GOLGI STUDIES ON INSECTS
PART II. THE OPTIC LOBES OF DIPTERA

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The optic lobes of Diptera have been examined by variants of the Golgi-Colonnier selective staining techniques and by reduced silver procedures. All, bar one, of the elements described by the earlier authors (Vigier 1908; Zawarzin 1913; Cajal & Sanchez 1915) have been seen, in part or in their entirely, in these preparations. Many other forms, hitherto unrecognized, have been found. Their perpendicular topographical relationships have been reconstructed in the optic lobe regions. Some lateral relationships have also been reconstructed between elements in regions whose columnar arrangement is clearly discernible in Golgi preparations; these include the lamina and the medulla. In the Diptera the projection pattern of the retina mosaic into the lamina neuropil involves complex chiasmata between the two regions (Braitenberg 1967); these have been confirmed from these species. The retina–lamina mosaic is, essentially, homotopically preserved in the columnar medulla, via long visual fibres and monopolar cells. The medullary mosaic is preserved through its strata by transmedullary cells and the longest small-field amacrine cells. The mosaic is projected to the two regions of the lobula complex by class I cells (see part I). The organization of the tangential cell processes suggests that some of them may interact with large or whole field aggragates of the relayed retinal mosaic. Others, especially in the lobula, may interact with small oval or narrow strip-field aggragates. Although there are many differences of neural form and number of neurons between species, both the Lepidoptera and Diptera have the same fundamental plan of neuroarchitecture.

INTRODUCTION

The Diptera have been the subject of much of the research on the insect visual system. The Calliphorinae, in particular, have been used for electrophysiological, optomotor and optical studies (see reviews by Bullock & Horridge 1965; Goldsmith 1964; Burtt & Catton 1966; and works by Autrum & Stumpf 1953; Autrum & Burkhardt 1961; Burkhardt, De La Motte & Seitz 1966; Bishop & Keehn 1966; Kuiper 1962, 1966; Fermi & Reichardt 1963; Götz 1964; Langer 1967 *a*, *b*; Kirschfeld 1965, 1967; Kirschfeld & Franceschini 1968; Miller, Møller & Bernhard 1966; Seitz 1968; Scholes 1969). Recently the outermost geographical region of the optic lobe, the lamina and the retina have been studied by light and electronmicroscopy (Braitenberg

1966, 1967; Trujillo-Cenoz & Melamed 1966). Many of the observations in the histological studies of Cajal (1909, 1910) and Cajal & Sanchez (1915, 1921) were derived from preparations of Diptera, in particular *Musca*, *Tabanus* and *Calliphora*. Other workers using non-selective silver impregnations have described some of the gross features of the optic lobes and the mid-brain regions (Power 1943*a*, *b*; Larsen 1966).

The preceding paper (part I) described the morphological features and some topographical relationships of three classes of neurons of two species of Lepidoptera. This study is extended here to include five species of Diptera; *C. vomitoria* L., *C. erythrocephala* Miegen., *Eristalis tenax* L., *Syrphus nitidicollis* Miegen., and *Syrphus elegans* Harris. Some individuals of *E. pertinax* L. and *S. torvus* Osten Sachen. were also stained. The two species of *Calliphora* were chosen in order to compare the neural architecture of two closely related Diptera and to check Cajal & Sanchez's original observations. The neuro-anatomy of the Syrphidae has not been previously recorded but some behavioural characteristics are known; they have a distinctive flight (Colyer & Hammond 1968; Coe 1953; Buckton 1895) and the phototactic behaviour and colour discrimination of some species has been studied (Dolley & Wierda 1929; Dolley & Golden 1947; Ilse 1949; Mittlestaedt 1949, 1951; Von Holst & Mittlestaedt 1950). However, they have been relatively neglected as experimental animals. These species are excellent histological material which stains remarkably consistently; they have little musculature in the head, and have large firm brains and relatively large neurons compared with the two species of *Calliphora*. Possibly they could provide ideal material for quantitative behavioural and electrophysiological studies as well as for further anatomical investigations.

The terminology used in this account is that adopted previously (part I). Any additions to it are made in the relevant sections. The terms 'ascendent' and 'descendent' mean, respectively, that the course of a process is either directed peripherally or centrally within a region with respect to its origin.

Cajal & Sanchez's (1915) account is again referred to simply as Cajal & Sanchez, without date; likewise for Zawarzin's (1913) account. In addition to the Spanish authors' main thesis a summary was published by Cajal (1915) and an account conjointly by Cajal & Sanchez (1921).

Materials and methods

The techniques of selective and reduced silver impregnation have been described in the preceding paper (part I). Colonnier's (1964) method works especially well on the Syrphidae giving beautifully clear impregnation of the neural elements of both the optic lobes and mid-brain regions. Even old over-wintering *Eristalis* are receptive to this method. The two species of *Calliphora* are more difficult to stain; in particular the main tracts of fibres between the optic lobe regions are often congested with dense crystalline deposits. These artefacts can be overcome in about 50 % of the preparations by reducing the concentration of the impregnating bath to 0.5 % silver nitrate in distilled water. The temperature of fixation and impregnation is especially critical in these species and must remain at 20 °C. In the author's experience smaller species of Diptera such as *Musca* and *Drosophila* are very difficult or impossible to stain so that several whole neurons can be visualized in their entirety in a single section.

Potassium dichromate can be replaced by ammonium dichromate for *Syrphus nitidicollis* but not in the other species: similar substitutions of dichromate salts have been described by earlier workers using Golgi procedures on vertebrate tissue. (Romeis 1948; Gatenby & Painter 1937)

Glyceraldehyde and paraformaldehyde have been found to give reasonably good fixation in the species of *Calliphora* but are no better than gluteraldehyde. Celloidin-embedded preparations were cut serially at either 60, 80 or 100 μm.

Photographs were taken on Adox KB 1435 mm film, on Ilford FP4 or Kodak microfile film, with a Zeiss Photomicroscope and developed in D.76. Blue, red and mauve Wratten filters were used to procure greater contrast in the case of some non-selective silver preparations. Nomarski interference and Zernicke phase-contrast illumination was used with thin Golgi stained sections to relate stained elements to their respective columns in the lamina or medulla. Drawings were made with the aid of a camera-lucida and a calibrated, squared eye-piece graticule on a Vickers M15C microscope. Measurements were made with a Vickers Filar micrometer eye-piece or a Zeiss or Watson graduated graticule.

The general features of the preparations and their interpretation

Interpretations of Golgi-stained material have been extensively discussed in the preceding paper (part I), but some additional criteria need to be clarified here.

Crystalline deposits on the surface of the brain and within the outermost 5 to 15 μm of the neural tissue are characteristic of Golgi-stained material. The outermost perikarya in the cell-body cortex around the neuropil are occluded by these precipitates. In the Diptera, however, the outer segment of the first optic chiasma lacks this cortex (figure 105, plate 23) and the crystalline deposits may extend into the chiasma itself and may sometimes obscure components in it. It is therefore necessary to define the conditions which allow discontinuous elements to be reconstructed and matched together. (1) A linking-fibre may be traceable up to and beyond a few overlying and semi-transparent crystals lying against a clear unimpregnated background; both 'pre-' and 'post'-crystal components are obviously continuous. (2) An array of components in the lamina may be traced part of the way across the chiasma before they are occluded, and so indicate the approximate positions at which their medullary endings should lie. The medullary array can often be correlated with the peripheral components in the lamina. For example, if a horizontal array of three radial monopolar components and one midget monopolar component in the lamina proceed (via the first optic chiasma) to an array of one dissimilar and three similar endings in the medulla, then it is likely that the former ending belongs to the midget monopolar cell and the others to the radial monopolar cells. (3) Some cell-types have linking-fibres with characteristic forms and sizes. Discontinuous distal and proximal fragments of these in the inner segment of the chiasma can sometimes be matched together by these features.

Reconstructions from the first method cannot be defeated. Those of the second and third are not without flaws but the results obtained from the present species agree with those from the Lepidoptera where complete neurons can be traced between the two outer regions. They also agree with observations of the Spanish authors (1915) on *Tabanus* and *Musca* and with recent observations of *Calliphora phaenicia*, *Musca domestica*, *Apis* and *Libellula* (Strausfeld, unpublished and in preparation).

The columnar arrangement of the medulla and lamina can be distinguished in Golgi-stained material as well as in non-selective silver preparations and in fixed unstained material viewed with phase-contrast illumination. These columns are useful points of reference for the study of lateral topographical relationships between class I elements and the perpendicular components

of the amacrine cells and some class II processes. Each column consists of the continuation of a medullary cartridge (part I) through the serpentine and inner layers. The main components of the columns are described in greater detail in a subsequent section and are illustrated in figure 170. The columns are arranged in regular arrays throughout the medulla as are the axis-fibres of class I cells. Most of these cell-types have their lateral extents radiating equilaterally and radially or bilaterally from an axis-fibre at characteristic levels. The extent of the unilateral bias of some unilateral cell-types can thus be expressed as a lateral extent equivalent to a definite number of columns.

This study is primarily qualitative; its purpose is to illustrate the forms of neurons in the optic lobes and their topographical associations with one another. Sophisticated quantitative and microscopical procedures have revealed the subtleties of neuronal stratification and three-dimensional shapes of dendritic spread in the mammalian cerebral cortex (Sholl 1953, 1956; Ramon-Moliner 1961 i and ii, 1962; Mannen 1968, among others). In mammalian material it is possible to correlate the Golgi studies with cell-body locations revealed by other non-selective methods, since these have a direct topographical relationship with their dendrites and axons (see, for example, Sholl 1956). Nissl stains reveal the optic lobe cell-bodies but apart from in the lamina it is not usually possible to relate them to their corresponding neuropil components nor to distinguish characteristic features in them, such as, for example, the arrangement of Nissl granules. Studies of cell-body populations of the insect brain are useful in their own right (Farrell & Kuhlenbeck 1964) but they do not reveal the relative proportions of individual types of neurons. Some regions of the insect central nervous system do, however, have perikarya at specific loci; for example in the corpora pendunculata (Kenyon 1896; Barendrecht 1931; Vowles 1955; Goll 1967) and the thoracic ganglia (Cohen & Jacklett 1967). Thus meaningful counts can be made at some regions of the brain (Witthöft 1967). But apart from the giant perikarya of some class II cells, which invest the lamina or medulla, and monopolar cells in the lamina (V. Braitenberg & N. J. Strausfeld, in preparation) this cannot be done for other cell types in the optic lobes. Non-selective methods reveal certain structures which are recognizable as belonging to specific cell-types; nevertheless, the types of components distinguishable by these methods are few in relation to the total number of different types of elements recognizable from Golgi preparations.

The stratification of the optic lobe regions has been reconstructed from selective and non-selective procedures (see part I). The spread and distribution of processes through the strata is characteristic for each species of neuron. These field-sizes are a fraction of the size of many vertebrate dendritic fields such as, for example, the pyramidal cells in the cerebral cortex, and can easily be identified as lying within particular levels.

Some forms of endings appear to be restricted to particular horizontal or vertical loci in a region, or they may have particular variations in the size of their lateral extents at characteristic vertical and horizontal locations in a stratum. These asymmetric distributions are discussed in a subsequent section (p. 192).

The gluteraldehyde-fixed brains appear to have smaller medullae and larger central bodies than in fresh material; thus there may be differential shrinkage and expansion between different brain regions during fixation: the lateral extents of neurons derived from selectively stained material do not necessarily reflect the absolute 'living' values. Thus all measurements in this study define the relative sizes of neurons in named regions of gluteraldehyde-fixed Golgi preparations and are expressed as maximal lateral extents of circular field-spreads unless

otherwise specified. The gross stratification of the regions, reflecting the geometrical organization of the neurons and their processes, has the same relative proportions in each region both in fresh and fixed material.

RESULTS

The gross architecture of the optic lobes

This has been fully outlined in the preceding paper (part I) and only a brief recapitulation is needed here. There are three main regions in the optic lobes; the *lamina*, *medulla* and *lobula complex*. In the Lepidoptera and Diptera the latter is divided into an anterior and posterior component, the *lobula* and *lobula plate*, respectively. The optic tubercle receives two of its three endings from the optic lobe regions (part I) and is here considered as part of the optic lobe complex.

The cross-section profiles of the regions are almost the same as those in the Lepidoptera: there is no lobula valley in the Diptera since the tracts to the mid-brain, derived from the medulla, pass behind this region (i.e. anterior to its inner margin) and not between it and the lobula plate as in the Lepidoptera.

In most other respects the gross architecture of the optic lobes is the same in both orders. The surface areas of the medullae of the Syrphidae, however, are greatly elongated vertically and are not discoid as in the Lepidoptera. Those of the species of *Calliphora* are oval, with a vertical long axis. The shape of the surface area of this region and the lamina reflects that of the retina.

The neural components of the optic lobes

The optic lobes contain three classes of neurons in addition to the first-order receptors (these are taken to include the long visual fibres as well as the retinula cells); class I (perpendicular) cells, class II (tangential) cells and class III (amacrine) cells. These have been defined in detail in the preceding paper (part I).

Some species of Calliphorinae and Syrphidae also have hair-sensillae situated between all, or some of the lenses of ommatidia. Nerve fibres project from each of these towards the lamina between ommatidia. Similar structures have been described by Sanchez (1920) in the bee, *Apis mellifica*. The fibres of these elements are extremely slender and have not been traced further than the fenestration layer of the lamina.

The lamina

Introduction

Reduced silver preparations and fixed unimpregnated laminae viewed with phase-contrast illumination show this region rigidly organized into discrete perpendicular columns. Each reflects an optic cartridge which in *Calliphora* usually consists of two axial first-order interneurons surrounded by a ring of six retinula cell endings. Each of these is derived from a separate ommatidium. A pair of long visual fibres (retinula cells nos. 7 and 8) is displaced laterally from each of these groups and projects through the lamina via the first optic chiasma to the medulla (figure 3, plate 11). Some analysis of the receptor cell projections from their parent ommatidia to their respective optic cartridges have been made by previous workers (Cajal & Sanchez 1915; Pedler & Goodland 1965; Braitenberg 1966, 1967; Trujillo-Cenoz &

Melamed 1966; Melamed & Trujillo-Cenoz 1967). Braitenberg's (1967) studies of *Musca* indicate that only one of the eccentric cells projects further than the inner face of the external plexiform layer. The other seems to be very thin and arranged close to the ring of retinula cell components in the cartridge.† Studies on *Lucilia* and *Phormia* show two long visual fibres projecting outside the optic cartridge towards the medulla (Trujillo-Cenoz & Melamed 1966). The projection patterns that have been described certainly show that at the lateral part of the retina, six retinula cells, from six different ommatidia, project to the same cartouche in the lamina. This arrangement has been correlated optically and physiologically (Kirschfeld 1967; Scholes 1969). Golgi studies support the extra-cartouche (satellite) arrangement of the long visual fibres. Reduced silver preparations also show the two long visual fibres outside an optic cartridge in *C. vomitoria* (figure 7, plate 11). In *E. tenax* both members of a pair of long visual fibres project outside the cartouche but at the edge of the retina this is not so obvious. The projection patterns of retinula cells of *C. vomitoria* and *E. tenax* have been reconstructed from Golgi preparations, phase-contract microscopy and from reduced silver preparations. It has not been possible to find any differences between these projection patterns and those of *Musca* described in detail by Braitenberg (1967). The projection pattern proposed by Pedler & Goodland (1965) for *C. vomitoria* could not be confirmed from any of the present species.

Possibly different species of Diptera have different projection patterns of their retinula cells and long visual fibres to the external plexiform layer; also the retinula cell complement at the edge of the retina may not be the same as that at its middle. It does seem that two retinula cells derived from a single ommatidium may project to the same cartouche at the dorsoanterior edge of the retina; but it must be stressed that this pattern has been derived from Holmes–Fraser-Rowell silver preparations where the retinula components are visible but due to the curvature of the eye at this location they are difficult to trace, in their entirety, the whole distance into the inner margin of their respective optic cartridges. There is also evidence that optic cartridges situated at the dorso-ventral mid-line edge of the lamina may have seven or eight retinula cell endings rather than the six characteristic of the more laterally placed cartouches.

