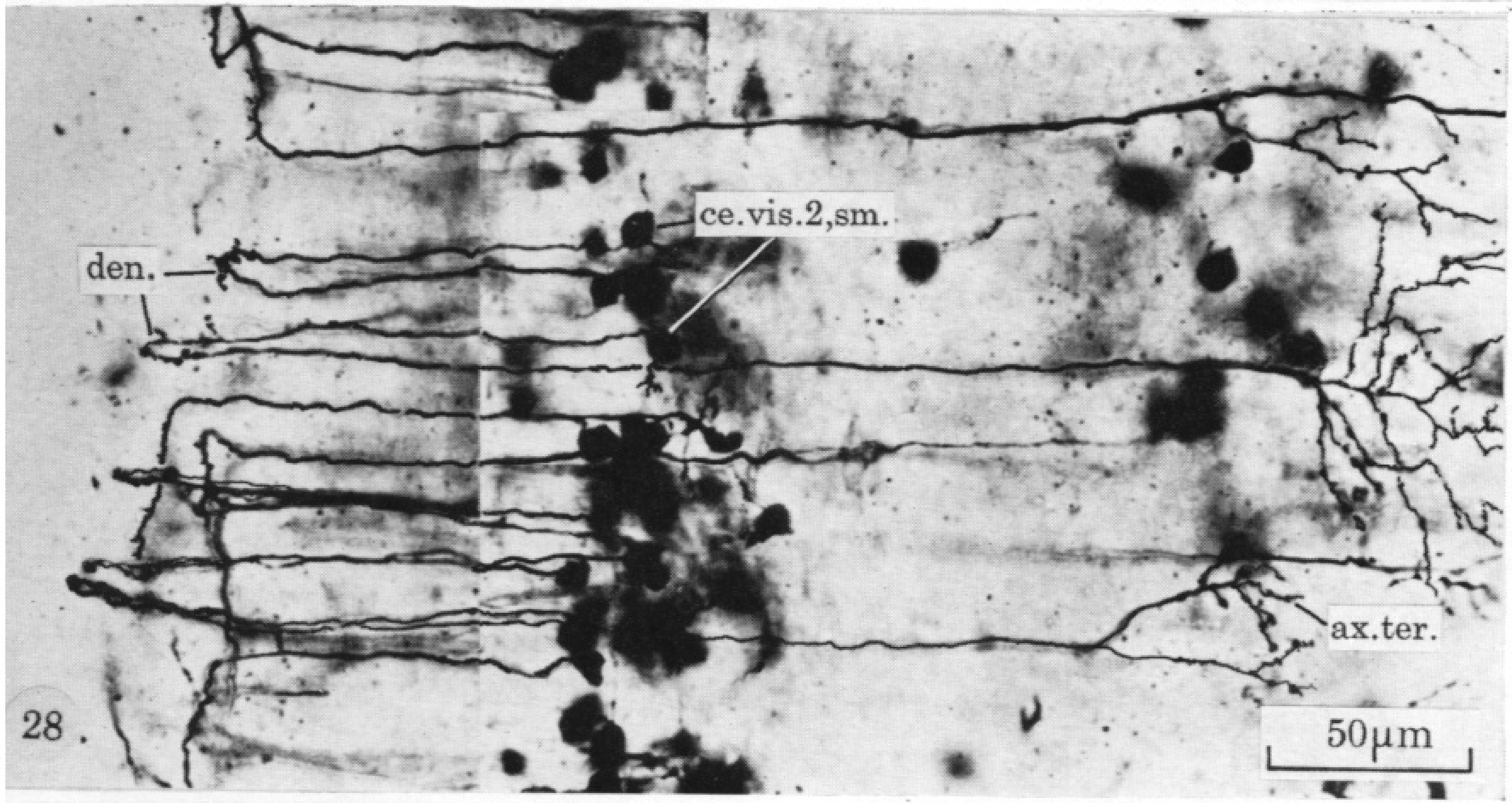
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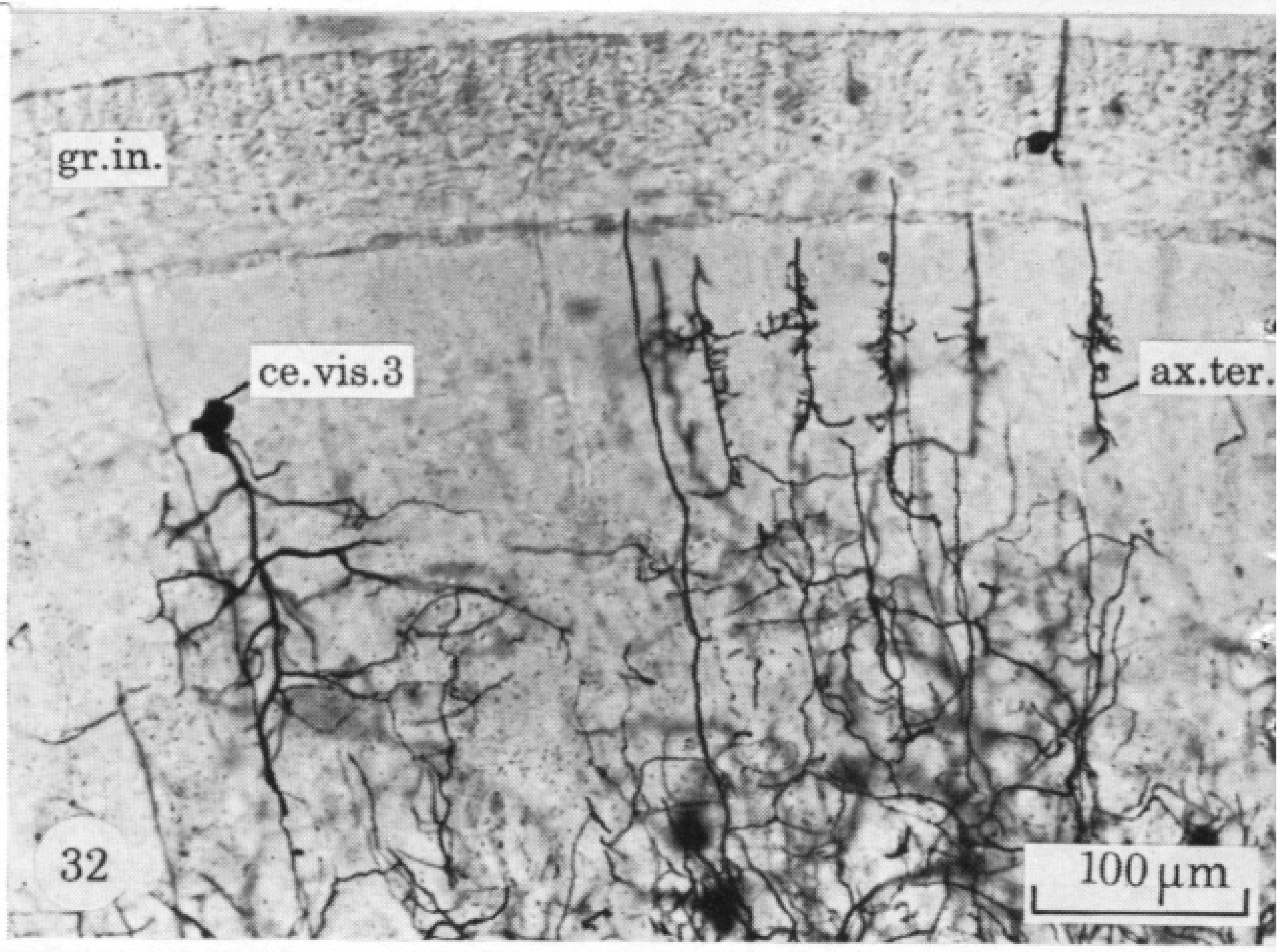
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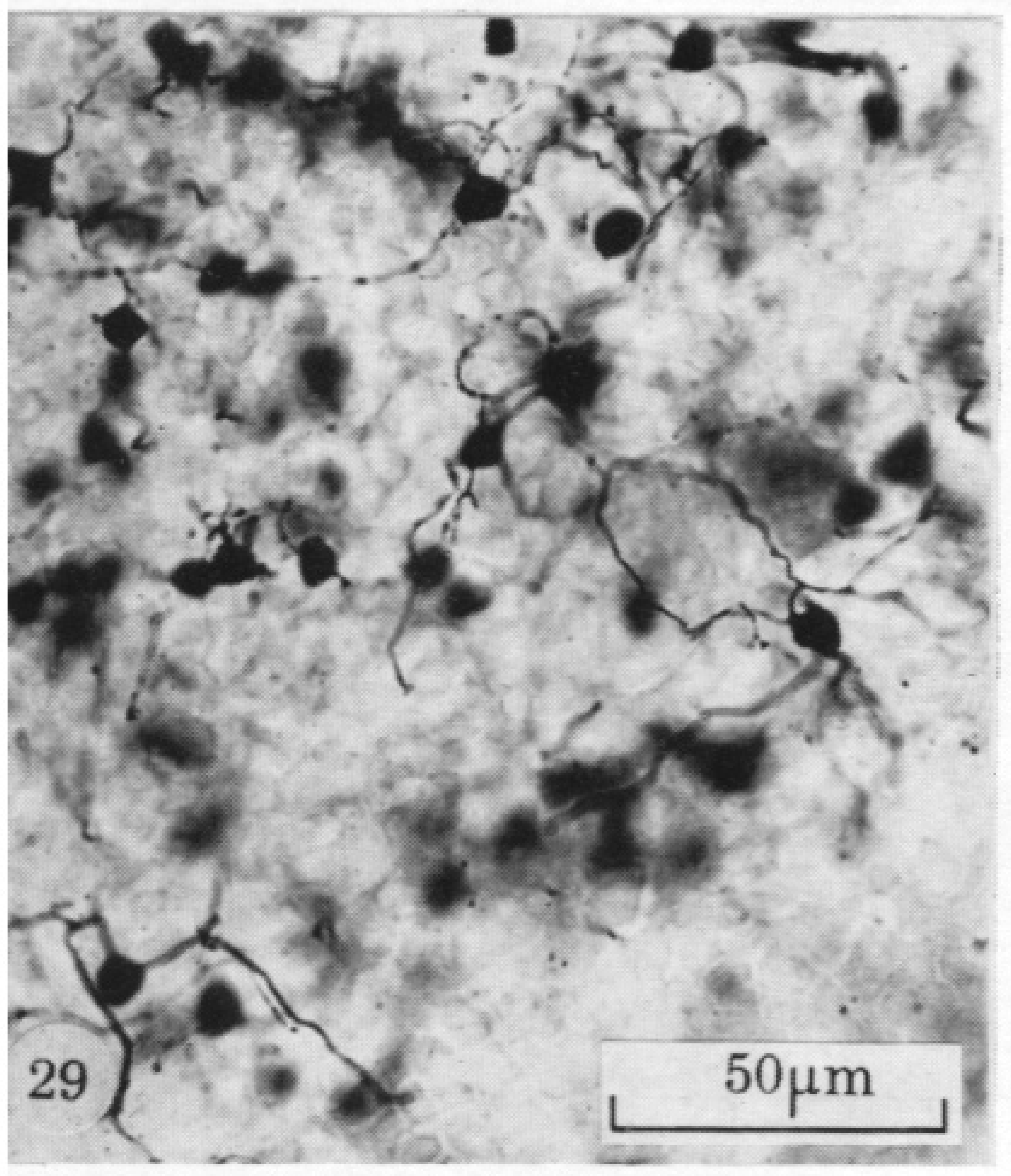
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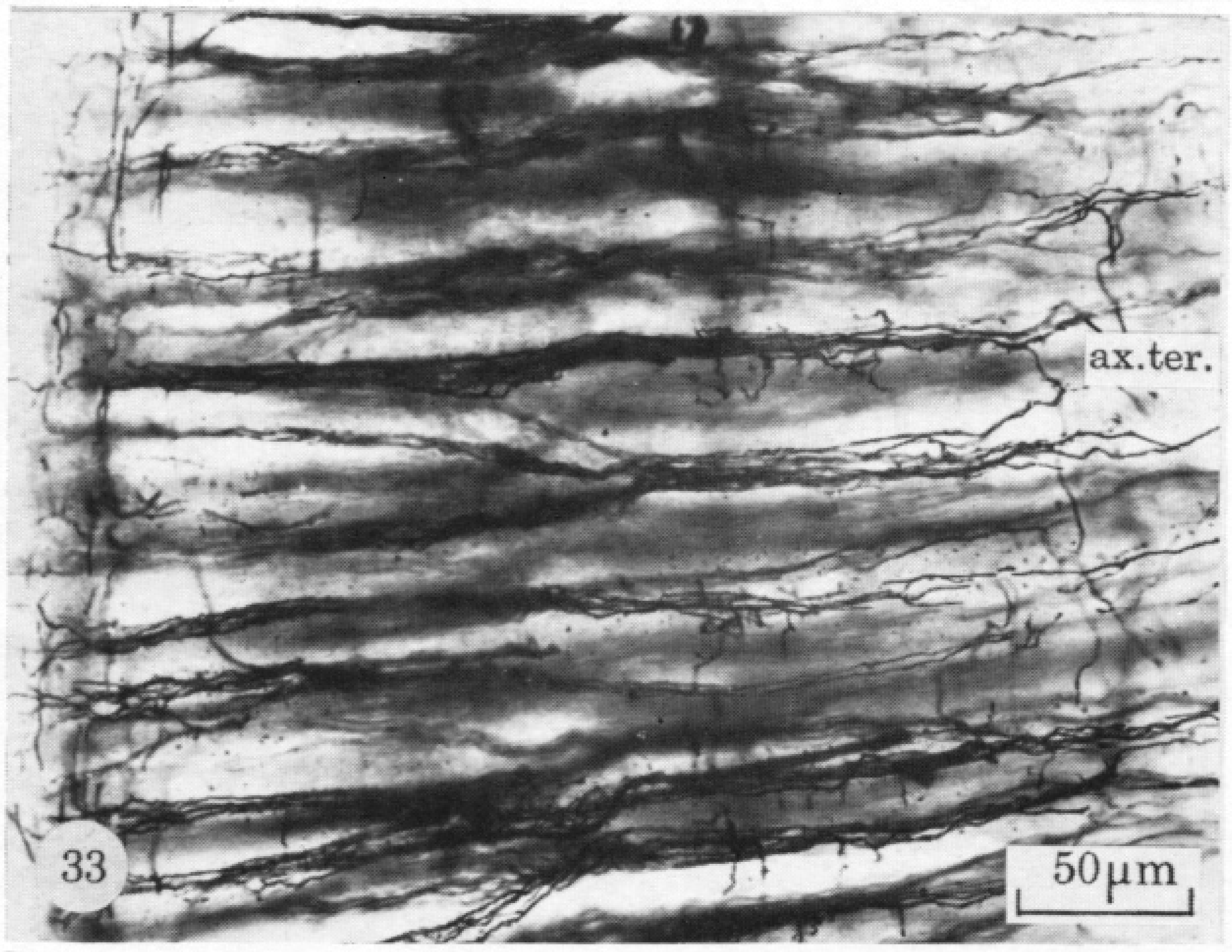
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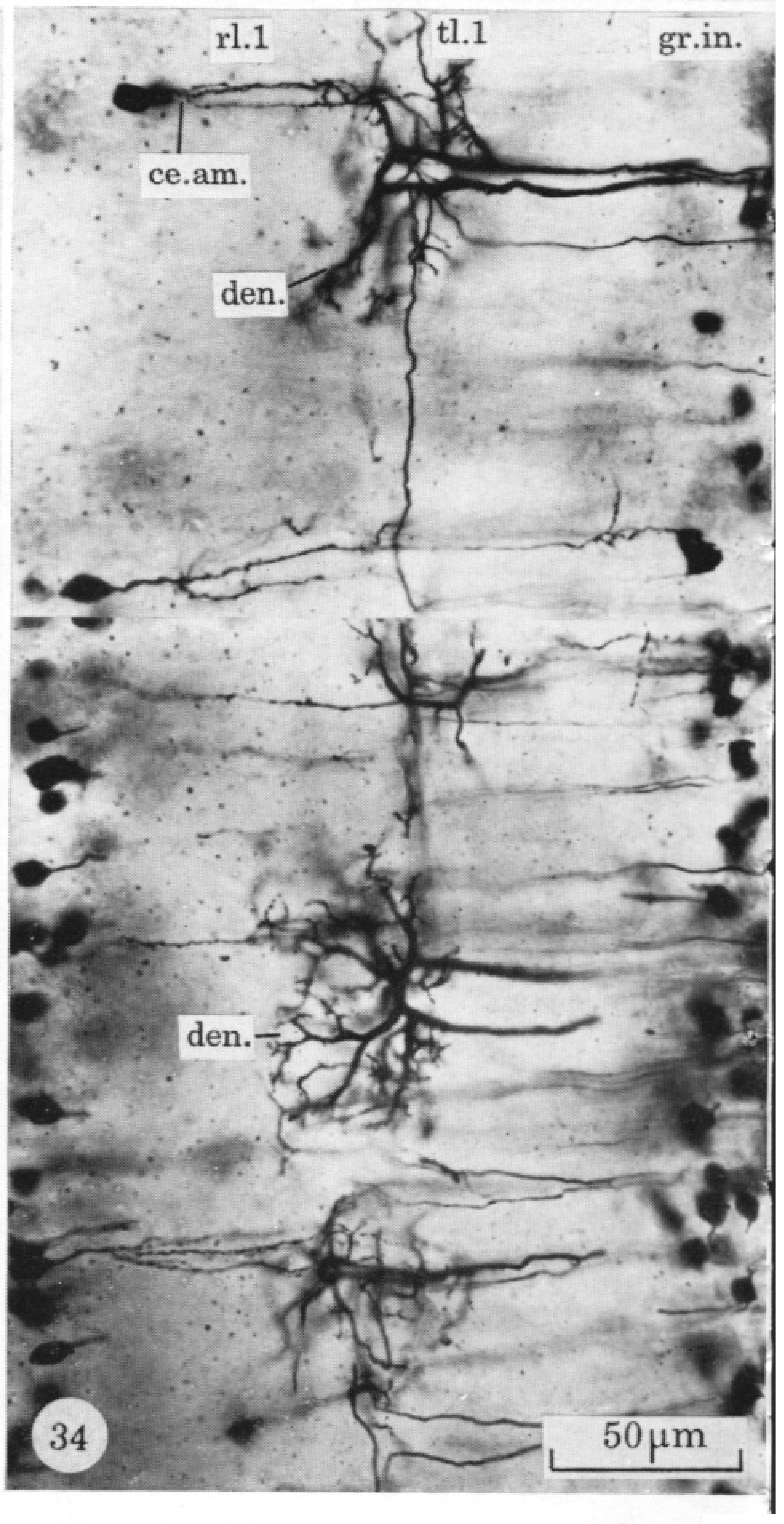
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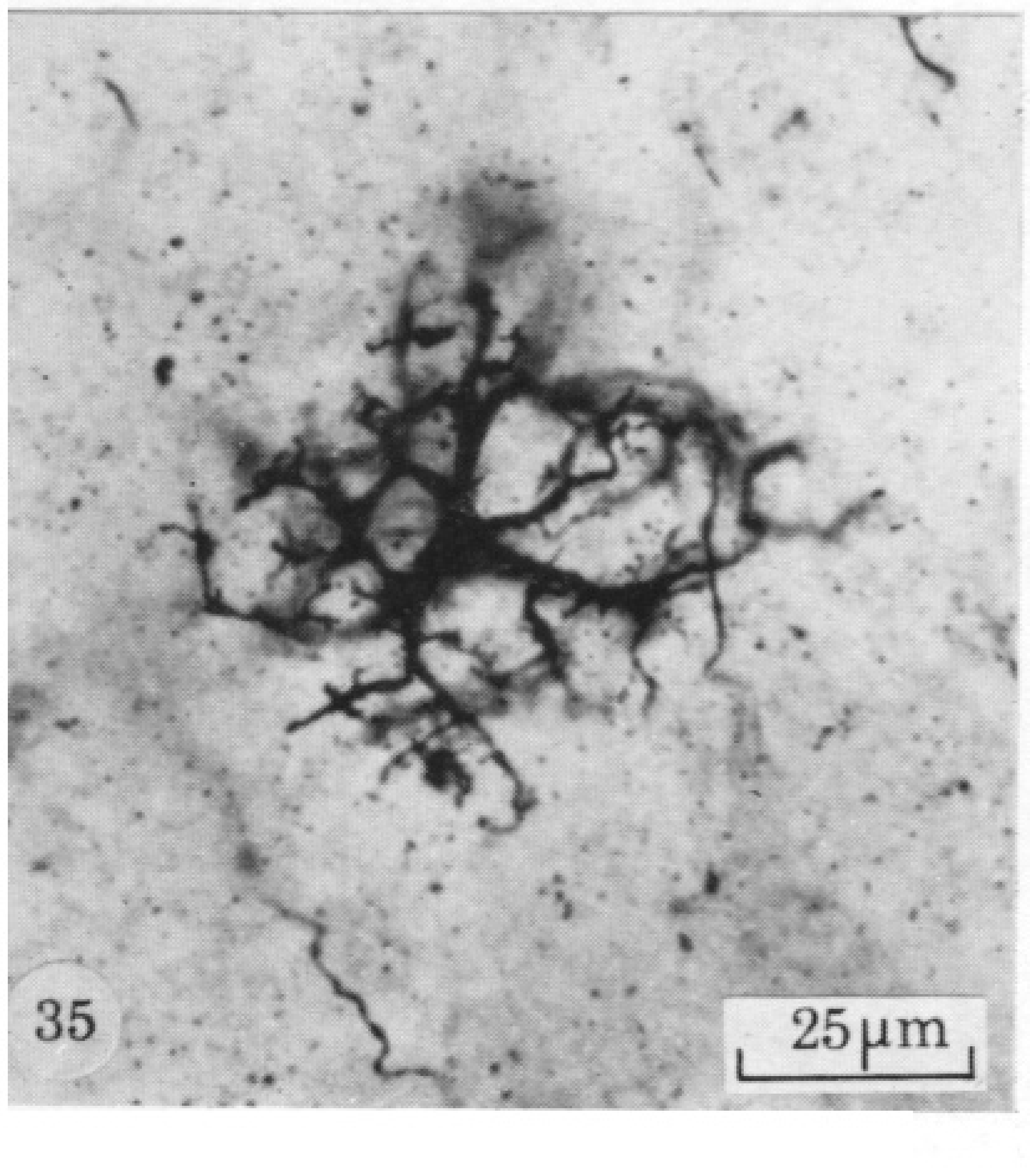
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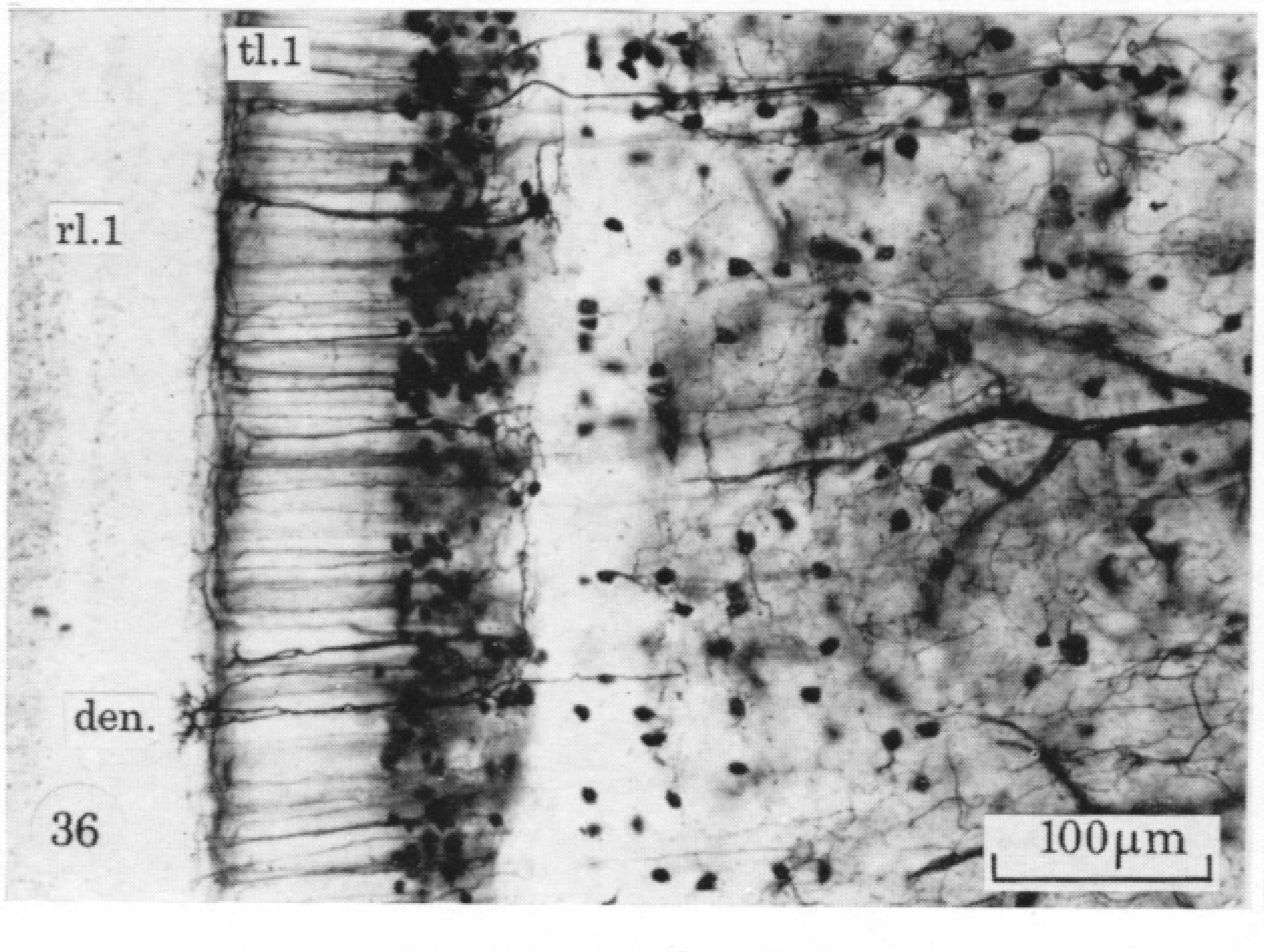
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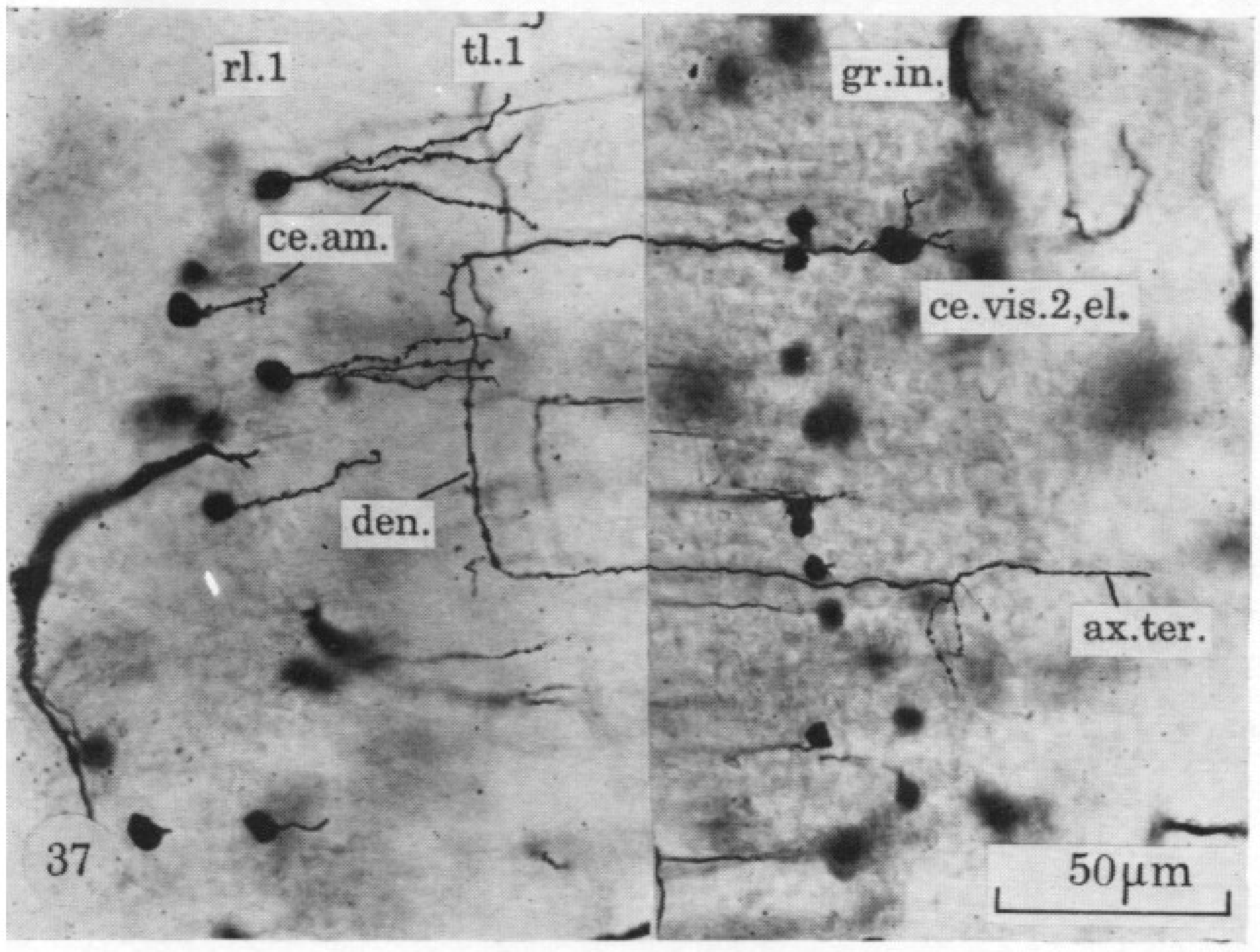
Figures 27–36. For description see opposite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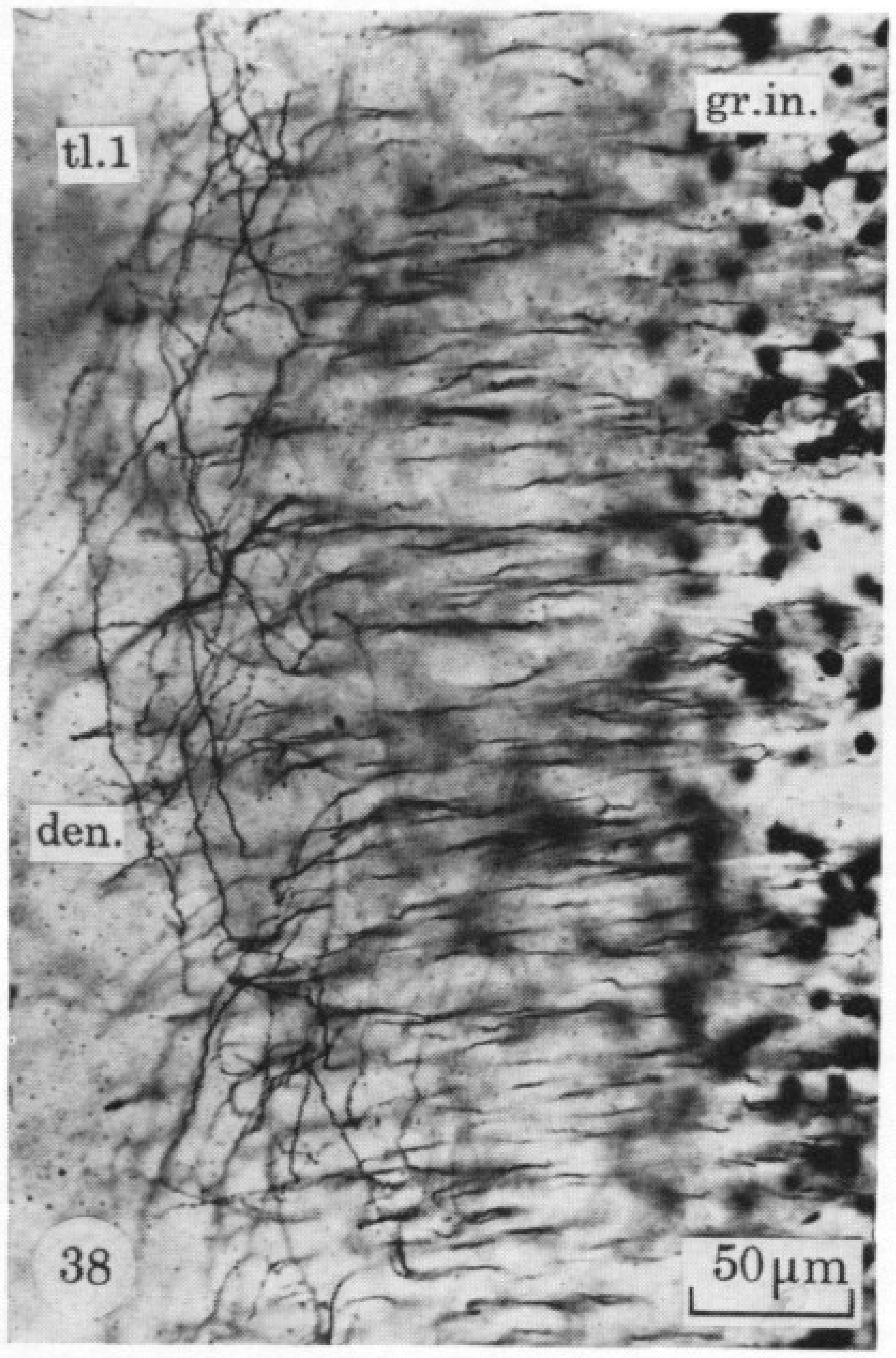
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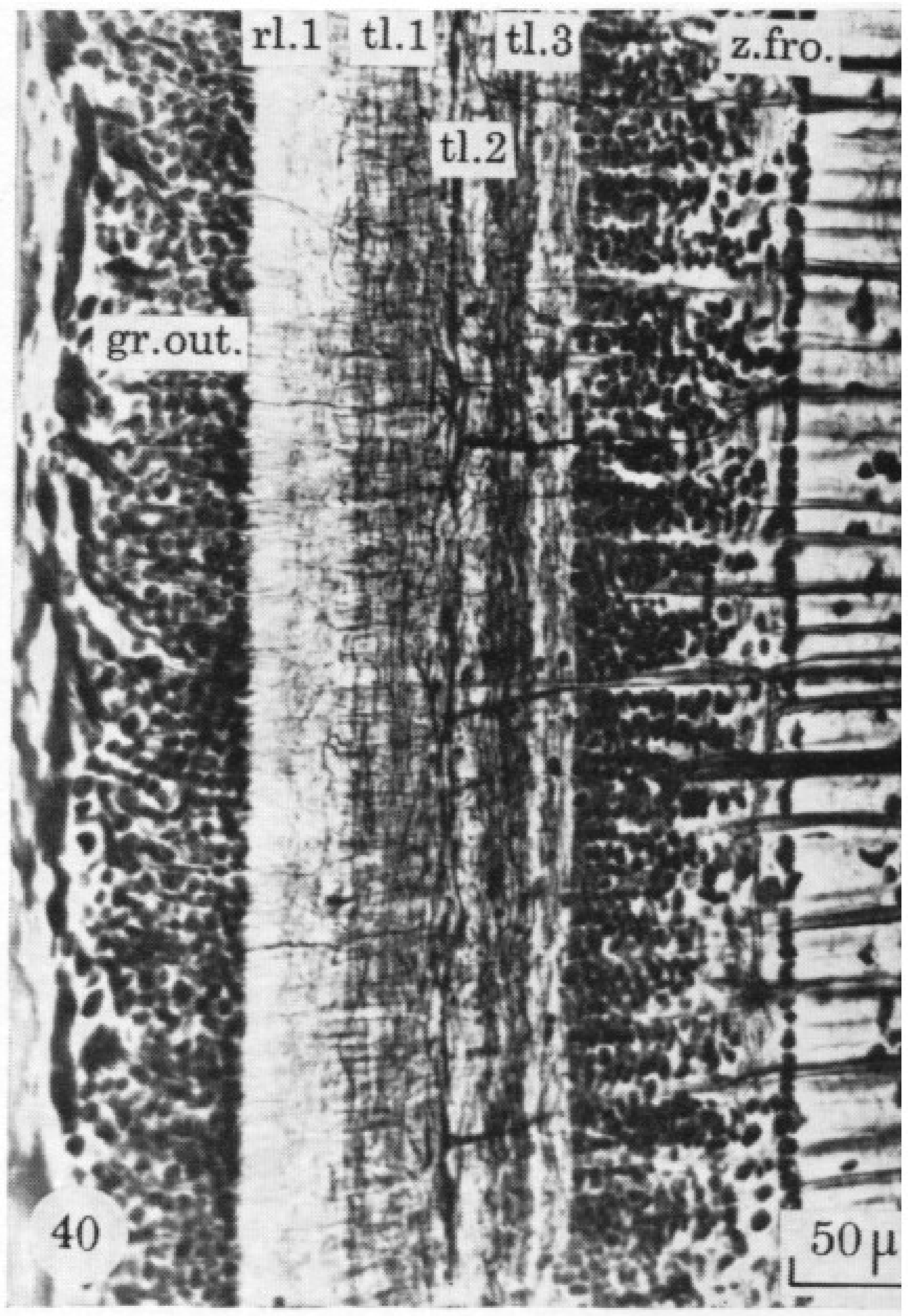
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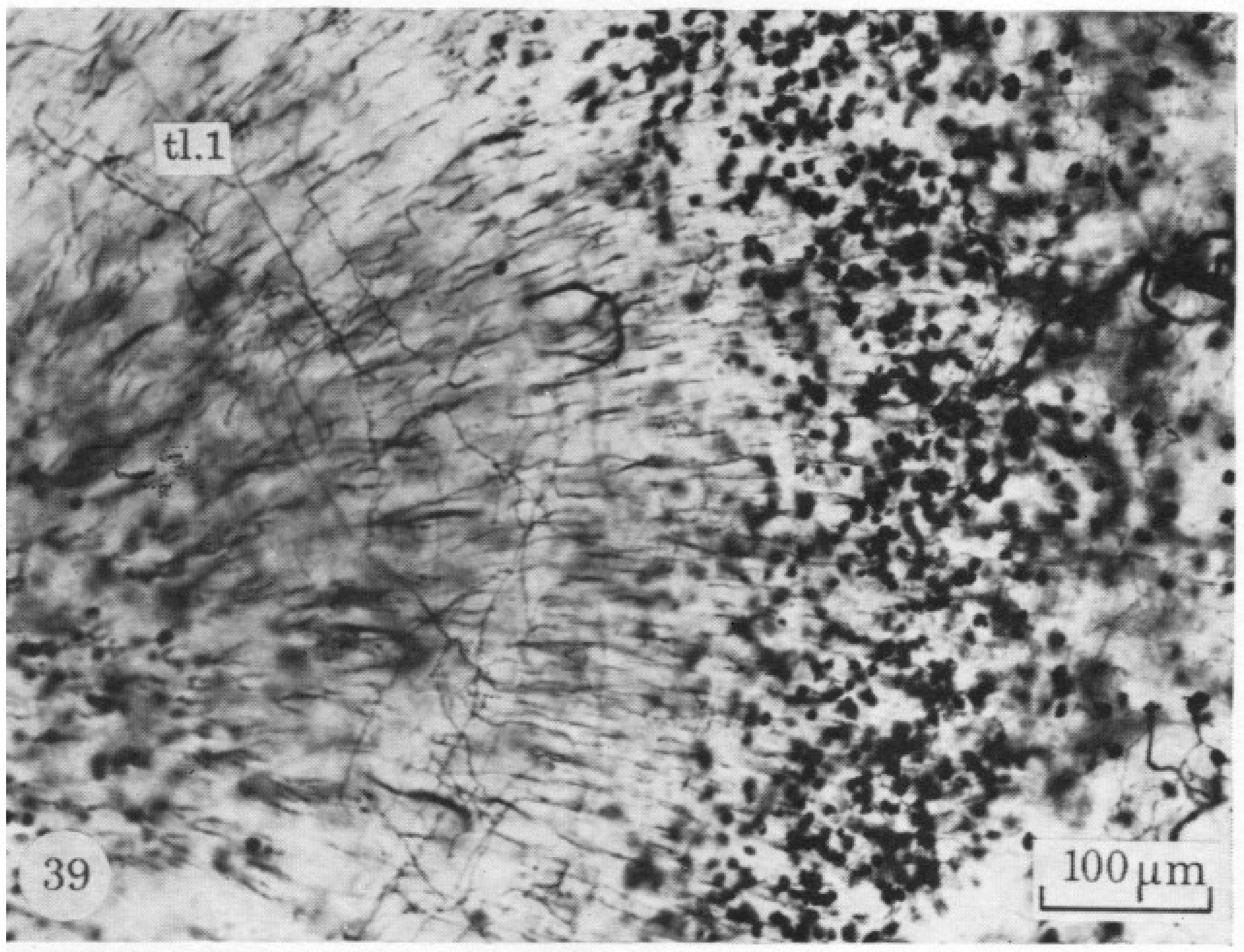
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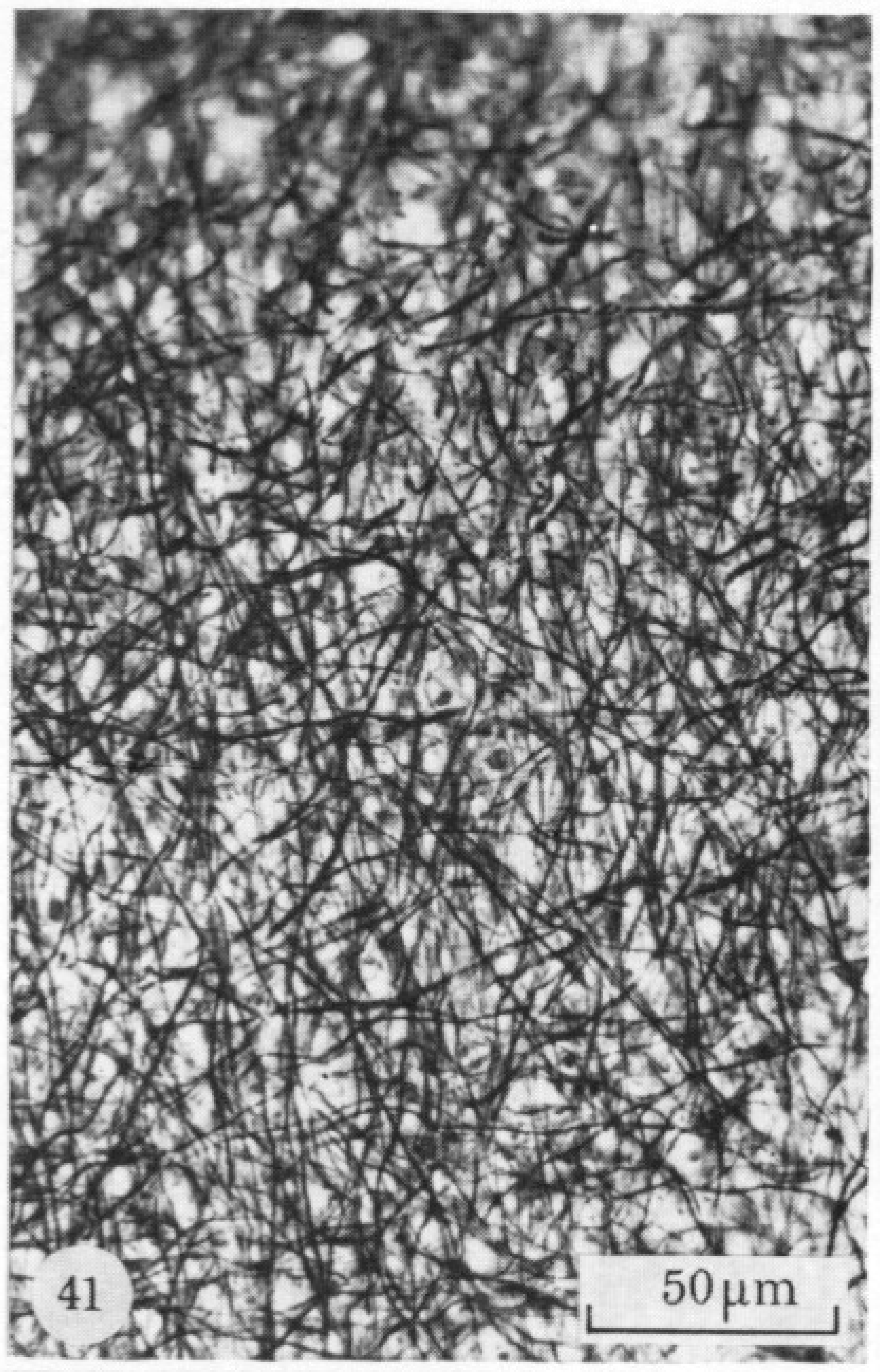
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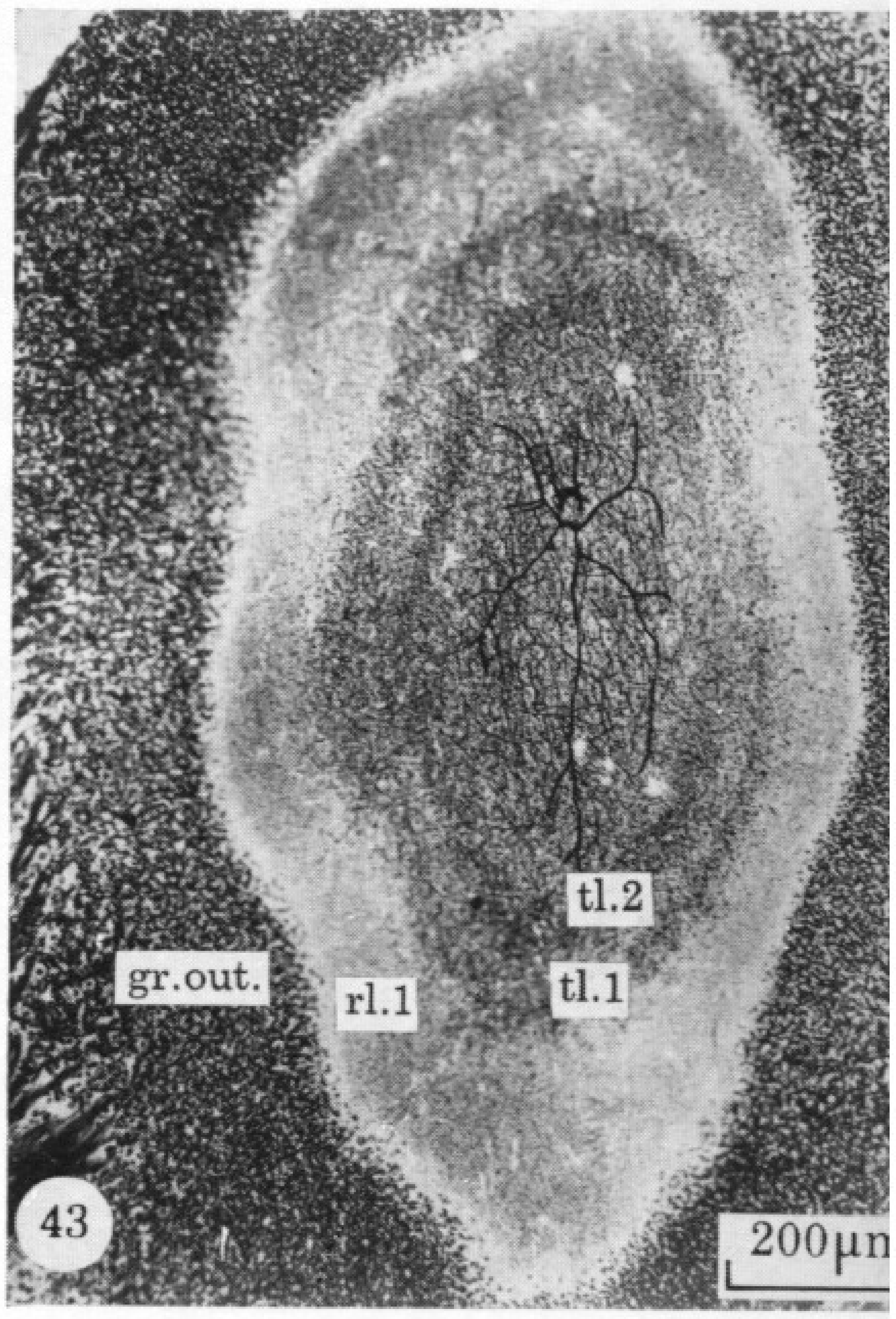
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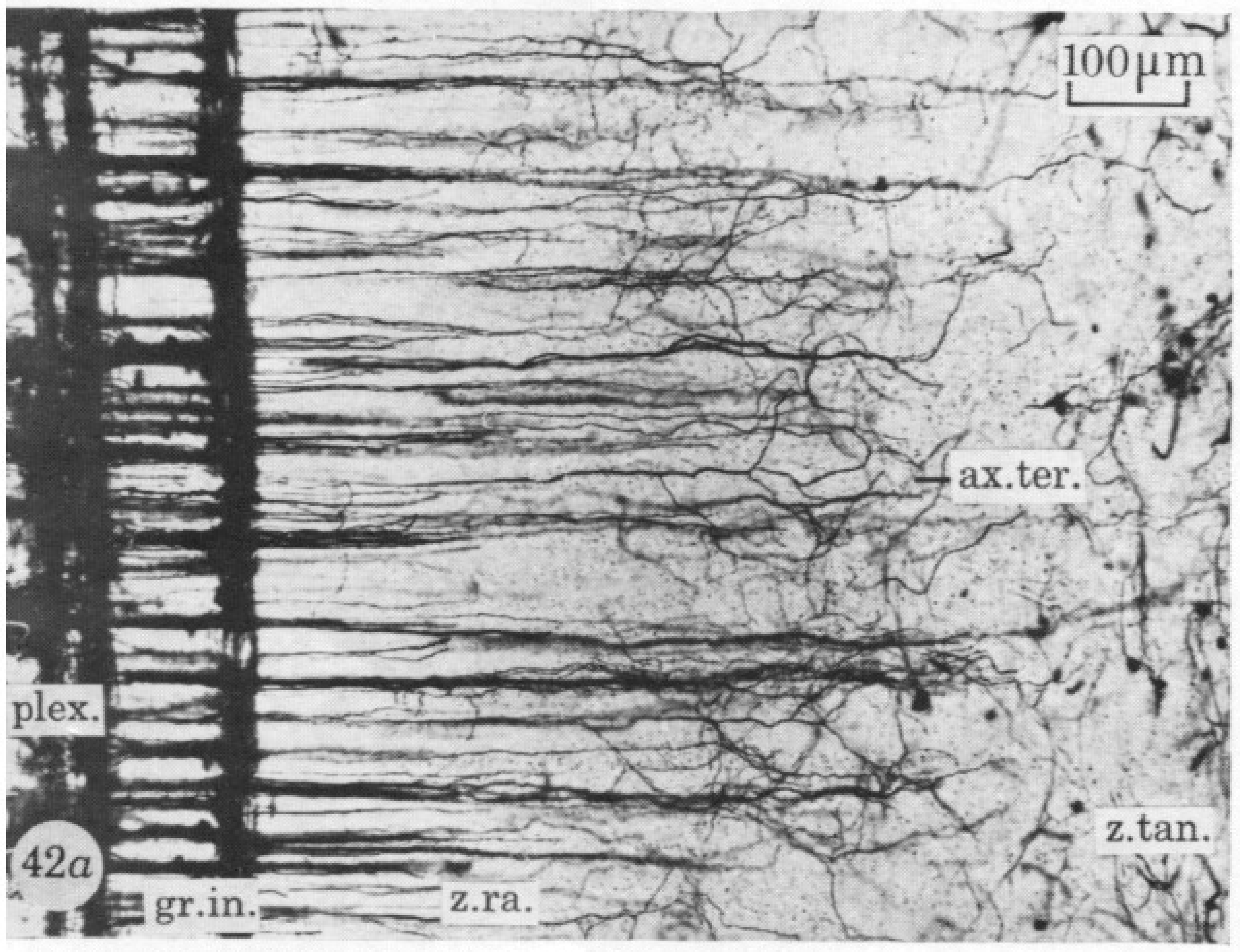
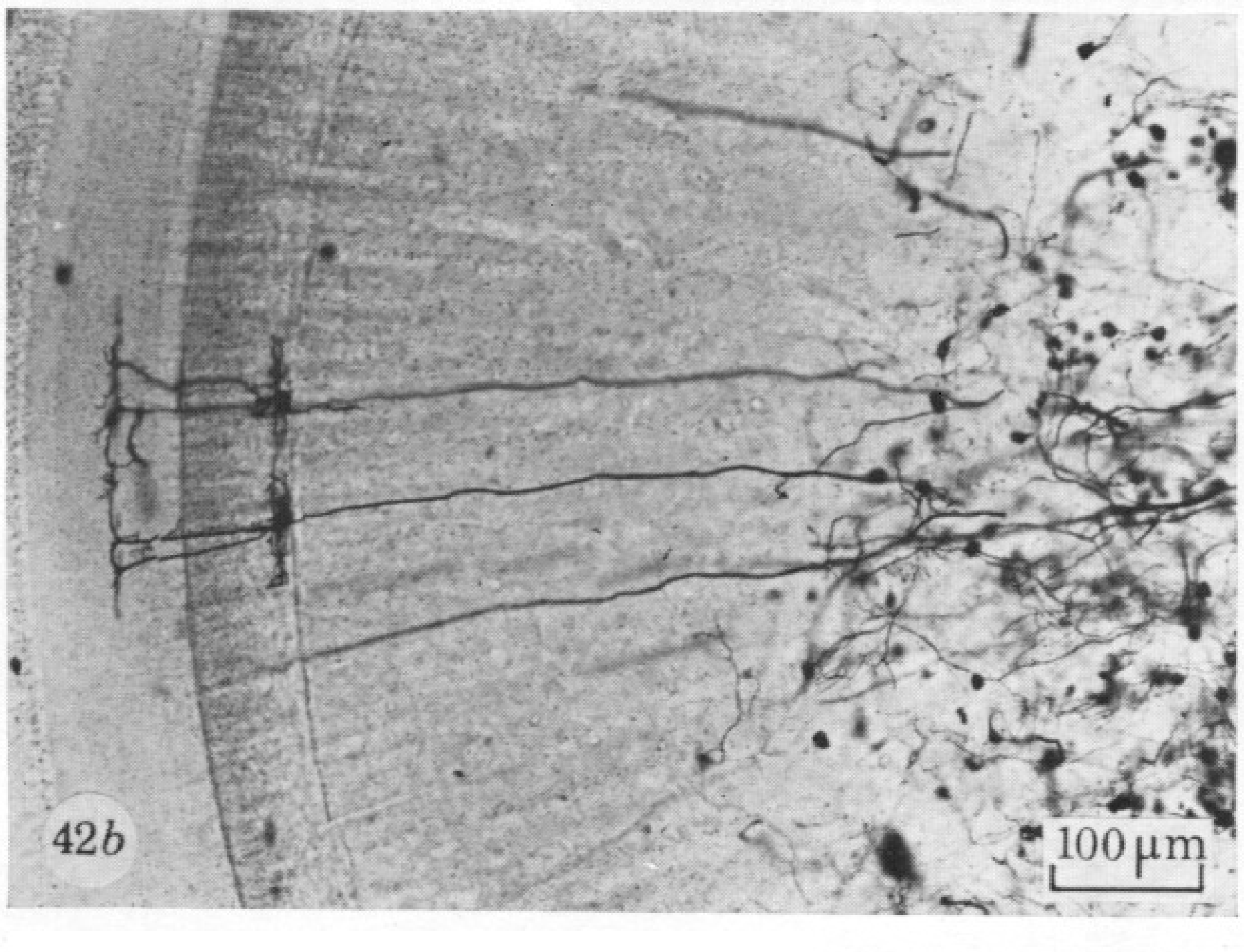

42*a*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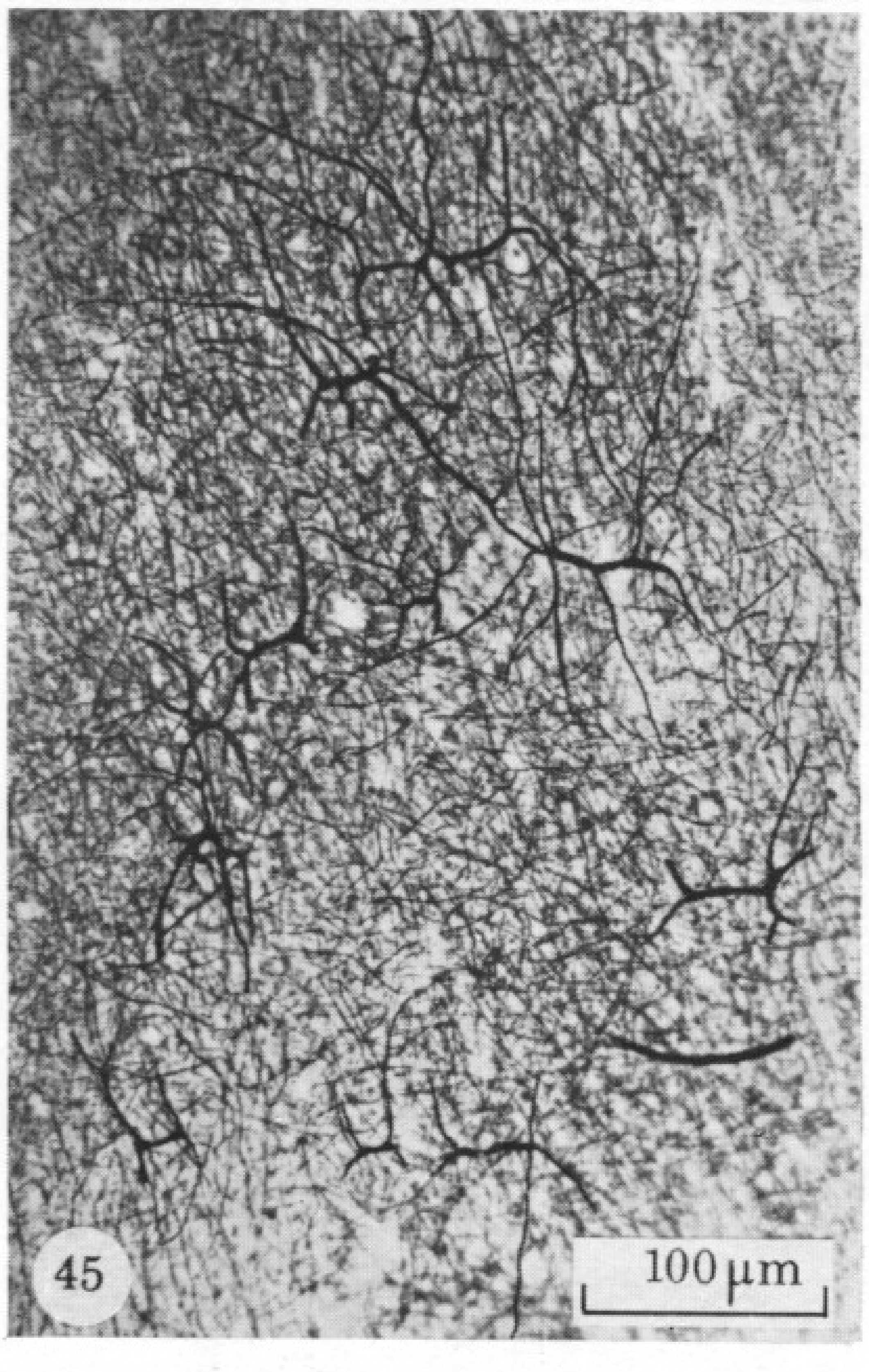
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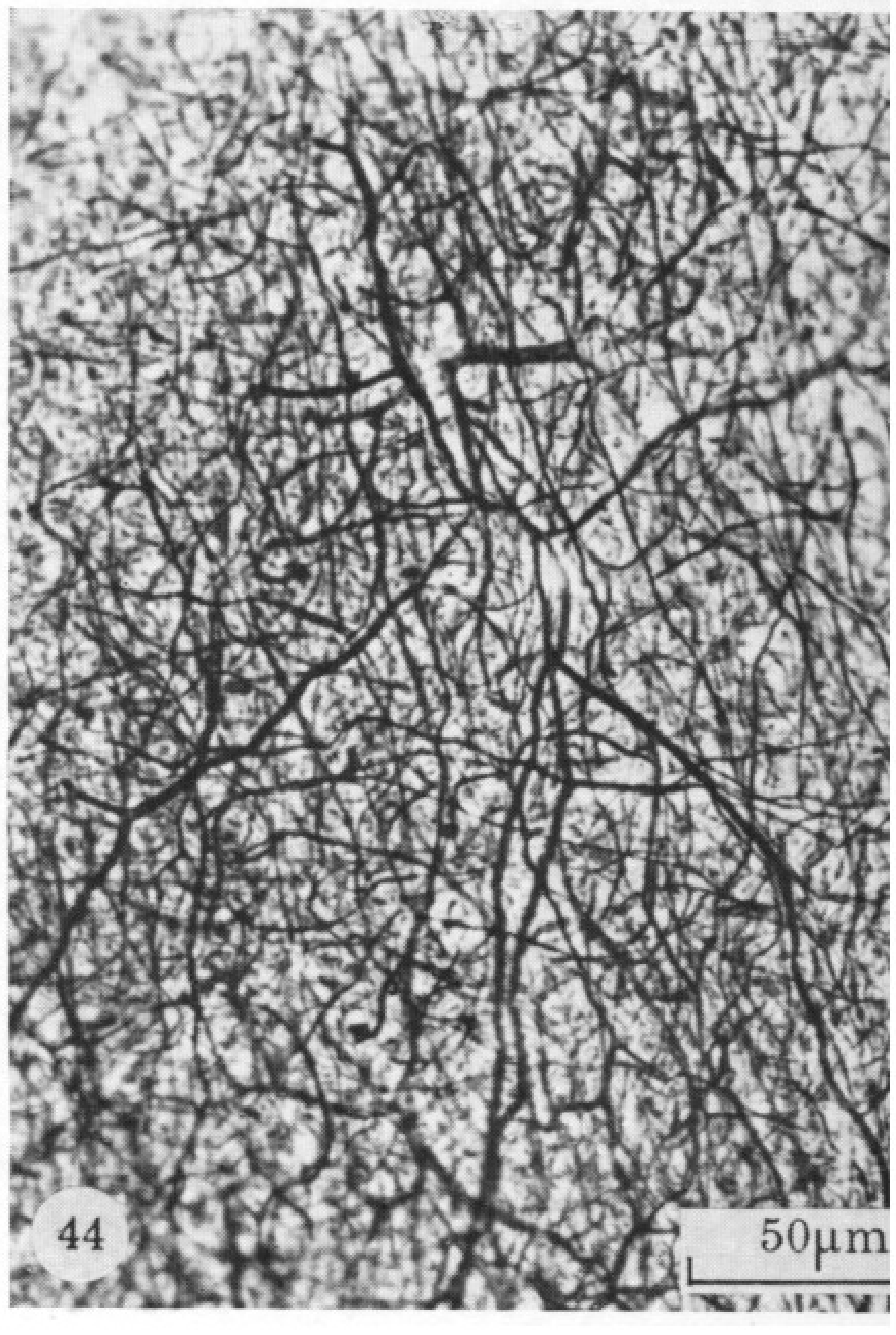
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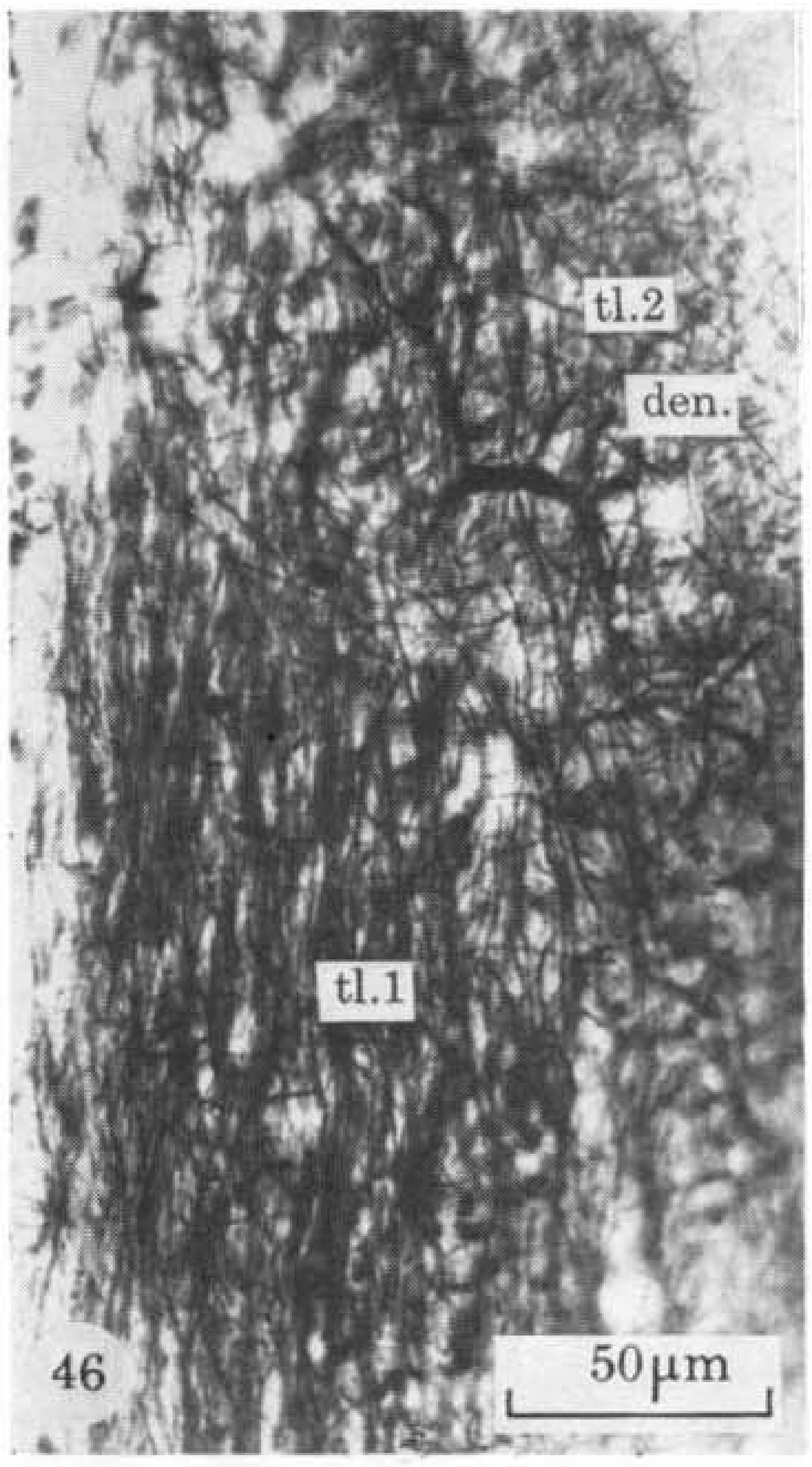
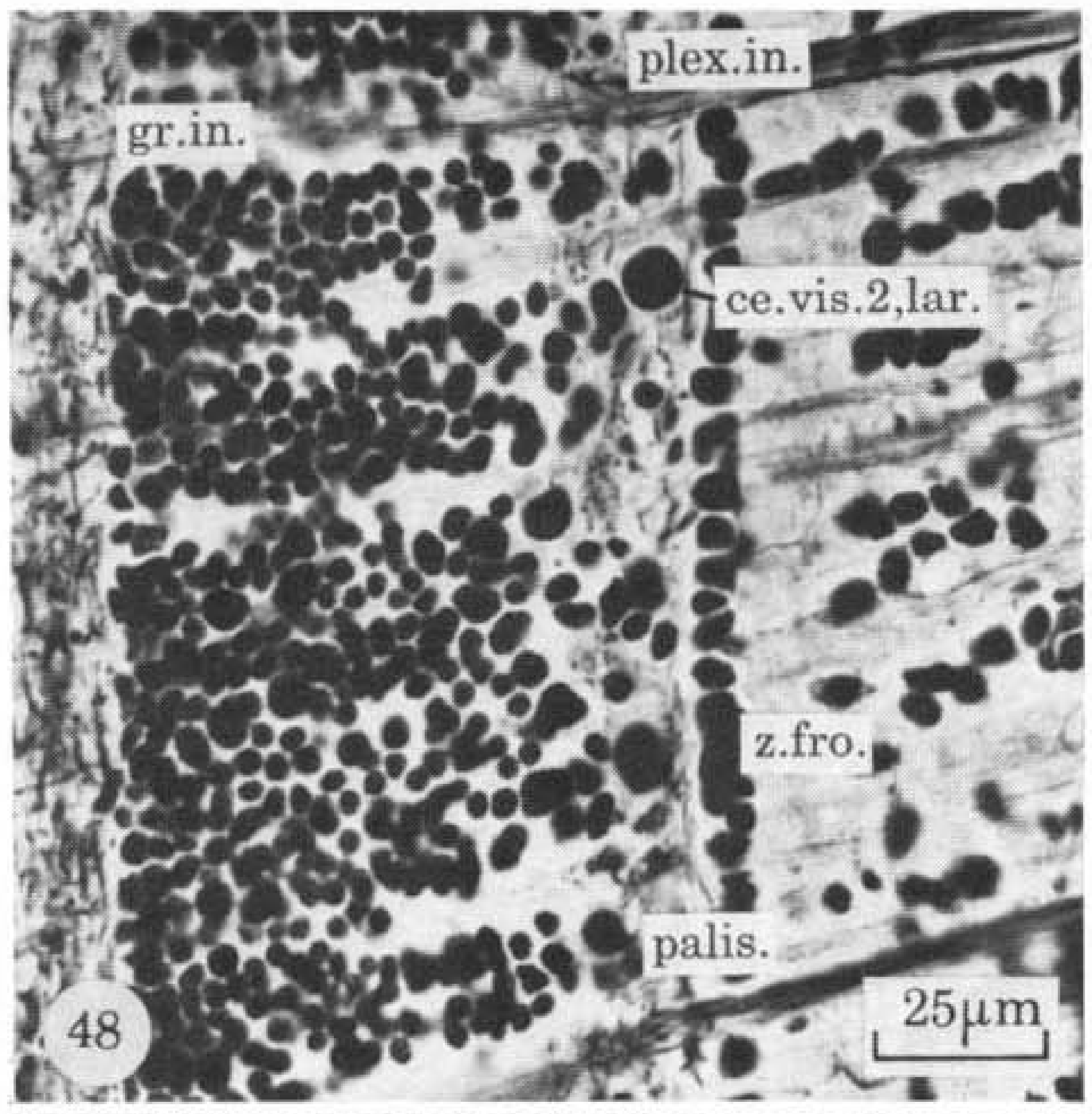
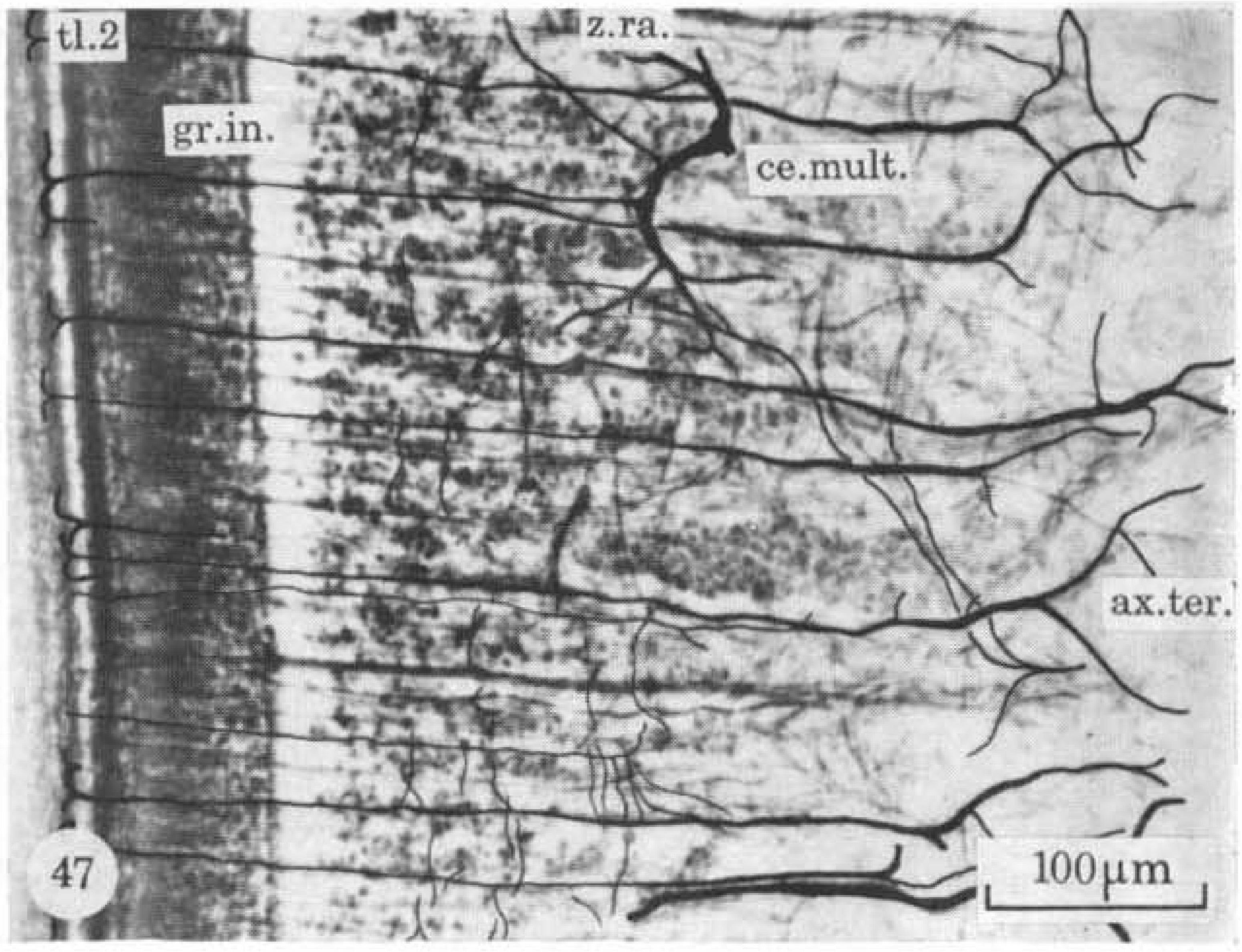
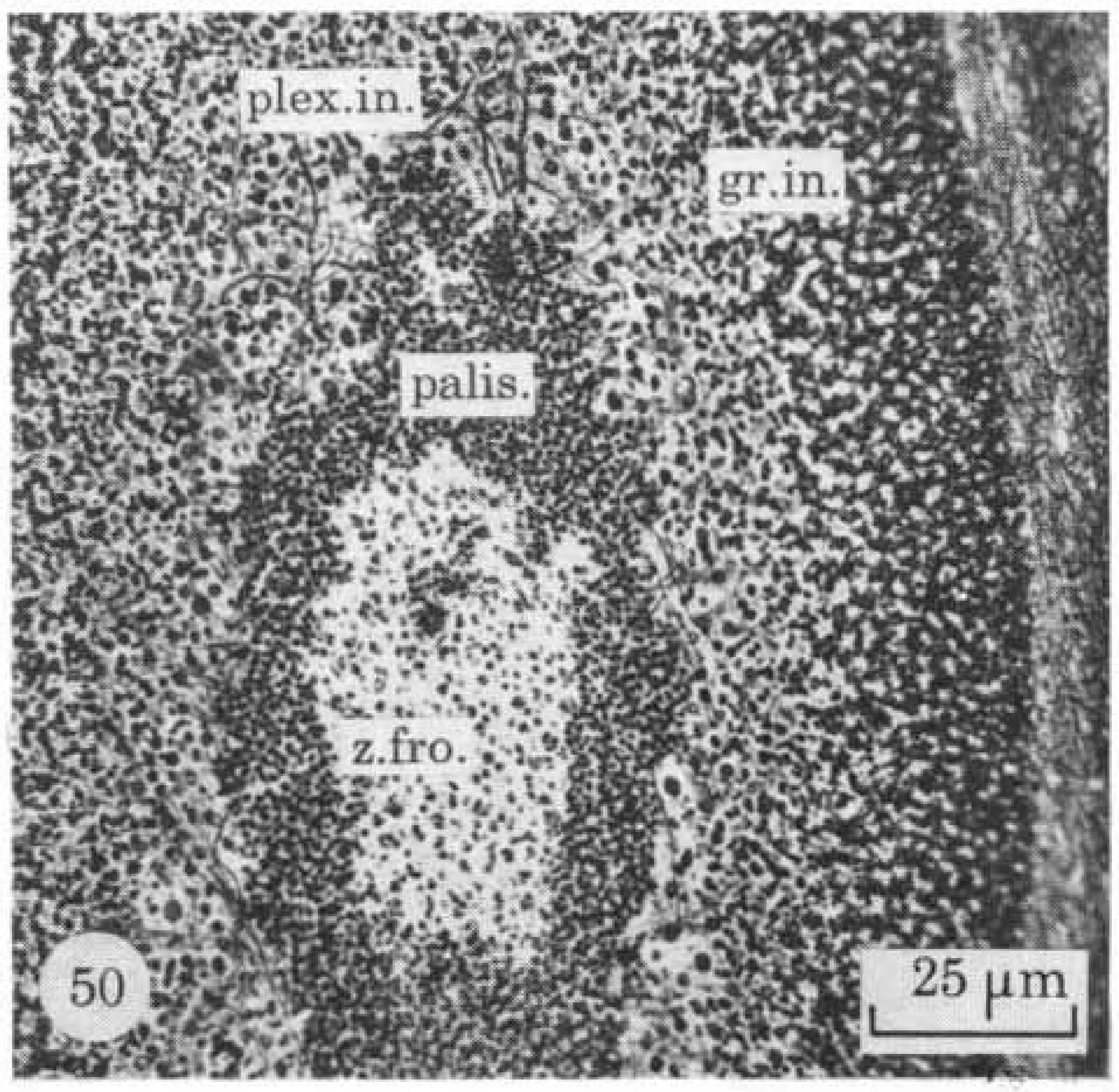
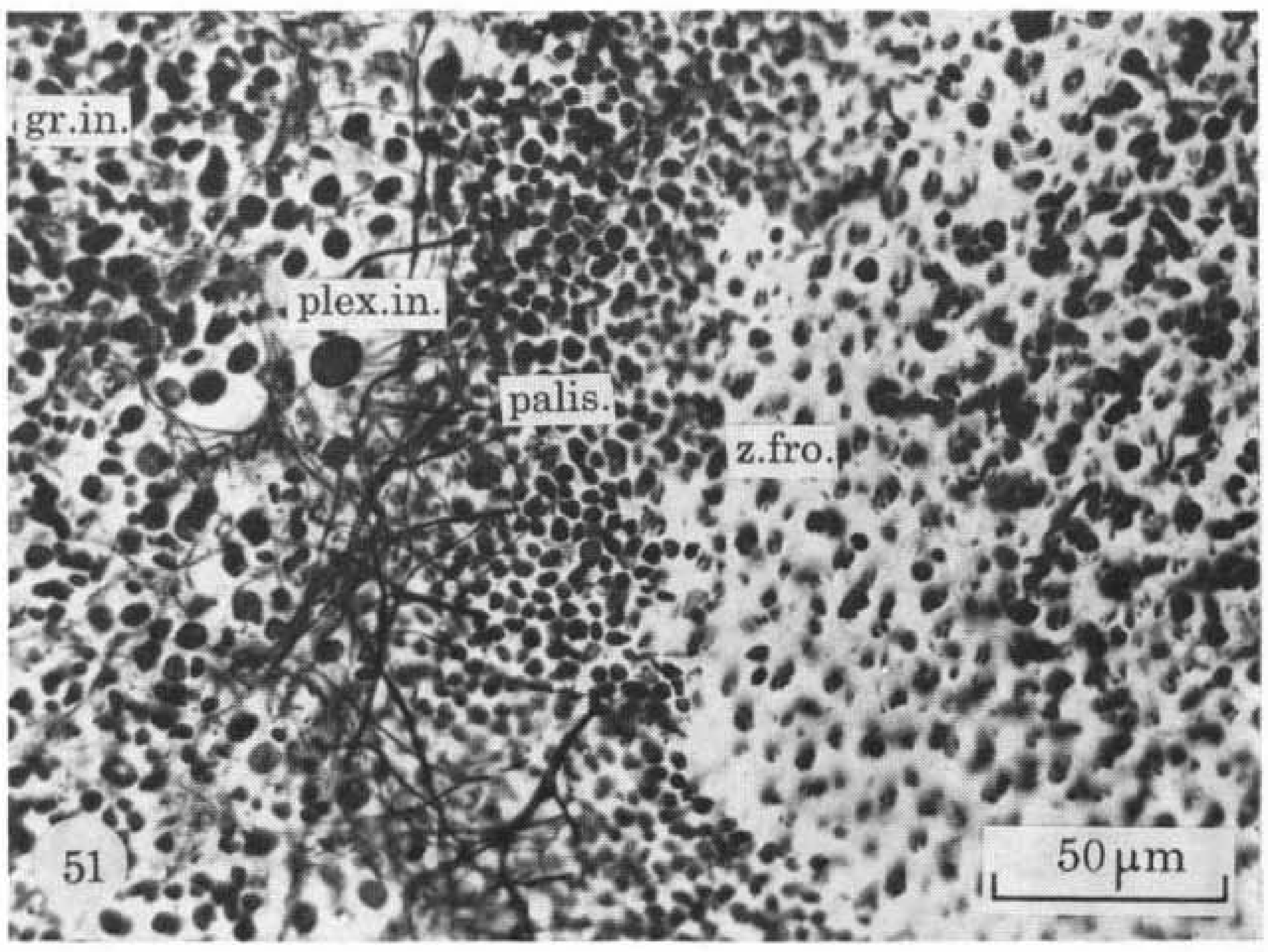
FIGURES 37–45. For description see opposite