Observations on lamina components derived from the retina

There is only one shape of retinula cell-ending in the lamina of the Diptera. This is the unbranched type I terminal described in the preceding paper. It has the form of a simple plug ending which may appear somewhat tuberous or varicose (figure 1, plate 11). This single morphological type does not, however, exclude the possibility that there is more than one physiological type of retinula cell throughout the retina (see Discussion, p. 210).

Three forms of long visual fibres project through the lamina *en route* to the medulla; these are the smooth, spiny and wide-field forms described previously. The former two have been detected in both species of *Calliphora* and in the species of Syrphidae. The wide-field long visual fibre has only been detected in *E. tenax* and the species of *Syrphus*. These forms are illustrated in figures 4 to 6, plate 11.

Pairs of long visual fibres leave their parent ommatidium closely apposed to one another (figures 3 and 4, plate 11). In the previous study it was suggested that the members of a pair had particular relationships with each other in the external plexiform layer. In the Diptera those pairs that have been detected contain the following combinations of partnership: two

† At the time of going to press V. Braitenberg (personal communication) has confirmed the paired projection of both long visual fibres from an ommatidium through the lamina of *Musca*.

smooth long visual fibres, a smooth and spiny long visual fibre and a smooth and wide-field long visual fibre. The last has only been detected in *S. nitidicollis* and *E. tenax*. Spiny and wide-field types have never been detected together in a pair.

Observations on first-order interneurons in the lamina (monopolar cells)

Monopolar cells project to the outer layer of the medulla via the first optic chiasma. At least one form of these cells, axial to the ring of retinula cell endings, has been described as being postsynaptic to the retinula cells of a cartridge (Trujillo-Cenoz 1964; Trujillo-Cenoz & Melamed 1966). All the monopolar cells in the present species of Diptera have been classified as small-field elements. The giant monopolar cells typical of *Locusta*, *Schistocerca*, *Apis* and some Lepidoptera have not been seen in the present species of Diptera nor are they figured by the Spanish authors for *Tabanus* or *Musca*.

There are three main types of small monopolar cells (part I); these are midget, radial, and bilateral elements. They may have unistratified, bistratified or diffuse arrangements of lateral processes from their axis-fibres. The classification of these variants is shown in figures 8 to 12, plate 12, and figures 34 and 35 and described in the accompanying text figures.

The bilateral (type 1a) monopolar cells have two sets of lateral processes arranged linearly down the length of each axis-fibre within the external plexiform layer. The two sets are not invariably arranged at 180° with respect to one another on the same fibre and occasionally they have been clearly seen at right angles (figures 23 to 25, plate 14). Each process bifurcates at its end to form two spines; the distance between them in *S. elegans*, is between 0.7 and 0.9 μm. The cross-sectional width of a retinula cell ending is between 1.2 and 2 μm. Figures 23 and 24, plate 14, shows one set of these lateral processes closely applied to a retinula cell ending so that

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Description of plate 11

The lamina

Figure 1. *C. erythrocephala*. Retinula cell endings in the lamina; only a small proportion of the retinula cells have been impregnated. Note the decussation of retinula cells 2 and 6 (Re 2 and Re 6) from ommatidium (a) and the single Re 6 from ommatidium (b). This latter ending can be seen close to another retinula cell ending in the same cartridge derived from a more ventrally placed ommatidium. Retinae cut tangentially show more complete projection patterns but these are not amenable to photography (see figure 34). 1 = retina, 2 = fenestration layer, 2a = cell-body layer, 3 = external plexiform layer.

Figure 2. *C. erythrocephala* (copper-protargol-S impregnation)†. Detail of the decussation pattern of the retinula cell fibres at the interface between the cell-body layer (2) and the external plexiform layer (3). This pattern of local chiasmata has been shown extremely clearly in *Musca* (see Braitenberg 1967) from tangential sections.

Figure 3. *S. vitripennis*. A single ommatidium near the anterior median edge of the retina (Ret) gives rise to two smooth long visual fibres. These project as a pair through the basement membrane (Ba) and lamina (Lam) into the first optic chiasma (1st O.C.).

Figure 4. *C. vomitoria*. A pair of smooth long visual fibres in the lamina.

Figure 5. *S. nitidicollis*. A wide-field long visual fibre in the lamina.

Figure 6. *C. vomitoria*. A high power photomicrograph showing the spiny long visual fibre (sLf). A midget monopolar (mM) cell is in the background.

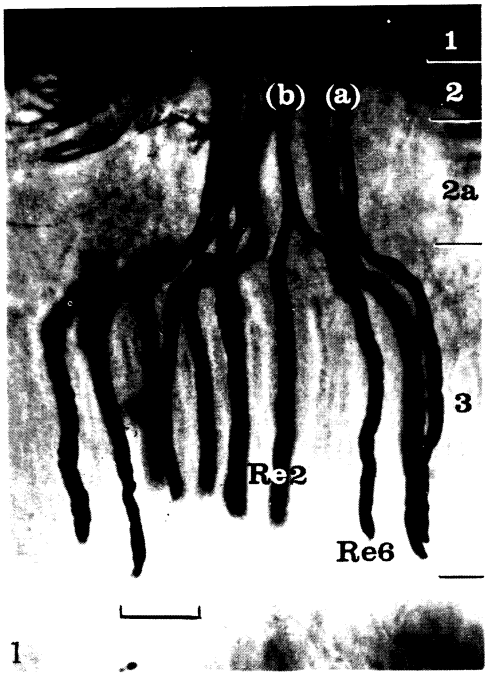
Figure 7. *C. vomitoria*. Gros-Schultze preparation.‡ Optic cartridges are arranged in linear arrays. Each consists of a ring of six retinula cells which surrounds a pair of monopolar cell axis-fibres (M). The pairs of long visual fibres (Lf) are satellite to an optic cartridge (see figure 34*a*).

Scales: Figures 1, 3 to 5, 10 μm; figures 2, 6, 7, 10 μm.

† See Chen, J. S. & Chen, M. G. M. 1969 *Stain Technology*. **44**(1), 50–51.

‡ See Romeis (1948).

Phil. Trans. Roy. Soc. Lond. B, volume 258, plate 11



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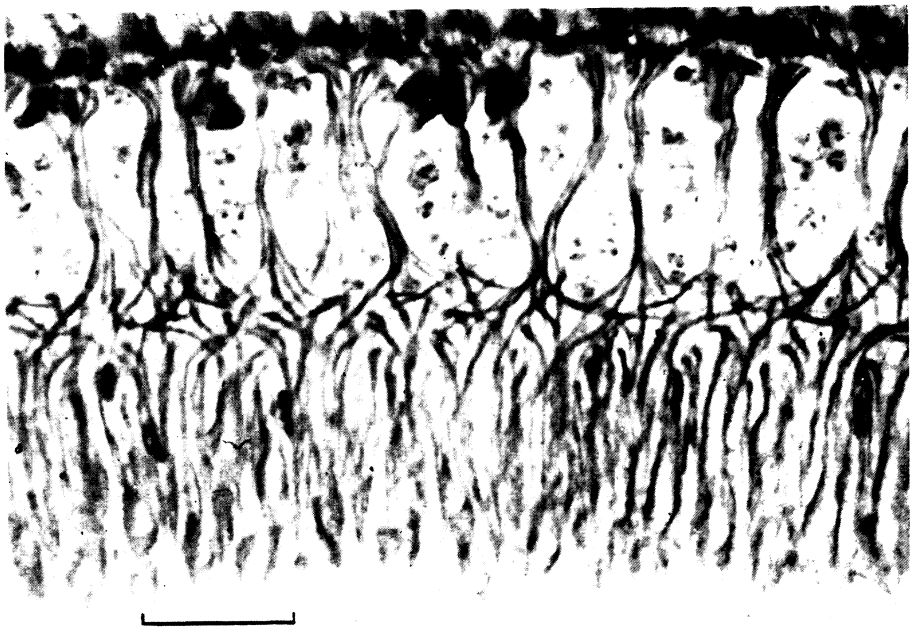

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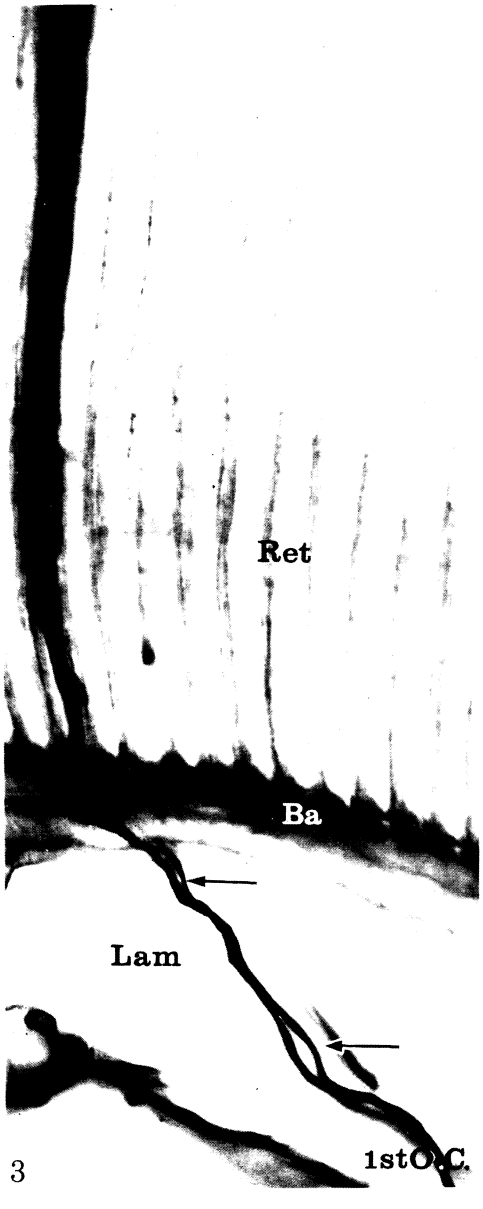

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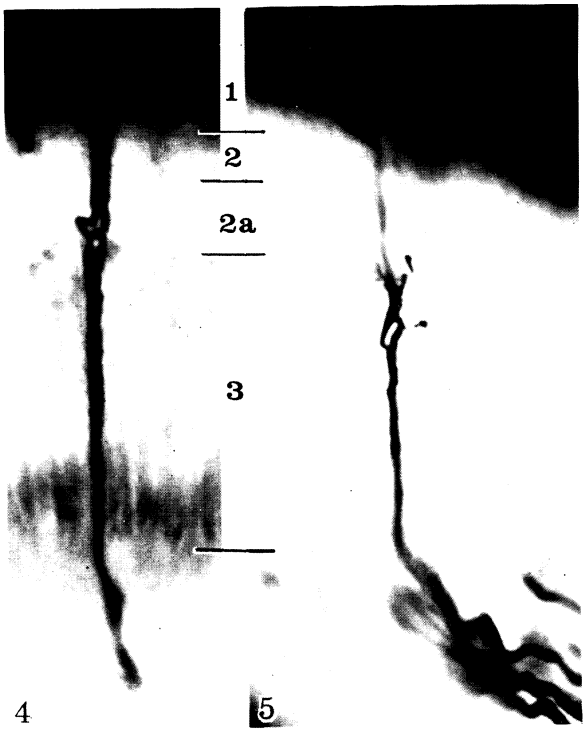

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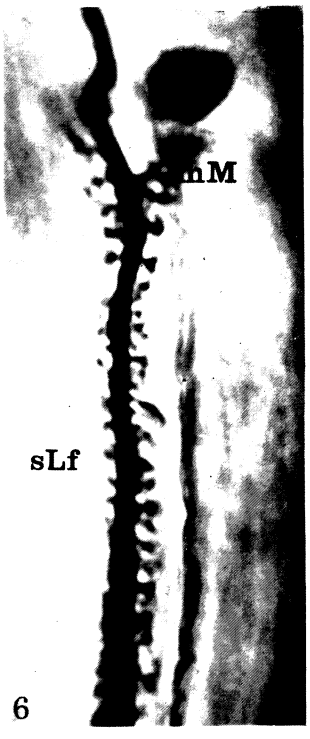

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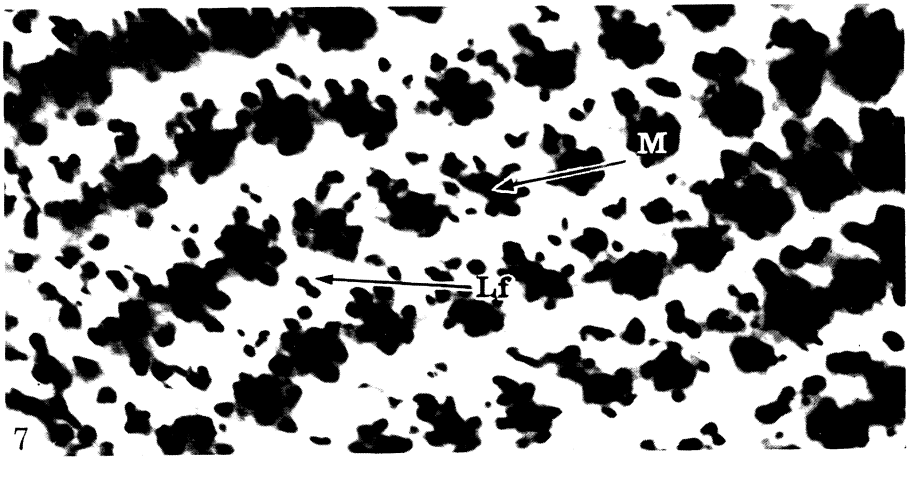

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(*Facing p.* 112)


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they appear to embrace or plug into it via the spines. Figure 25, plate 14, shows that the second set of processes, arranged at right angles to the first, is revealed on its own. The retinula cell with which it is most probably intimate is unimpregnated.

Unistratified midget monopolar cells (type 2a) have one or two lateral processes situated at the outer margin of the external plexiform layer. They are not spined but appear more like lateral swellings of the axis-fibre near to the perikaryon. Bistratified midget monopolar cells (type 2b) have one or two spines at the same location as the type 2a cell and an additional spine or swelling at the inner margin of the external plexiform layer; these bistratified variants have only been detected in the Syrphidae.†

The radial unistratified monopolar cell (type 3) has between four to six lateral processes at the outer margin of the external plexiform layer derived from the axis-fibre, just beneath the cell-body.

Bistratified radial diffuse monopolars (type 1b) have their cell-bodies situated close to the inner margin of the cell-body layer. Their outermost processes are varicose and wider than the inner group whose spiny processes are radially arranged from the axis-fibre down its length in the plexiform layer. Fragments of a third variant (type 1c) have been detected in two species of Syrphidae; this cell has bilaterally arranged varicose processes, similar to those of the outer group of 1b, restricted to the cell-body layer of the lamina. Possibly the outer processes of adjacent type 1b and 1c monopolar cells may be intimate with one another or with retinula cell fibres at the level of their chiasmata before they converge into their respective optic cartridges.

Observations on 'centrifugal' elements in the lamina

Efferent and afferent fibres cannot be distinguished from light microscopy observations. Thus the terms dendrites, axons and axon terminals have been omitted from this and the

† At the time of going to press, bistratified midget monopolars have been stained in *Calliphora phaenicia*, and in *Musca domestica*.

Description of plate 12

The lamina

Figure 8. *S. elegans*. Unistratified radial monopolar cell. The processes are disposed radially from the axis-fibre.

Figure 9. *E. tenax*. Unistratified radial monopolar cell. The processes are characteristically Y-shaped and tuberous.

Figure 10. *E. tenax*. Radial bistratified diffuse monopolar cell. Note the wider processes near the cell-body (arrowed).