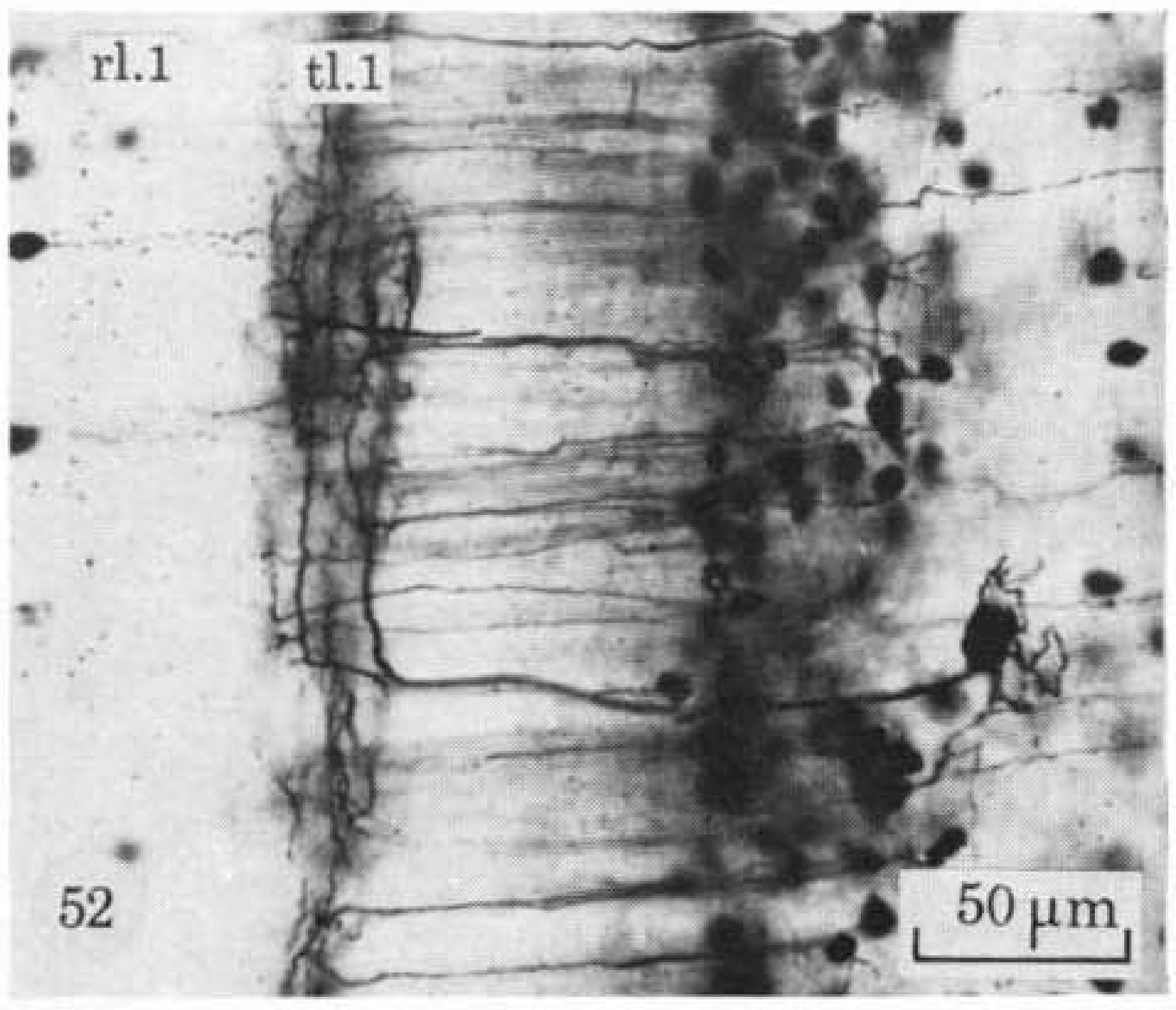


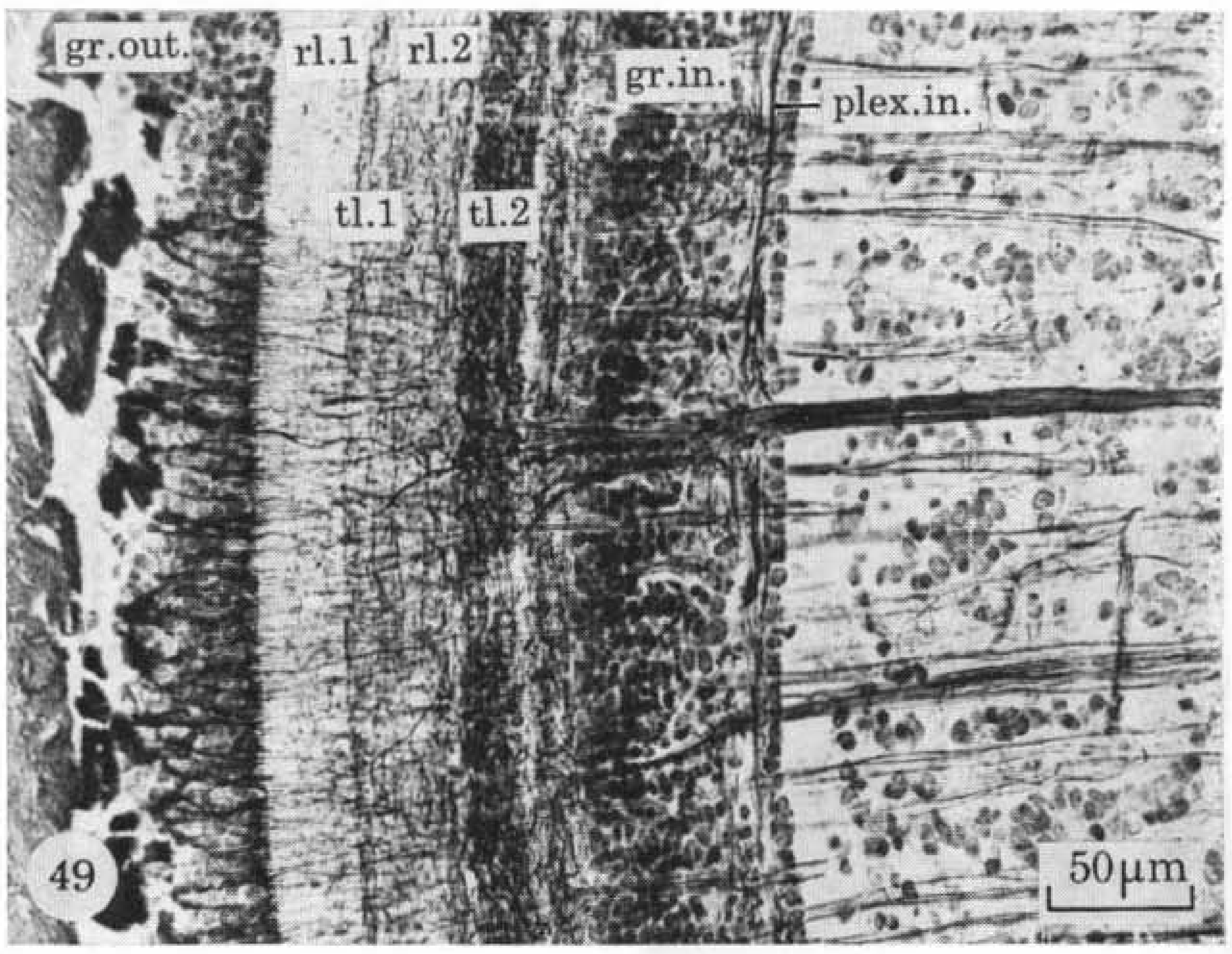


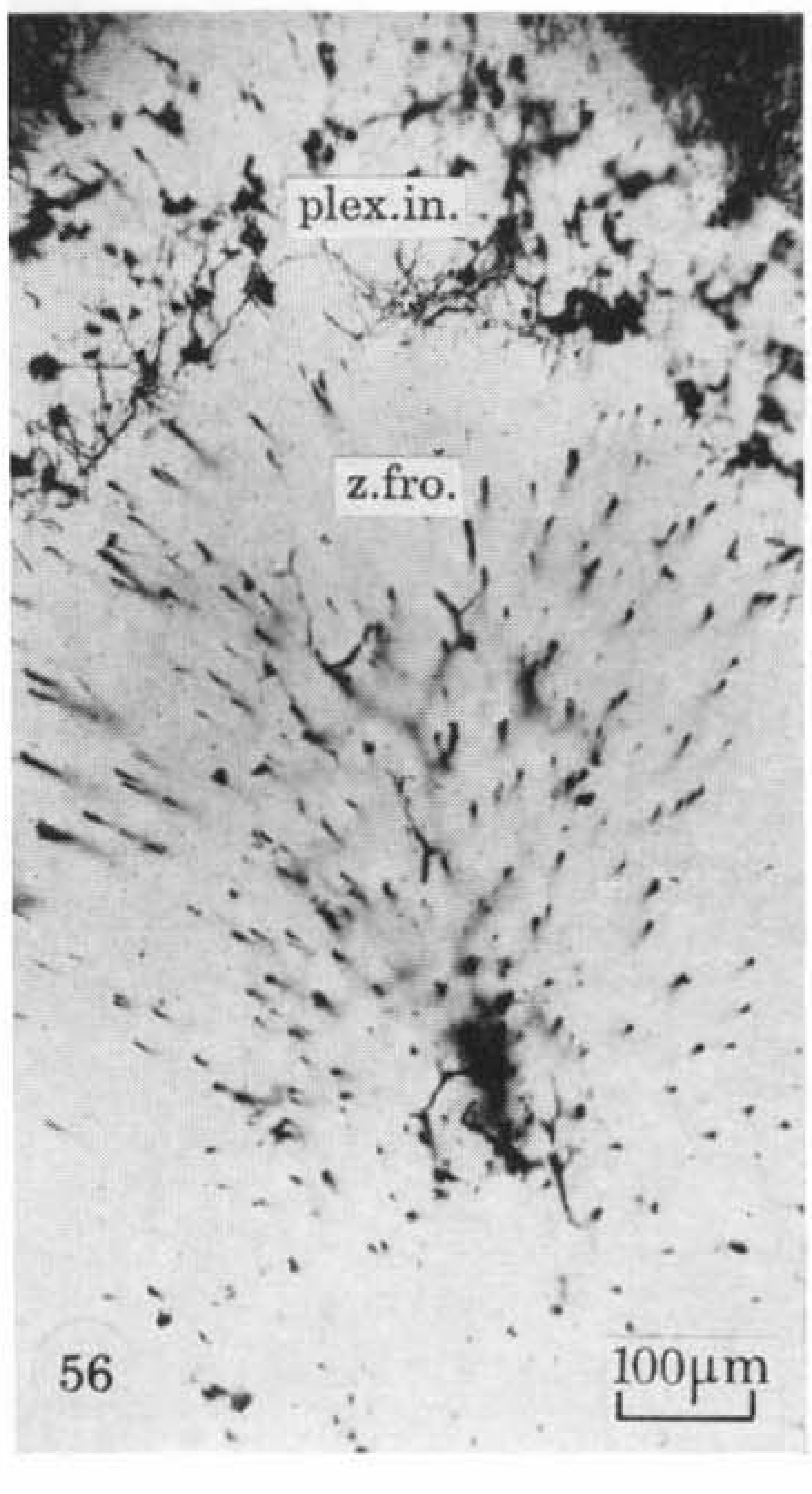


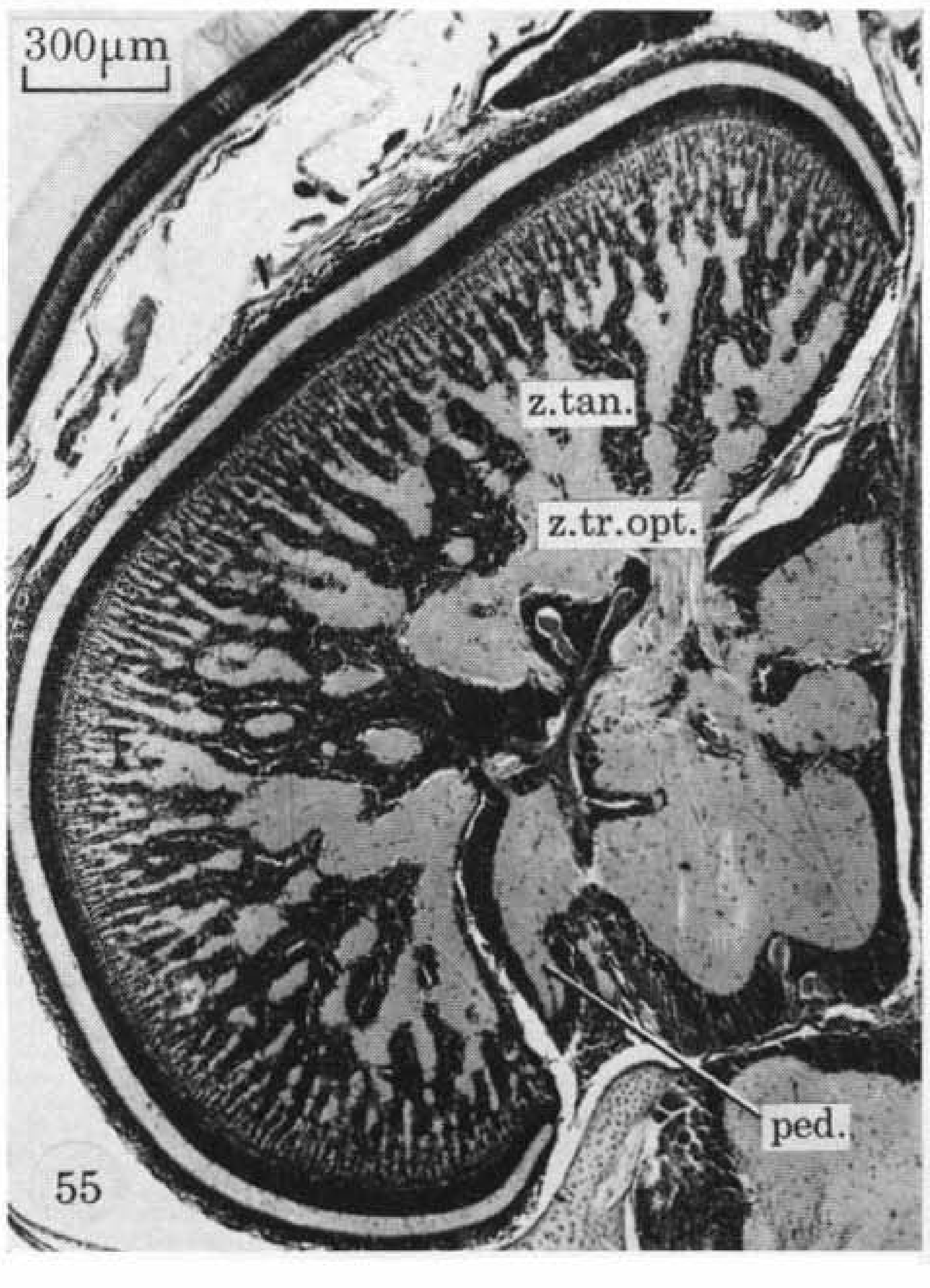


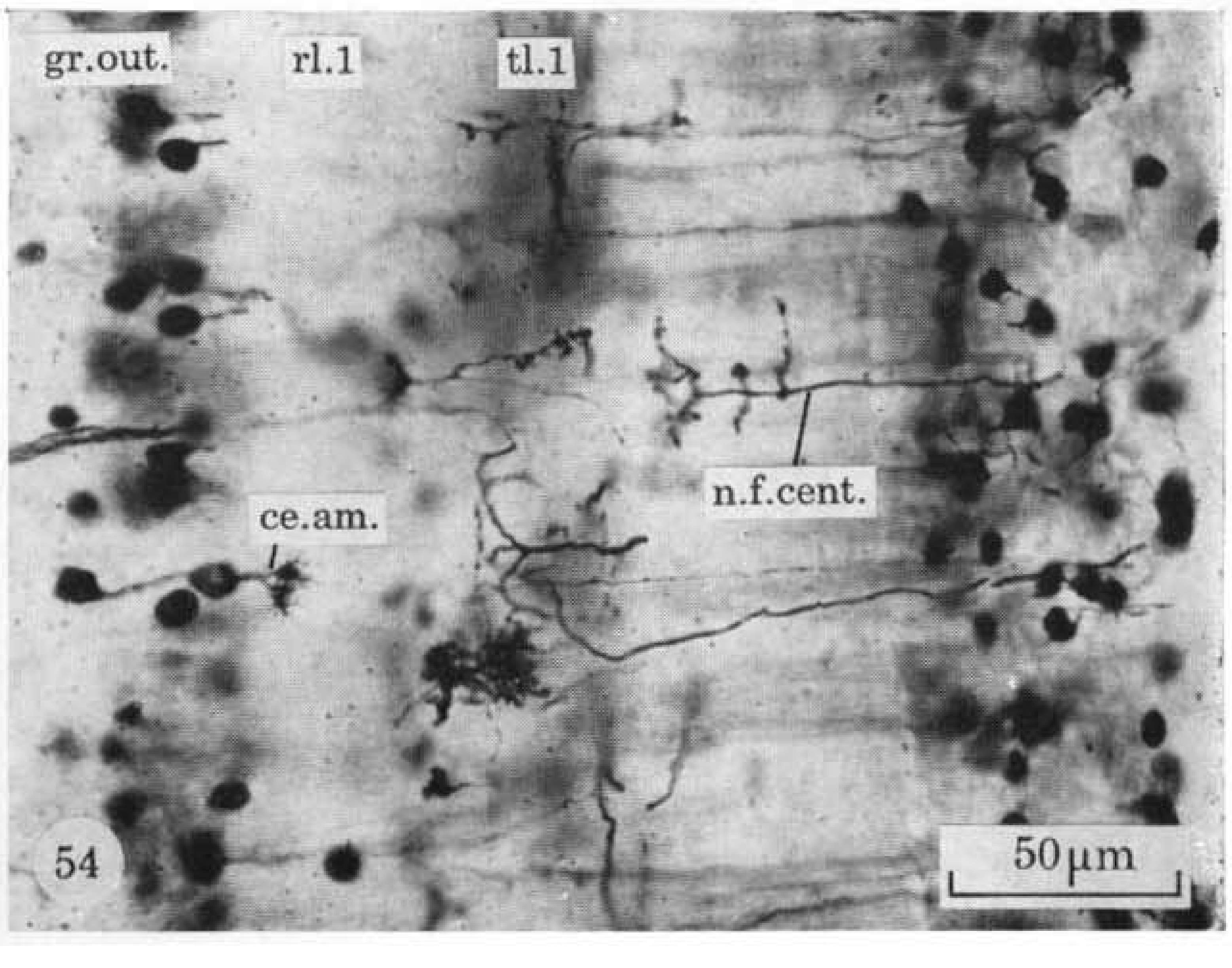




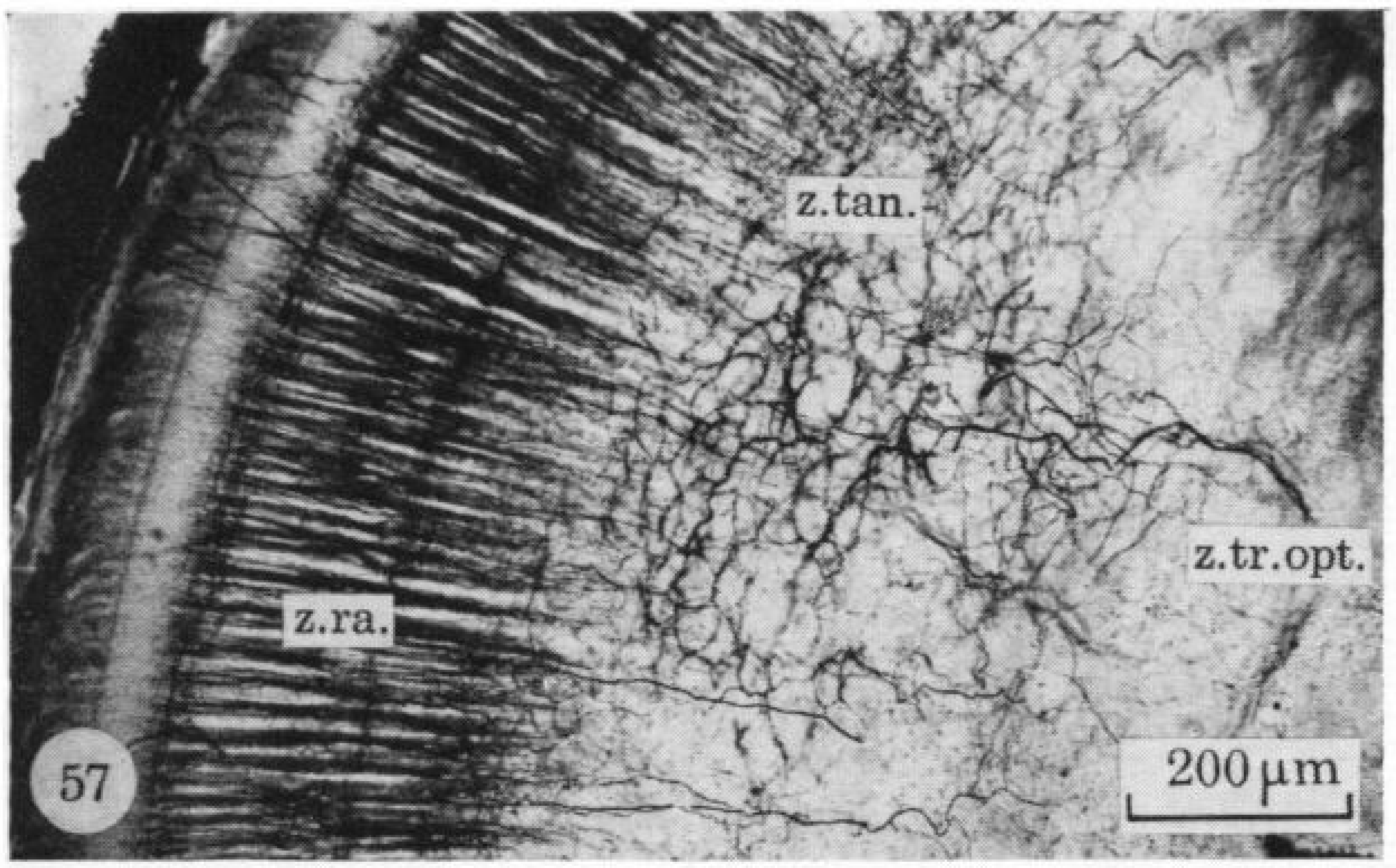


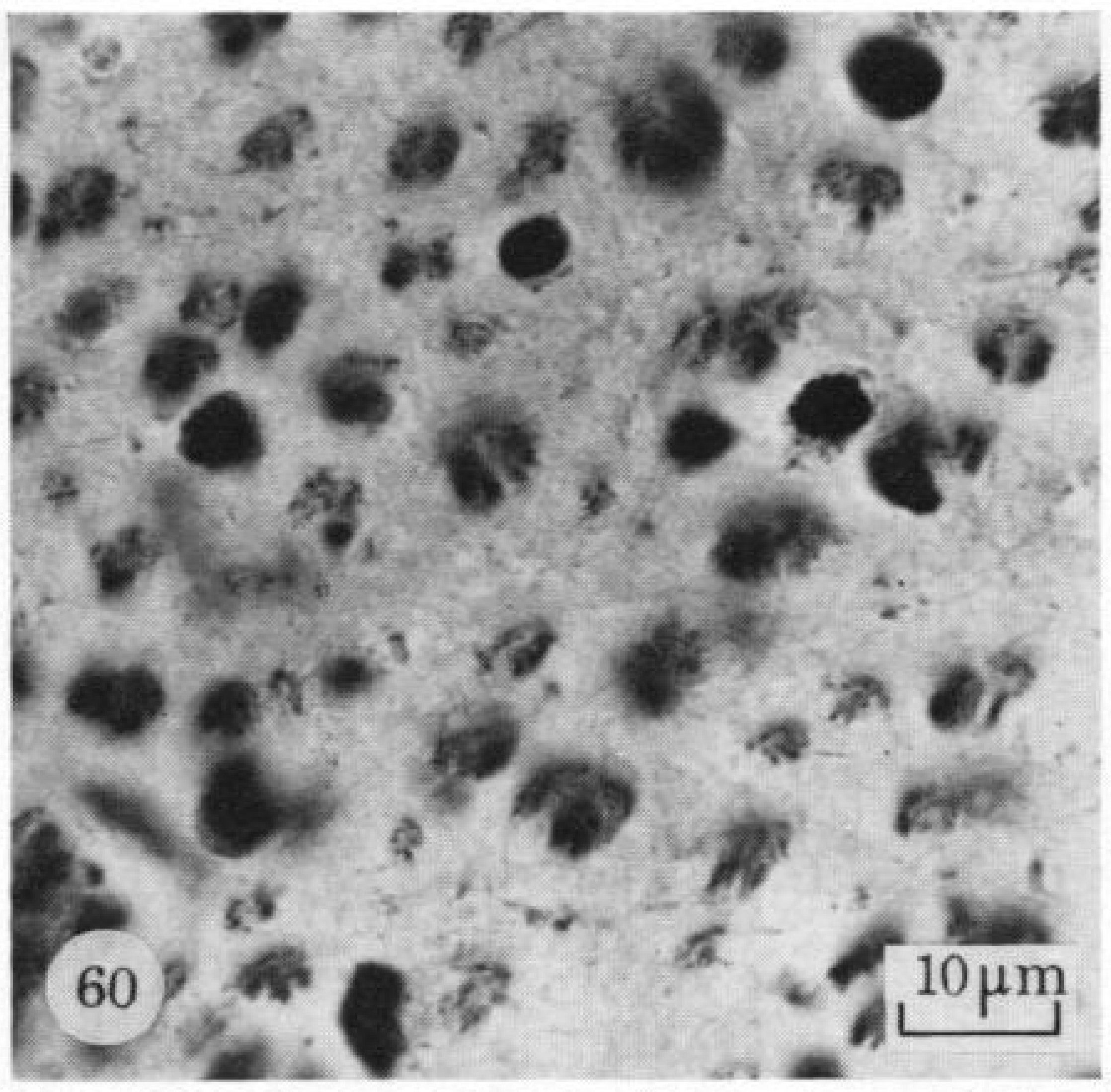


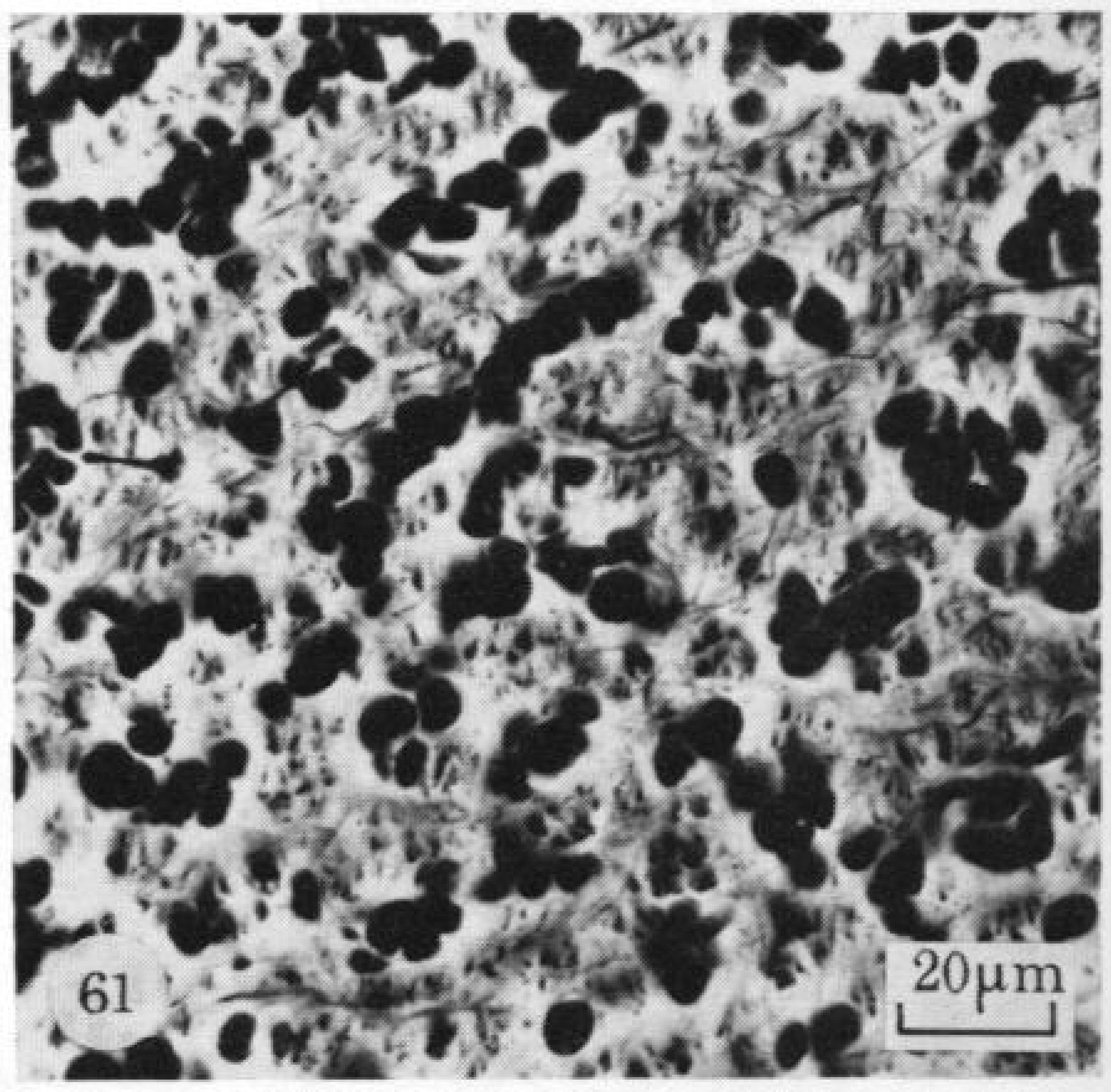


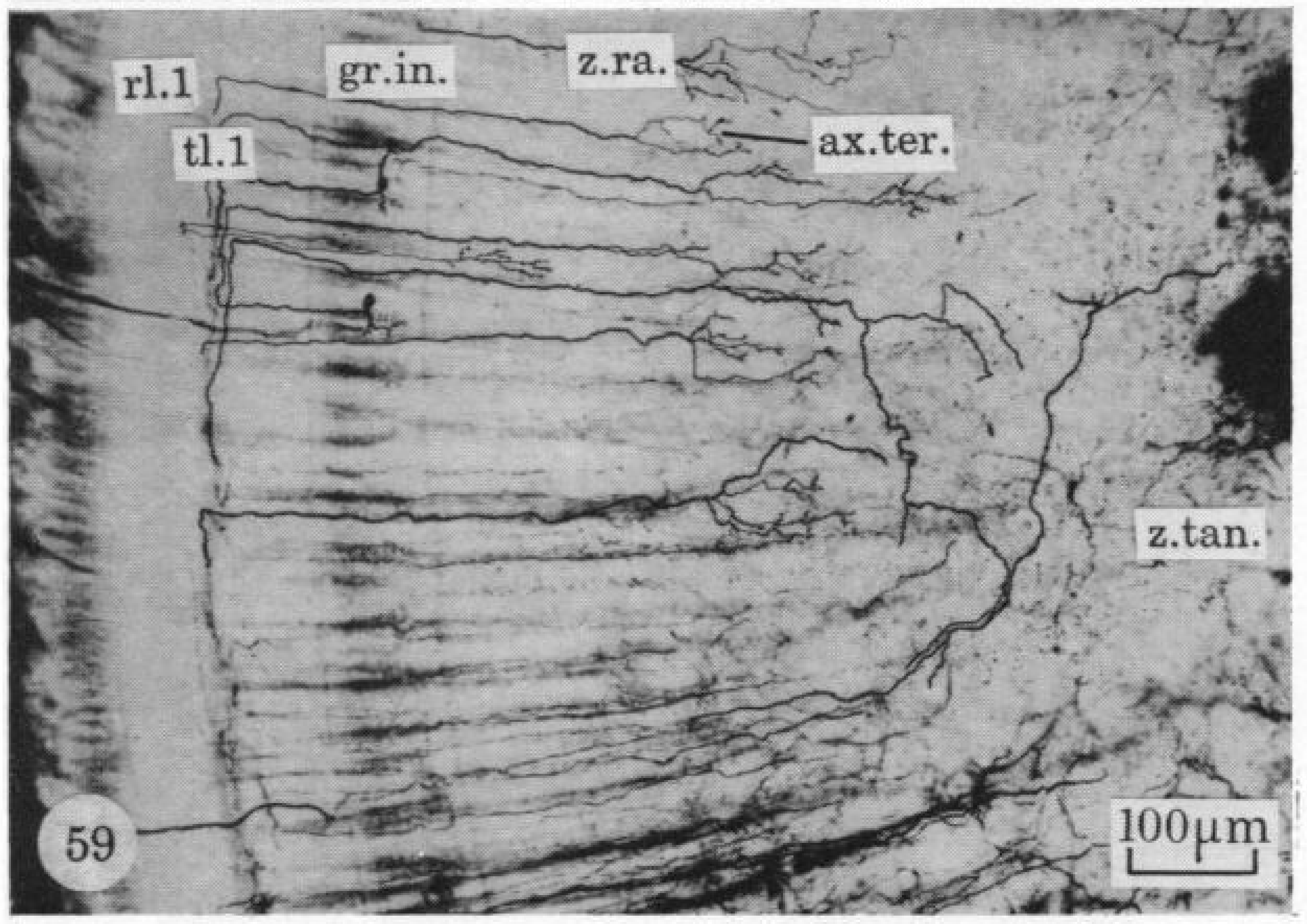


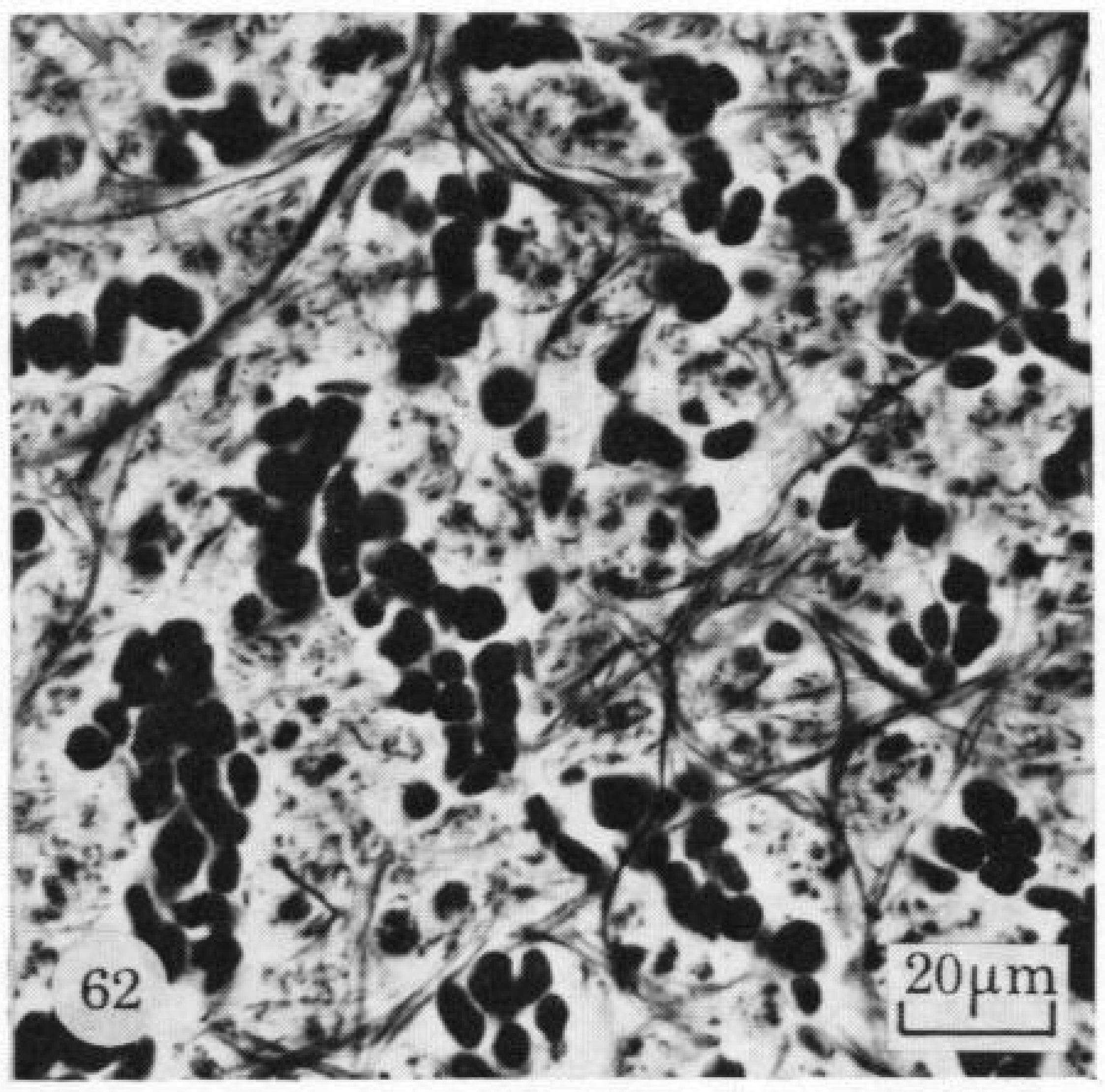
FIGURES 46–56. For description see opposite

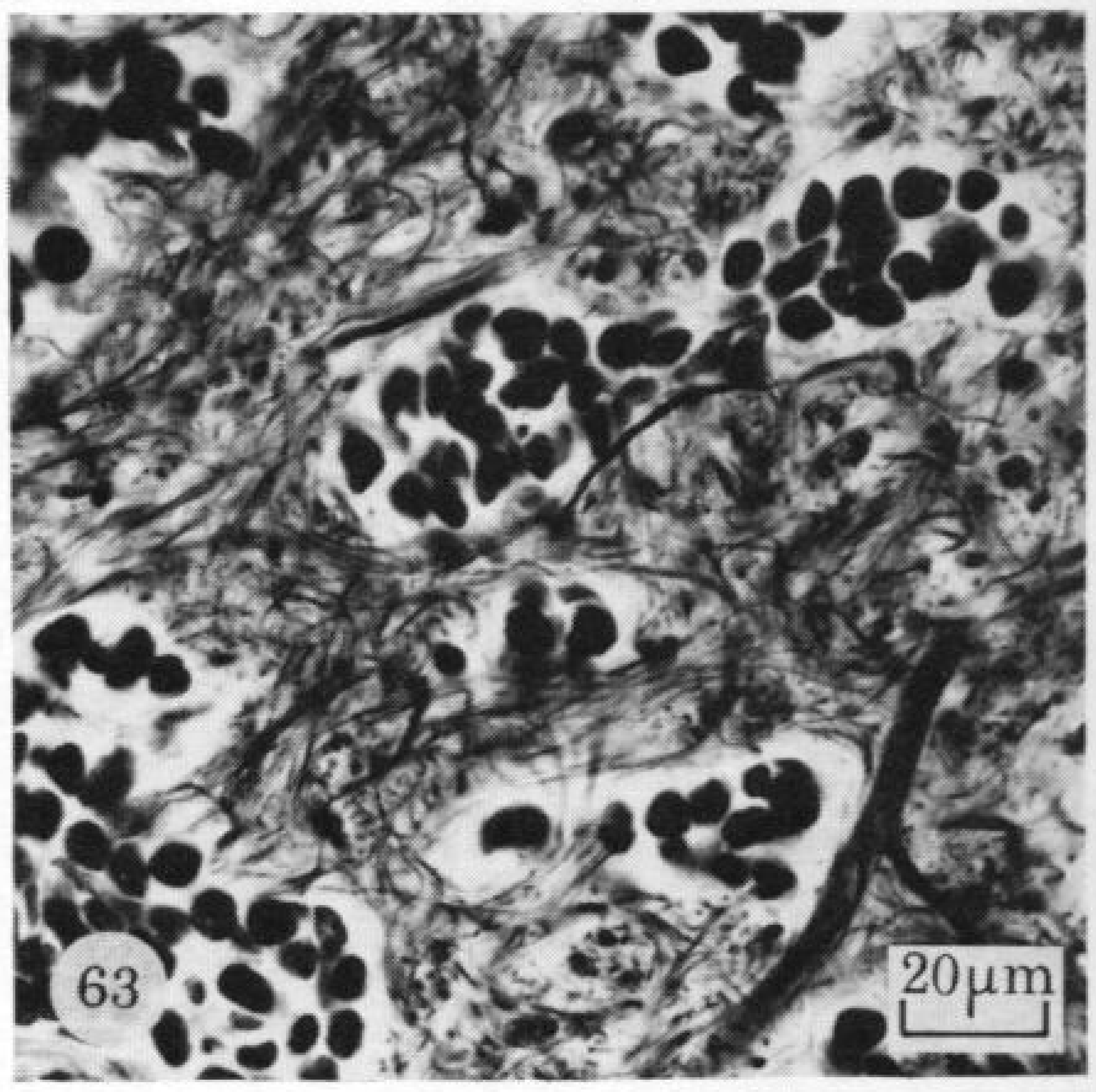


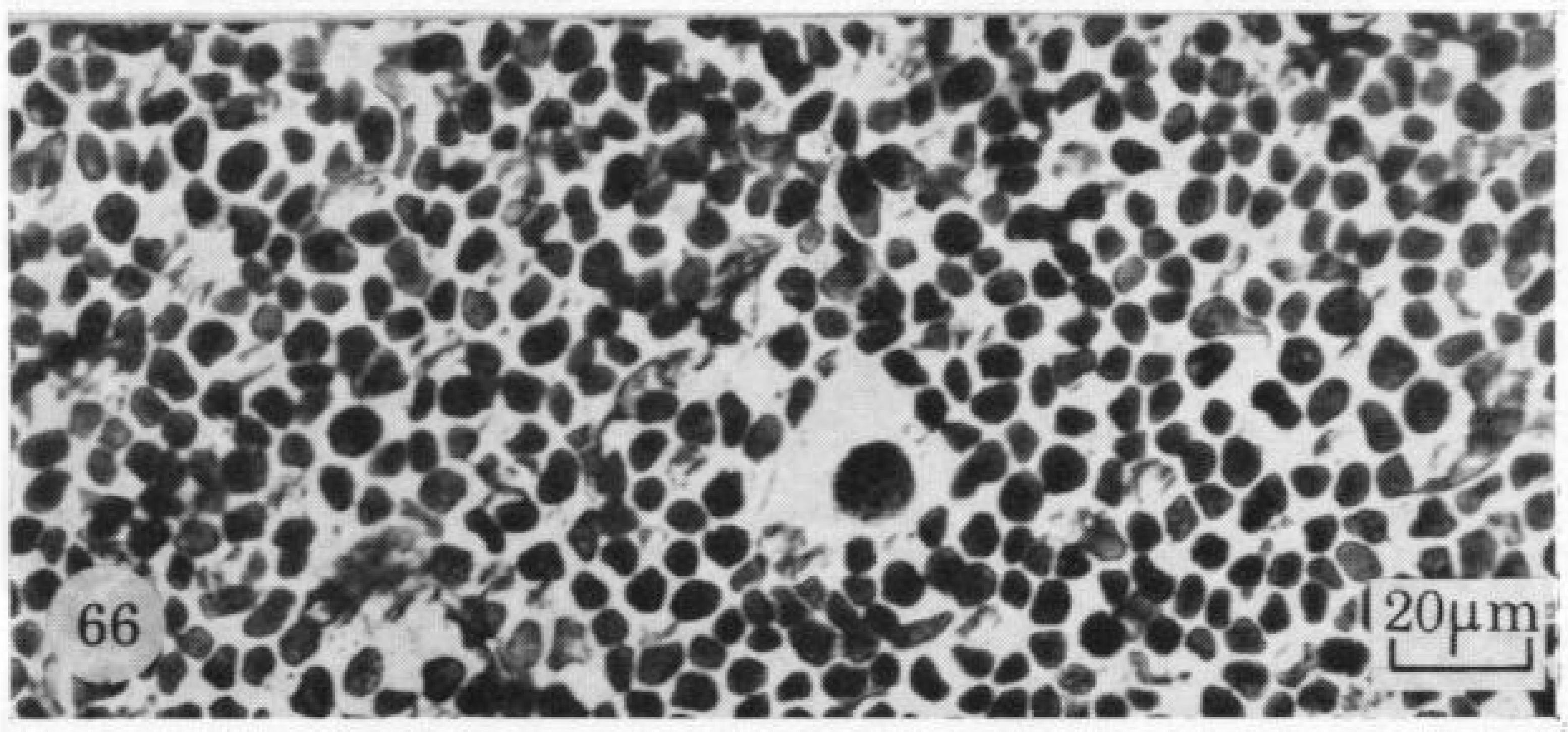


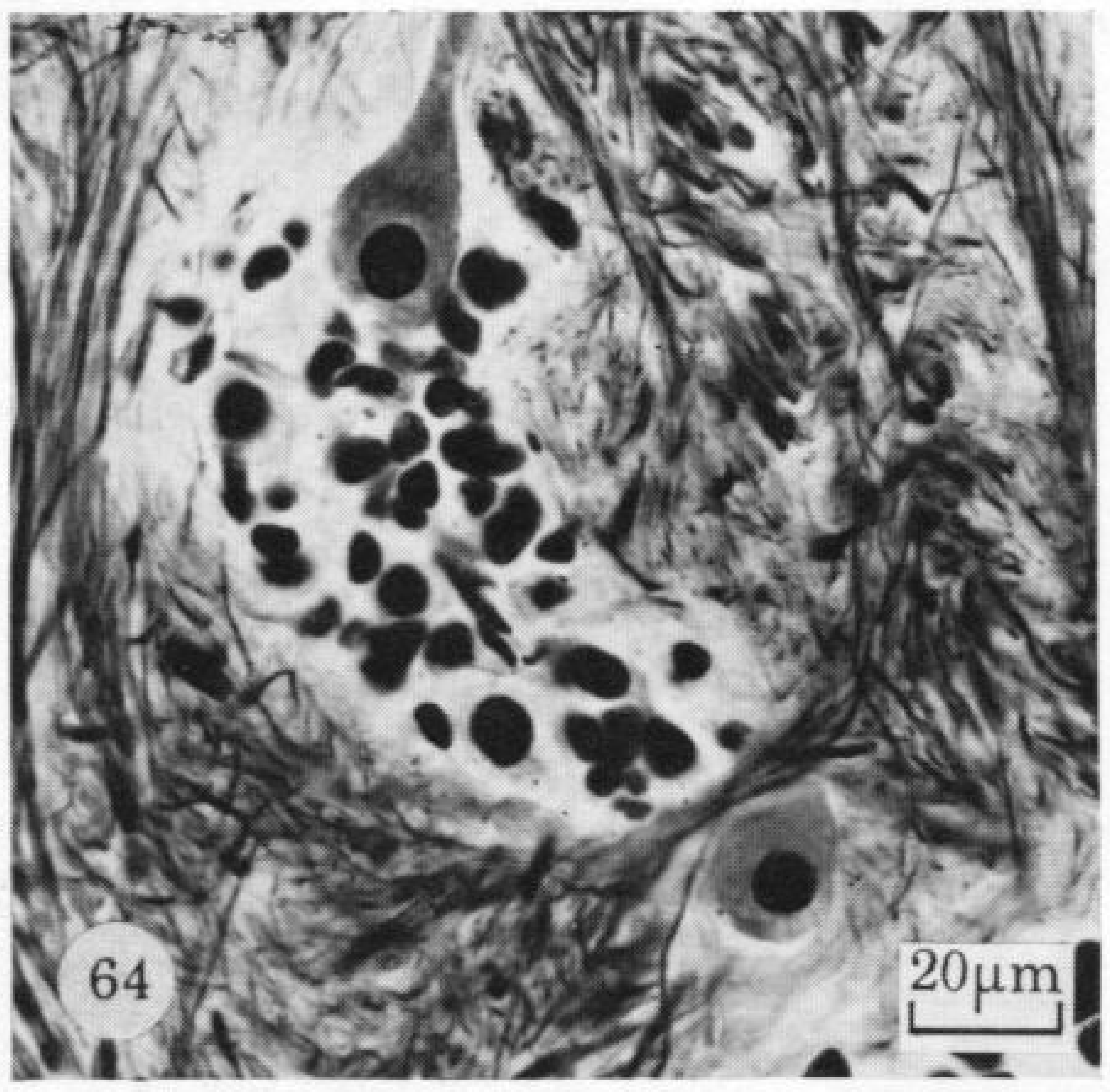


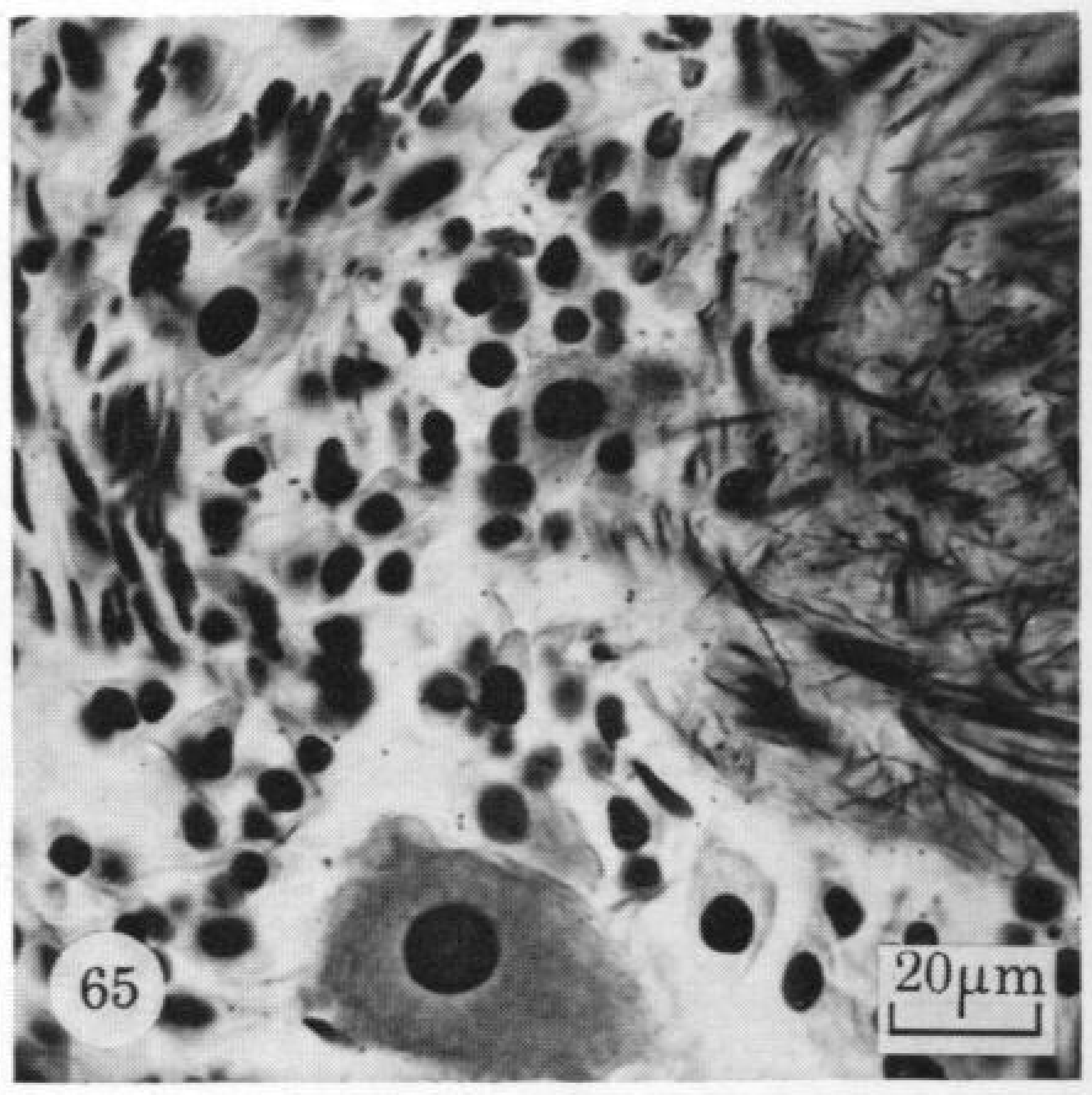


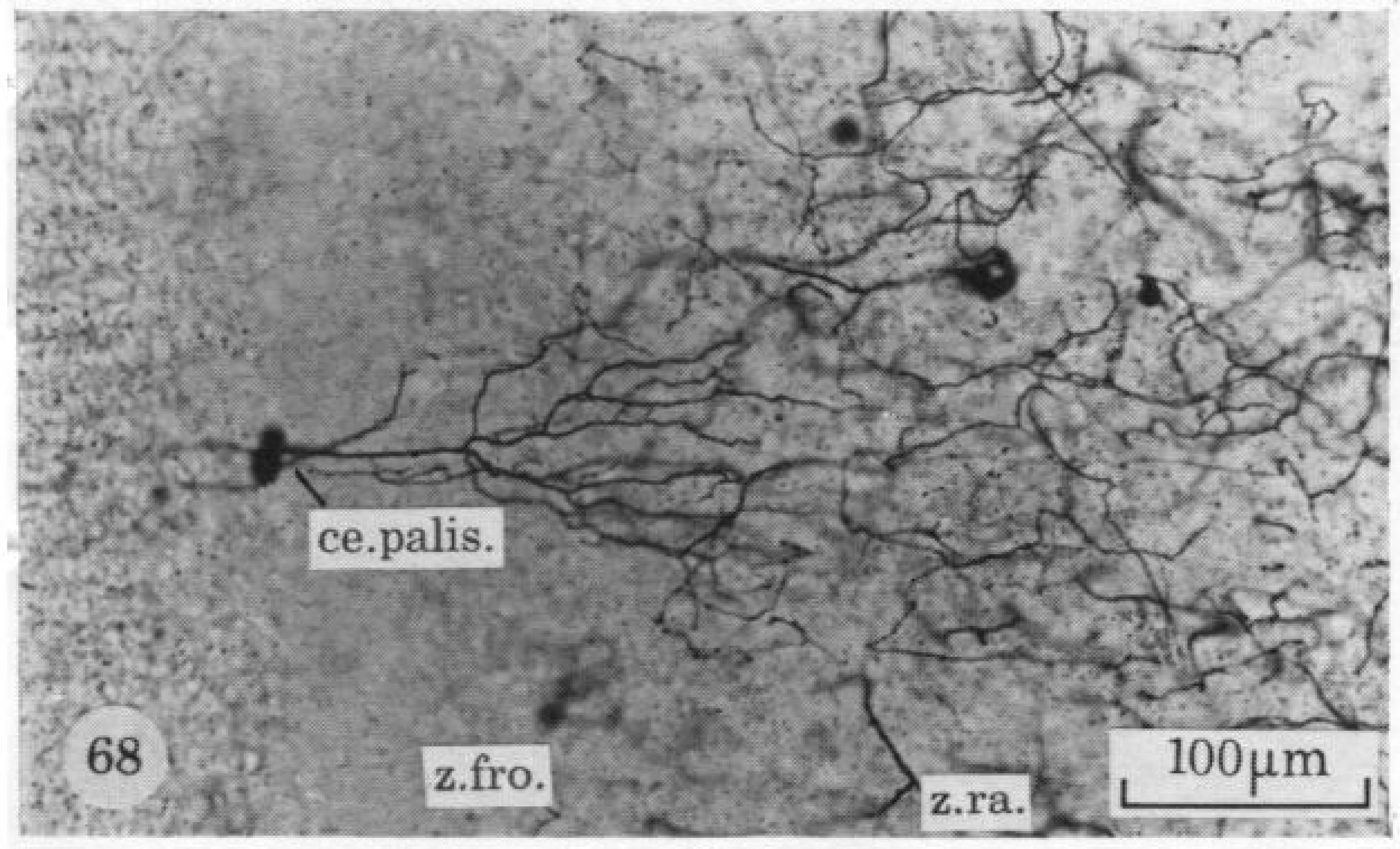


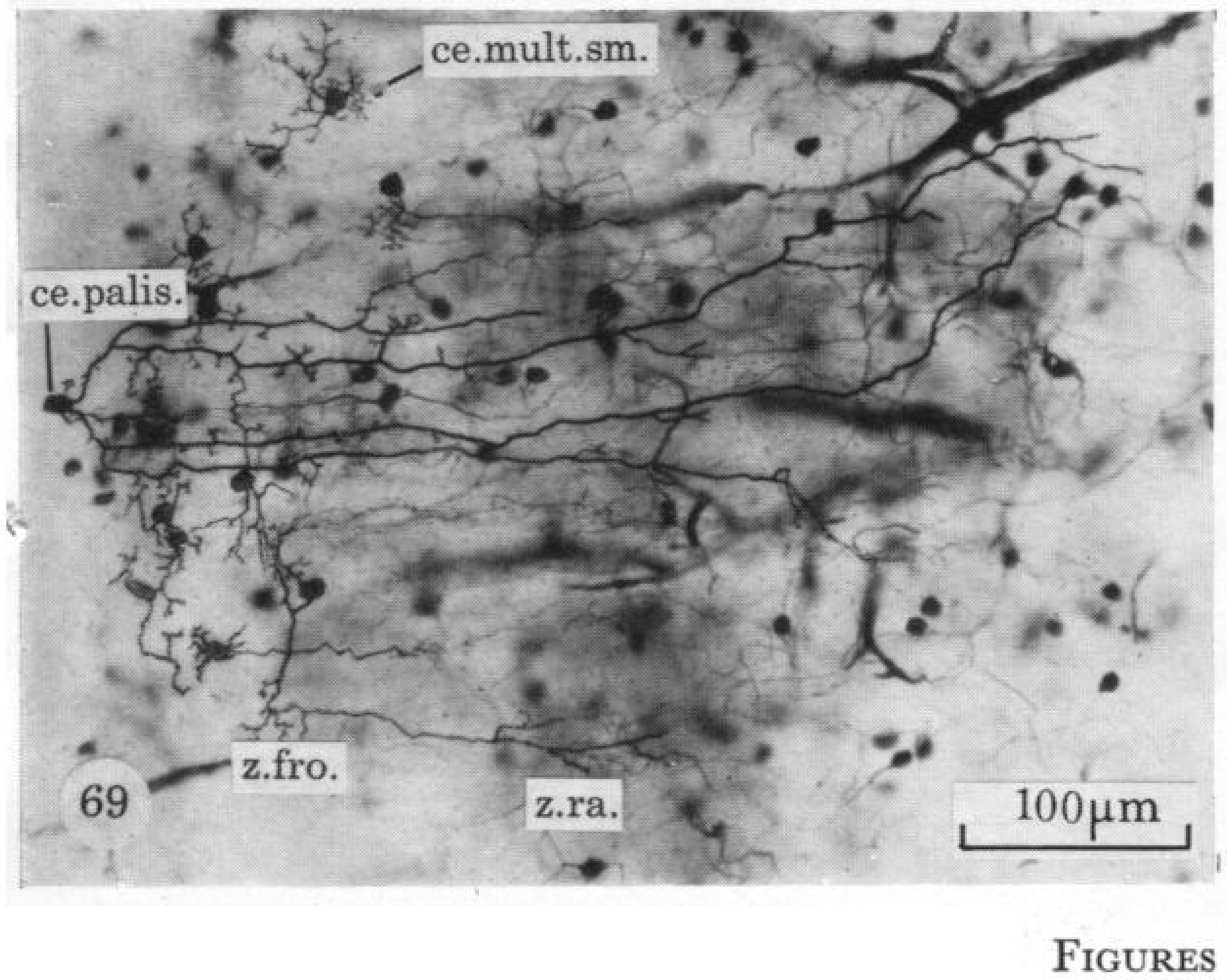


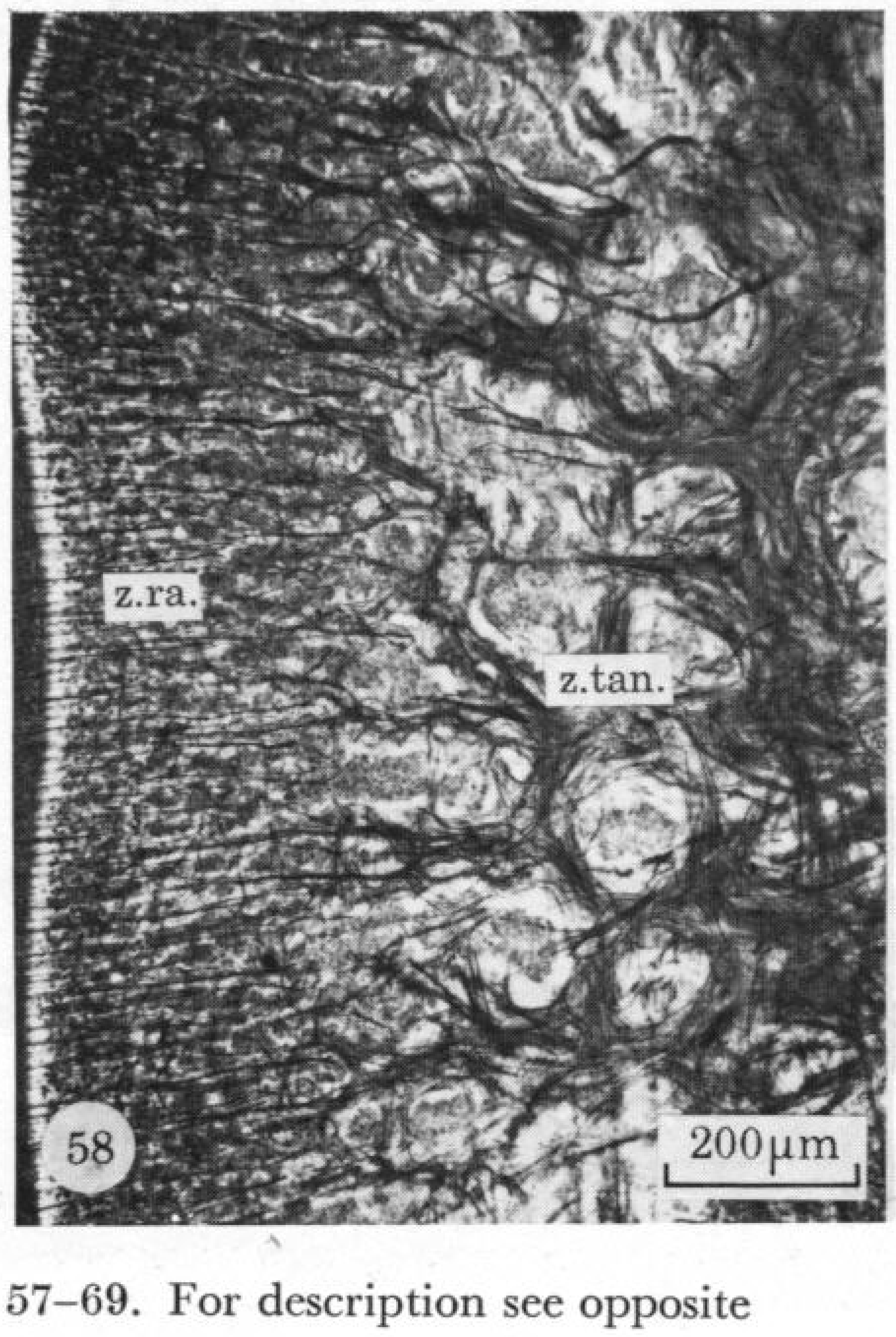


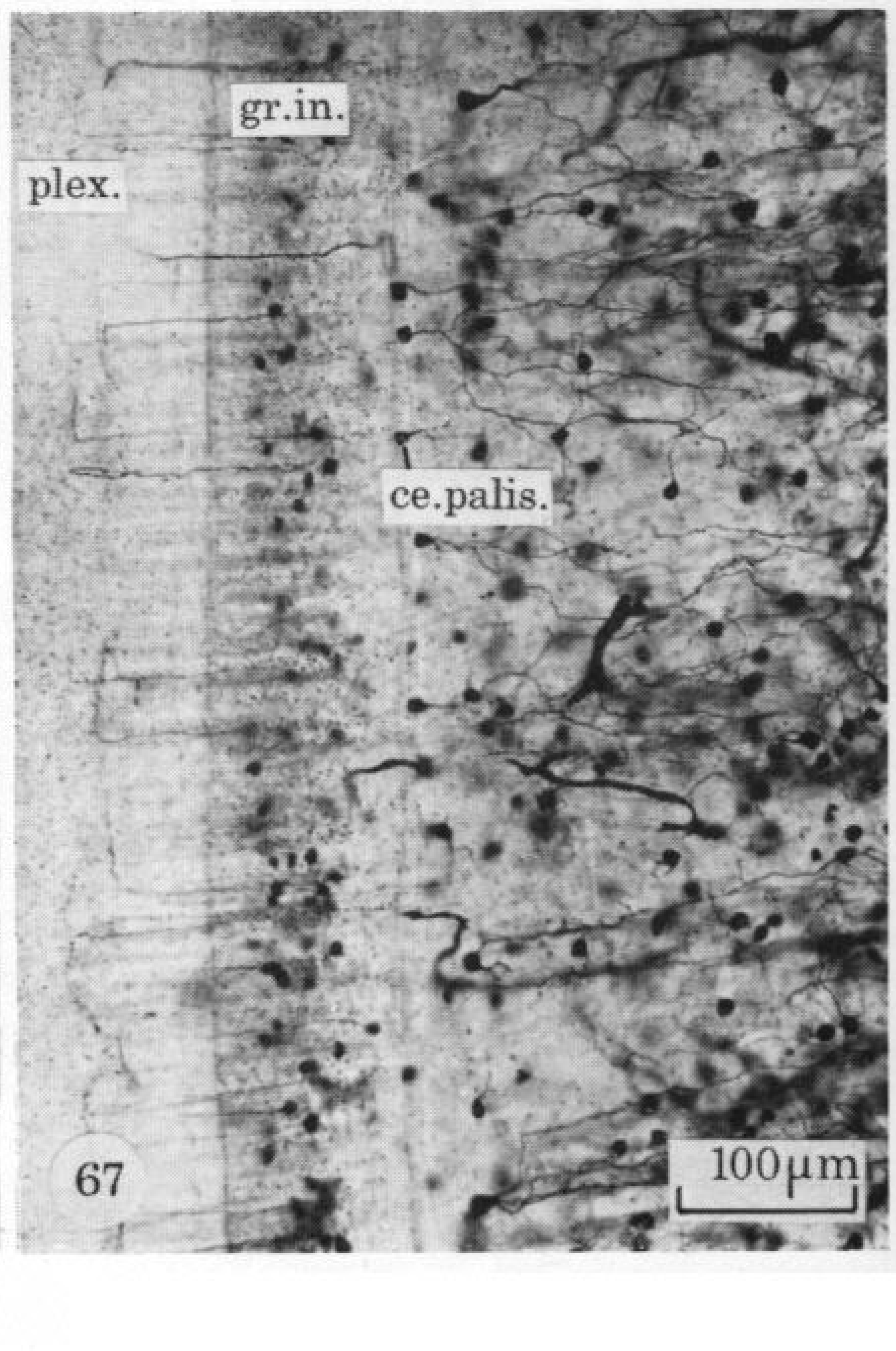




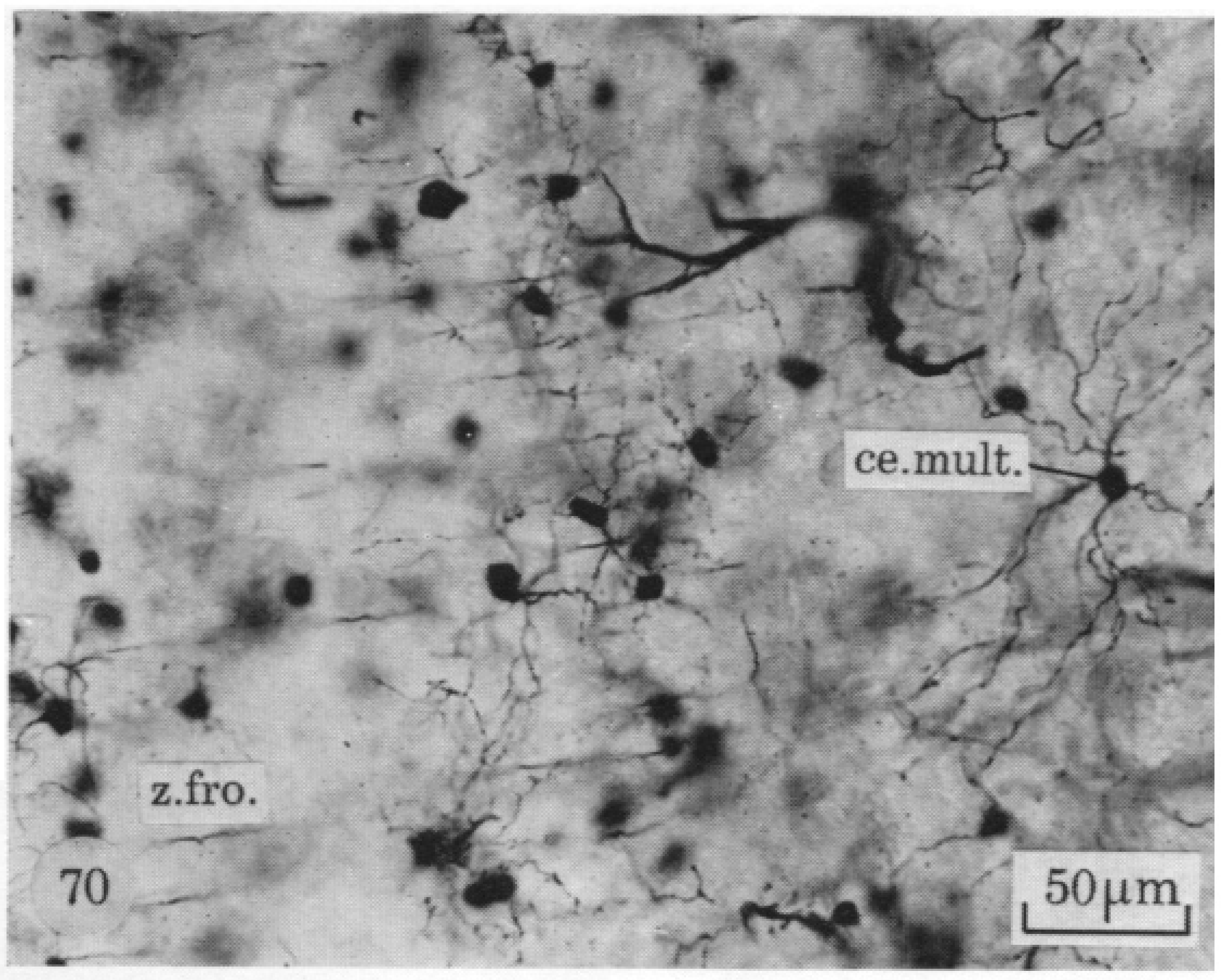








Figures 57–69. For description see opposite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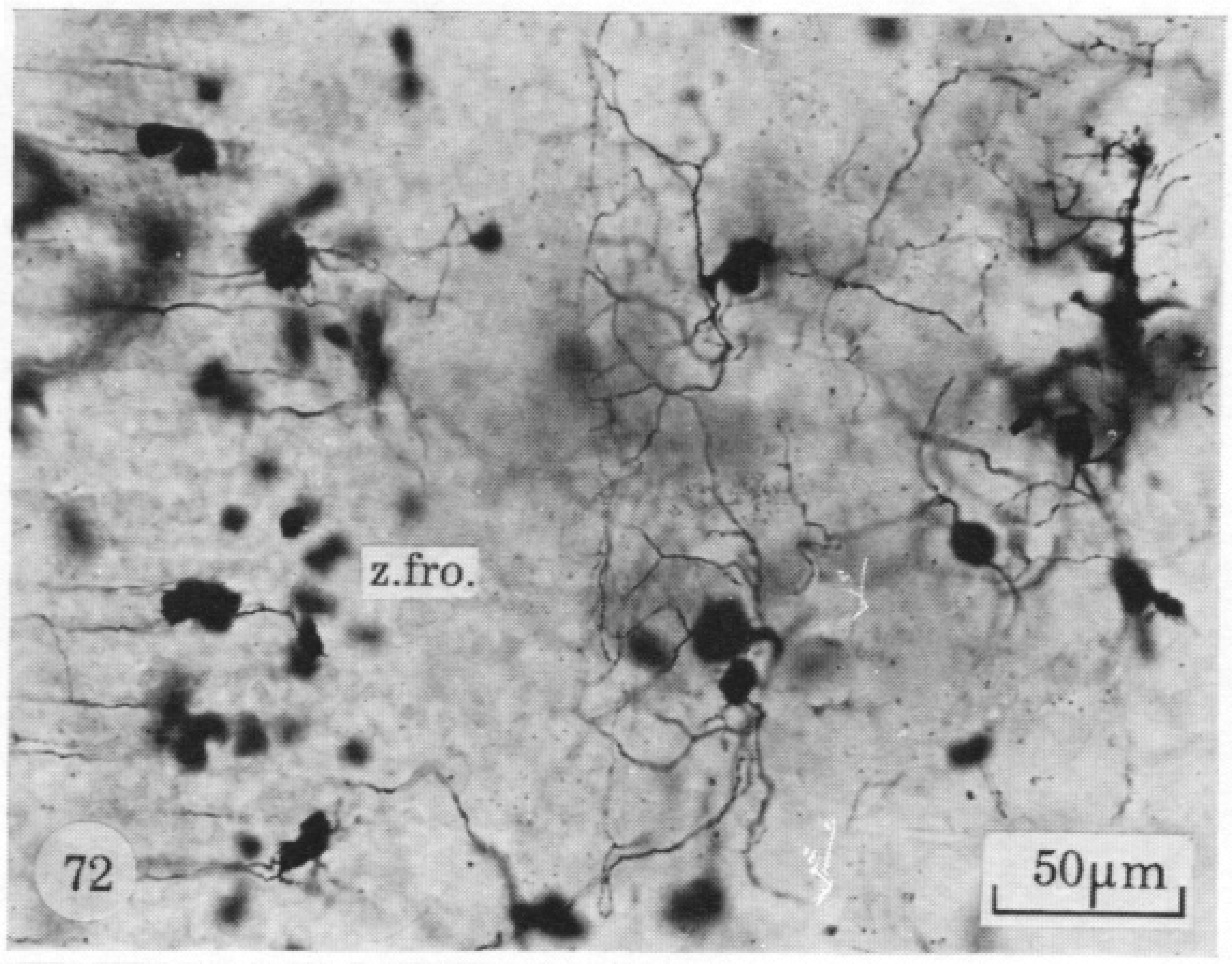
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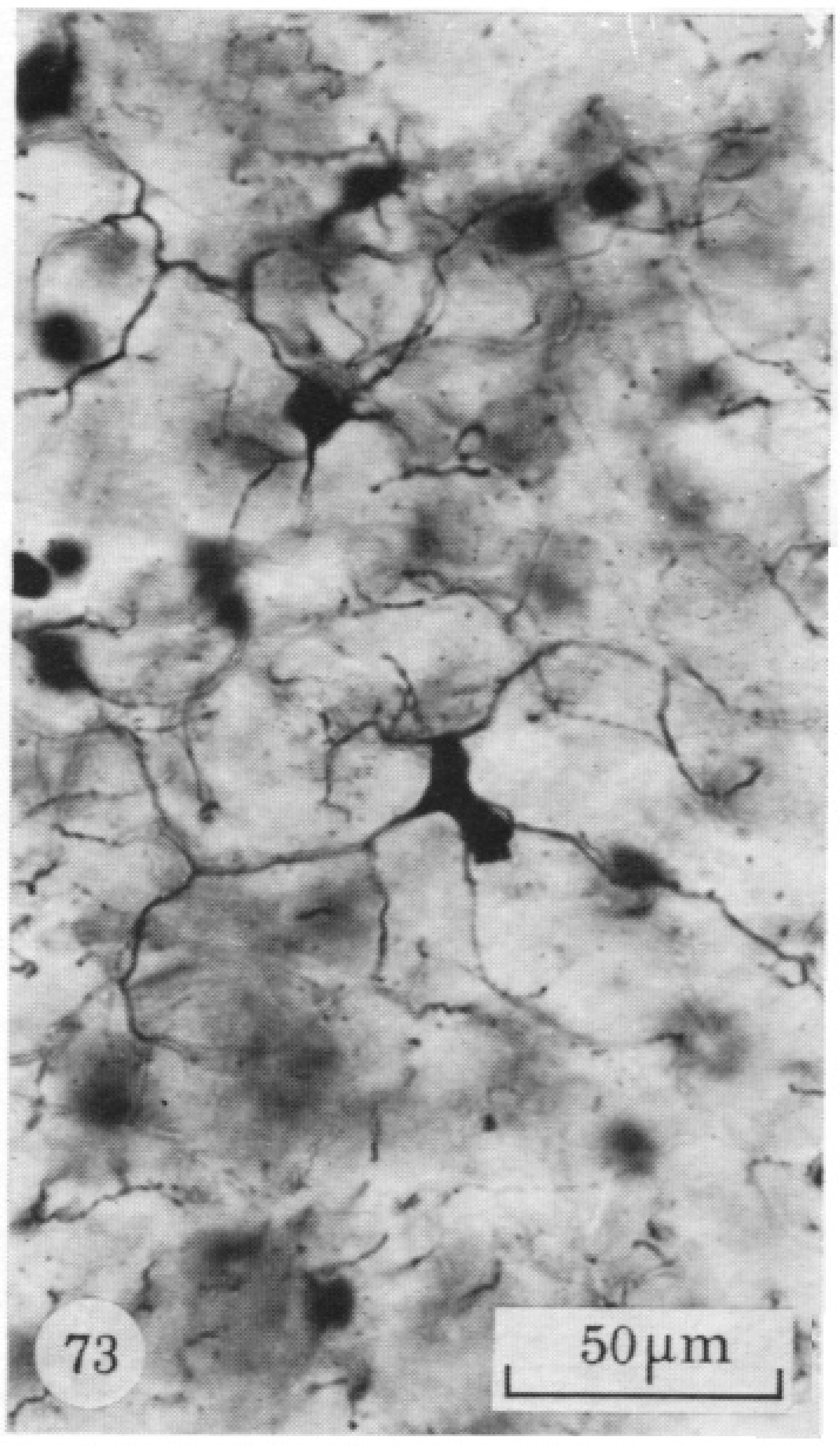
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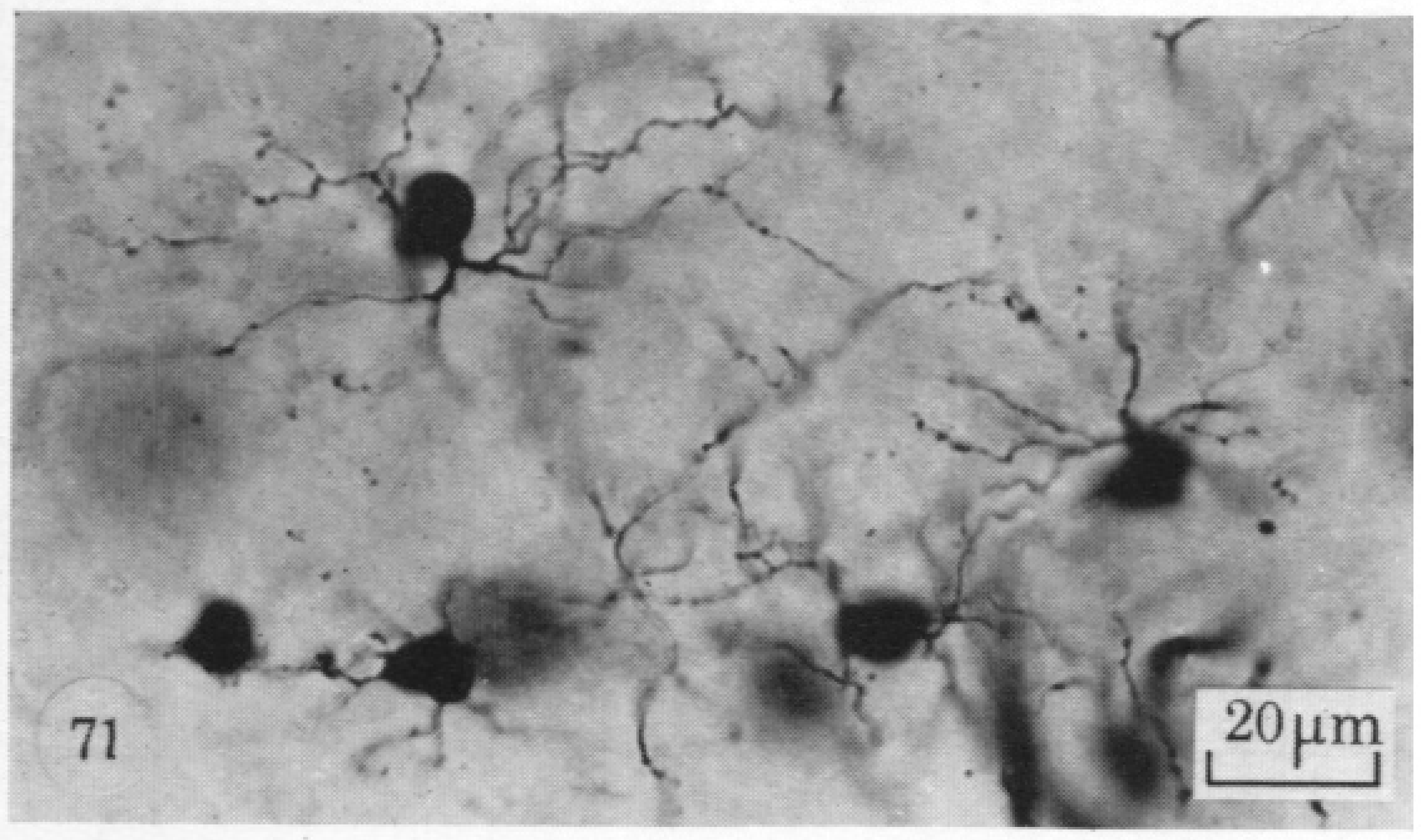
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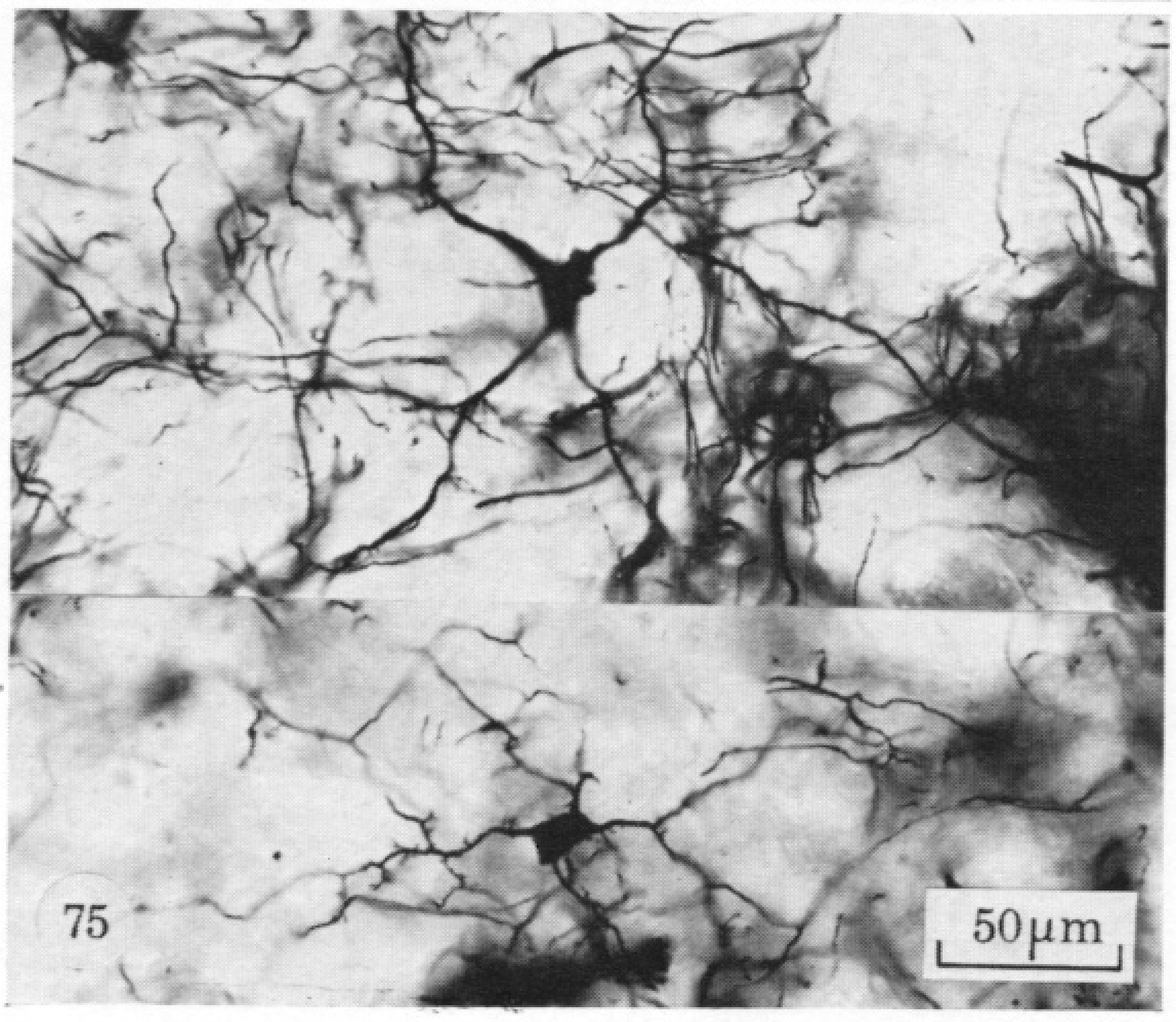
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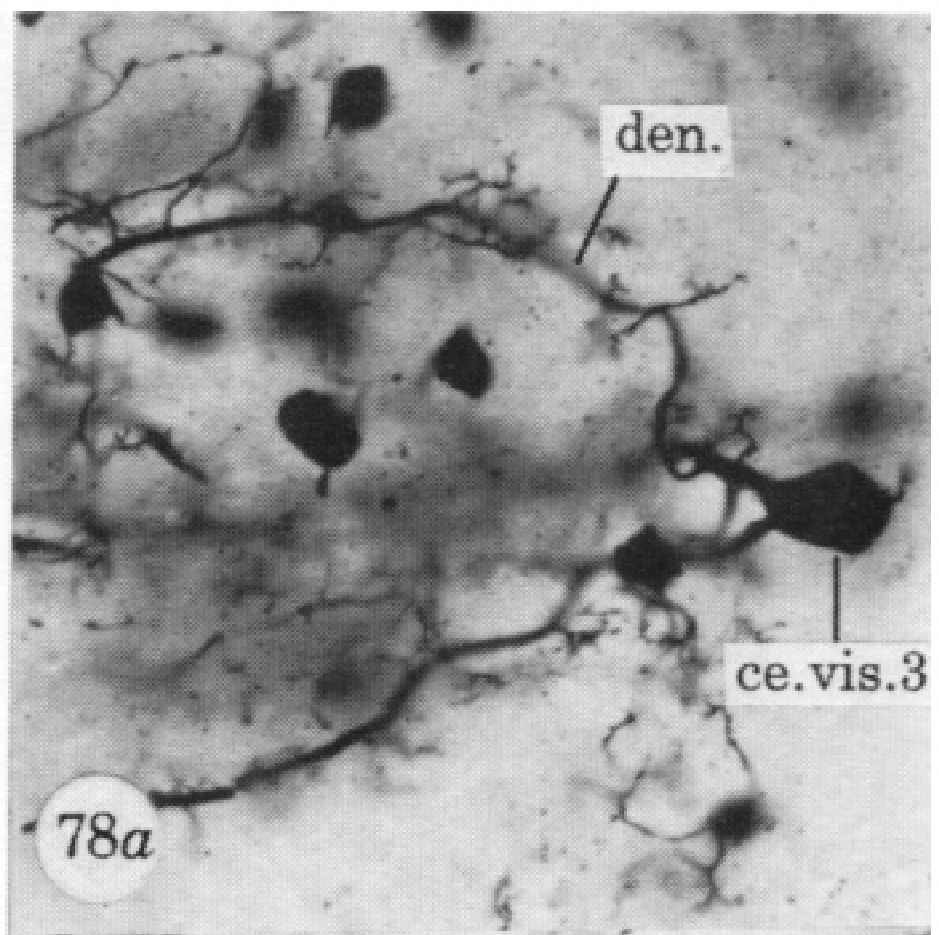
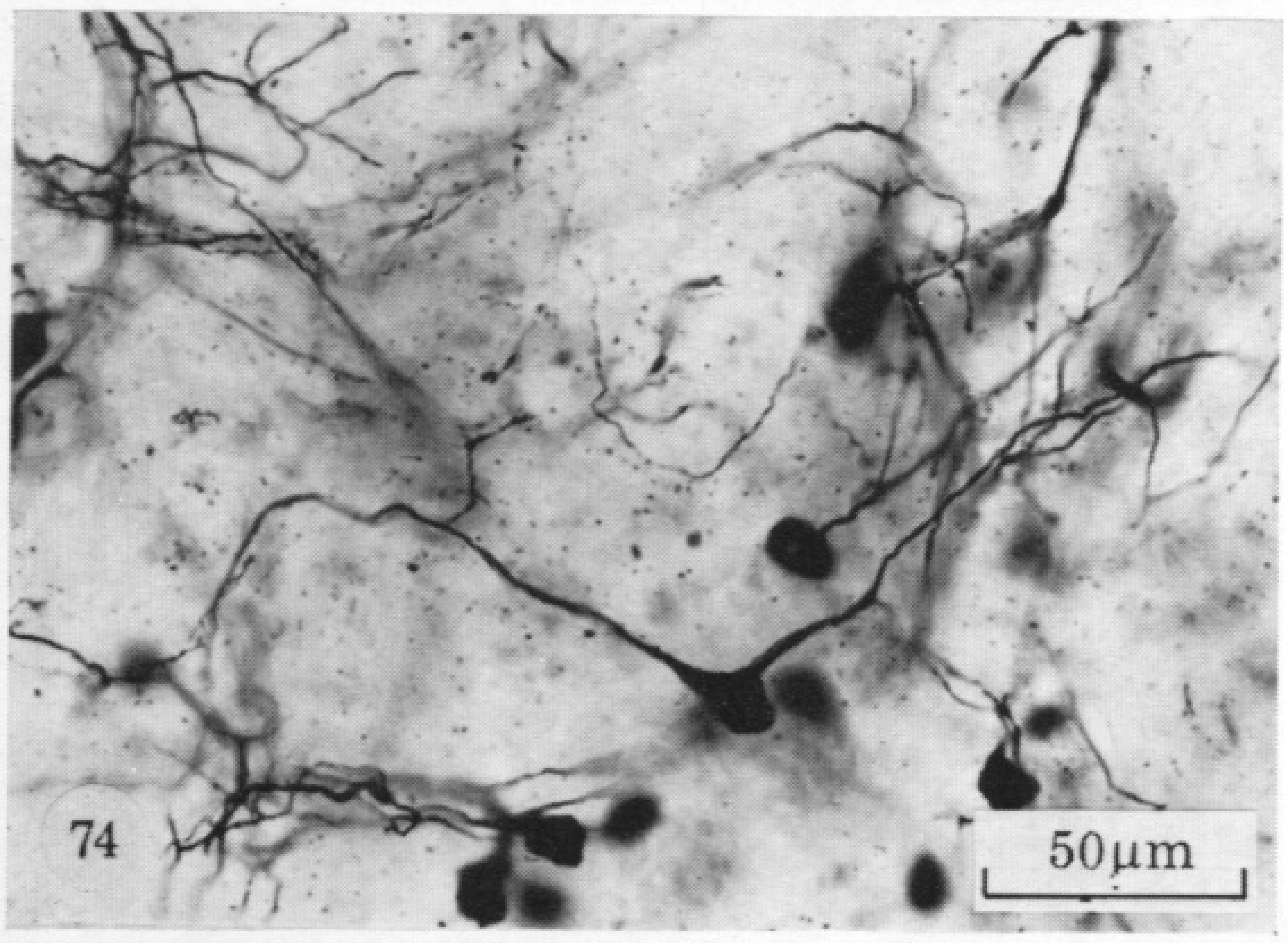

78*a*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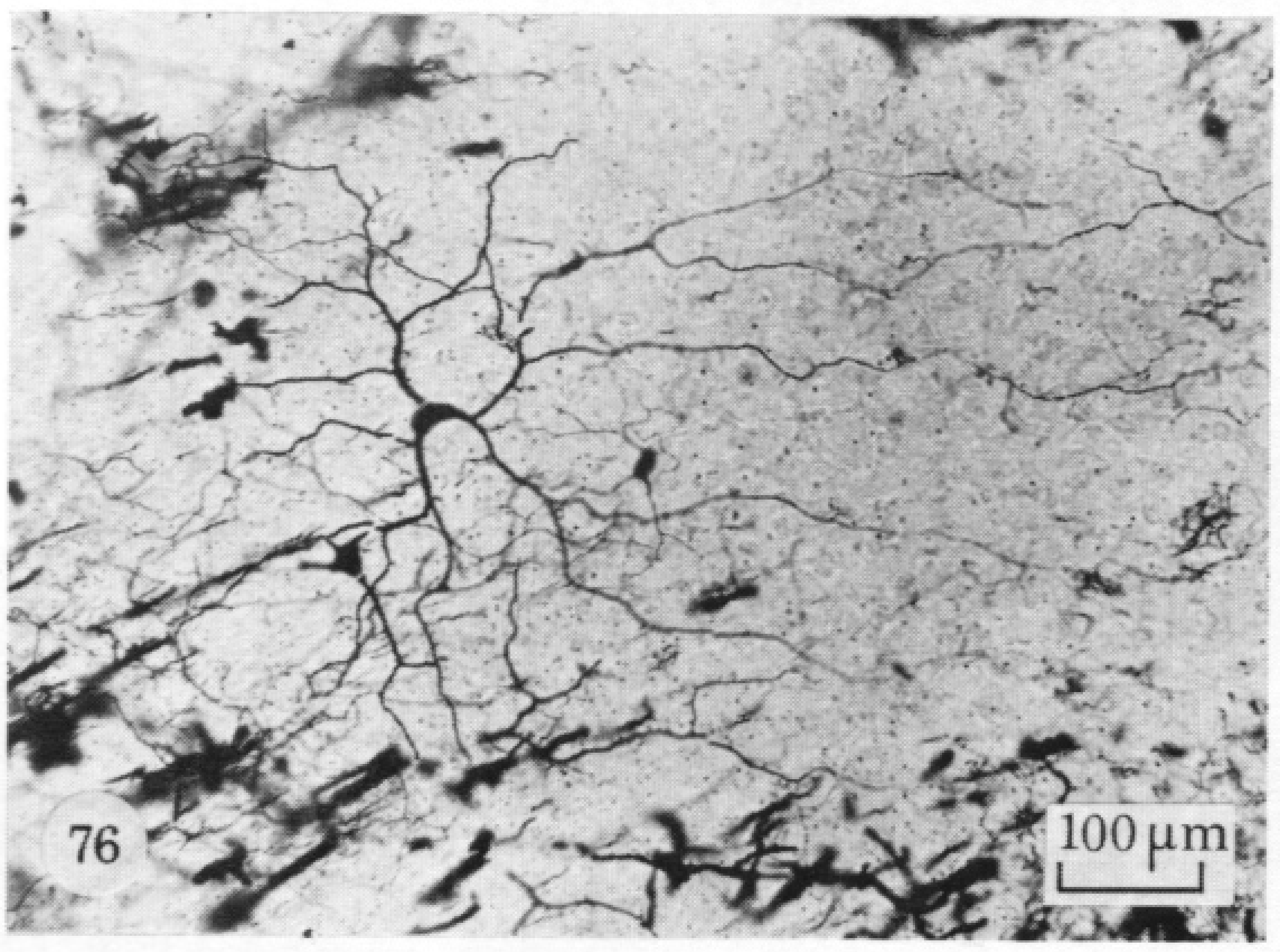
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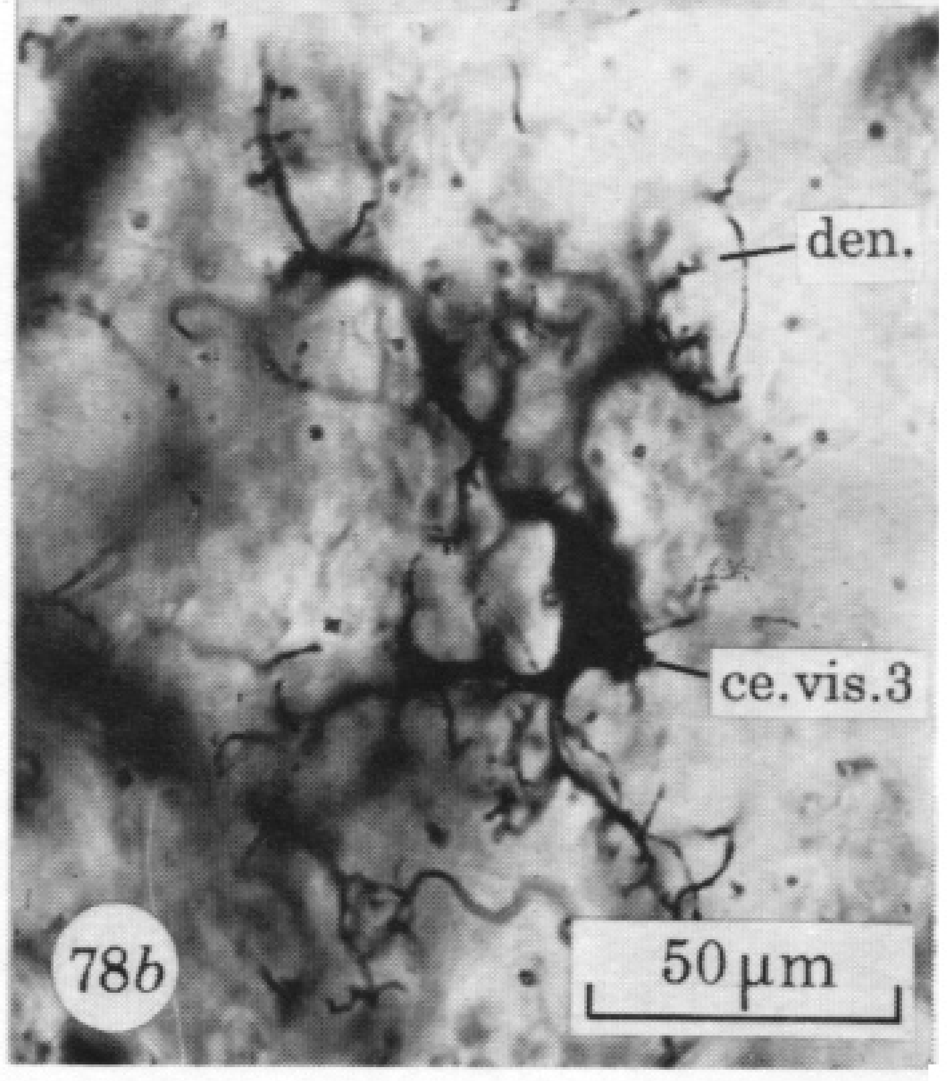
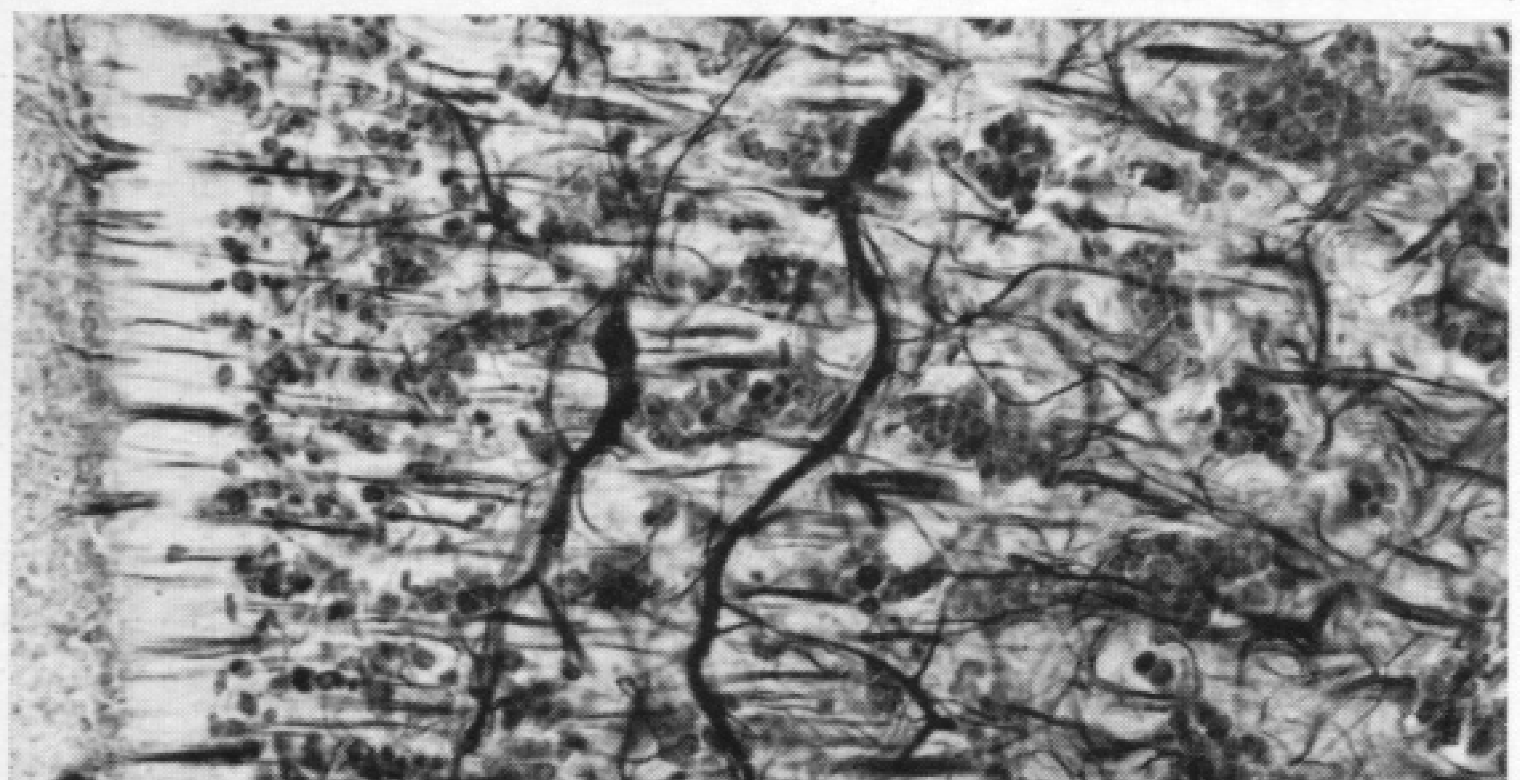