Figure 11. *E. tenax*. Bilateral diffuse monopolar cells. The cell-bodies are out of section. Note the extremely thick axis-fibre (between 2 and 4 μm diameter).

Figure 12. *E. tenax*. Bistratified midget monopolar cell. Note the outer unilateral process and the inner swelling, at the outer and inner margin of the external plexiform layer, respectively (arrowed). A pair of smooth long visual fibres (2 Lf) is shown nearby.

Figure 13. *C. erythrocephala*. 'Basket' endings of T_1 cells in the lamina. The unimpregnated retinula cells can be seen in the unstained background.

Figure 14. *S. elegans*. A type 3 (climbing) ending in the lamina. It is characterized by the unilateral arrangement of knobs along the outermost 2/3 of its length.

Figure 15. *E. tenax*. A type 2 (capped) ending in the posterior median lamina. A process of the type 1 lamina tangential is applied to the basal branch of the centrifugal ending.

Figure 16. *C. erythrocephala*. The type 2 centrifugal ending is essentially similar to that of *E. tenax*. However, its distal-most specialization is comparatively smaller. The arrows in figures 15 and 16 indicate the bistratified arrangement of this element.

Scales: Figures 8 to 16, 10 μm.

preceding paper. As in Cajal's earlier study on the avian retinae (1888) the term 'centrifugal' has a purely morphological definition; it denotes endings in the lamina and medulla that are derived from initial groups of processes which are themselves derived from cell-bodies located more centrally in the brain. These centrifugal endings must be clearly distinguished from initial groups of processes derived from a cell-body directly below them; this latter structure is applicable to the amacrine cells of the lamina and the T-cell components in the medulla which project centripetally to the lobula complex.

Four forms of centrifugal endings can be detected in the laminae of these species of Diptera. Three of them have been described by the Spanish authors.

The type 1 and 1a medulla-lamina T-cell (T_1 and T_{1a})

Perikarya in the cell-body cortex around the inner segment of the first optic chiasma give rise to initial groups of processes in the medulla. A linking-fibre extends from each of these and terminates as a 'basket ending' in the lamina. Each of the type 1 endings in *Calliphora* consist of between 10 and 14 terminal perpendicular processes, all of which are restricted to the inner plexiform layer. In *E. tenax* each basket ending consists of between six and eight processes. In all the species these extremely slender fibres are distributed around the cartouche of six retinula cells that enclose the two axial monopolar cell axis-fibres. The basket-ending processes are characteristically varicose and give rise to lateral tuberous prolongations (figure 13, plate 12) which are directed inwards towards the optic cartridge axis; i.e. between and around the retinula cell endings and axial monopolar cell components (figure 26, plate 14). Some basket endings have a peculiar terminal extension of their perpendicular processes; these are oriented tangentially with respect to the outer face of the external plexiform layer and extend over the margins of adjacent cartridges. They are characteristically blebbed; the fibres are usually less than 0.2 μm in diameter, and barely resolvable as faintly impregnated ghosts.

Cajal & Sanchez described and figured a double basket cell ending in *Tabanus*. This was apparently composed of two adjacent components derived from the same linking-fibre from the medulla. There is no evidence for these forms of endings in any of the species studied for this account. The lamina is, however, prone to crystalline deposits by the Golgi stain and some components do appear fused together. Possibly the double basket ending described by these authors could be derived from such artifacts. Even so, they may possibly be present in Tabanids and must await further investigation.

The type 1a centrifugal ending in the lamina

This terminal component of a second type of medulla-lamina T-cell consists of between four and six perpendicular processes of unequal length. They are characteristically varicose, without lateral projections, and are invariably restricted to the inner plexiform layer. The lateral extents of these endings cannot be measured accurately since they are only detectable at the perimeter of the lamina where its curvature is greatest and the optic cartridges are somewhat distorted. However, it seems that they do not have a spread greater than between one and two optic cartridges in any plane of section. These type 1a endings have been detected at the entire perimeter of the lamina of the two species of *Calliphora* and in the dorsal perimeter of the lamina of *E. tenax*. They have not been seen in the two species of *Syrphus*. There is evidence that their medullary endings are likewise restricted to these perimeter locations (see p. 200).

The type 2 endings (C_2)

This form of ending was described and figured by the Spanish authors who called it a 'capped ending'. Their nomenclature is an apt one; the ending consists of a terminal prolongation of a linking-fibre, derived from the medulla, which extends as far as the external plexiform layer. There is a basal swelling at the inner margin of this layer and a terminal bilateral 'cap' at its outer margin. These are illustrated in figures 34 and 35, and figures 15 and 16, plate 12. In *E. tenax* this ending has a basal unilateral process and its terminal specializations consists of a disk-like swelling. In some preparations blebbed processes, derived from the type 1 tangential element, have been detected closely opposed to the basal component (figure 15, plate 12).

The type 3 (climbing) ending (C_3)

This ending is also restricted to the external plexiform layer: it consists of a perpendicular extension of a linking fibre from the medulla. The terminal is characterized by an extremely slender fibre with a diameter of less than 0.5 μm from which is derived a set of unilateral knobs (figure 14, plate 12). The lateral extent of this array is between 2 and 4 μm in *C. vomitoria* and between 3 and 4.5 μm in *E. tenax*. The knobs have been detected closely opposed to a midget monopolar axis-fibre (figures 29 and 30, plate 14). Whether this reflects synaptic intimacy between the two is not known. The medullary components of the centrifugal cells are described in a subsequent section (p. 155).

Observations on class II components in the lamina

There are two types of class II components in the laminae of the species of *Calliphora*, and three forms in *E. tenax* and in at least two species of *Syrphus*.

Type 1. The diffuse lamina: bistratified medulla tangential cell. (Lam: tan 1)

This neuron has been identified in all the species of Diptera. Its medullary component was figured by the Spanish authors who considered it to be derived from an amacrine cell-body. It has the following characteristics: a large cell-body, between 15 and 20 μm in diameter, situated below the lamina, gives rise to a stout fibre that projects as far as the inner face of the external plexiform layer. There it gives rise to several branches which invest both the outer and inner margins of this layer and extend as anteroposteriorly oriented strip-fields through the whole of the horizontal width of the lamina and through about an eighth of it in the vertical plane. The outer branches bear many lateral processes which extend into the external plexiform layer among the optic cartridges. These processes are extremely thin, often less than 0.3 μm in diameter and are characterized by regularly spaced blebs along their length. Each of the horizontally oriented subfields of these tangential cells have several collateral linking-fibres which extend, via the first optic chiasma, to the medulla where they end as characteristic bistratified components (figure 35). These are described in detail in a subsequent section.

Short ascendent processes have also been detected arising from the branches at the outer margin of the external plexiform layer. These project towards the basement membrane but invariably stop short of it (figure 17, plate 13). They do not appear to have any form of lateral projections. It is conceivable that they may represent interaction between this class II element and another non-visual form of receptor fibre. Hair cells between the ommatidia of *Eristalis* and *Apis* give rise to first-order receptor fibres which seem to by-pass the lamina and deeper

optic lobe regions entirely. Extremely small sensillae are also apparent between some lenses of the retinae of *Calliphora* and *Pieris* which project to the level of the ascendent branches of the type 1 tangential fibres in the fenestration layer.

Type 2. The diffuse lamina: diffuse medulla tangential (Lam: tan 2)

This cell component has been clearly seen in *S. nitidicollis* and *E. tenax*, and is probably present in the other syrphidae. It has not been seen in *Calliphora*. The arrangement of its branches and lateral processes is essentially similar to that of the type 1 tangential cell; however, its branches at the outer margin of the external plexiform layer are characteristically tuberous and varicose, while its processes among the optic cartridges are predominantly smooth. Its projections to the medulla are still obscure: a stratified diffuse ending in the medulla is certainly derived from the lamina at a position directly peripheral to it (i.e. anterior components in the medulla stem from the anterior lamina) but cannot be definitely assigned to a lamina component (figure 35). The imperfectly impregnated linking-fibres that have been seen arising from the type 2 lamina tangential components appear to cross directly to the medulla and not via the first optic chiasma. Several of these fibres are derived from one type 2 tangential field in the lamina. Similarly, in *Pieris*, some fibres have this atypical decussation between the two regions (figure 106, plate 23).

Type 3. The monostratified tangential component (Lam: tan 3)

A branching system of fibres is located at the interface between the fenestration layer of the lamina and the cell-body layer. It is rarely impregnated and is difficult to trace for any distance. Its processes are thin (0.5 to 0.2 μm in diameter) and blebbed (figure 18, plate 13) and are similar in appearance to the tangential component described from *Sphinx* (part I).

The cell-body locations of lamina class II components and their projections to other regions

Reduced silver preparations show up between 10 and 16 large unipolar perikarya beneath the external plexiform layer amongst the fibres of the first optic chiasma. Some of these cell-bodies undoubtedly belong to the type 1 lamina tangential (figures 17 and 21, plate 13). But nothing is known of the perikarya location of the remaining two types of tangential components in the outermost region. There is little cause for confusion between these type 1 lamina tangential cell-bodies, the perikarya of amacrine cells and the somata of glia. Amacrine cell-bodies are regularly arranged beneath the external plexiform layer; they are unipolar with diameters ranging between 7 and 10 μm and there seems to be a one to one relationship between them and the number of optic cartridges. Glia cells are characteristically small, elongate and multipolar and are scattered throughout the first optic chiasma.

The cell-bodies of the remaining two types of tangential elements in the lamina need not be assumed to be located in the ipsilateral lobe. Possibly both these types are terminal components derived from the mid-brain or contralateral lobe. Alternatively these elements could be derived from cell-bodies situated behind (anterior to) the ipsilateral lobula and thus be intrinsic to the optic lobe. The embryology of the lobes of some insects is complex (see Malzacher 1968) and involves extensive migrations of the regions during development. Possibly the movements may take place after the positions of some cell-bodies have been established (with respect to the cell-body cortex) and may result in their respective neuropil components lying some distance from them.

In *S. nitidicollis* a thick fibre has been traced from the third type of lamina tangential towards the mid-brain; it bypasses the medulla anteriorly and is closely opposed to the actual margin of the brain itself at the extreme periphery of the cell-body cortex. This prolongation is either a linking-fibre which projects to a central or contralateral region or it may be derived from a cell-body fibre situated near the lobula. In *Apis* fibres have been detected which project anteriorly from the lamina to the mid-brain and by-pass the medulla *en route* (Kenyon 1896; N. J. Strausfeld, unpublished). A similar tract has been described by Zawarzin (1913) from preparations of *Aeschna*, and there is some evidence for the same projection in the Lepidoptera. Reduced silver preparations reveal another tract in *Apis* which projects from the retina, antero-dorsally in the lamina, and towards the mid-brain (these fibres are not derived from the hair sensillae described by Sanchez (1920)). In *C. vomitoria* two tracts have been detected anterior to the perimeter of the outer margin of the medulla; one of these is derived from a surface tangential on the outer face of this region (M: tan 3), the other is most probably derived from the lamina.

Amacrine cells in the lamina: introduction

Class III cells were previously defined in part I as having processes in only one geographical region. The term 'amacrine' is used to describe them, after Cajal & Sanchez. The functions of these cells in the insects are unknown. Some of the cells intrinsic to the medulla extend throughout its depth, and bear several discrete groups of processes at different levels. They may, in fact, be receiving information at one medullary level and transmitting it to another, but it is convenient to treat the medulla, despite its complexity, as one geographical region, and hence to classify such cells on morphological grounds as amacrines.

Observations

The perikarya of lamina amacrine cells are situated beneath the external plexiform layer. Only one form of these cells has been detected in the present species of Diptera and in those described by the Spanish authors.

Each perikaryon gives rise to an extremely short process which branches two or three times below the external plexiform layer. Slender branches arise from these which invest the space around an optic cartridge and its associated long visual fibre and centrifugal elements (figure 34).

This form of amacrine cell has features which make it appear quite unlike other neurons seen in the insect brain. The cell-body fibre is unusually short and thick (3 to 6 μm long and 1 to 1.5 μm wide) and the subsequent processes are derived from it unusually near the perikaryon. These processes are completely smooth without any of the lateral prolongations typical of other neural elements which usually have bags, blebs, spines or other specializations. Neither is it like any form of glia cell (Cajal & Sanchez 1915; Sanchez 1935); these commonly have lateral lamellae arranged along their lengths within a geographical region. The epithelial cells (Cajal 1909) have lateral knobs and swellings. The diameters of the knobs range from between less than 0.2 and 0.3 μm and probably correspond to the capitate projections described from electron-microscopy by Trujillo-Cenoz & Melamed (1966), even though, in Golgi preparations they are slightly larger. The marginal glia cells (Trujillo-Cenoz 1964) have been detected by non-selective methods. Similar shaped elements have been seen in the cell-body cortex and amongst the fibres of the inner segment of the first optic chiasma (part I).

There are two forms of lamina cells in *E. tenax* which have not been detected in other species

(figure 35); both are multipolar. The form shown in figure 19, plate 13, has an extremely small cell-body, less than 7 μm in diameter and looks more like a peripheral abdominal multipolar element described by Zawarzin (1913) and Orlov (1924). Its processes lie closely opposed to tracheae in the fenestration layer. The other element has blebbed processes which are oriented tangentially at the interface between the cell-body layer and external plexiform layer. It has only been seen in one preparation, but similar shaped elements have been detected in the larva of *Libellula* lying at the inner margin of the plexiform layer (N. J. Strausfeld, unpublished).

The significance of both multipolar elements is unknown; however, multipolar elements have been described in the lamina of the lobster *Homarus* (Hamori & Horridge 1966) which were suggested to have a neurosecretory role. Possibly the multipolar elements in the fenestration layer of *E. tenax* may have a similar function.

Some lateral topographical relationships of cells in the lamina

In Golgi preparations the columnar arrangement of the lamina provides a means of locating the positions of the optic cartridges, either by adjustment of the condenser, or by employing Nomarski phase-contrast illumination (figure 22, plate 14). The unstained retinula cells, monopolar cell-bodies and axis-fibres can, in excellently fixed material, sometimes be distinguished in the unimpregnated background as can the satellite long visual fibres which project between optic cartridges. Certain additional neural components, other than receptor elements, can be spatially related to optic cartridges.

Type 3 centrifugal endings have been detected closely applied to midget monopolar cells within a cartridge; but there is also evidence that they may have a particular relationship with spiny long visual fibres. At present the evidence for them being related to one or other of these elements is equivocal. When they are detected alone against an unimpregnated background they appear to be situated within or at the posterior edge of an optic cartridge. If the centrifugal elements have a special relationship with only one or two types of centripetal elements the possibility of detecting them by electron-microscopy will largely be a matter of

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Description of plate 13

The lamina

Figure 17. *S. vitripennis.* The type 1 lamina tangential. Note the bistratified arrangement of processes at the outer and inner margins of the external plexiform layer and the large cell-body. Branch b extends out of the section, posteriorly, to give rise to another strip subfield. Smooth processes (2) extend into the cell-body layer. Their population is similar to that of the interommatidial hairs at the surface of the retina (see Strausfeld 1968). The branches at the outer margin of the external plexiform layer (o) give rise to many descendent processes (x) which invade this stratum. Only a small part of the linking-fibre to the medulla (lf) is visible in this section.