78*b*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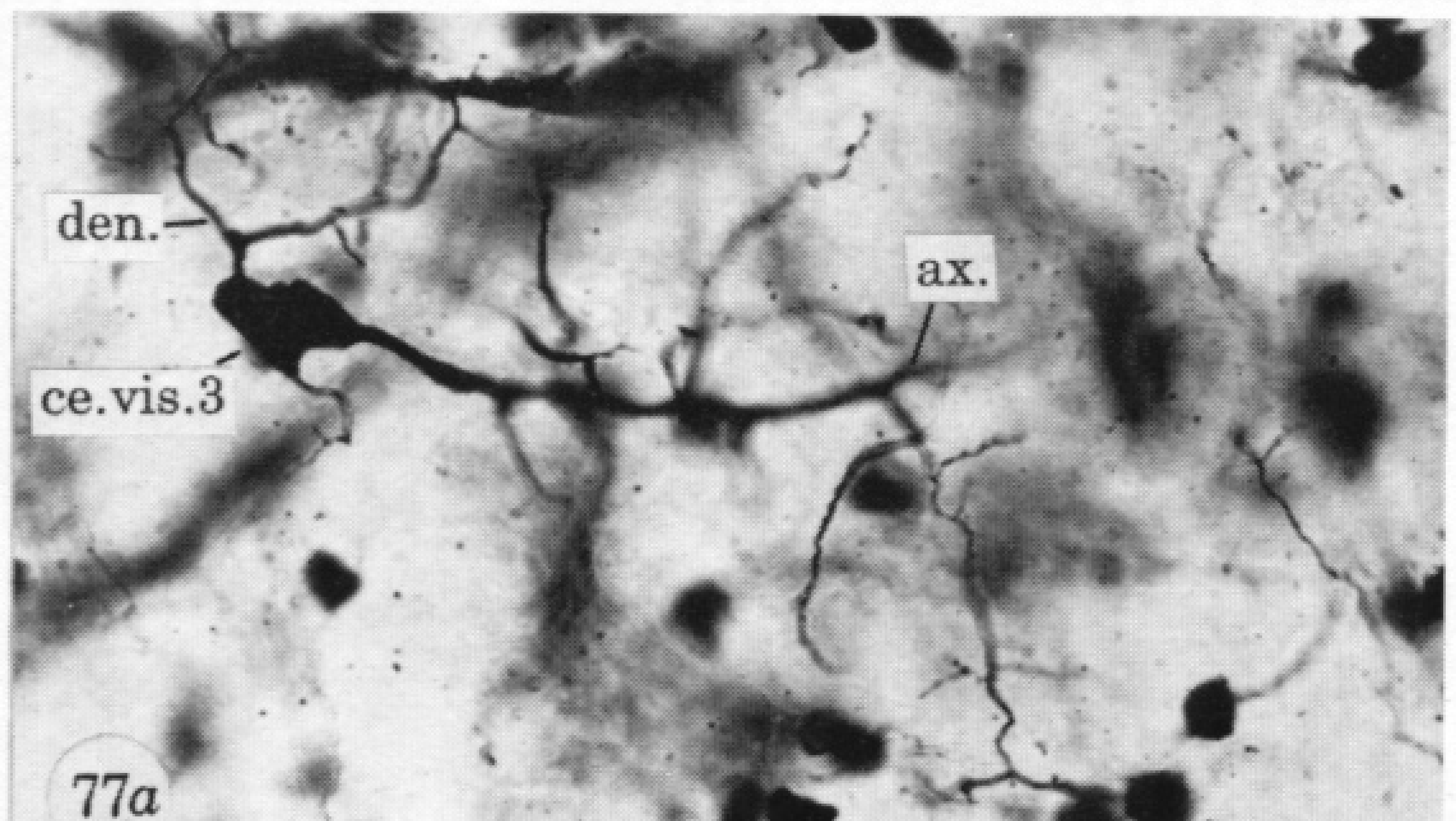
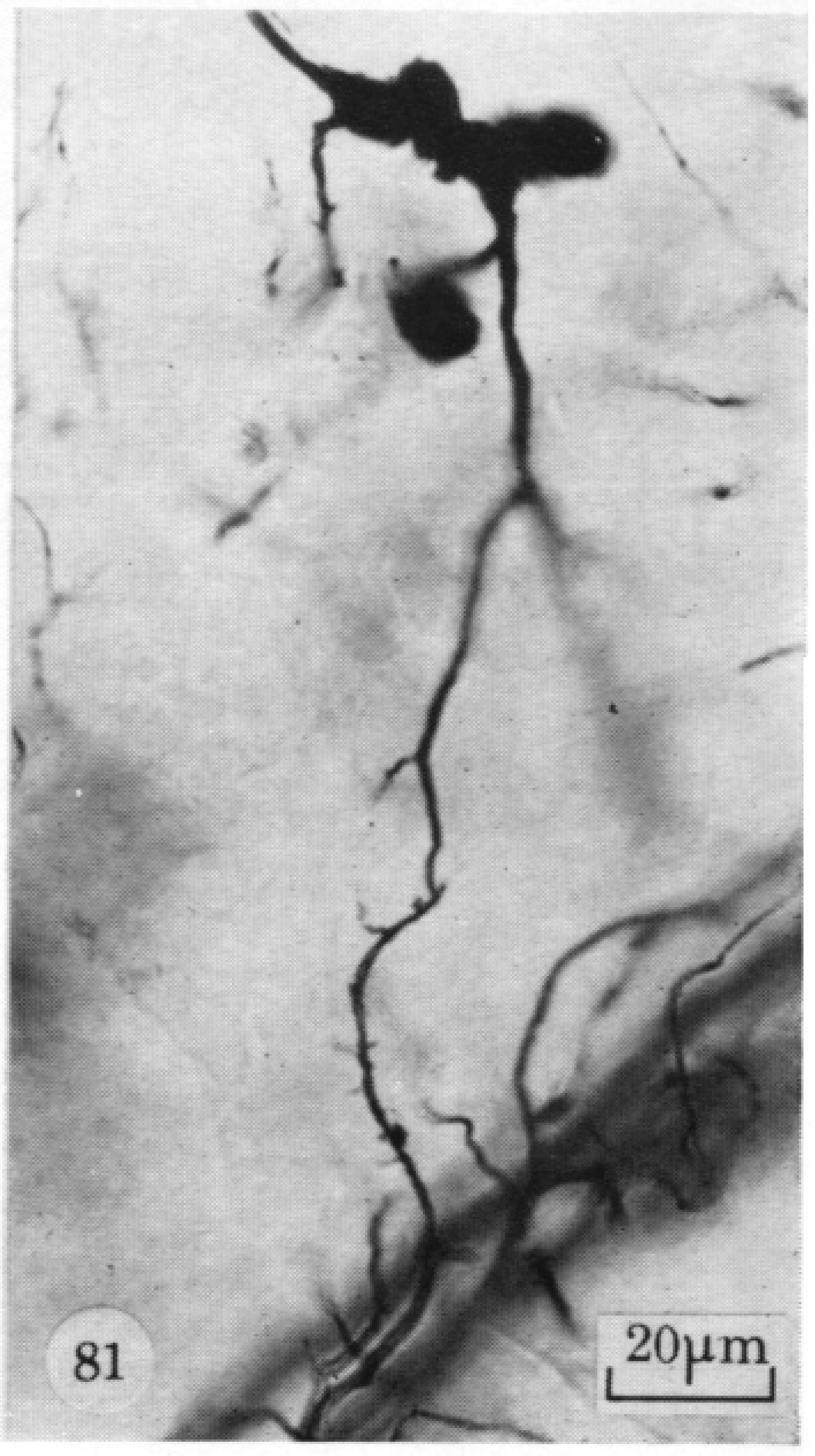

77*a*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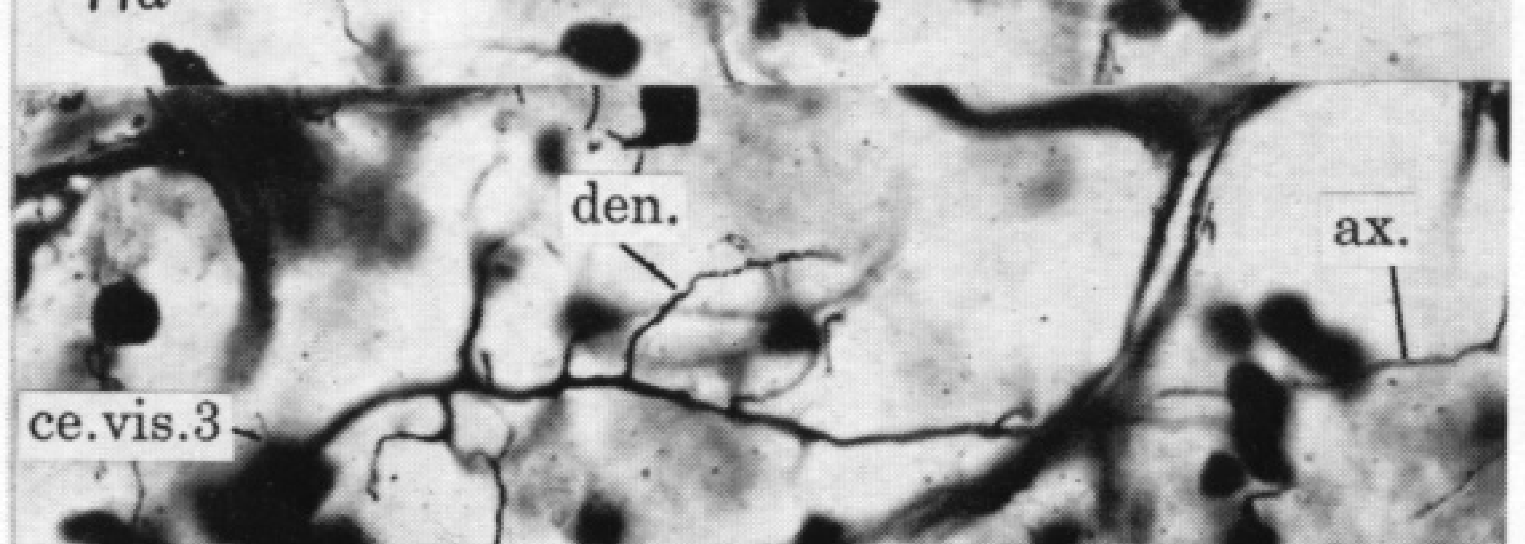
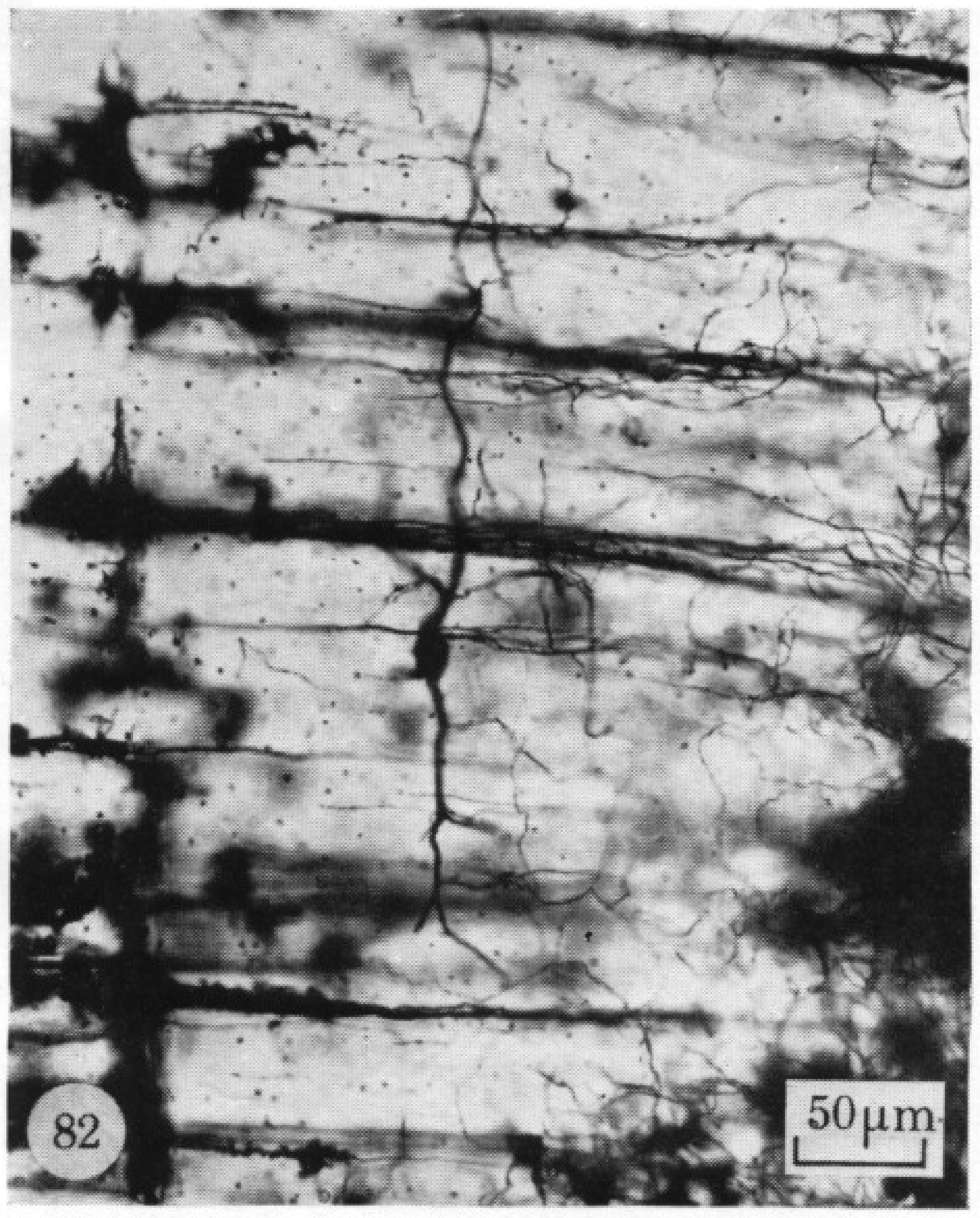
80


77*b*

FIGURES 70–81. For description see opposite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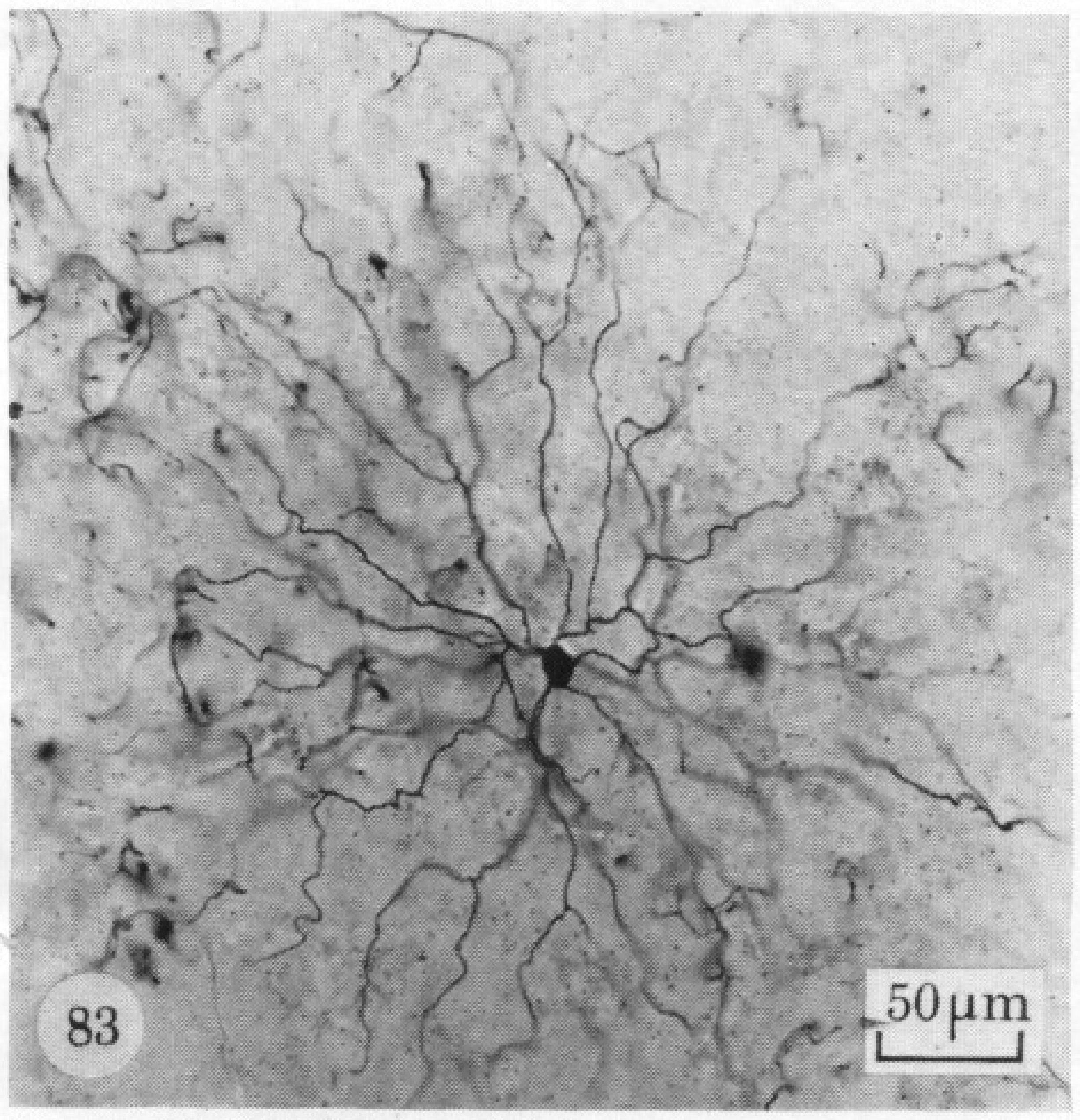
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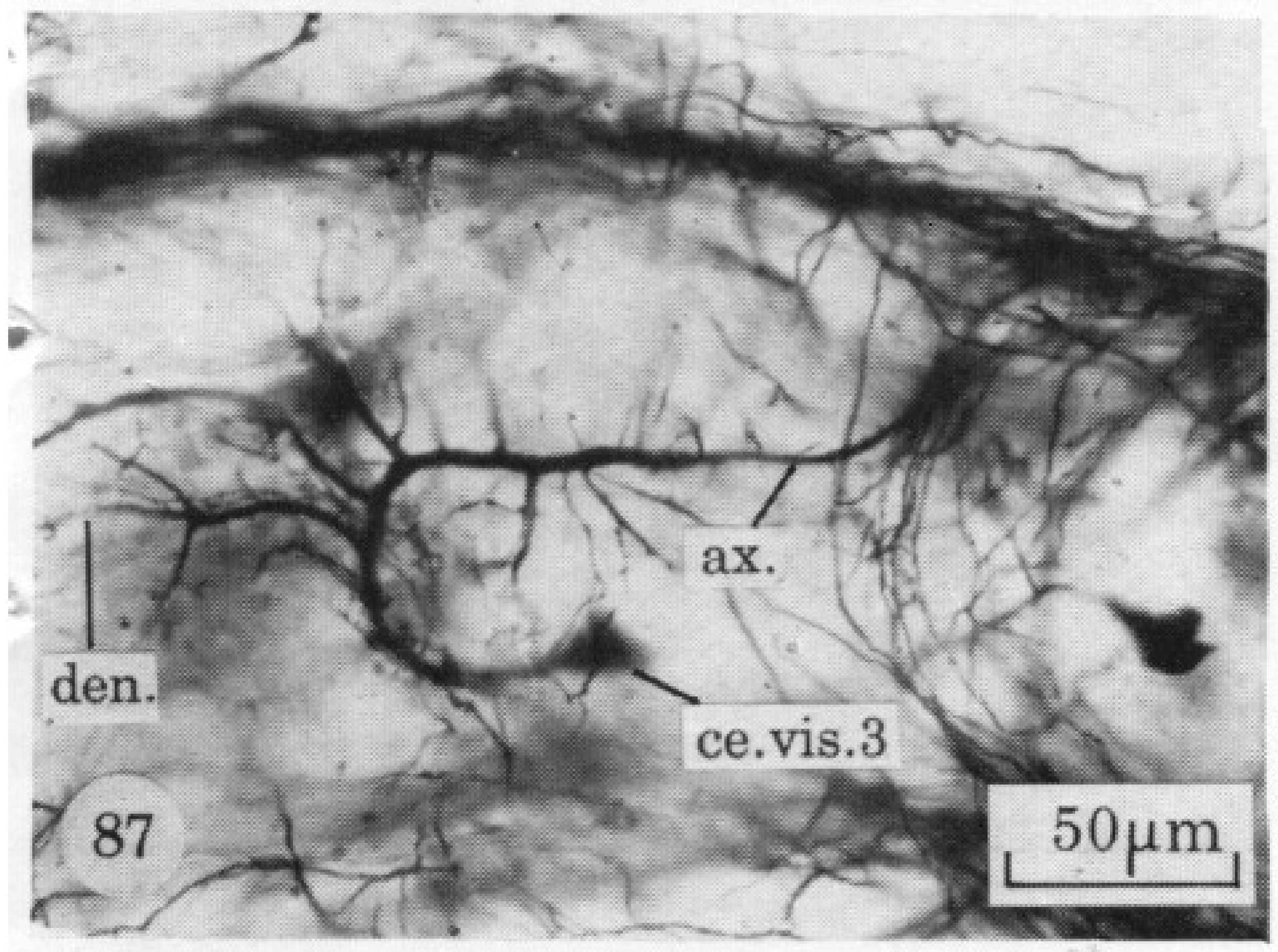
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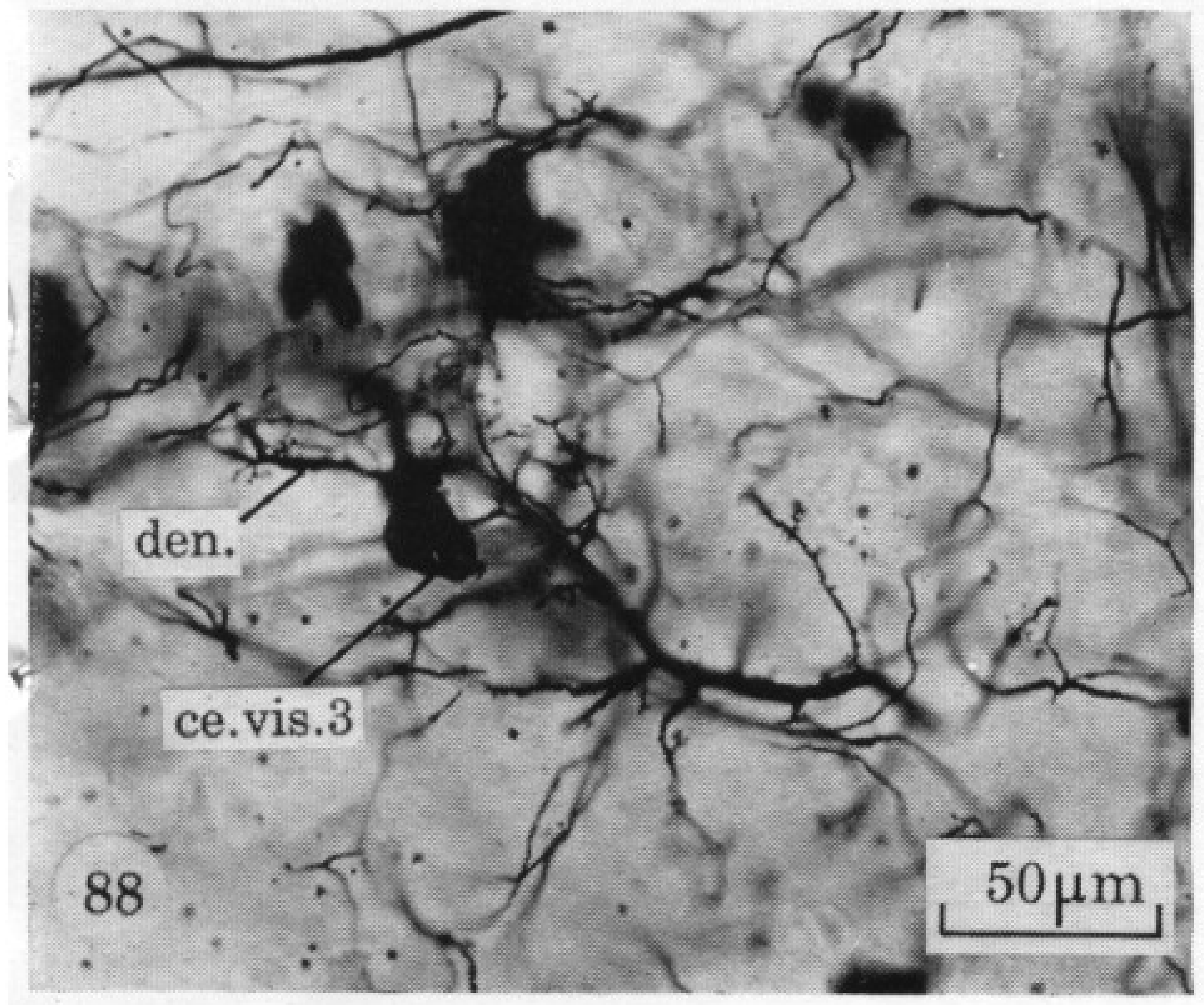
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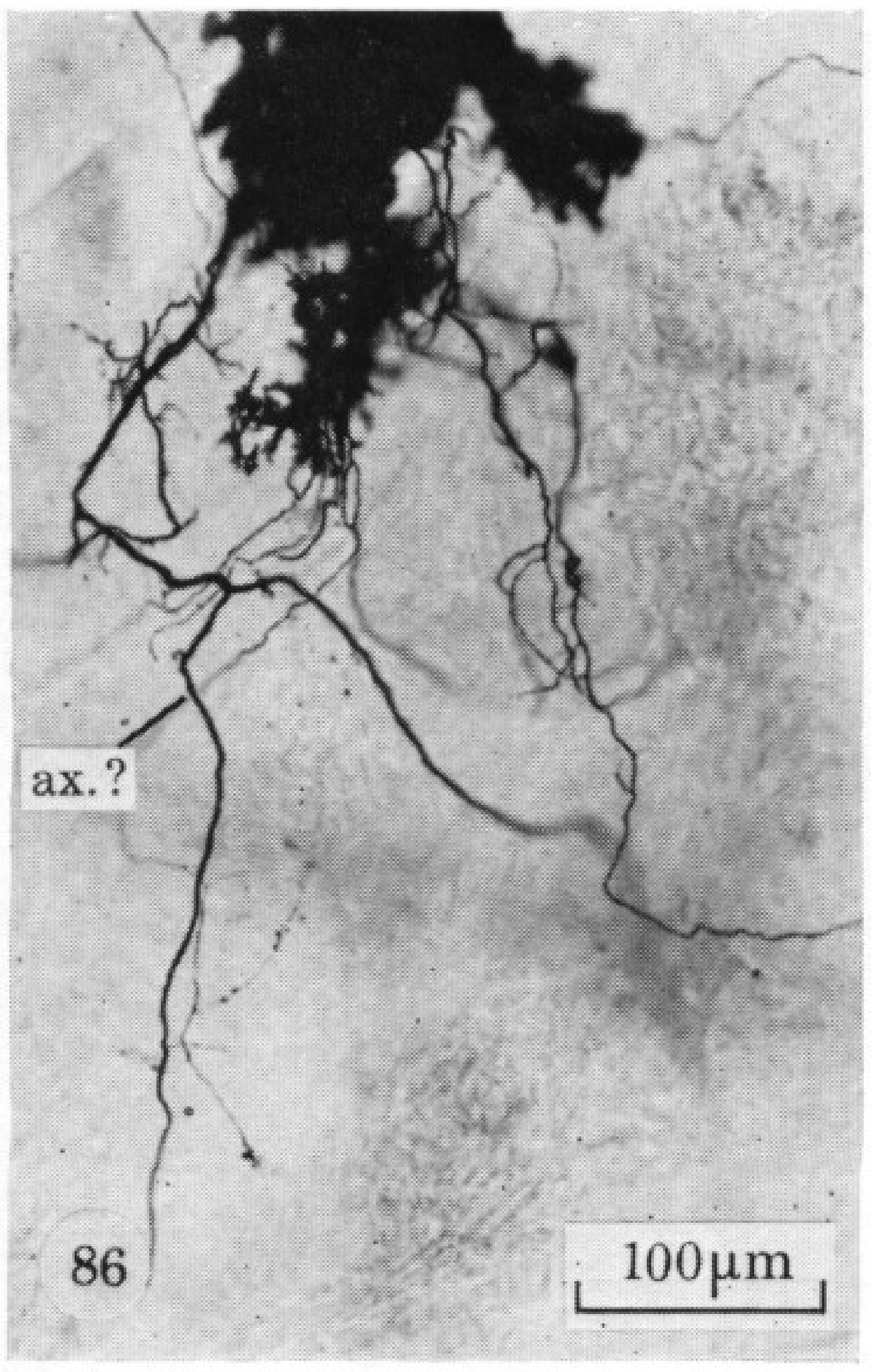
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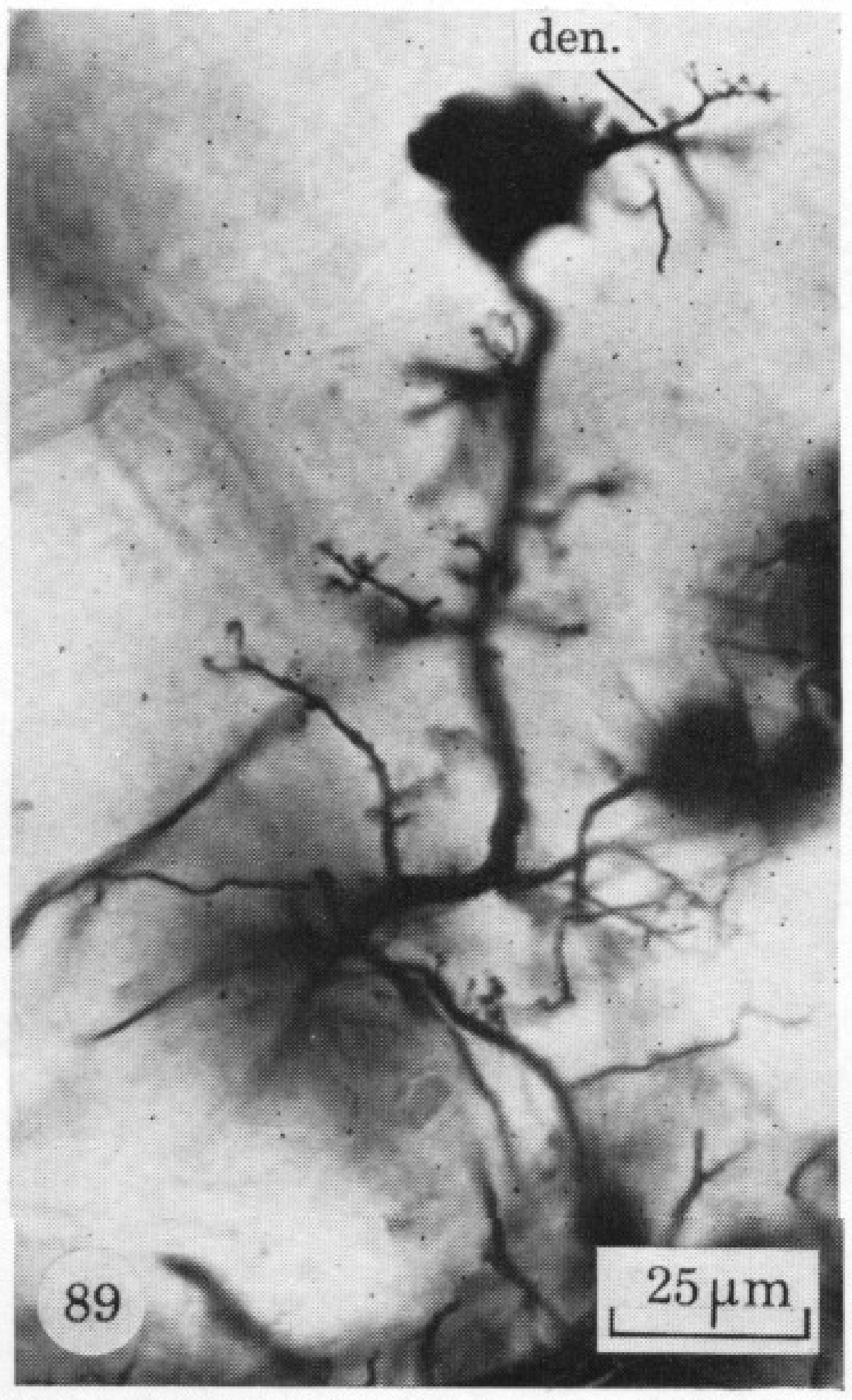
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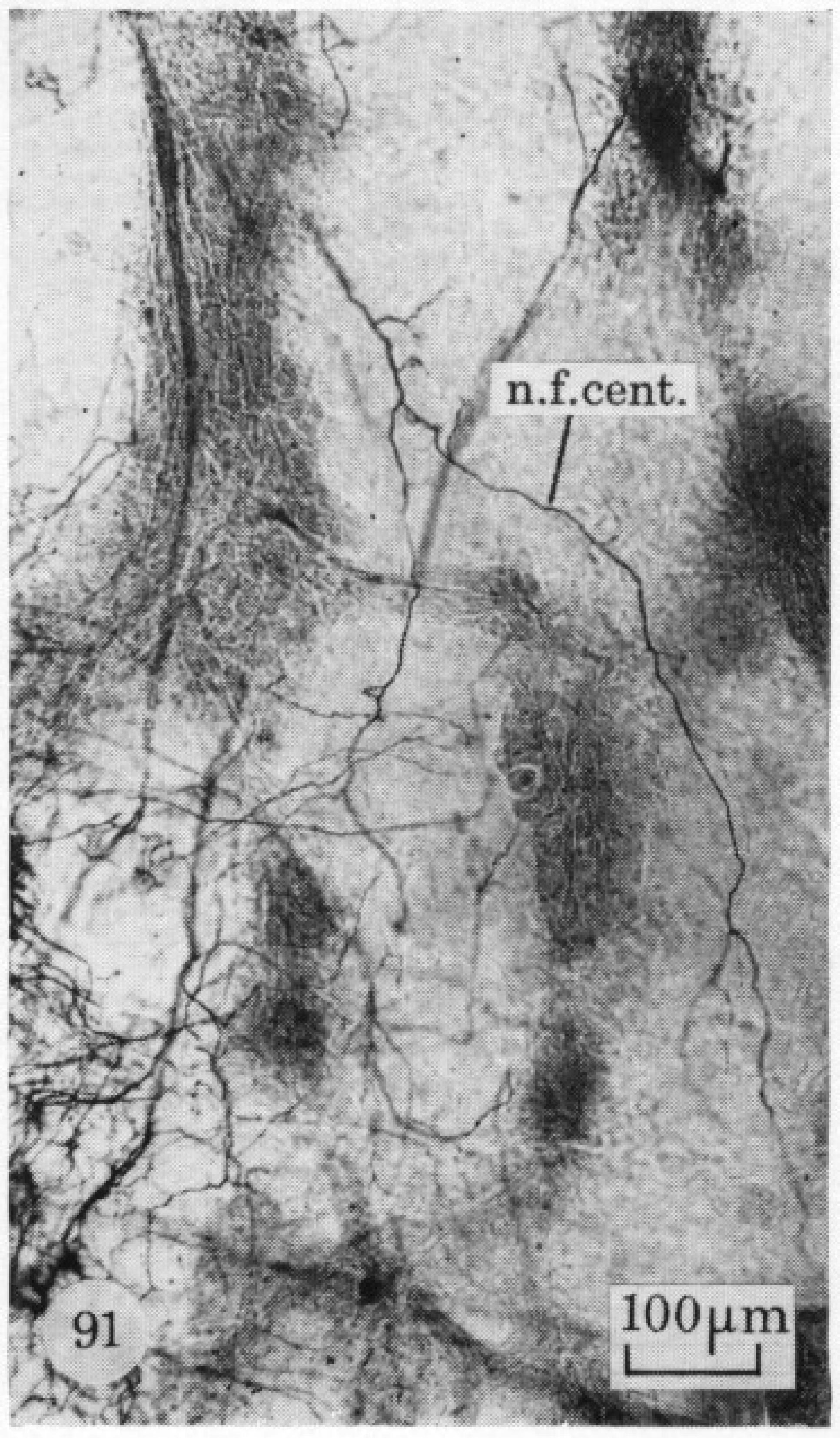
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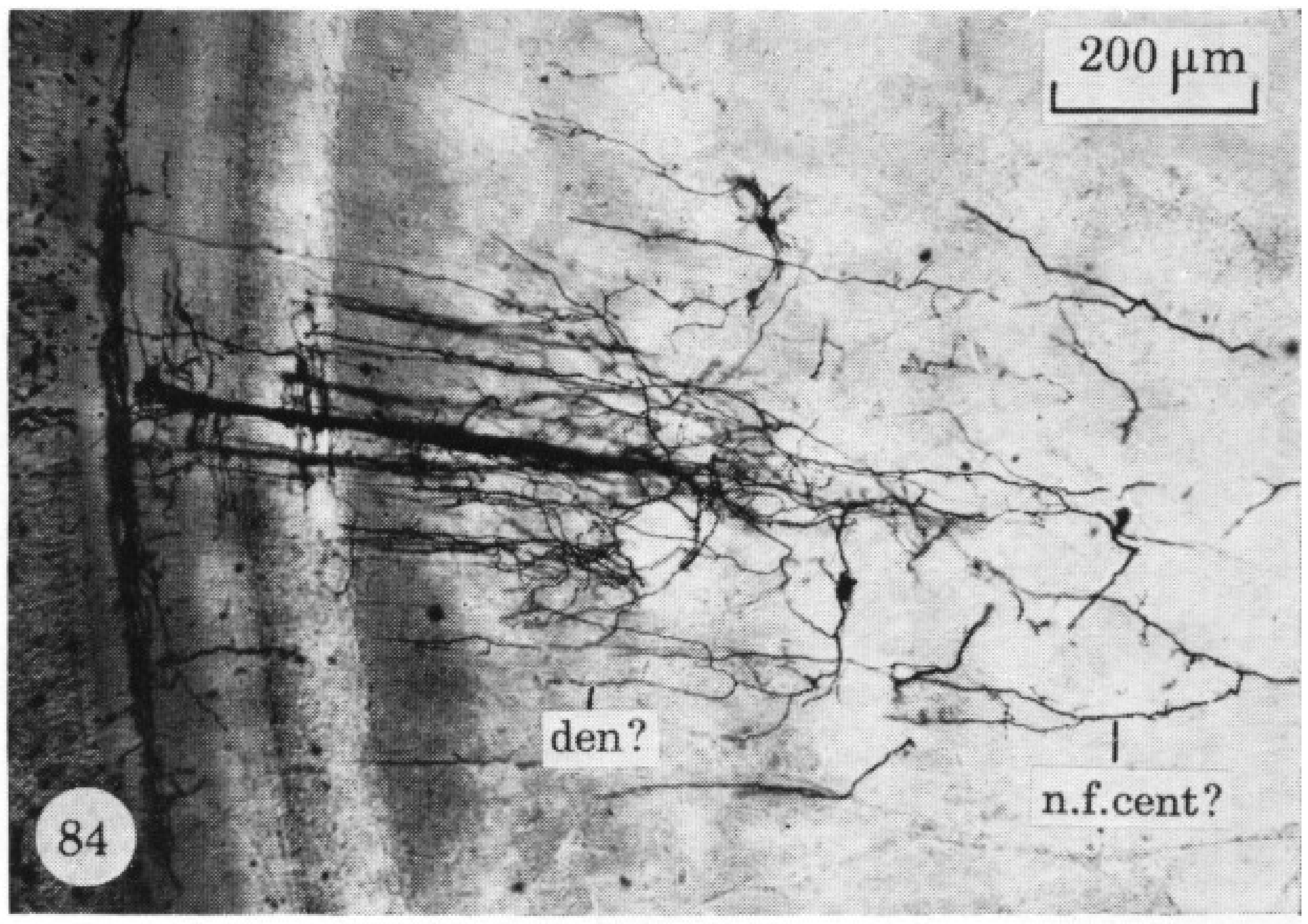
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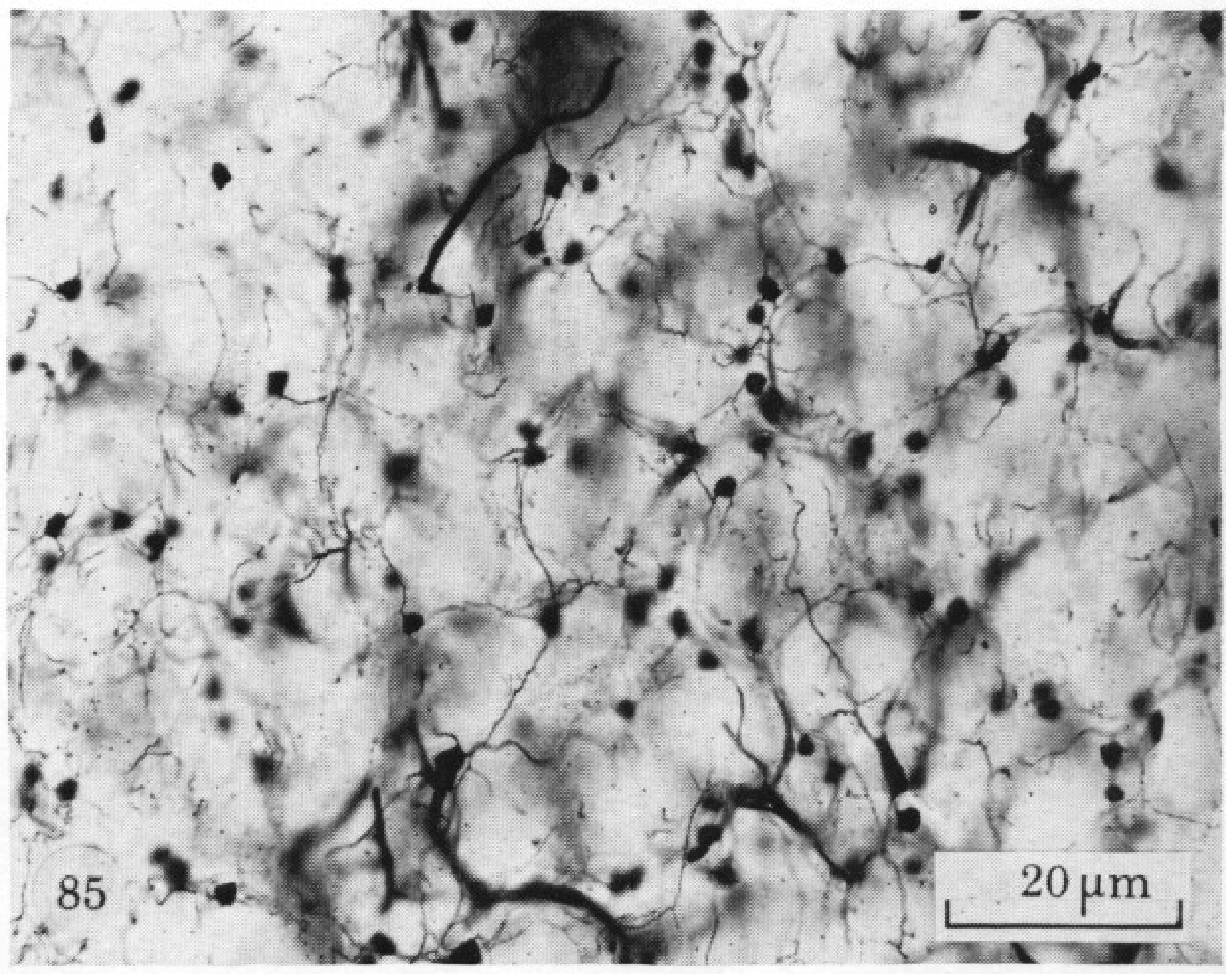
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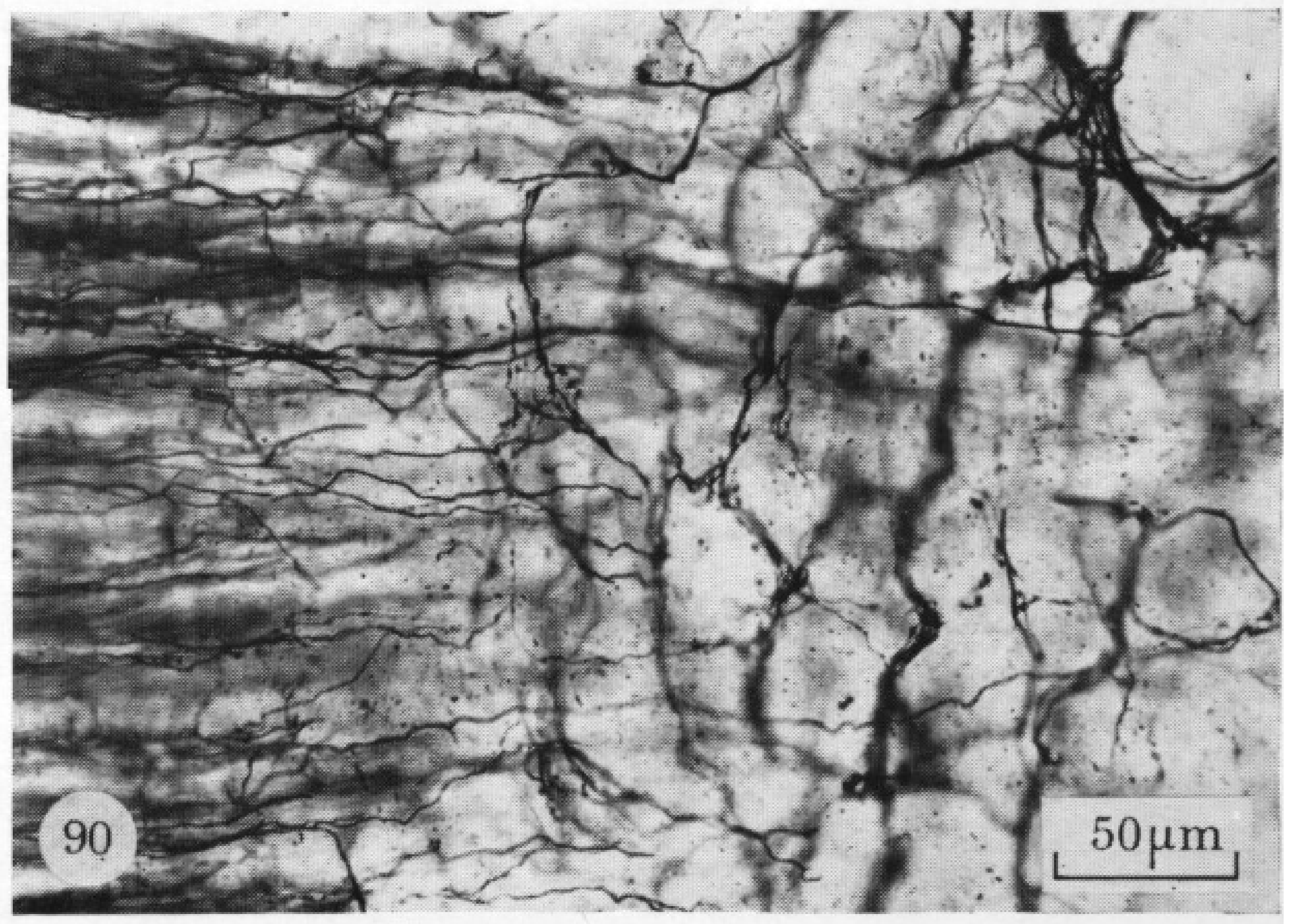
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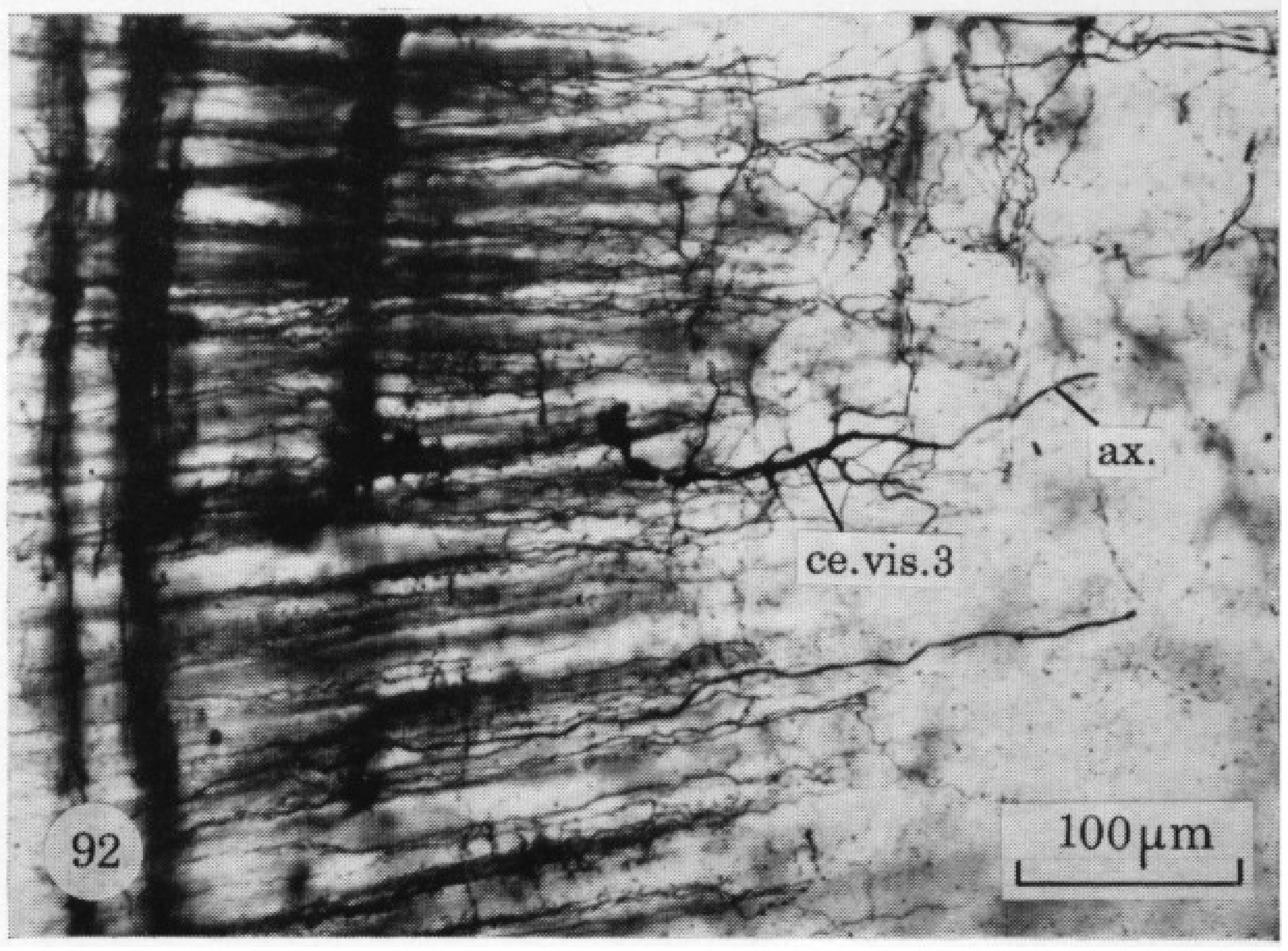
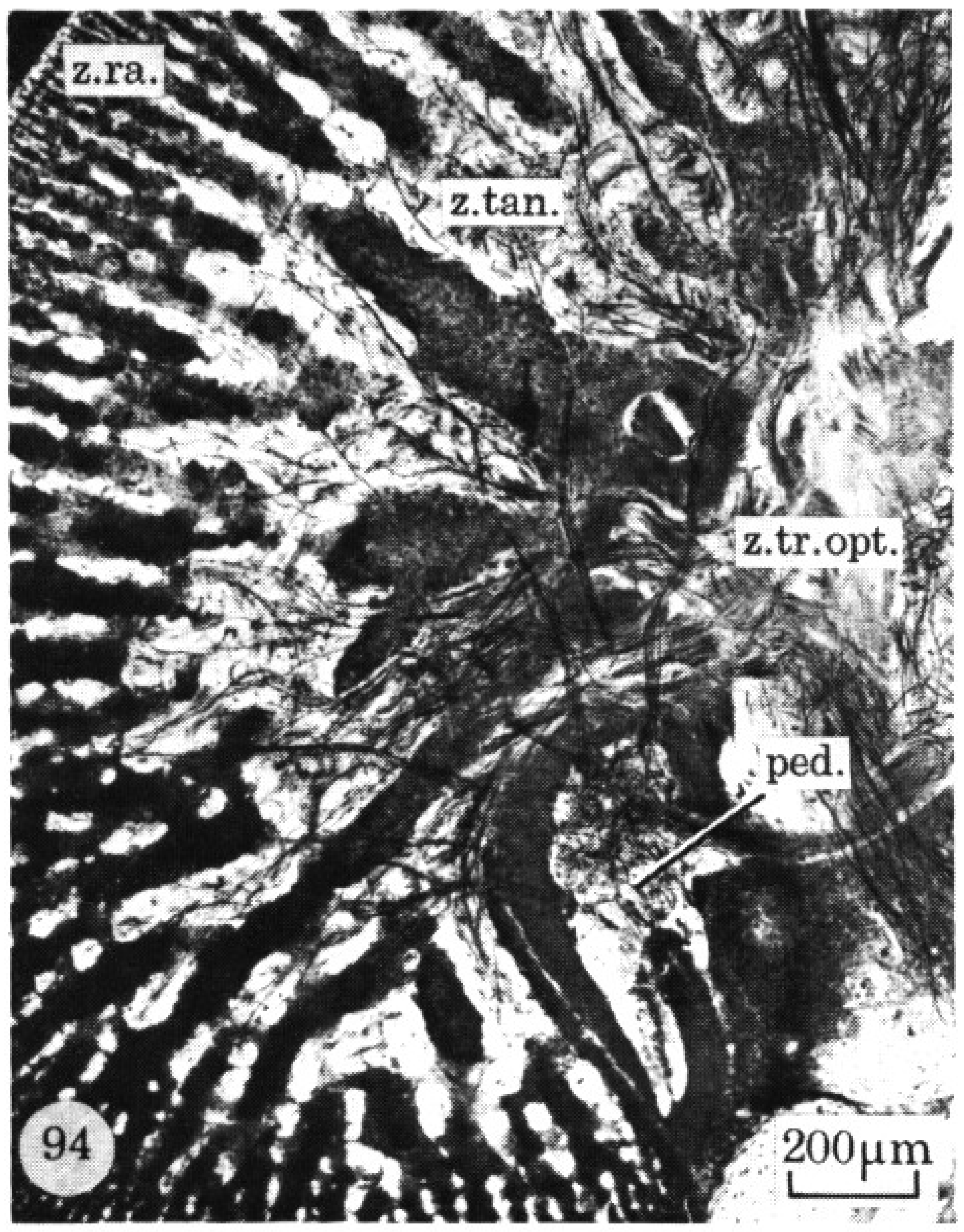
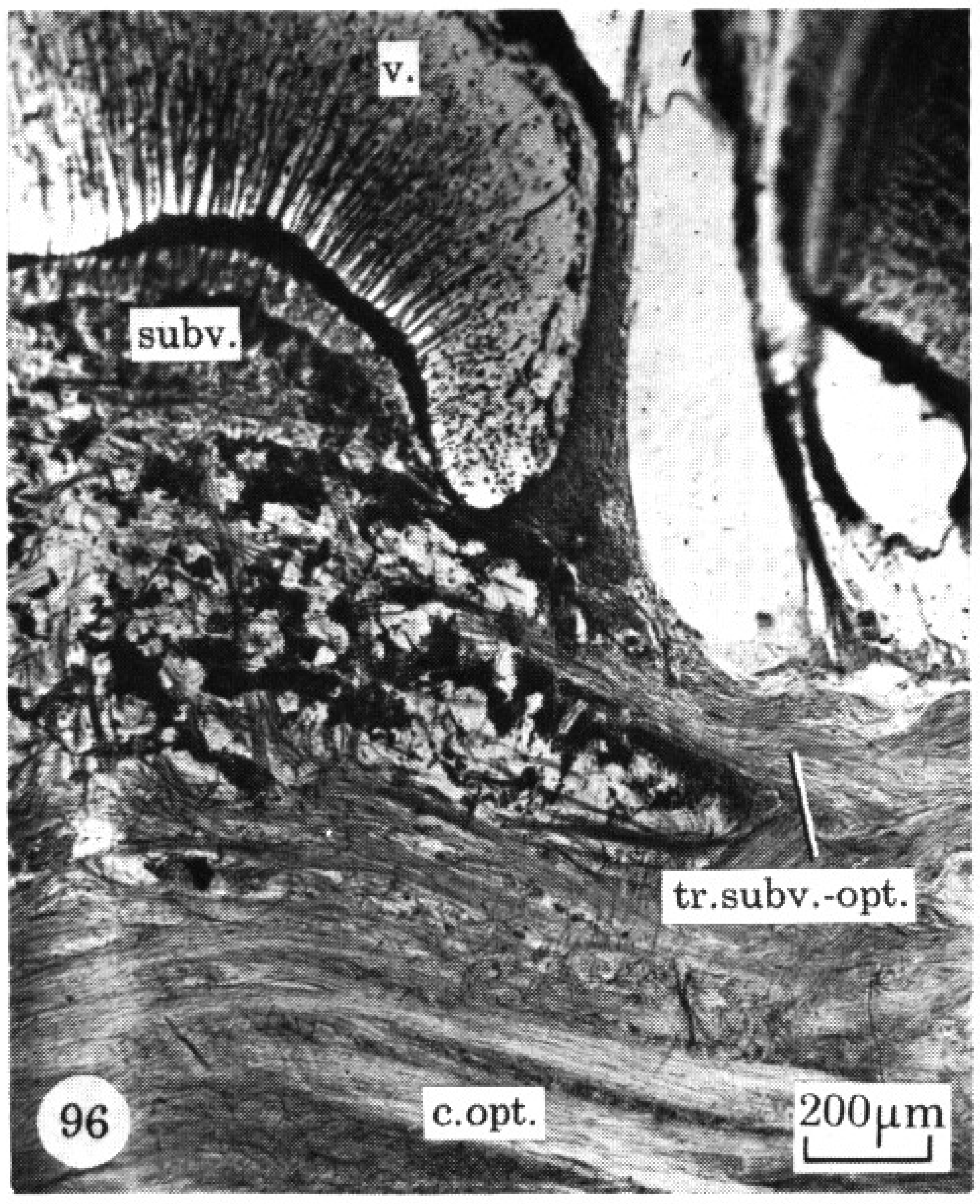
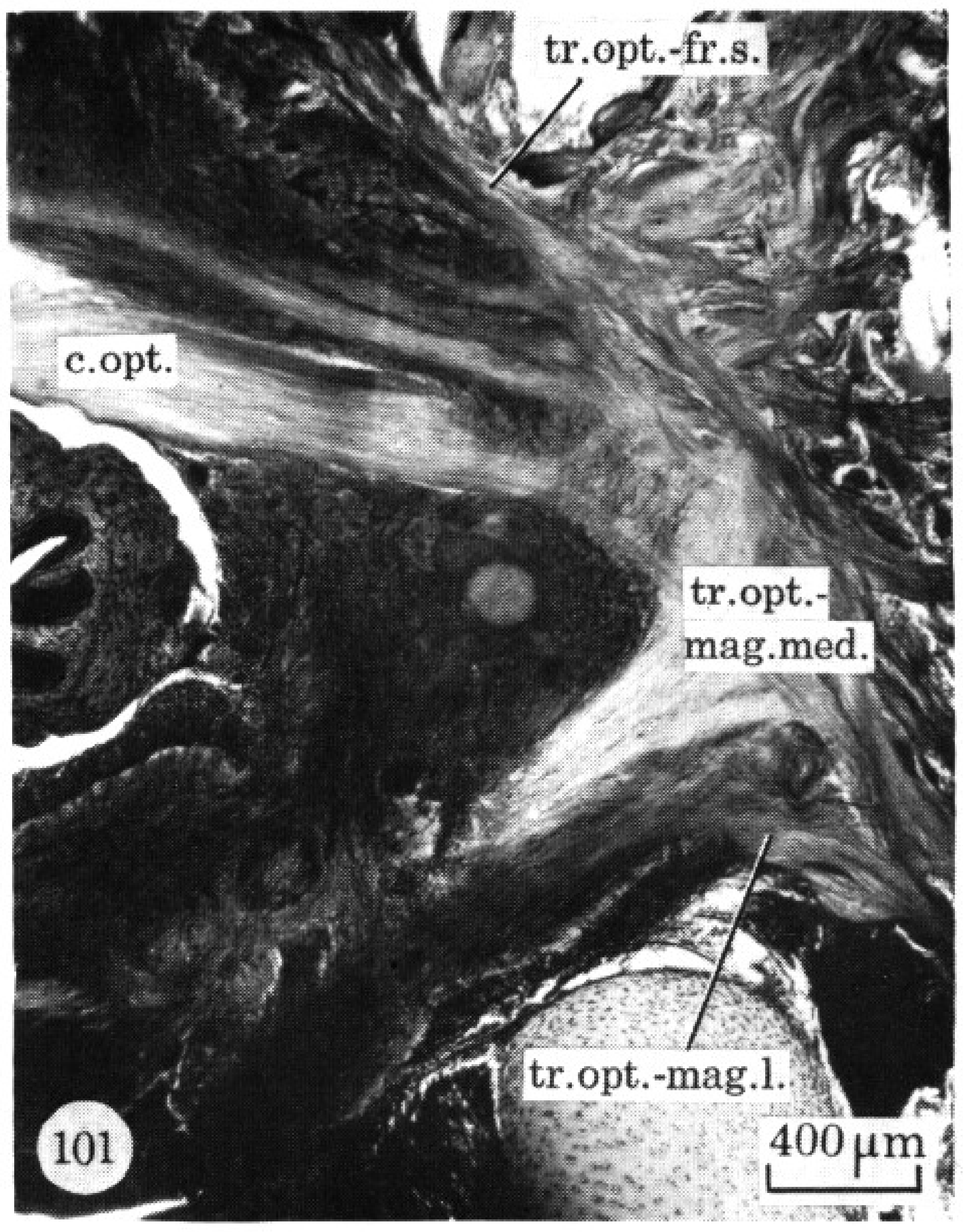
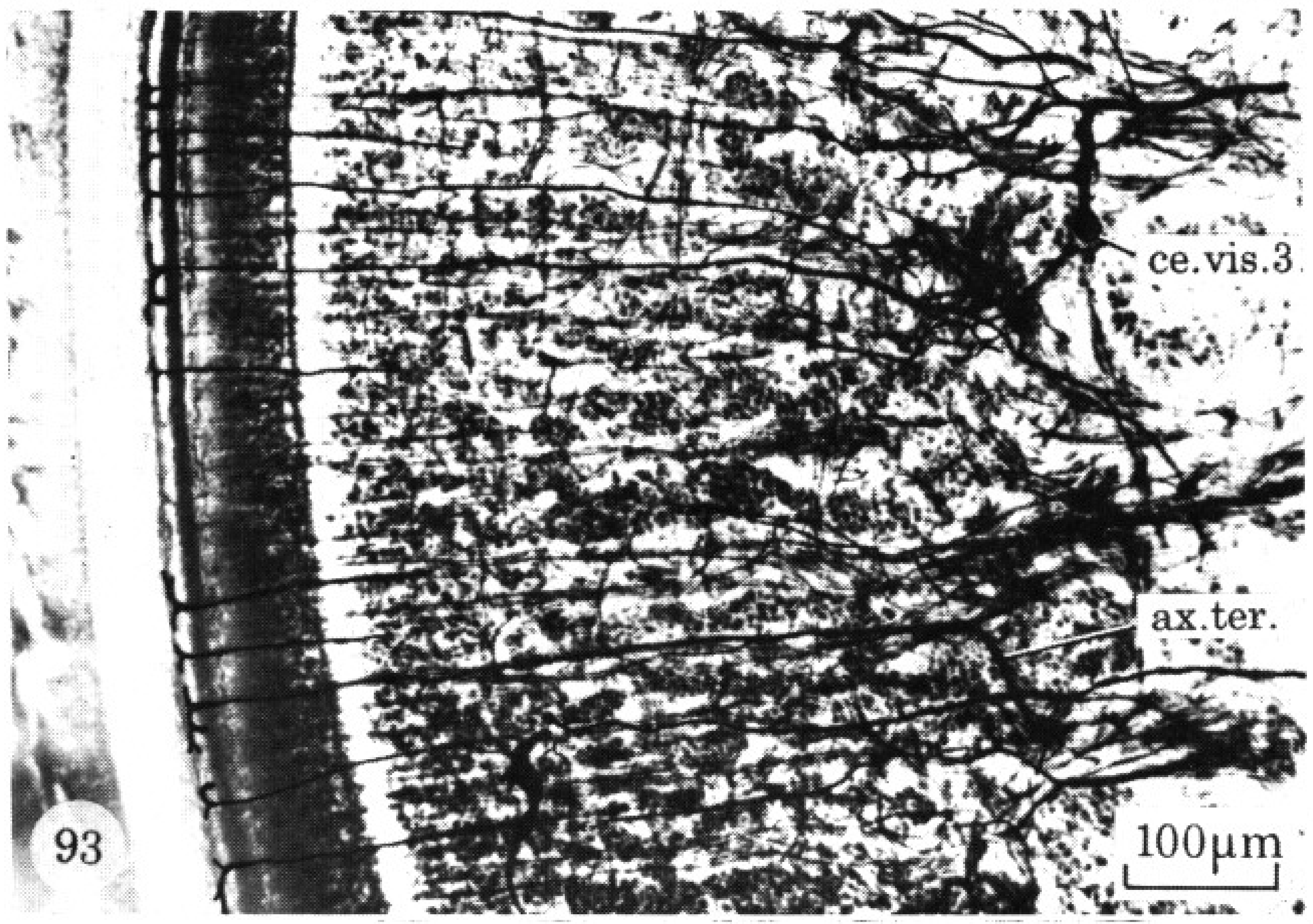