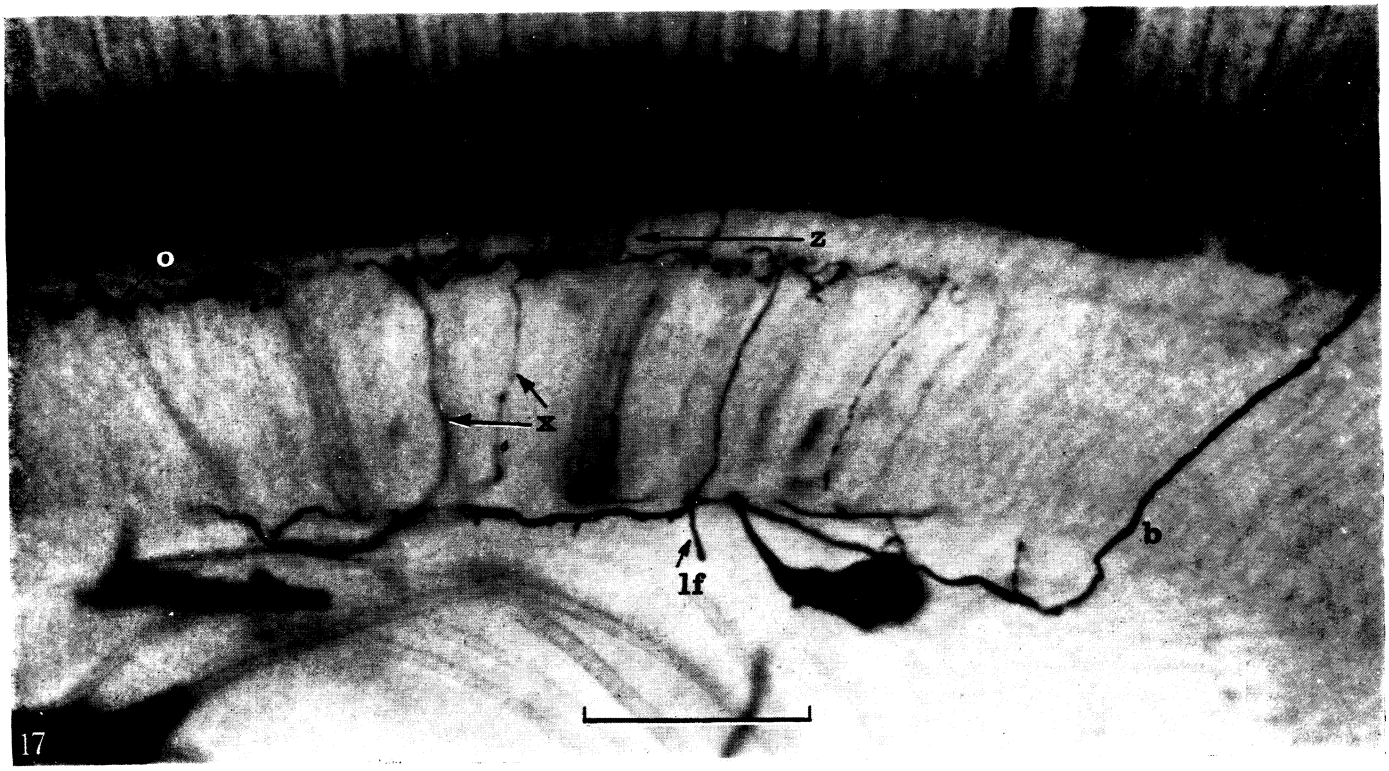
Figure 18. *C. vomitoria* (tangential section). The characteristically blebbed processes of the type 3 (unistratified) tangential component located in the fenestration and cell-body layers.

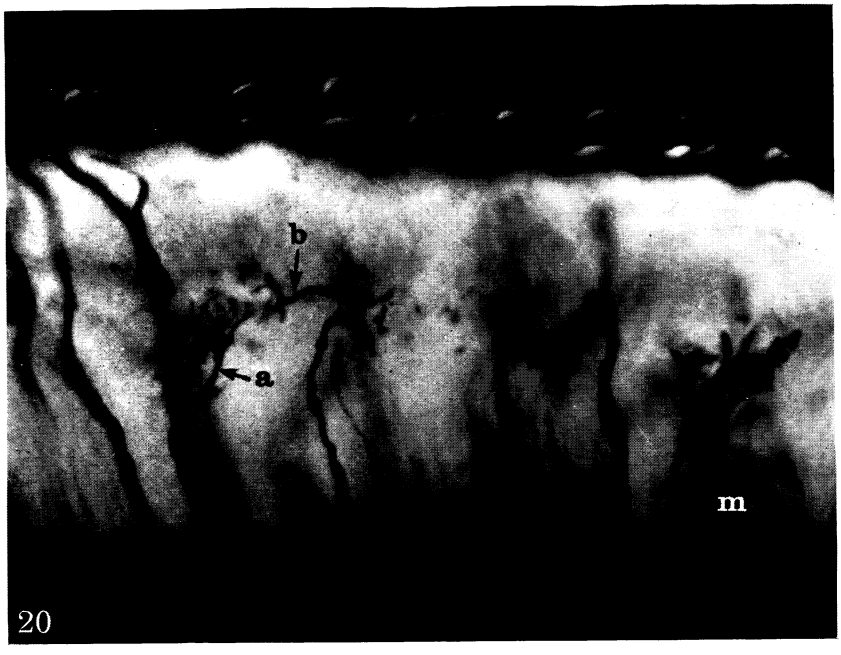
Figure 19. *E. tenax.* The multipolar cell at the outer margin of the cell-body layer. Note the weakly impregnated trachea (tr) (see also, figures 109 and 111, plate 22).

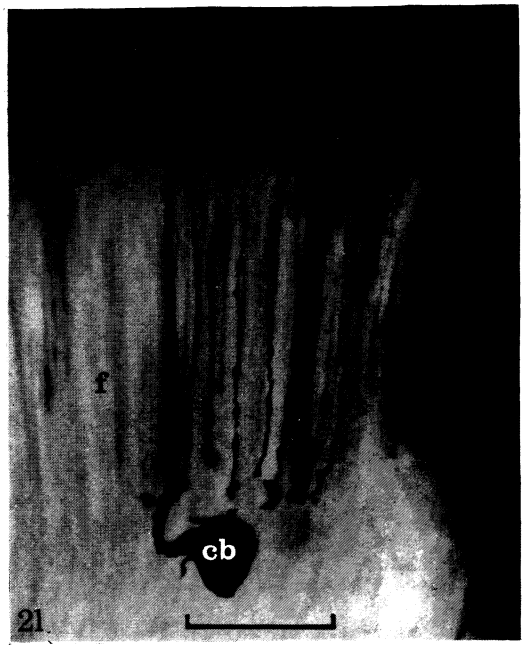
Figure 20. *S. nitidicollis.* Lateral processes (a) of the wide-field long visual fibres are at the same level as those of the type 3 tangential component (b) in the cell-body layer. Radial monopolar cells (m) are just discernable in the plexiform layer.

Figure 21. *E. tenax* (vertical section). Part of a type 1 lamina tangential element. The blebbed processes in the external plexiform layer are especially clear in this preparation. The cell-body (cb) is relatively small compared to that of the same element in *S. vitipennis.* This section shows the vertical extent of the horizontal strip subfield (f).

Scales: Figure 17, 50 μm; figure 19, 5 μm; figures 19 to 21, 25 μm.







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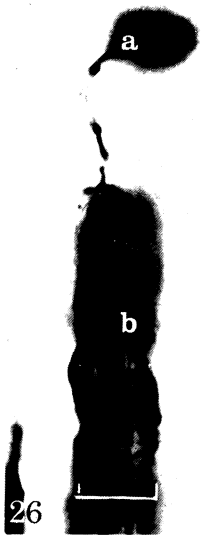

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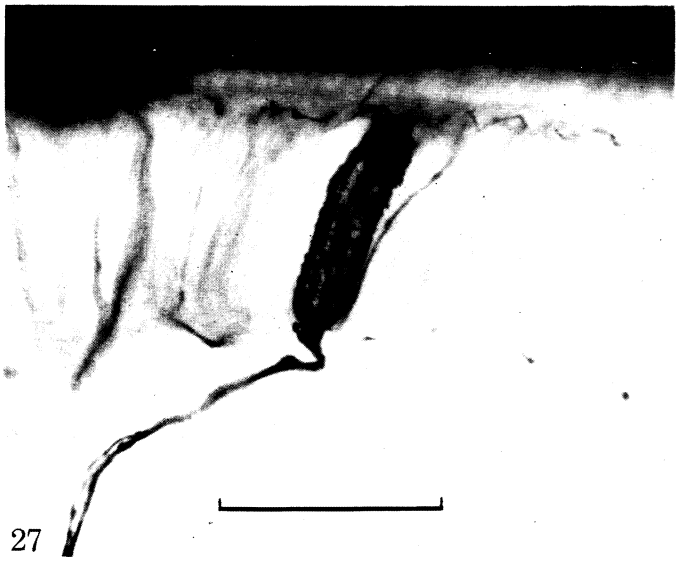

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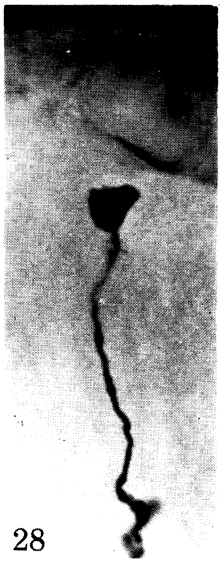

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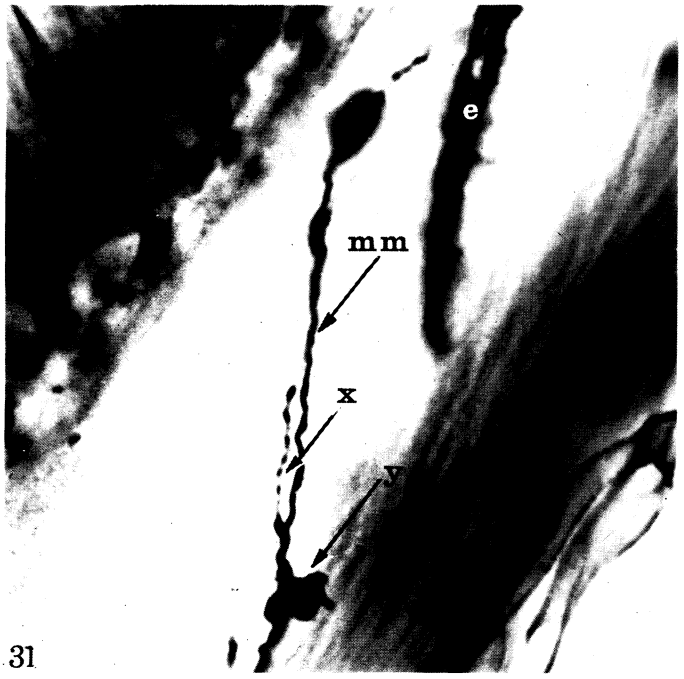

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chance; not all cartridges may contain a midget monopolar cell axis-fibre, and not all the pairs of satellite long visual fibres may contain a spiny variant. The axis-fibres of the type 2 centrifugal endings have been related to the spaces between cartridges which also contain the satellite long visual fibres. But again these may have a particular relationship with certain elements that do not have a homogenous distribution in the lamina.

Golgi preparations give the impression that at most only one of these centrifugal elements is associated with each column in the medulla. In a subsequent section (p. 153) it is proposed that each optic cartridge and its satellite pair of long visual fibres are represented by two columns in the medulla, each of which contains one long visual fibre ending and one monopolar cell ending. If each column contains either a type 2 or a type 3 centrifugal element each optic cartridge would then have two centrifugal endings associated with it in addition to a type 1 or 1a T-cell ending. Although this seems the case in these preparations it can only be resolved by more sophisticated reduced silver studies (N. J. Strausfeld & V. Braitenberg, in preparation). Some, but not all, basket endings have flat tops (figure 34). Possibly these lateral extensions serve to bring some adjacent basket endings into contact with one another. They may, however, allow contact between basket endings and receptor cell-fibres at the zone of their decussation just above the outer margin of the external plexiform layer.

The class II components in the lamina are clearly divided into separate sublayers. The type 3 element lies above the external plexiform layer among the monopolar cell-bodies. It could not possibly be intimate with any of the centrifugal endings. In the Syrphidae these tangential fibres lie at the same level as the bilateral processes of the wide-field long visual fibres (figure 20, plate 13). In *S. nitidicollis* these two types of elements are clearly applied against one another. But this does not necessarily imply synaptic intimacy between them although the arrangement

Description of plate 14

The lamina

Figure 22. *S. vitripennis.* Nomarsky phase contrast of Golgi-stained material. The impregnated retinula cell endings can be located to their respective optic cartridges. Unimpregnated fibres are also resoluble.

Figure 23. *C. erythrocephala.* Retinula cells nos. 2 and 5 from the same ommatidium end in antero-posteriorly adjacent cartridges. Retinula cell 5 appears closely applied to the spiny lateral processes of a bilateral monopolar cell (m). This latter element has its two sets of processes set at right angles to one another from the axis-fibre.

Figure 24. A high resolution photomicrograph of the spiny processes applied against the surface of the retinula cell ending.

Figure 25. The second set of processes is facing the camera. The double row of spines is clearly visible. These probably plug into the unstained retinula cell ending 1 or 6 (dotted parallel lines).

Figure 26. *C. vomitoria.* A basket cell (b) ending enclosing one of the two monopolar cells (a) in an optic cartridge.

Figure 27. *C. vomitoria* (vertical section). The perpendicular topographical relationship between fibres of the type 1 tangential element and a basket ending.

Figure 28. *C. erythrocephala.* The unistratified midget monopolar cell.

Figures 29 and 30. *C. vomitoria.* Two planes of focus of the same restricted portion of the lamina showing a type 2 centrifugal ending alone (figure 29, arrowed) and the same type of ending applied a to a midget monopolar cell (figure 30). The unimpregnated retinula cells are visible in the background.

Figure 31. *E. tenax.* A bilateral monopolar cell (mm) and its association with the flat end (y) of a type 1 tangential cell process (x). Epithelial cell (e).

Figure 32. A detail of the association between the inner processes of the bistratified midget monopolar cell and the flat end of the tangential process.

Figure 33. The flower-like flat-ended process, impregnated alone.

Scales: Figures 22, 23, 28 to 31, 33, 15 μm; figures 24, 25, 32, 5 μm; figure 26, 10 μm; figure 27, 50 μm.

is suggestive of it. The thin processes of the types 1 and 2 tangential elements appear to be dispersed both between and within the optic cartridges. The processes of the type 2 tangential cells are invariably blebbed. Those of the type 1 cell are either blebbed or smooth with a characteristic flattened, flower-like, ending (figure 21, plate 13, and figure 33, plate 14); these have been detected closely applied to the inner swellings of the bistratified midget monopolar cells (figures 31 and 32, plate 14). The inner swelling of a type 2 centrifugal ending seems to have a special relationship with the blebbed processes of either type of tangential element (figure 15, plate 12). Neither the bistratified midget monopolar cells nor the flattened ends of the type 1 tangential fibre processes have been detected in the two species of *Calliphora*.These species have unistratified midget monopolar cells with one or two short lateral processes at the outer margin of the plexiform layer, and a slight swelling or kinking of the axis-fibre towards the ring of retinula cells at the inner margin of the plexiform layer (figure 34*c*).

Golgi preparations have not revealed optic cartridges with more than two monopolar cells that are axial to the whole length of the ring of retinula cells. Occasionally the basket ending of the T_1 cell and a monopolar cell axis-fibre have been detected together at the same medullary cartridge (figure 26, plate 14). This further substantiates evidence from other authors (Trujillo-Cenoz & Melamed 1966) that thin centrifugal fibres surround a cartridge. None of the 400 impregnated optic lobes have shown conclusive evidence that an optic cartridge contains more than one monopolar of the same type within it. More radial monopolar cells have been impregnated than any other type and the Golgi preparations give the impression that each cartridge usually contains one radial cell and one other type. Midget monopolars can be related to within the cartridges at their outermost level in the plexiform layer and external to them elsewhere in this layer. The amacrine cell processes invade the spaces between cartridges. In *Calliphora* one amacrine cell embraces a cartridge and its basket ending, whereas in *Eristalis* and probably the other Syrphidae one amacrine cell embraces up to six cartridges. These initial reconstructions of the topographical relationships between the lamina components are illustrated in figures 34 and 35. Elements in the lamina are illustrated in plates 11 to 14.