92

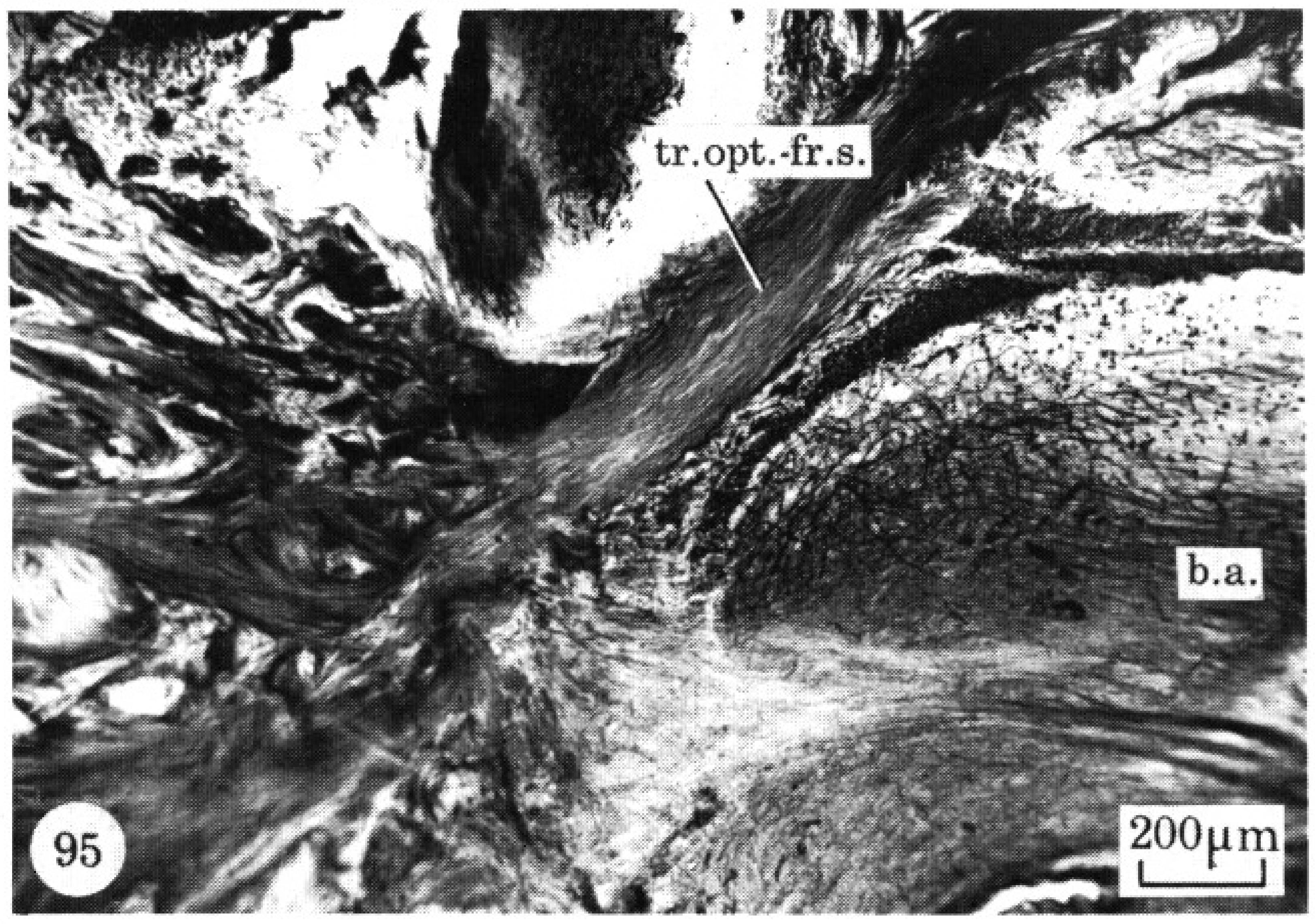
FIGURES 82–92. For description see opposite

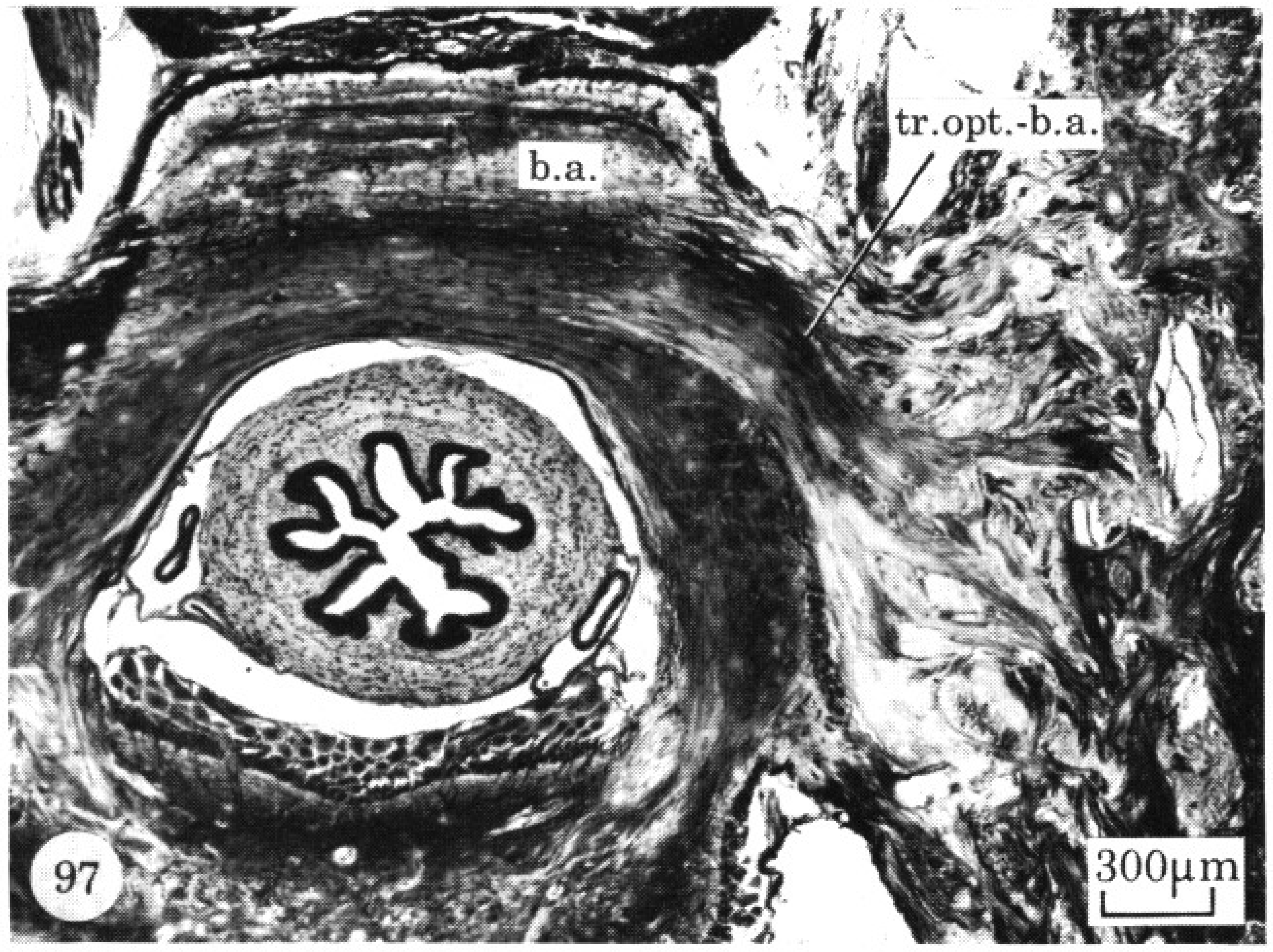


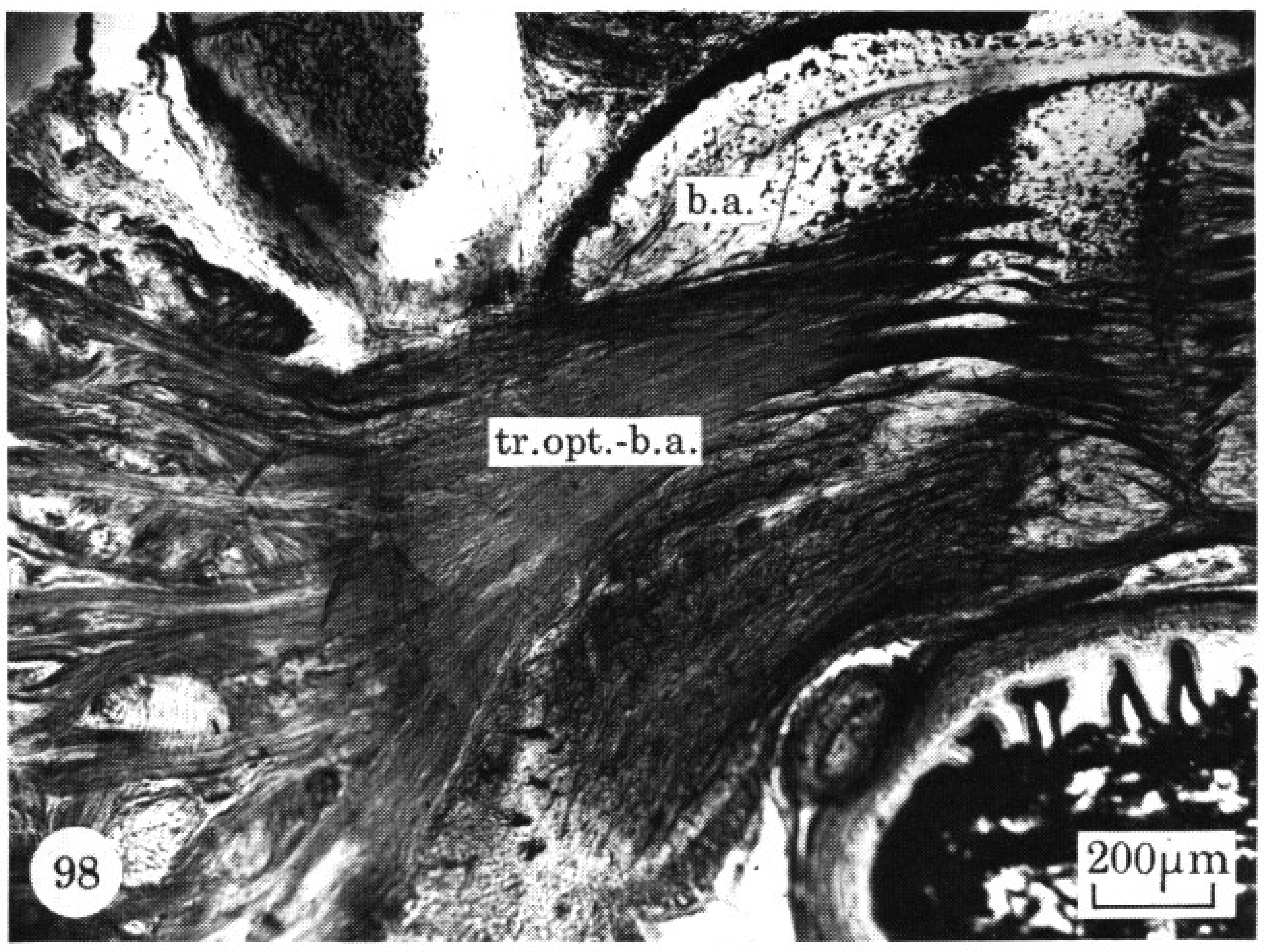


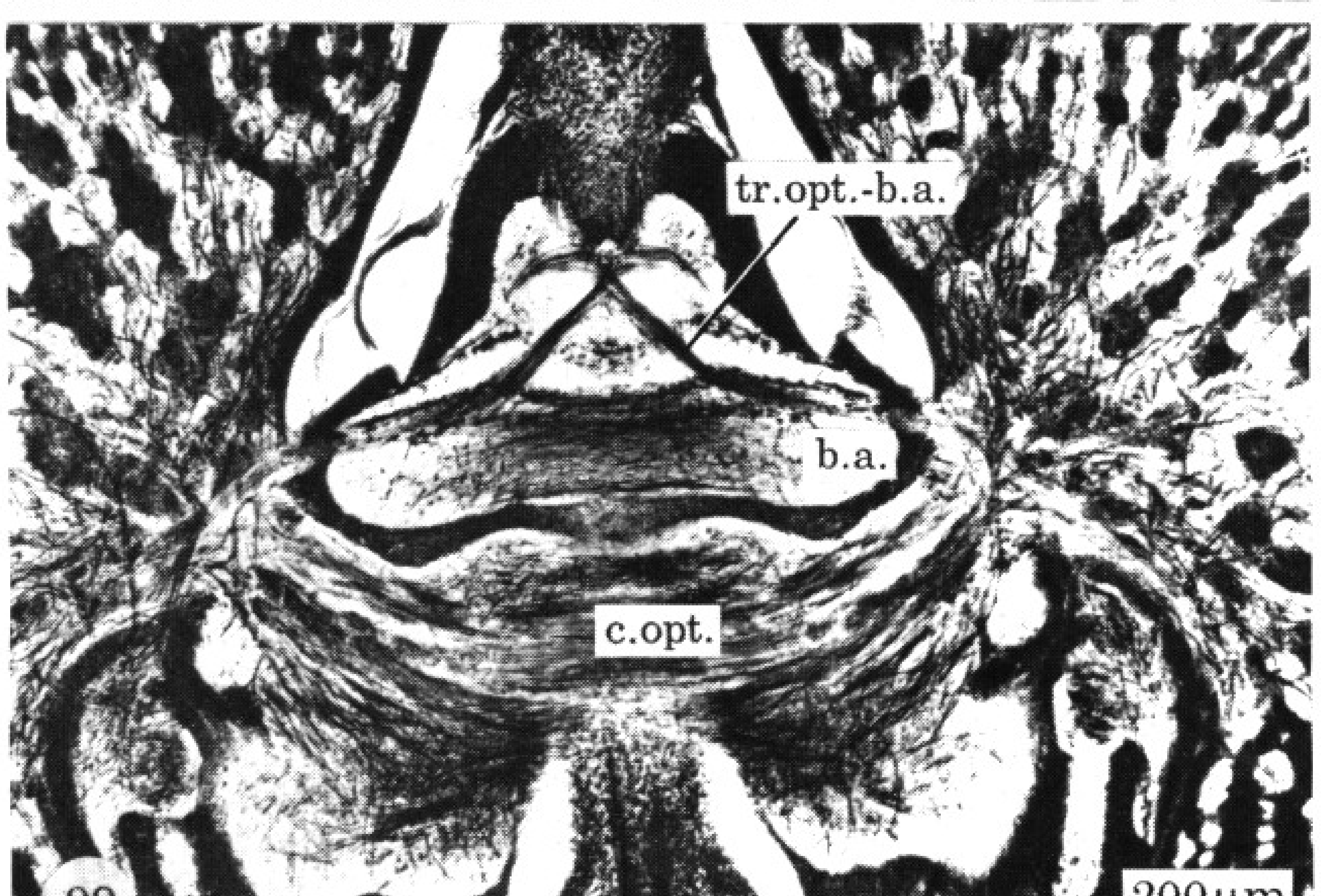


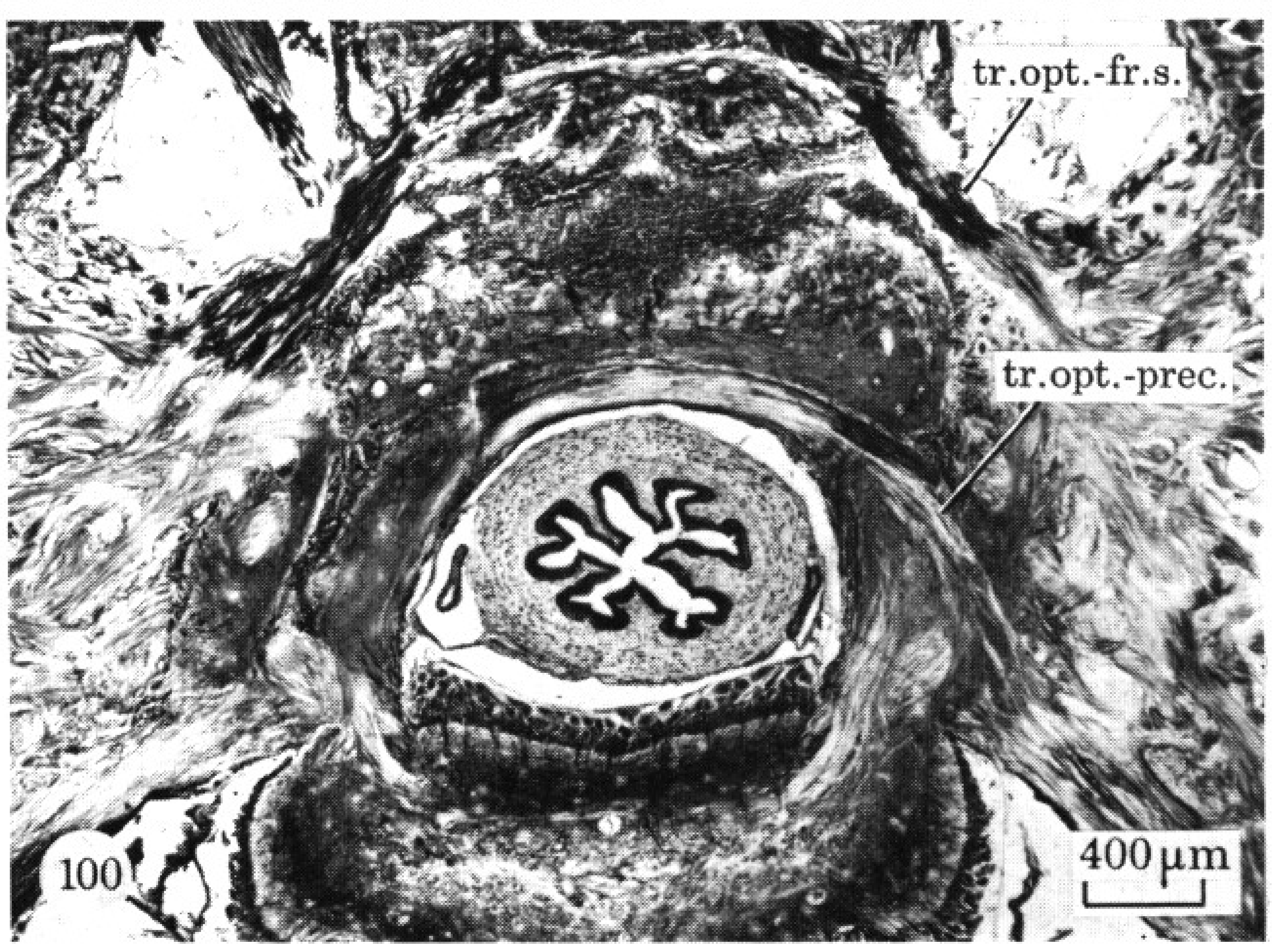




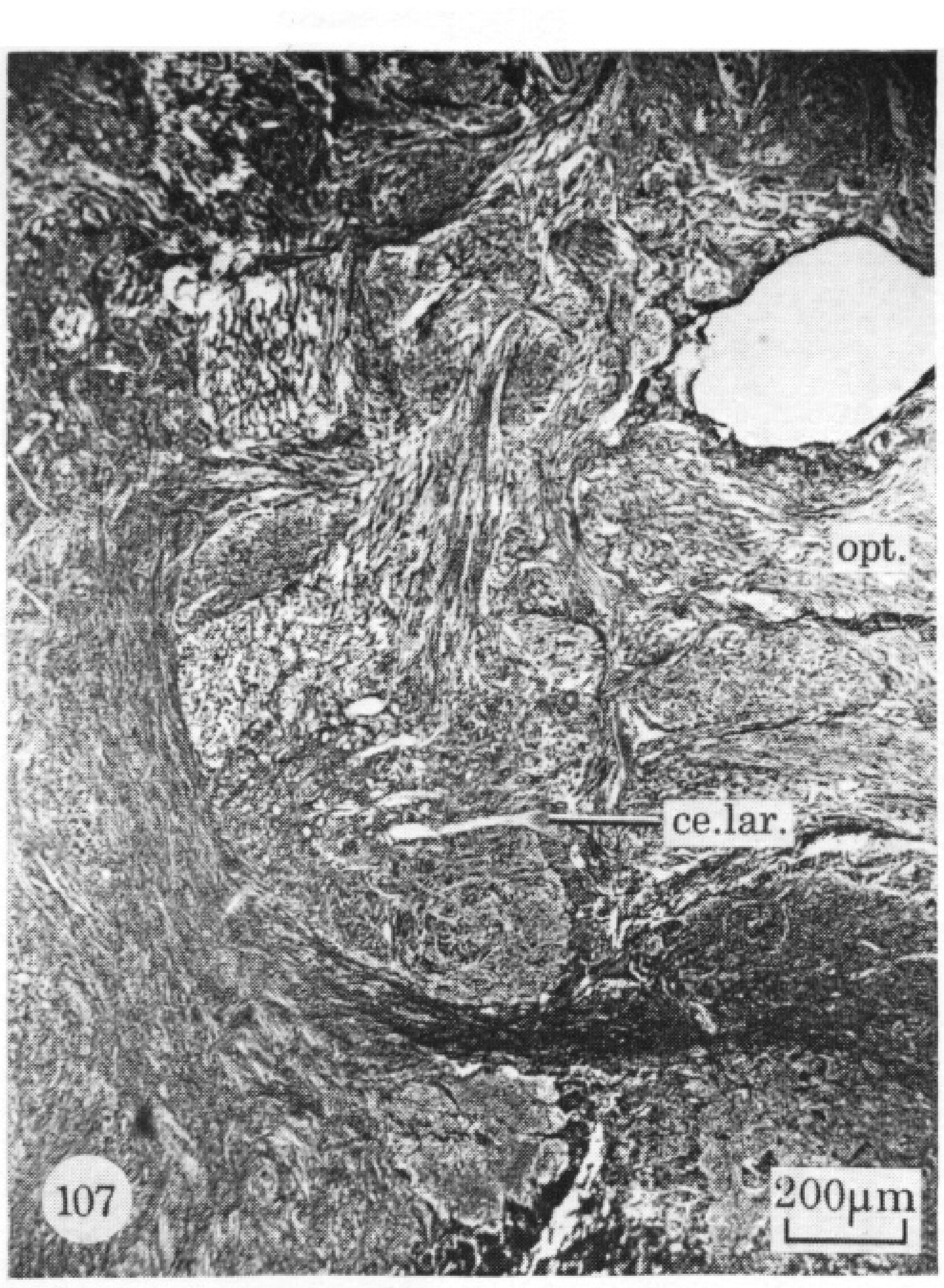


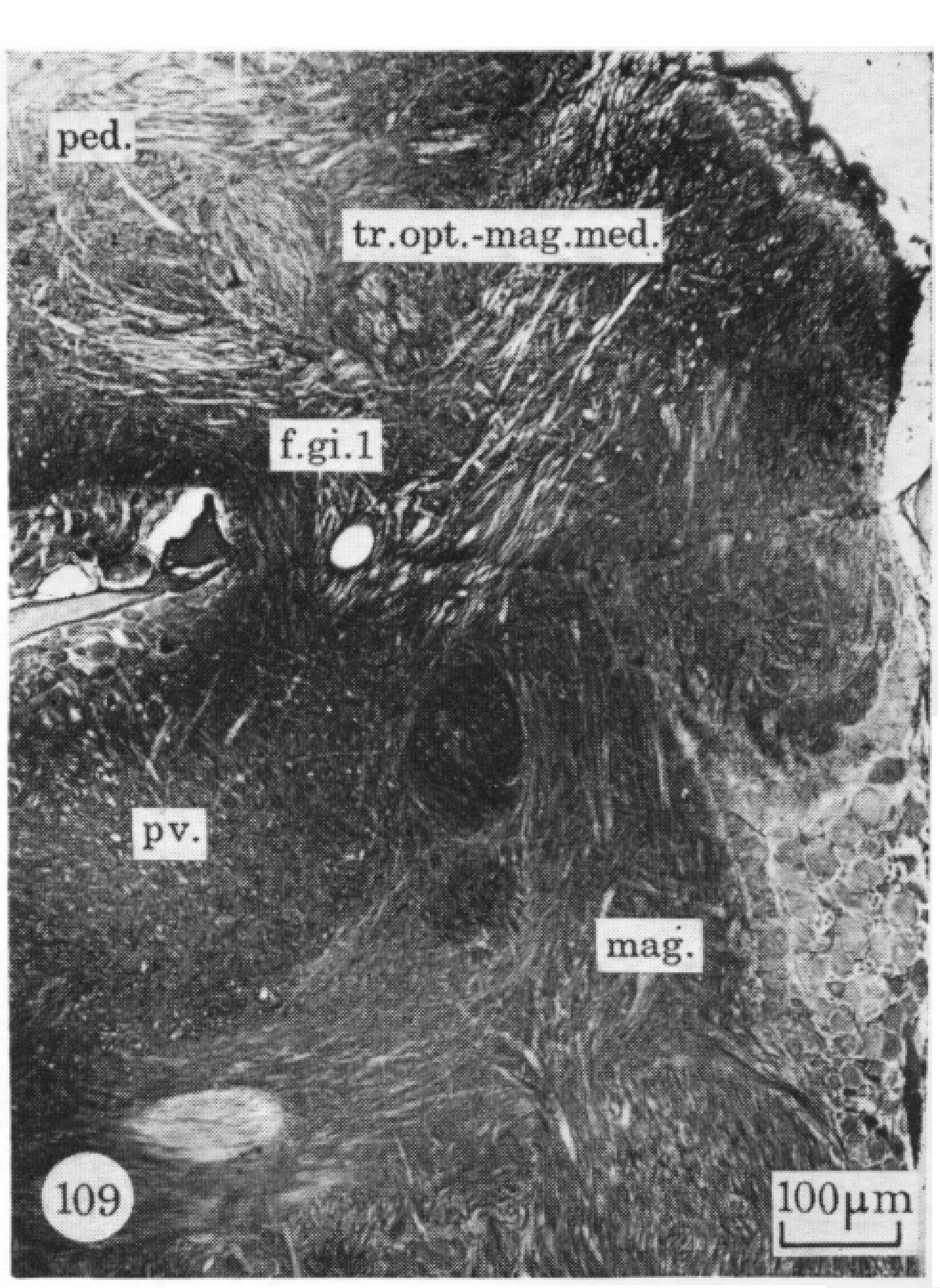


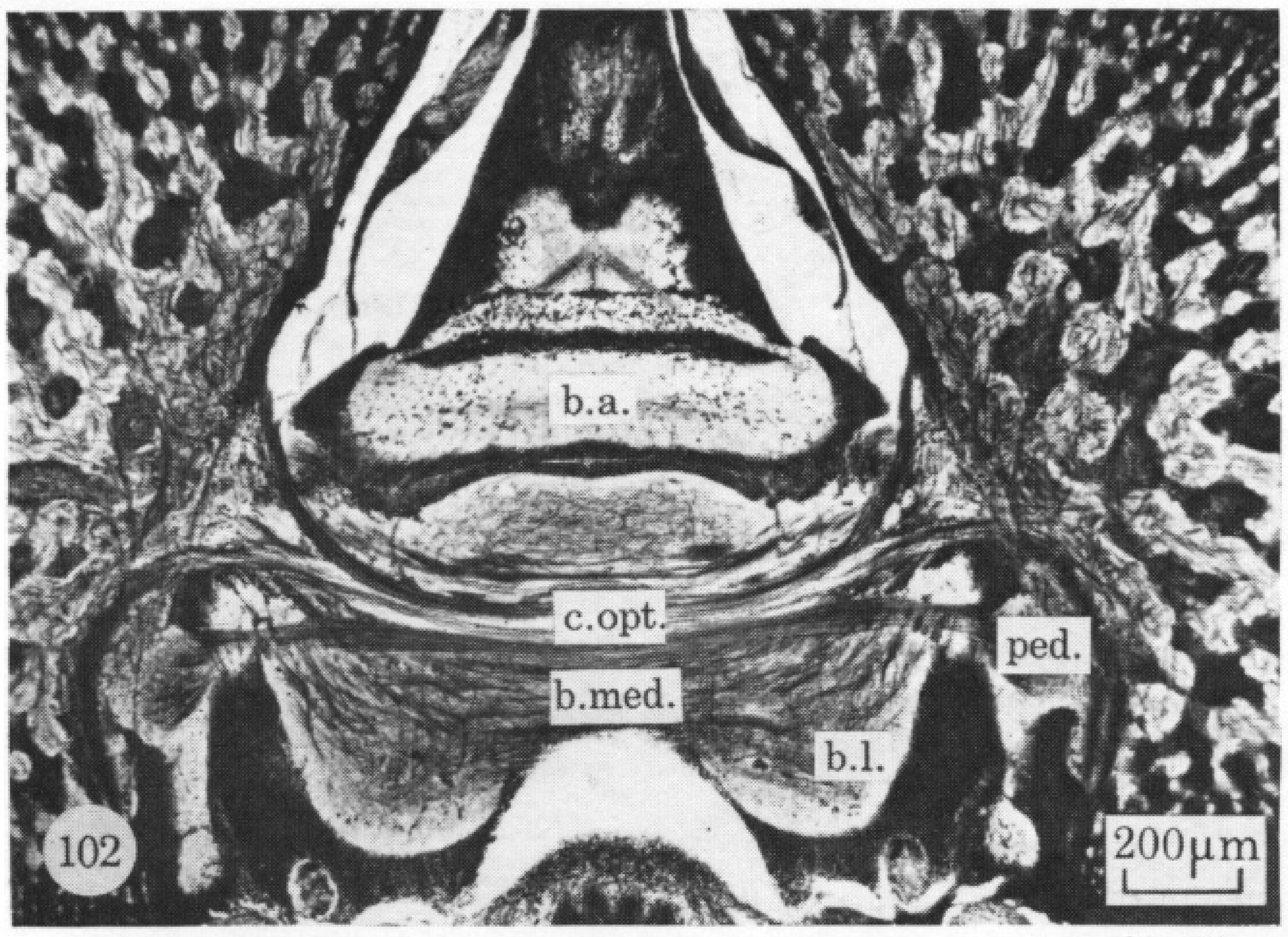


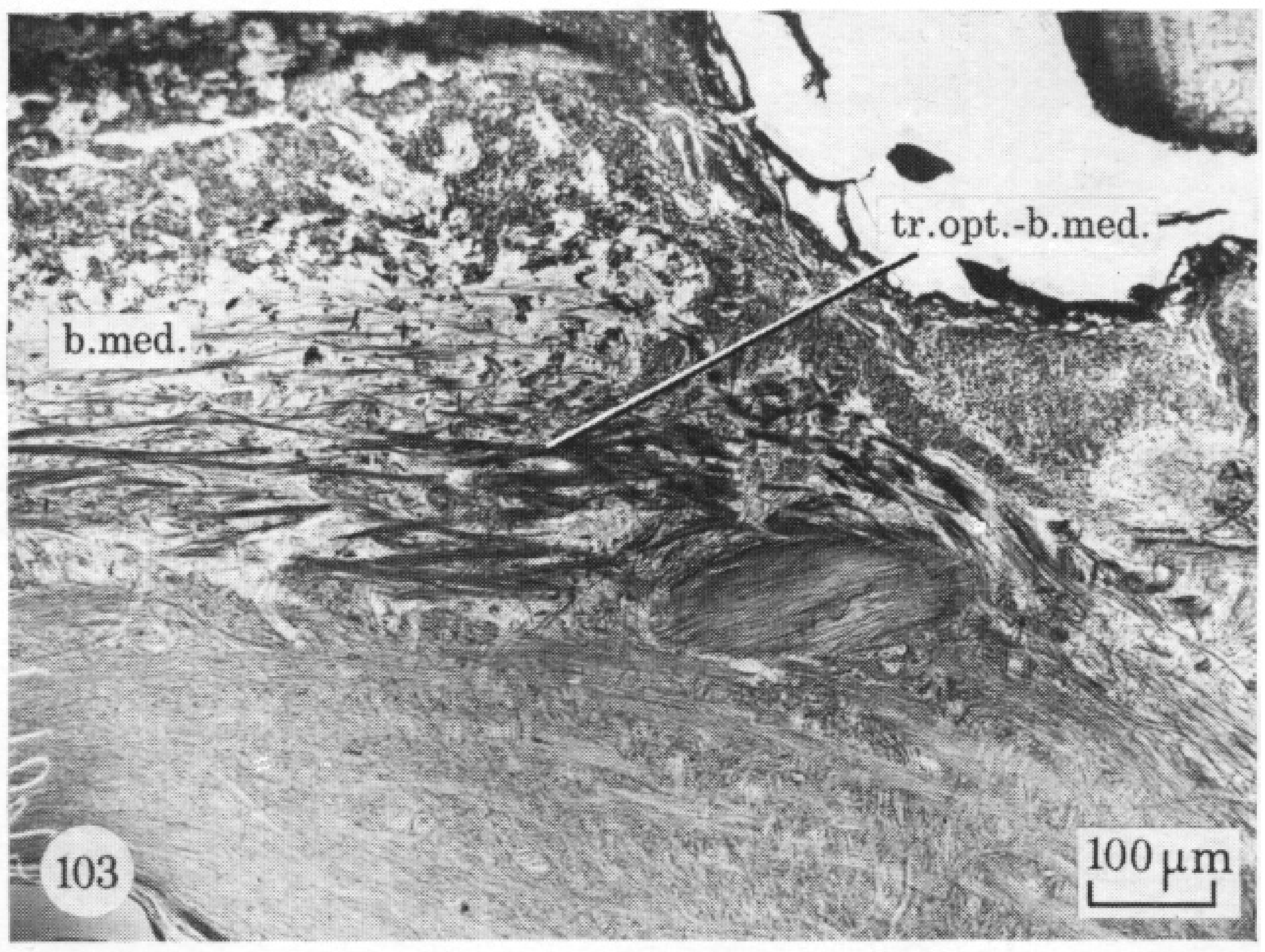


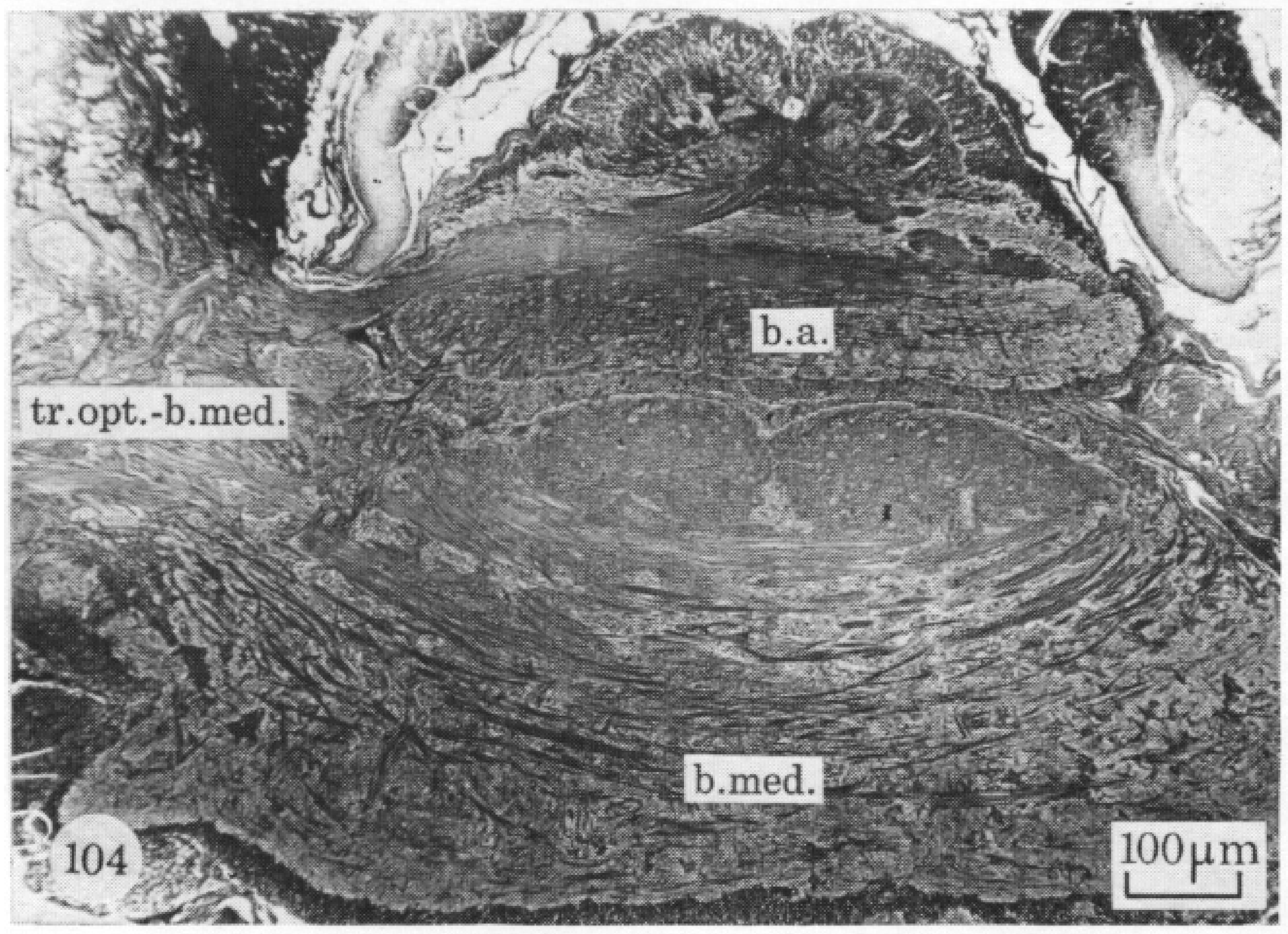
FIGURES 93–101. For description see opposite

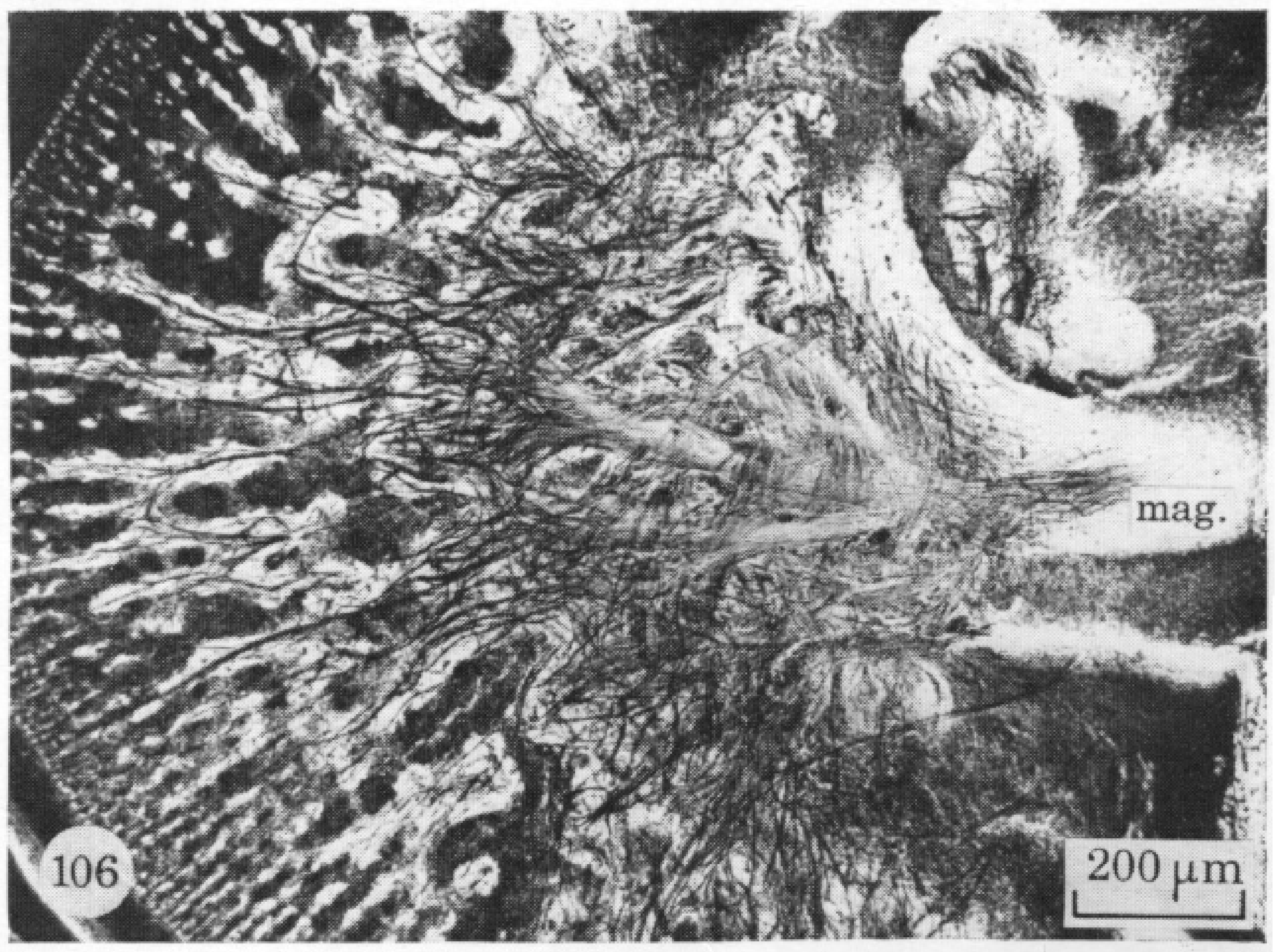


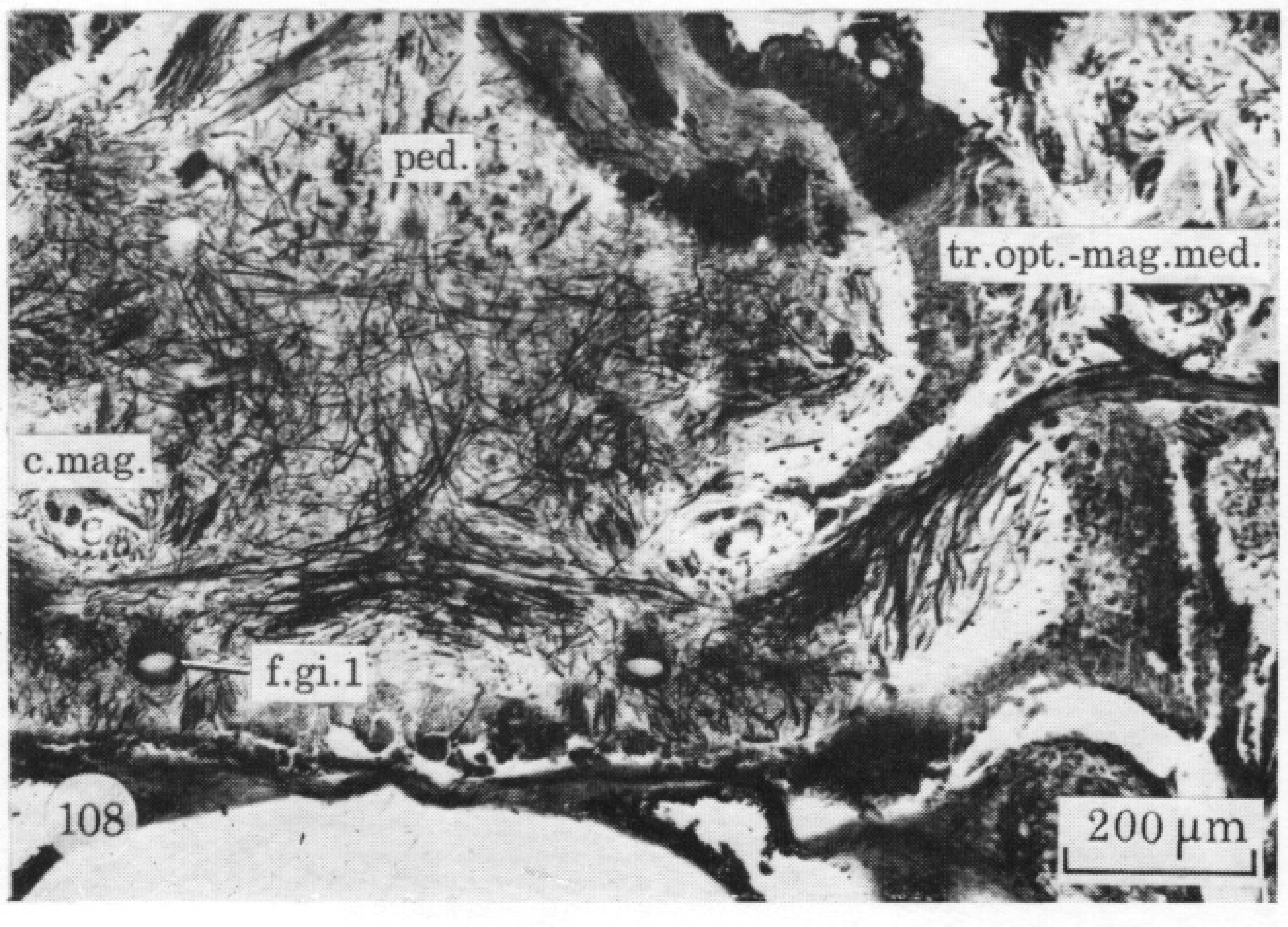


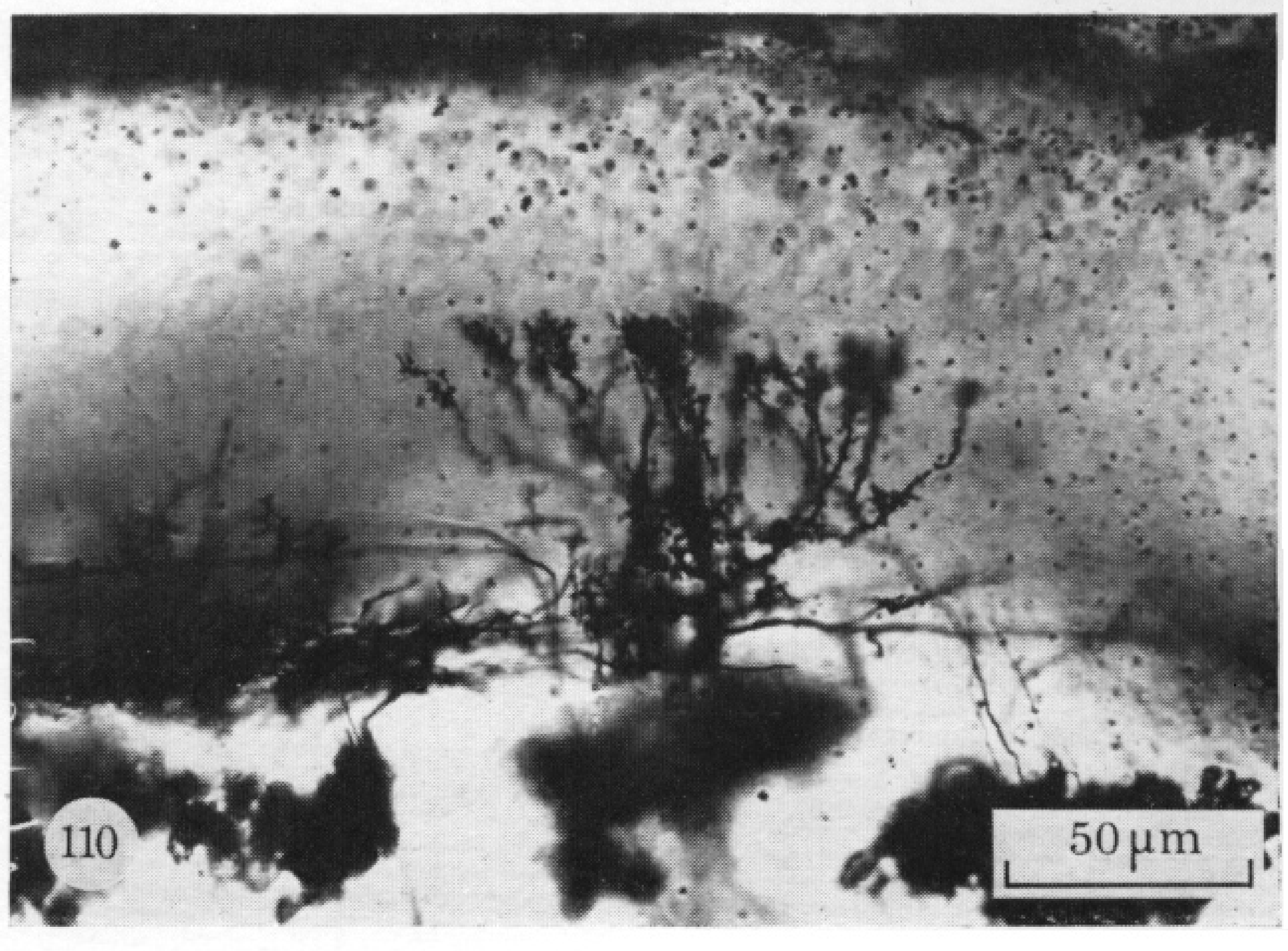












FIGURES 102–110. For description see opposite