The medulla

Observations on the long visual fibre endings

There are three forms of this ending in the medullae of all these species of Diptera. These are illustrated in figures 39 to 45, plates 15 and 16, and in figures 54 and 55, plate 17. They have been termed plug, forked and miniature endings. The former two end more deeply than the latter. The axis-fibres of plug endings characteristically have a unilateral bulge at the surface of the medulla; axis-fibres of forked endings may have a similar specialization or short lateral processes disposed radially from the axis. The miniature endings, illustrated in figure 54, plate 17, are slender and difficult to resolve. Extremely thin lateral processes have been detected from them (less than 0.3 μm diameter) along all or part of their length. Plug endings in the Syrphidae have also been detected with thin lateral processes which extend between 3 and 5 μm from the swollen tip of the axis-fibre (figure 55, plate 17). In this respect they appear similar to some long visual fibre endings in *Pieris* and *Sphinx* (see part I).

A fourth form of long visual fibre ending has been seen in *E. tenax* and *S. elegans*. This terminal has three groups of bilateral processes (figure 40, plate 15) each of which is composed of two lateral prolongations set at right angles to each other. This characteristic configuration is reflected by the outermost processes of a bistratified diffuse amacrine cell at the same level

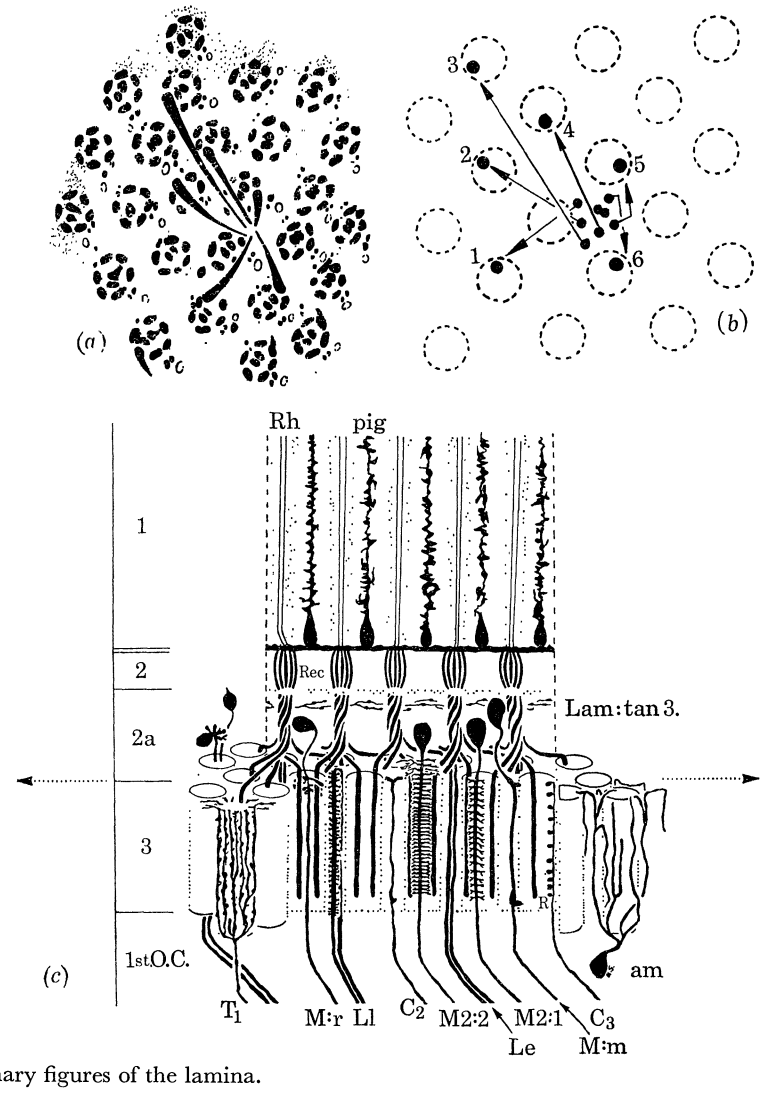


FIGURE 34. Summary figures of the lamina.

(*a*) A tangential section of the lamina, taken from a Holmes–Blest silver preparation, showing the arrangement of the optic cartridges (six retinula cell endings around two axial monopolar cells) and the pairs of satellite long visual fibres. The projection pattern of the retinula cells, from one ommatidium to their respective cartridges, has been derived from Golgi preparations of *Eristalis* and *Syrphus nitidicollis* and is superimposed upon the cartridges.

(*b*) A schematized representation of retinula cell projections of the present species of Diptera from an ommatidium to optic cartridges. Retinula cells are numbered according to Dietrich's (1909) nomenclature. In these species of Diptera the long visual cells project as pairs outside cartridges.

(*c*) (*Calliphora*) This diagram illustrates the lateral topographical relationships between classes I and III elements in the lamina. Each complete cartridge is represented as a cylinder, others (transversed) as half cylinders. Five groups of receptor elements (Rec) leave five ommatidia. The complete decussation is shown of the retinula cell compliment of the group on the extreme left. Parts of the decussation of the others are shown in horizontal section. Long visual cell pairs (Ll) project between cartridges, monopolar cells project through or between cartridges and are surrounded by retinula cells (R). With the exception of the extreme left-hand cartridge others are shown with, at most, only one of their pair of monopolar cells. The basket cell endings (T_1) embrace cartridges. Amacrine cell processes (am) extend through the spaces around one cartridge; the distal-most portions of these processes are characteristically recurrent and extend part of the way down the margins of adjacent cartridges. Capped centrifugal endings (C_2) are located between optic cartridges and the climbing endings (C_3) are located within a cartridge close to its margin.

Rh = Rhabdom. pig = pigment cells. R = retinula cell. Lam: tan 3 = unistratified (type 3) lamina tangential. M: r = radial monopolar cell. M2: 2 = bistratified diffuse radial monopolar cell. M: m = midget monopolar cell (note its kinked course through the plexiform level). M2: 1 = bilateral monopolar cell. 1 = retina. bas = basement membrane. 2 = fenestration layer. 2a = cell-body layer. 3 = external plexiform layer. 1st O.C. = first optic chiasma. The depths of the external plexiform layer varies between species. *Calliphora* sp., stratum 3 = 30–55 μm; *E. tenax*, stratum 3 = 45–70 μm; *S. elegans*, stratum 3 = 35–60 μm; *S. nitidicollis*, stratum 3 = 28–63 μm (maximum depths at the centre and posterior edge of the lamina disk, minimum depths at the anterior edge).

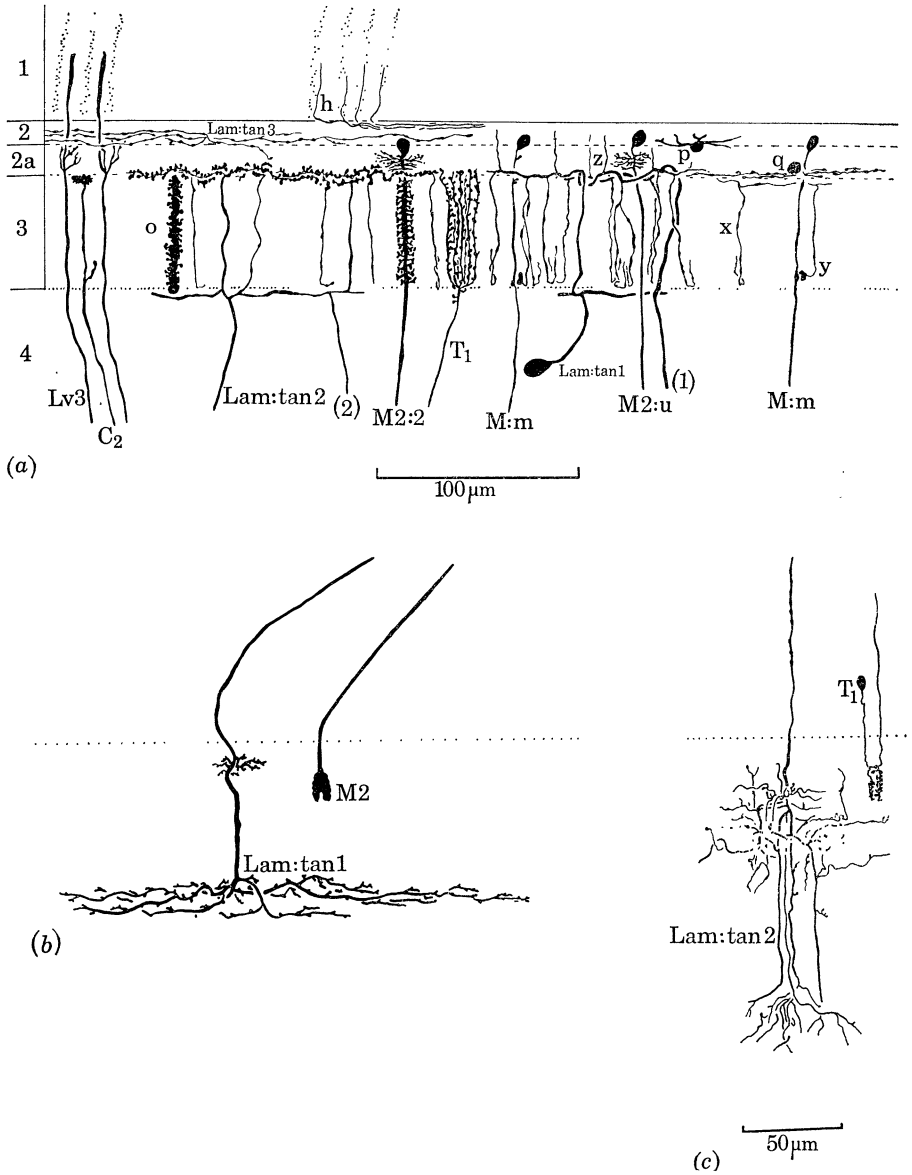


FIGURE 35. *E. tenax.* Summary diagram of the tangential elements of the lamina and their medullary components.

(*a*) The types 1 and 2 lamina tangentials have characteristic forms of processes at the outer margin of the external plexiform layer. The processes of the wide-field long visual fibres and the type 3 lamina tangential are disposed in the same stratum. The processes of the unistratified bilateral monopolar cells (M2 : u) are at the same level as those of the bistratified radial monopolar cell (M2 : 2). Note the two forms of processes of the type 1 tangential in the external plexiform layer (x and y). The epithelial cells (o) are sometimes impregnated by the Golgi stain; they are characterized by their columnar appearance and many small lateral knobs. The basket endings in *E. tenax* consist of only between five and eight perpendicular processes. Two multipolar elements, at two characteristic levels have also been seen in this species (p and q). Lv3 = wide field long visual fibre. C_2 = capped centrifugal ending. Lam: tan 1 = type 1 lamina tangential; (1) its linking-fibre to the medulla. Lam: tan 2 = type 2 lamina tangential; (2) its linking-fibre towards the medulla. z = the outer processes of Lam: tan 1 in the fenestration layer. M: m = midget bistratified monopolar cell. h = fibres from interommatidial receptors (hair apparati) at the retinal surface. Lam: tan 3 = unistratified type 3 lamina tangential.

(*b*) The bistratified medullary ending of Lam: tan 1 with a lobed ending of a radial monopolarcell (M2).

(*c*) A bistratified diffuse element in the medulla. This is most probably the medullary component of Lam: tan 2 (see text). An initial bi-lobed component of a centrifugal T-cell (T_1) to the lamina is shown adjacent to it.

which also projects to the innermost stratum of the medulla (figure 97, plate 22). The lateral processes of both these cell types are oriented strictly antero-posteriorly and dorsoventrally.

Observations on monopolar cell endings in the medulla

These elements end at two distinct levels in the medullae of both the Diptera and the Lepidoptera. A similar stratification of these endings has been detected in other insects; for example in *Libellula*, *Apis*, *Locusta*, *Vespa* and *Calliphora phaenicia* (N. J. Strausfeld, unpublished), in *Tabanus* and *Musca* (Cajal 1910; Cajal & Sanchez 1915) and in *Aeschna* (Zawarzin 1913). Hanström (1924) also showed a similar disposition of analogous elements in many crustacea.

There are four major forms of monopolar cell components detectable in the lamina of the present species of Diptera and similarly four variants of monopolar endings in each of their medullae. Some variations of their lateral extents have been detected at the perimeter of this region where its curvature is greatest and where the medullary columns are widest and somewhat curved. Completely impregnated and reconstructed neurons from serial sections in *Pieris* and *Sphinx* indicate that in these species the midget and small-field radial monopolars end less deeply than the other types. Similarly, in the Diptera there are two forms of shallow endings and two forms which end between 5 and 10 μm deeper. Reconstructions of whole monopolar neurons from serial sections lead to the conclusion that the unistratified and bistratified midget monopolar cells and unilateral bistratified monopolar cells end shallowly, and that others lie in the stratum directly beneath them. This arrangement agrees with observations of other species by the Spanish authors and with observations of *Apis* (N. J. Strausfeld, unpublished). The forms of these monopolar cells in the two species of *Calliphora* and in *E. tenax* are summarized in figures 79 and 80. The deep monopolar endings are characteristically lobed: each lobe is compressed dorsoventrally. The lateral spread of this ending is equivalent to the embrace of type 1a transmedullary cell processes at the same level (figure 170).

The projection of centripetal fibres from the lamina to the medulla

Quartets of four fibres can be detected in Holmes–Blest reduced silver preparations which leave the lamina directly beneath its inner face. It is sometimes possible to trace two of the four fibres peripherally, through the axis of an optic cartridge, back as far as the monopolar cell bodies, and the others as far as the basement membrane of the retina. Phase-contrast illumination of gluteraldehyde-fixed material indicates the same arrangement. All four fibres have diameters equivalent to those of monopolar cell fibres and long visual cell fibres. The thinner fibres of the centrifugal cells to the lamina cannot be detected by these methods and it is extremely difficult to resolve them by phase-contrast illumination. However, in *Calliphora* each quartet of centripetal fibres can be traced through the outer segment of the first optic chiasma into its inner segment as far as between 20 and 40 μm from the medulla surface. There the quartet appears to split into two components each consisting of a pair of fibres (figure 37, plate 15). These project separately into the medulla where one fibre of a pair ends shallowly and the other deeply (figure 38, plate 15). The depths of these endings are equivalent to those of monopolar cells and long visual fibres, respectively. Thus, instead of the 'Quads' of endings characteristic of *Pieris* (part I) and *Apis* (unpublished) the first-order receptor inputs (visual cells 7 and 8) and first-order interneuron (monopolar cells) inputs to the medulla of these Diptera commonly end in pairs. Golgi preparations also reveal that a pair of terminals from the retina contains a shallow monopolar cell ending and a deep long visual fibre ending within

the same medullary column (figure 43, plate 15 and figures 44 and 47, plate 16). Surface sections of this region reveal these paired fibres in cross-section as regularly spaced stipples (figure 42, plate 15). In *Pieris* each of these stipples is commonly composed of the cross-sections of four fibres. Golgi stains of this species reveal four input elements ending in the same medullary column. In the Diptera the stipples cannot be accurately counted simply because of the technical difficulty of cutting a whole medulla so that all the sections are tangential to its surface. This region is much flatter in the Lepidoptera and the clarity of staining is superior. However, a rough estimate of the proportions of these stipples to optic cartridges can be derived by a somewhat devious and indirect approach; in the horizontal cross-section the length of the medulla's surface is approximately equivalent to that of the retina at the level of the basement membrane. The ommatidia are represented in a 1 : 1 ratio by the optic cartridges. If these latter units are similarly represented in the medulla one would expect the spacing of medullary columns to be equal to that of the ommatidia at the level of the basement membrane. However, there are approximately two medullary columns per ommatidium in horizontal sections and slightly more in vertical sections. The actual distances between columns in the horizontal plane is, on average, 9 μm although at the perimeter of the medulla this increases to between 11 and 15 μm. It is not absolutely certain that every optic cartridge is represented by two columns in the medulla. Occasionally two long visual fibres have been detected lying closer together than this inter-column distance; both together are accompanied by a single monopolar cell ending and thus comprise a triplet of fibres (figure 61). Since it seems that at least one type of monopolar cell is effectively looking in the same direction as those retinula cells which synapse onto it (Scholes 1969) more than one monopolar cell 'looking' at the same restricted portion of the

Description of plate 15

The medulla

Figure 36. *C. erythrocephala* (Holmes–Blest preparation). The centripetal fibres from the lamina in the inner segment of the first optic chiasma (1st O.C.) enter the outer face of the medulla. Groups of fibres are arranged at the medulla's surface more or less equidistant from one another. The medulla is stratified (1 to 8) and columnar.

Figure 37. *C. vomitoria* (Holmes–Rowell preparation). Quartets of fibres (arrowed, a) from the lamina split into pairs in the inner segment of the chiasma near the medulla's surface. Each pair (arrowed, b) is clearly identifiable at the surface of this region. The two pairs derived from a quartet are displaced obliquely from another. However, the distance between them very rarely exceeds 15 μm (see figure 169), and is usually between 7 and 11 μm.

Figure 38. *C. vomitoria* (Holmes–Blest preparation). Each pair of endings consists of a shallow terminal (monopolar cell, m) and a deep terminal (long visual fibre, Lf).

Figure 39. *E. tenax*. Three club endings of long visual fibres. Note the characteristic swelling from each at the surface of the medulla.

Figure 40. *E. tenax*. The medullary ending of a wide-field long visual fibre.

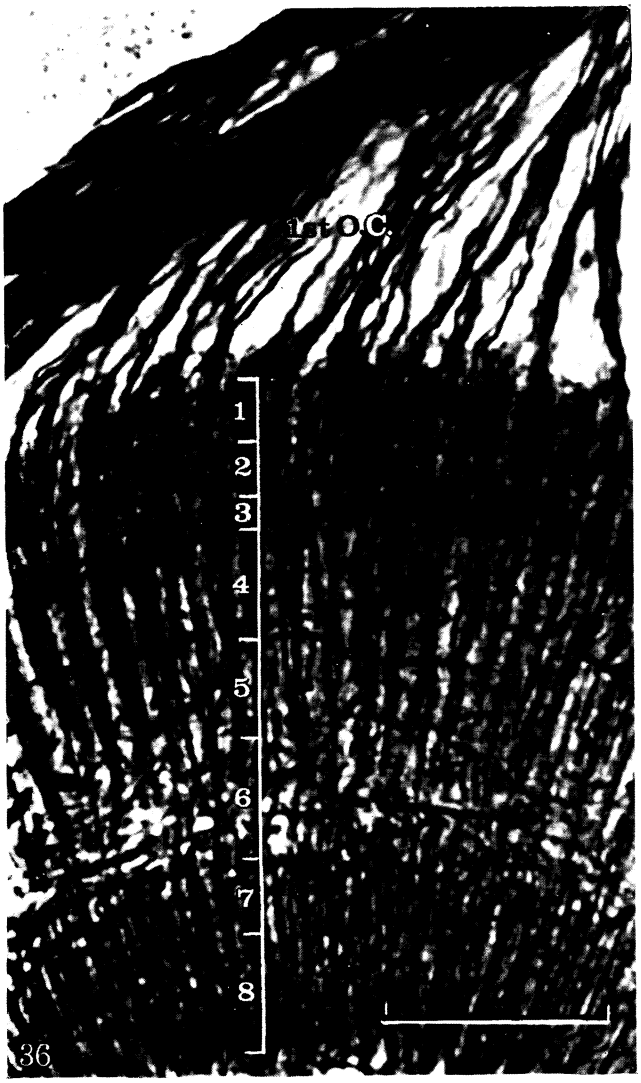
Figure 41. *E. tenax*. Left: a long visual fibre forked ending with lateral processes near the outer surface of the medulla. Some forked endings lack these components completely, others may have extremely small processes at this level. Right: a pair of endings in the same column; the outermost is derived from a bilateral monopolar cell and the deeper terminal from a smooth long visual fibre.

Figure 42. *C. vomitoria*. (Bielschowsky preparation).† Tangential sections of the medulla surface are stippled: each stipple represents a pair of fibres (ringed) from the lamina (a long visual fibre and monopolar cell fibre). Note the regular distribution of these input pairs.

Figure 43. *C. erythrocephala*. High-power photomicrograph of the two lobes of a long visual fibre forked ending.

Scales: Figure 36, 40 μm; figures 37, 38, 42, 10 μm; figures 39 to 41, 10 μm; figure 43, 10 μm.

† See Romeis (1948). The whole block impregnation method can be modified for wax impregnated material (N. J. Strausfeld & V. Braitenberg, in preparation).



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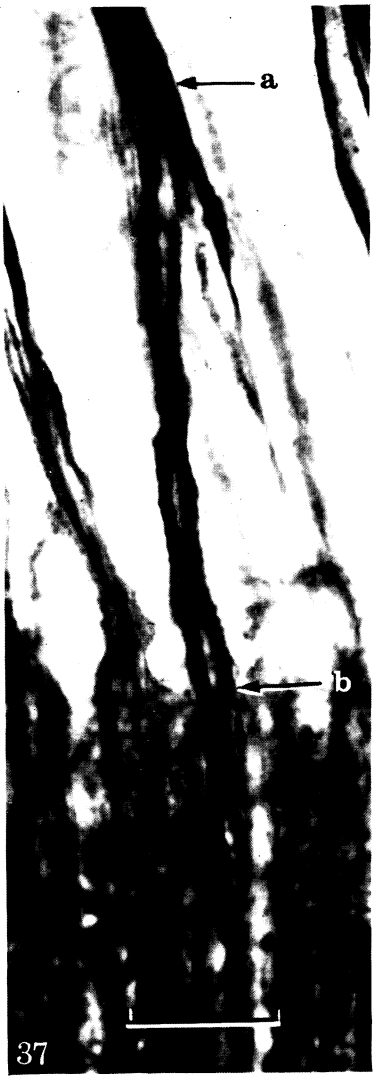

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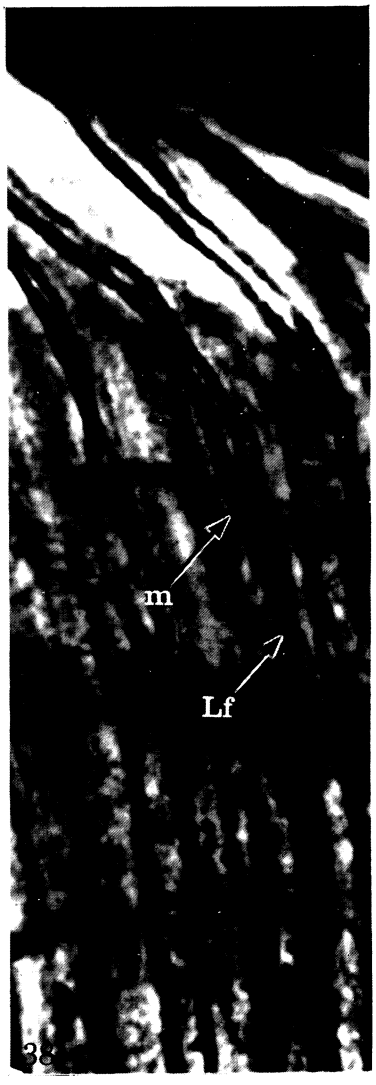

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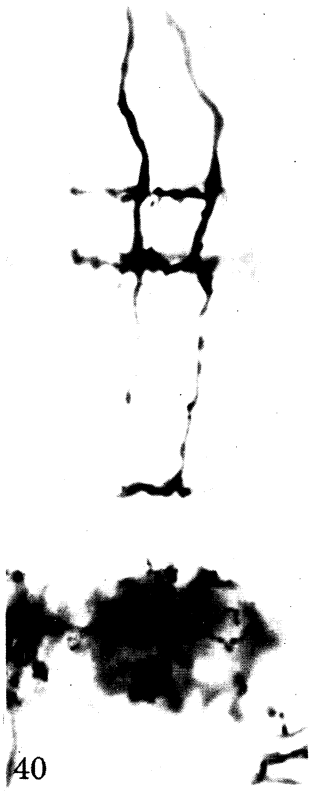

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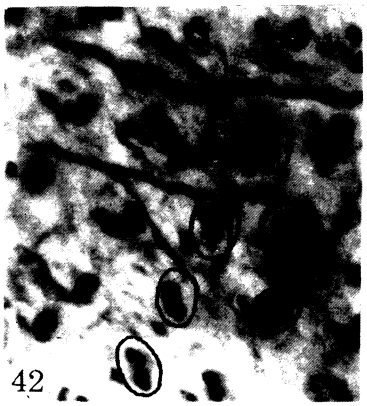

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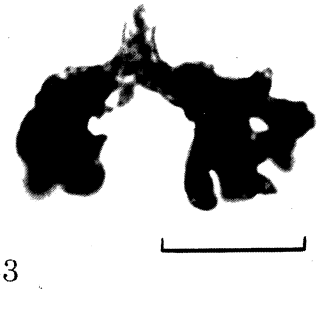

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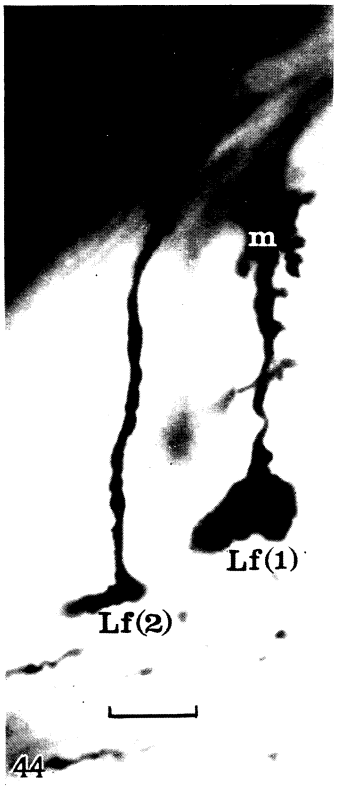

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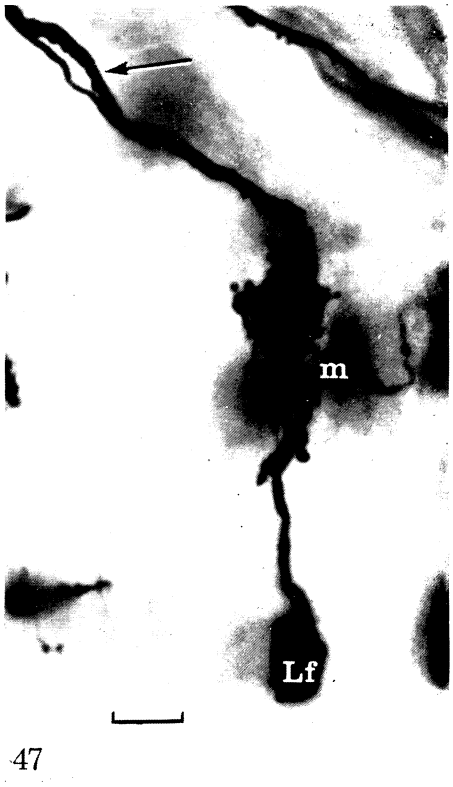

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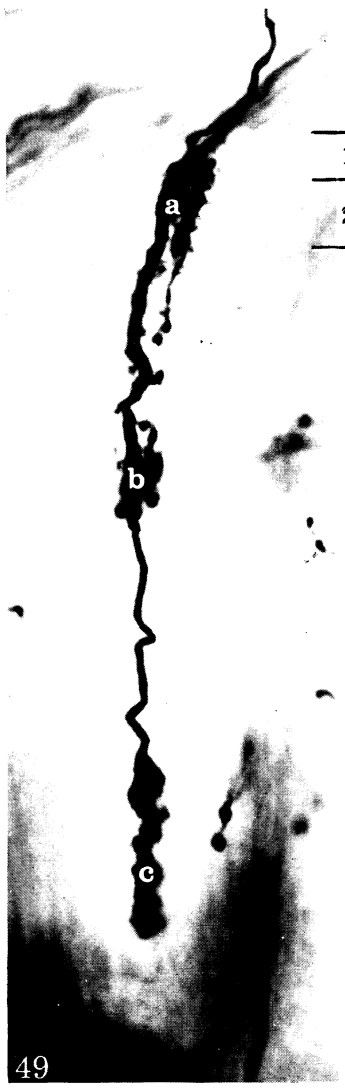

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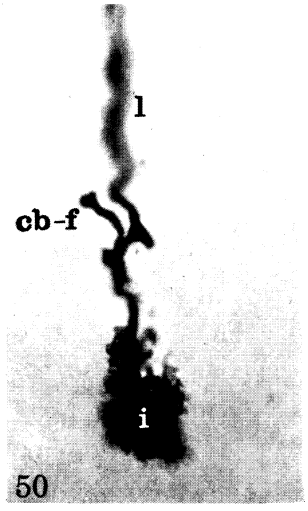

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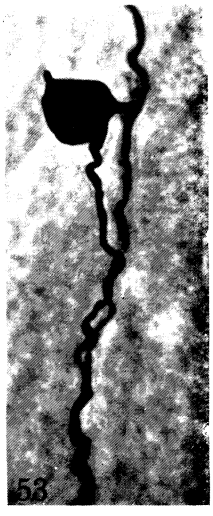

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total visual field may have to make contact with the same small-field element in the medulla. If this is so, and it must be pointed out that this is merely speculation, some convergence of their topographical lateral relationships might be expected if two optic cartridges had a closely similar optic alignment. Such local variations of projection pattern between first-order interneurons converging at the same medullary column might have a similar functional basis as the local chiasmata between retinula cells from the retina to the lamina (Cajal 1909; Trujillo-Cenoz & Melamed 1966; Braitenberg 1967).

Observations on centrifugal elements to the lamina

The type 1 and 1a T-cells

The medullary components of the type 1 T-cells lie in the outermost strata, between monopolar cell endings. In *E. tenax* and the two species of *Syrphus* they consist of two identical sets of processes at the same level, each of which is closely apposed to the deeper monopolar endings from the lamina in two adjacent columns (figures 35 and 170). The cell-body and linking-fibres of these T-cells, the shallow monopolar endings and the type 2 centrifugal cells all have characteristic unilateral 'ruffles' in the inner segment of the first optic chiasma (figures 51 and 52, plate 16). They have been seen in every successful impregnated preparation and appear to be a characteristic feature of these fibres (both Golgi–Colonnier preparations and osmium-fixed material consistently shows these structures). Cajal & Sanchez, using a different Golgi procedure, also figured similar short lateral projections from these linking-fibres. Some mid-brain fibres also have similar lateral protuberances within tracts and others may have distinct blebbed collaterals outside the clearly demarcated mid-brain regions. The cell-bodies of the medulla to lamina T-cells sometimes appear to be multipolar. That is to say they have, in addition to the cell-body fibre, other lateral extensions restricted to the cell-body cortex (figure 53, plate 16). Cajal & Sanchez figured and also described these from the cell-bodies of type 1 T-cells in the bee and in *Tabanus*. They also detected 'multipolarity' of one type of monopolar cell-body in the lamina of *Agrion*. Cell-bodies in the calyces of corpora penduculata have similar prolongations (Kenyon 1896; Sanchez 1933; Strausfeld, in preparation). In all three instances different Golgi stains were used.

Description of plate 16

The medulla

Figure 44. *C. vomitoria*. Two long visual fibre forked endings, Lf (1) and Lf (2). Lf (1) is accompanied by a lobed ending of a radial monopolar cell (m).

Figure 45. *C. erythrocephala*. Vertical section. A forked ending and the initial component of a medulla-lamina T-cell. These lie between the axes of adjacent medullary columns, in the horizontal plane.

Figure 46. *S. elegans* (vertical section). Three lobed endings of radial monopolar cells in three adjacent medullary columns.

Figure 47. *S. elegans*. A bilateral monopolar cell ending (m) and a long visual fibre club ending (Lf) in the same column. The paired arrangement of their two linking-fibres is clearly visible (arrowed).

Figure 48. *C. erythrocephala*. The bistratified medullary subfield of the type 1 lamina tangential.

Figure 49. *C. erythrocephala*. The tristratified initial component of a type 1a medulla-lamina T-cell.

Figures 50, 51. *C. erythrocephala*. Two different planes of focus of an initial component of a type 1 medulla-lamina T-cell. Note the tightly packed arrangement of processes in the medulla (figure 50) and the unilateral ruffles from the linking-fibre in the first optic chiasma (figure 51). l = linking-fibre; cb-f = cell-body fibre; i = initial component.

Figure 52. High resolution photomicrograph of the unilateral ruffles.

Figure 53. *S. elegans*. The characteristic 'multipolar' T_1 cell-body of the Syrphidae.

Scales: figures 44 to 46 and 48 to 51, 10 μm; figures 47, 53, 10 μm; figure 52, 5 μm.

The initial components of the type 1a centrifugal cells are bi- or tristratified. The outermost group of processes look like those of the type 1 element; they are densely branched and have minute spines and blebs. Each group gives rise to a perpendicular fibre which descends as far as the deepest stratum of the medulla where it branches to form between five and seven short tuberous processes: these have, together, a lateral extent equivalent to a medullary column. Fine descendant collaterals have been seen from the outer groups, in *E. tenax*, which extend as far as the level of the miniature and tristratified long visual fibre endings. There are also short lateral processes from the axis-fibre in stratum 5 or 6. The lateral extents of the deeper groups of processes are also equivalent to a single medullary column.

The type 2 and 3 centrifugal cells

Both these elements are derived from cell-bodies situated beneath the inner face of the medulla. Cell-body fibres of the type 2 cells project to the inner face of this region and continue through all its strata as perpendicular axis-fibres. These extend further from the surface of this region as linking-fibres to the lamia via the first optic chiasma, where they terminate as capped endings. The medullary component of this cell-type is tristratified; there is a characteristic vertical bilateral set of processes in the deepest stratum, another at the same level as the deepest long visual fibre endings and a third at the outer face of the medulla. This latter portion consists solely of a local thickening of the axis-fibre and a single recurrent process at the same level together giving the appearance of a tuberous inverted U (figure 60, plate 17). The lateral spread of the deepest processes in the species of *Calliphora* is between 15 and 20 μm either side of the axis-fibre. In the Syrphidae it does not exceed 15 μm. The processes of the middle group have been seen 'climbing' over the club-endings of long visual fibres. Those in the deepest stratum have been detected intermingled amongst shallow T-cell processes. Both types of processes appear extremely closely applied against one another as do those of adjacent type 2 centrifugal cells.

The cell-body fibres of the type 3 centrifugal cells project as far as the serpentine or outer layer of the medulla where they give rise to perpendicular axis-fibres. These either extend

Description of plate 17

The medulla

Figure 54. *C. erythrocephala* (phase contrast of thin Golgi stained sections). Shallow long visual fibre endings. Note the extremely slender lateral processes.

Figure 55. *E. tenax*. Variants of long visual fibre club endings. These have only been detected posteriorly in the medulla. Note the thin lateral processes from the swollen tips.

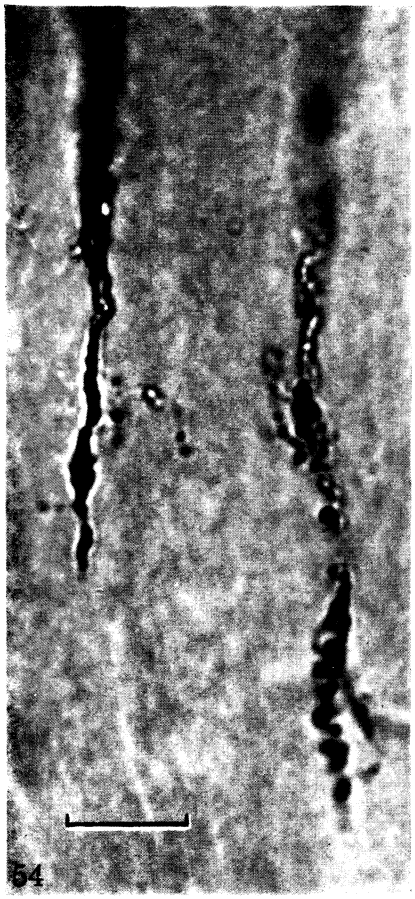
Figures 56, 57. *E. tenax*. The perpendicular topographical relationships between an initial component of a T_1 cell, long visual fibre club endings (Lf), a lobed (radial) monopolar cell ending (m), the outer and middle specializations of a type 2 centrifugal cell to the lamina (Co and Cm, respectively) and a diffuse medullary amacrine cell (am).

Figure 58. *C. vomitoria*. Initial components of bistratified T_{1a} cells and unistratified T_1 cells, together at the anterior perimeter of the medulla.

Figure 59. *C. erythrocephala*. A pair of endings from the lamina (Lf, long visual fibre ending; m, monopolar cell ending) and a tristratified initial component of a T_{1a} cell.

Figure 60. *C. erythrocephala* (vertical section). The medullary component of two type 2 centrifugal cells to the lamina. Note the inverted U arrangement of the outermost specialization (Co), the vertically oriented bilateral processes in the serpentine layer (Cm) and the processes adjacent to the inner face of the medulla in stratum 8 (Ci). A shallow T cell (T_3) is also shown. The spacing of the axis-fibres of these elements indicates that they are located in adjacent columns.

Scales: figure 54, 5 μm; figure 55, 20 μm; Figures 56, 57, 20 μm; figures 58 to 60, 10 μm.



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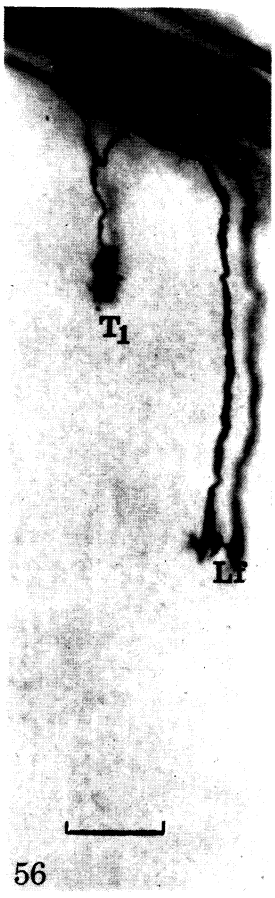

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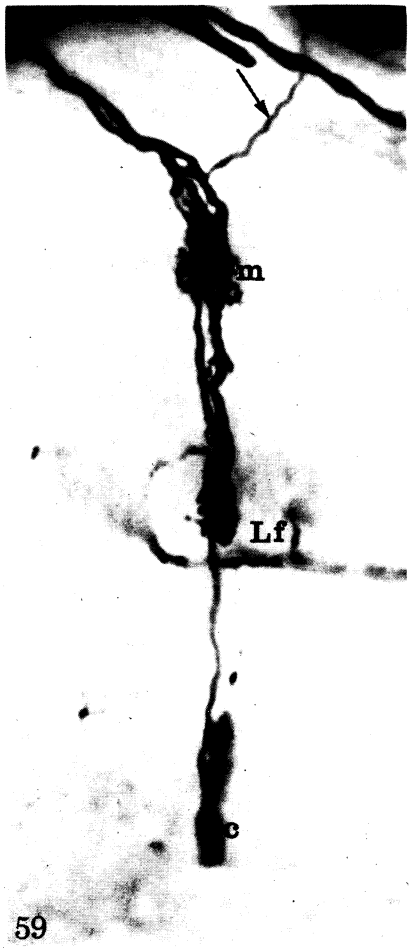

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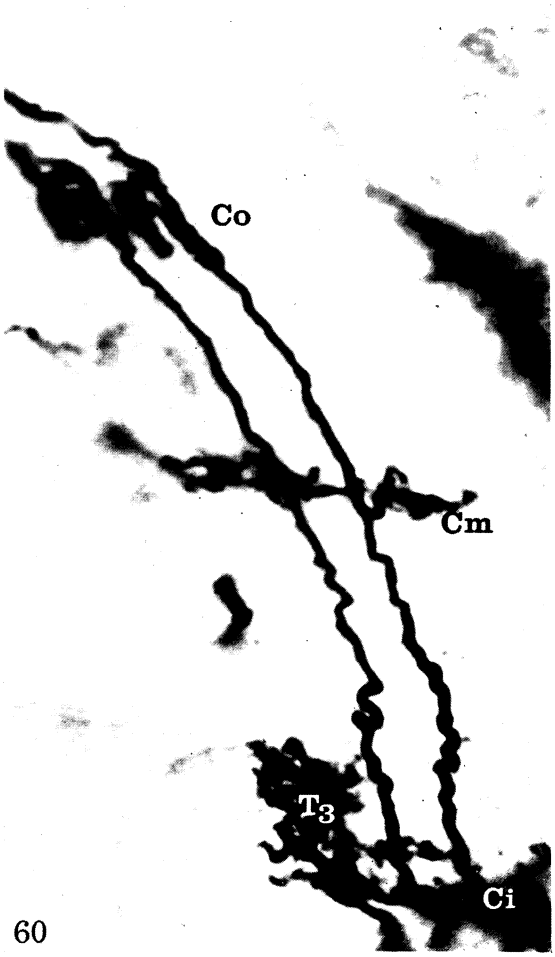

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through all levels of this region or within the outer and serpentine layers. In either case they are tristratified; the outer group of blebbed processes is located at the same level as the monopolar cells; the middle group is arranged bilaterally from the axis-fibre, like those of the type 2 cells, at the level of the deep long visual fibre endings. The innermost group consists of a cascade of fine processes which pass through the inner layer of the medulla or a group of blebbed processes restricted to strata 7 and part of 8. The lateral spread of these groups is equivalent to $1\frac{1}{2}$ medullary columns. Each perpendicular axis-fibre extends, via the first optic chiasma, to the lamina where it terminates as a climbing ending. Both the medullary components of the types 2 and 3 centrifugal cells are shown in figure 62.

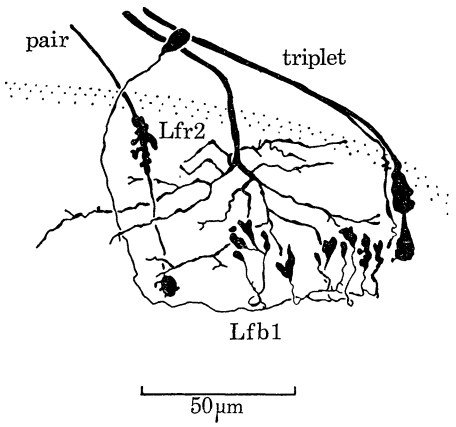

FIGURE 61

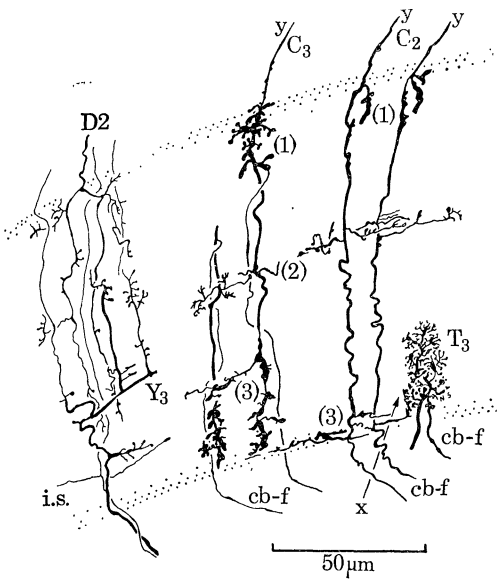

FIGURE 62

FIGURE 61. *C. erythrocephala* (camera lucida drawing of an oblique horizontal section of the medulla). Endings from the lamina usually end as pairs; some, however, end in triplets. The third ending is usually a shallow long visual fibre terminal and is displaced between 3 and 5 μm laterally from the other. A large-field bilateral amacrine cell (Lfb1) has swollen tuberous processes arranged so that they are disposed directly beneath long visual fibre club endings. A large-field radial unistratified amacrine cell is also situated at the same level (Lfr2).

FIGURE 62. *C. erythrocephala* (camera lucida drawing of a vertical section of the medulla). The medullary components of two type 2 centrifugal elements to the medulla (C_2) and the whole, and a part of another, type 3 centrifugal element (C_3). Both these components are tristratified (1, 2 and 3). The cell-body fibres (cb–f) of C_2 prolongate as axis-fibres in the medulla. Cell-body fibres and axis-fibres of C_3 form T-junctions in the outer layer of the medulla. Deep lateral processes of C_2 climb over the initial components of shallow T-cells (T_3) and adjacent C_2 processes. Deep processes of C_3 are restricted to one medullary column in medulla stratum 8 but extend through adjacent columns in stratum 7. A variant of a deep Y-cell (Y_3) is als oshown; its processes interdigitate with those of a diffuse amacrine cell (D2). Fine fibres (between 0.4 and 0.2 μm diameter) have also been detected climbing over Y_3 cell processes. These are included as *incerta sedis* (i.s.). y = linking fibres to the lamina.

Observations on class II components derived from the lamina

Each subfield of the type 1 tangential cell gives rise to several axis-fibres that end in the medulla. Each terminal consists of an outer group of processes at the level of the shallowest monopolar cell endings in stratum 1 and a second group directly beneath the deepest monopolar cell endings in stratum 3. The branching pattern and field shape of this deeper component (figure 48, plate 16) is mirrored by that of the wide-field amacrine cell at the same level.

The outermost group is compressed dorsoventrally so that it has a lateral spread through 2 or 3 pairs of class I endings derived from the lamina. The second group of processes embraces a disk-shaped subfield whose diameter is equivalent to between 20 and 30 medullary columns. Adjacent deep subfields overlap but the extent of this is not yet clear. The outer groups are clearly separated from one another by intervals of at least 15 columns.

Incerta sedis

Cajal & Sanchez described and figured a third form of ending in the medullae of *Tabanus*, *Calliphora* and *Apis* which they claimed was derived from the lamina. But this form of ending (no. 10 in Bullock & Horridge's 1965 classification) is remarkably similar to the stratified diffuse amacrine of the Lepidoptera and Diptera, which have their cell-bodies located at the extreme periphery of the cell-body cortex surrounding the first optic chiasma. Incompletely impregnated cell-body fibres can easily be confused with other class I linking-fibres between the lamina and medulla. There is, though, another form of stratified diffuse ending in the medullae of *E. tenax* and *S. nitidicollis* which is certainly derived from the lamina (figure 35) even though it does not appear to cross over via the first optic chiasma. Although this fibre has not been followed the whole way back to its respective lamina component it seems likely that it is derived from the second species of tangential element (see p. 146) in the outermost region of these insects.

Some extremely fine processes, between less than 0.2 and 0.5 μm in diameter have been seen in the first optic chiasma that arise from cell-bodies in the cortex. These fibres pass through the medulla as far as the lobula where they become so slender as to be unresolvable. No lateral processes have ever been detected from these fibres and it is doubtful whether they should be considered noteworthy components of the optic lobe's architecture. There is recent evidence that morphogenetic death might occur amongst optic lobe neurons when they may be presumed not to have established relationships with other elements (Nordlander & Edwards 1968). Possibly it is these cells that are sometimes impregnated. They are most frequently detected in young emergent animals but rarely if ever in older flies. A possible 'non-relationship' with other elements may be reflected by their characteristic lack of lateral processes.

Class I elements in the medulla destined for the lobula complex

Observations on transmedullary cells

These cells link the medulla and lobula. Their cell-bodies invariably lie above the outer face of the medulla and they all have two or more distinct groups of processes in this region.

One type of transmedullary cell, common to every species† that has been stained (see also part I) ends in the outermost stratum of the lobula. There are at least three forms common to each species of Diptera; these include the former (type 1) cell, the type 2 elements that end more deeply in the lobula and the type 3 (diffuse) cells. Other forms of transmedullary cells are characteristic of families or are species specific in form (see figures 63 to 69, plate 18, and figures 80 and 81). There are at least six distinct types of transmedullary cell in the present species of *Calliphora* and in *Eristalis* there are at least nine.

The type 1 (Tm1) cell has two distinct groups of processes; outer processes are arranged bilaterally (vertically) from the axis-fibre and have been seen wrapped around radial monopolar cell endings: the inner group lies at the same level as the bushy T-cells. Outer processes

† These also include: *Apis mellifica*, *Vespa silvestris*, *V. germanica*, *Bombus rupestris*, *Musca domestica*, *Calliphora phaenicia*, *Locusta migratoria*.

are characteristically spiny and the inner are tuberous or varicose. Both groups have lateral extents equivalent to one medullary column in the species of *Calliphora* and *Syrphus*. In *Eristalis* some processes near, and at, the surface of the medulla extend into adjacent columns.

The type 2 transmedullary cells have an outer group of spiny processes at both levels of the monopolar cell endings, and an inner group of blebbed processes at the level of the shallow T-cells, but above the bushy T-cells (see p. 203). The lateral extents of both outer groups are usually equivalent to $1\frac{1}{2}$ medullary columns, except at the perimeter of the medulla where the outermost processes extend through a maximum of five columns (see p. 199). The type 3 (Tm 3) transmedullary cells have processes arranged diffusely down the whole length of the axis-fibre. Other transmedullary cells have processes that may be clustered into groups (Tm 6, for example) and their lateral extents can vary between different strata. In addition, there are other forms which have wide-fields in the medulla that are usually tri- or quadristratified. All the variants of form are illustrated in figures 79 to 81, and described in the accompanying figure legends.

In all orders where both the types 1 and 2 cells have been identified the type 1 cells terminate in the outer stratum of the lobula and the type 2 cell beneath it in stratum 2. Other variants of transmedullary cells end in strata 2 and 3 or exclusively in stratum 3. These deeper endings have shapes that are again characteristic to their medullary components (see figures 140*a* and 141*a* and summary figure 141*b*).

The axis-fibres of the types 1 and 2 transmedullary cells together, as pairs, define the axes of medullary columns (see part I). They can be seen in reduced silver preparations as fibres that extend from the outer face of the medulla, through the region, into the second optic chiasma. Their lateral topographical relationships are difficult to determine from reduced silver preparations since these do not show lateral processes with any clarity. However, in some well stained Golgi preparations many of these cells are shown up in a single section. In the most dense populations they are spaced so that there is one of each type (1 and 2) per column-interval. The outer processes of type 1 cells do not overlap whereas those of the type 2 cells certainly overlap their immediate neighbours. Both types of outer processes lie at the same level as the monopolar cell endings and the outermost part of the long visual fibre endings. There seems to be a special relationship between the vertically oriented lobed endings of radial monopolar cells and the similarly oriented fields of the type 1 cell processes. The latter may also be intimate with other neurons, since they extend further into the medulla than do the first-order interneuron endings from the lamina.

All transmedullary cells have at least one group of processes that lie at the same level as efferent fibres from the lamina; this relationship is also implied by the arrangements of these class I elements in other orders (Zawarzin 1913; Cajal & Sanchez 1915; N. J. Strausfeld, unpublished). All the available information about these cells in the present species and others is summarized in table 1.

Observations on T- and Y-cells

T- and Y-cells link the medulla with the lobula or lobula plate, and the lobula and lobula plate, respectively. T-cell perikarya lie between the inner face of the medulla and the lobula plate or behind the posterior face of this region. In the Syrphidae the Y-cells characteristically have perikarya situated above the outer face of the medulla. In the species of *Calliphora* and the Lepidoptera these lie either between the medulla and lobula plate or above the medulla. The

cell-body fibres of T- and Y-cells project to the innermost stratum of the medulla where they give rise to characteristic sets of processes.

Three forms of T-cells link the medulla to the lobula or lobula plate. These have been described in the Lepidoptera (part I) and analogous forms have been seen in *Apis* and *Vespa* (N. J. Strausfeld, in preparation). In the Diptera the deep T-cell (T_2) extends as far as the level of the shallowest long visual fibre endings in the medulla and ends deeply in the lobula. It is characterized by the bistratified diffuse arrangement of the medullary processes (figure 67, plate 18); the inner group has a lateral extent through a maximum of $1\frac{1}{2}$ columns, the outer processes extend through between 2 and 6 columns. The processes of the shallow T-cells (T_3) have a characteristic arrangement in the two innermost strata of the medulla (figure 70, plate 18) and lie at the same level as the inner processes of the types 1 and 2 transmedullary cells. Their lateral spread is approximately equivalent to a single medullary column.

The bushy T-cells (T_4) have single sets of processes in the deepest stratum of the medulla that have a characteristic unilateral arrangement from their axis-fibres (figure 72, 73 and 74, plate 19). Their lateral extent just exceeds that of two medullary columns in the horizontal plane and only one in the vertical plane (figure 170). The deep T-cells end in the third stratum of the lobula: the shallow T-cell endings are situated in the second stratum of this region and the bushy T-cells end in the lobula plate. The field-spreads of their lobula plate endings overlap marginally in both planes. The field-spreads of the bushy T-cells in the medulla overlap marginally in the vertical plane (figure 75, plate 19), and by about one-quarter of their extent in the horizontal plane (figure 170). A giant form of the shallow T-cell has been detected in one preparation of *E. tenax*. No other giant T-cells have been detected in the medulla of Diptera although the deep T-cells have larger lateral extents at the perimeter of this region than they do elsewhere. There is also a giant diffuse T-cell in the Lepidoptera which has not been detected in the Diptera.

The Y_1 cells give rise to processes in the medulla which extend as far as the level of the long visual fibre endings. Those of Y_2 cells have a quasi-tangential arrangement within the innermost stratum of this region. The Y_1 cells have plug or narrow-field branched endings in the

Description of plate 18

The medulla

Figure 63. *E. tenax*. Type 1 transmedullary cells.

Figure 64. *E. tenax*. A type 2 transmedullary cell.

Figure 65. *E. tenax*. A type 3 transmedullary cell.

Figure 66. *E. tenax*. A wide-field variant of the type 2 transmedullary cell (Tm2). The lateral spreads of the outer swelling of the centrifugal element (C_2) and the monopolar cell ending (m) are equivalent to the width of a medullary column.

Figure 67. *C. vomitoria*. Three deep T-cells (T_2) and a shallow T-cell (T_3). The deep T-cells are bistratified; the inner group of processes is characteristically disposed in stratum 7. Those of the shallow T-cells are disposed in stratum 8 and the inner half of 7. Note their linking-fibres and cell-body fibres from the axis-fibres at the inner face of the medulla (i.f.).

Figures 68, 69. *E. tenax*. A diffuse transmedullary cell. Only part of this element can be resolved by direct illumination (figure 68). However, its slender descendant processes, from stratum 4, can be revealed by side illumination (figure 69).

Figure 70. *C. erythrocephala*. Two (shallow) T_3 cells in adjacent medullary columns. The inner stratum of processes of a T_2 cell is situated to the right, in the subadjacent column. cb-f = cell-body fibres. l-f = linking-fibre to lobula. 2nd O.C. = second optic chiasma. L.P. = lobula plate.

Scales: Figures 63 to 66 and 68, 69, 40 μm; figures 67, 70, 10 μm.

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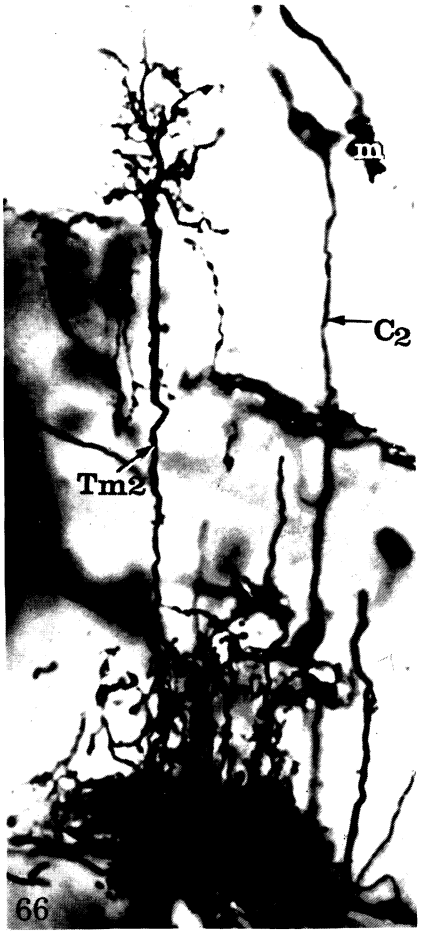
64


65



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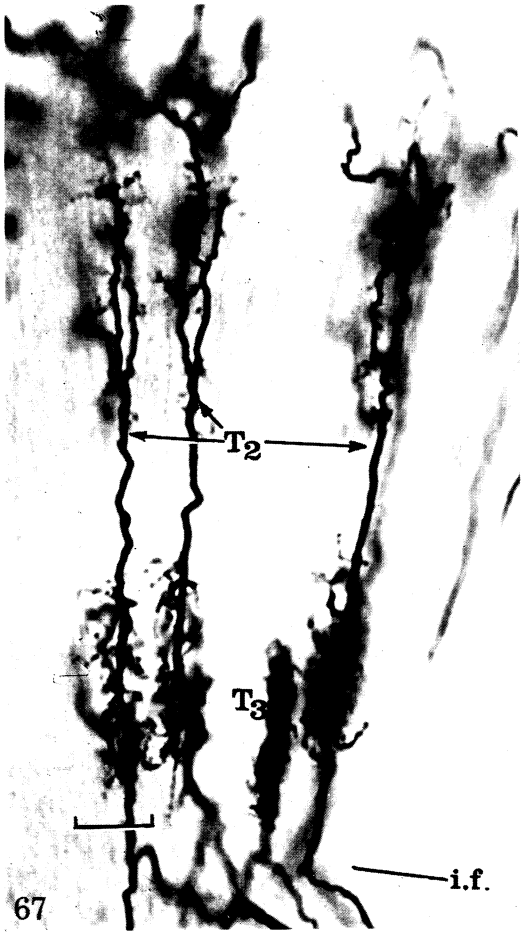

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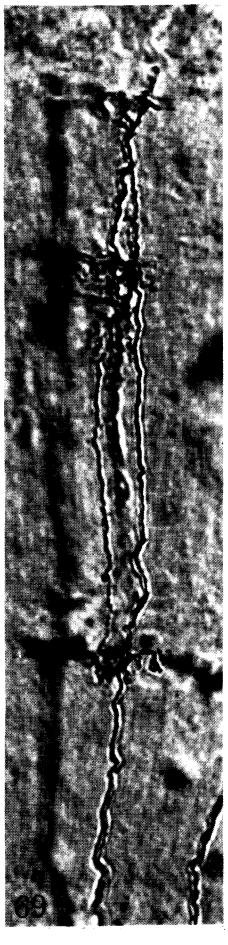
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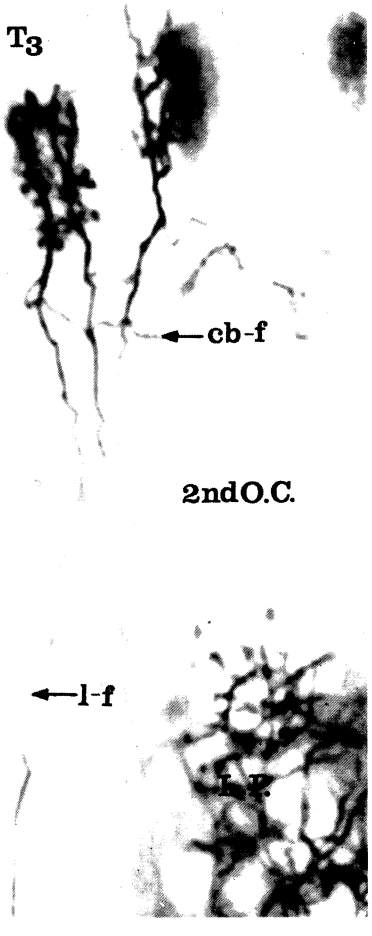

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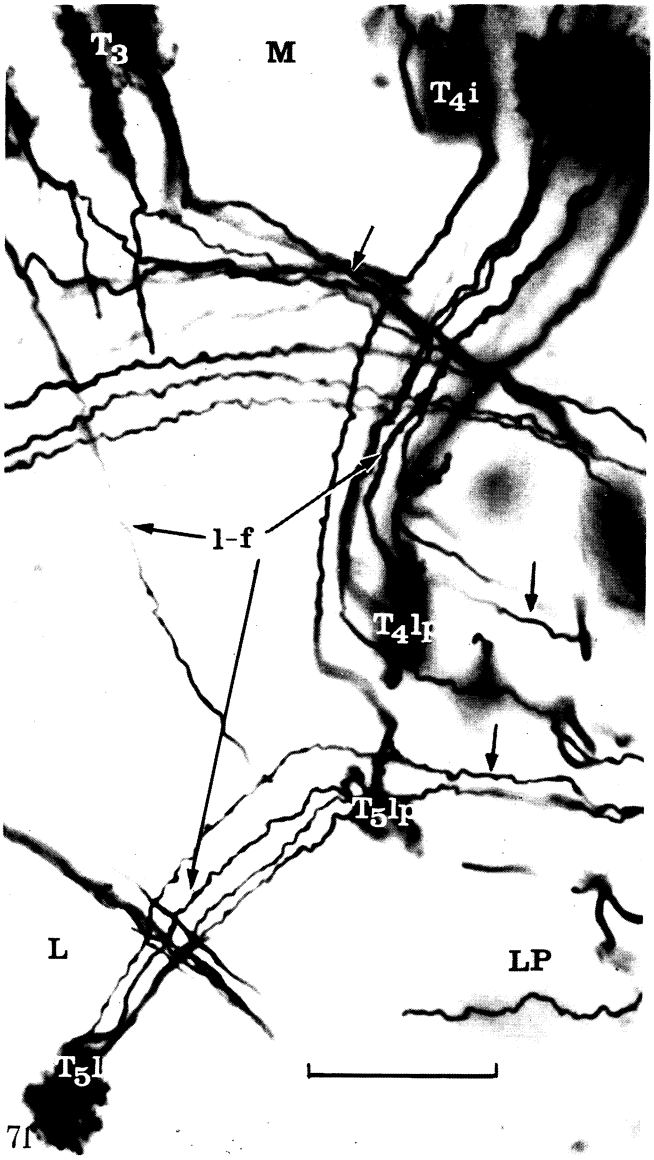

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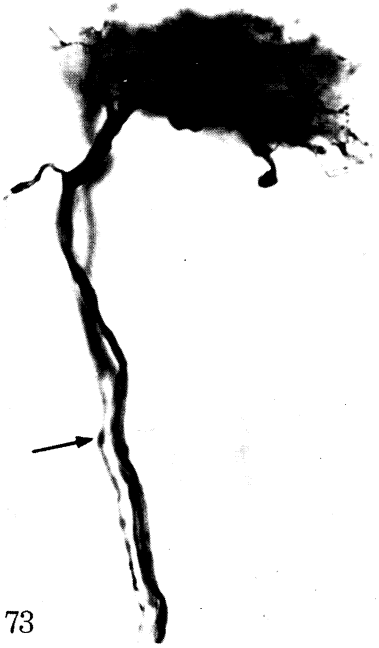

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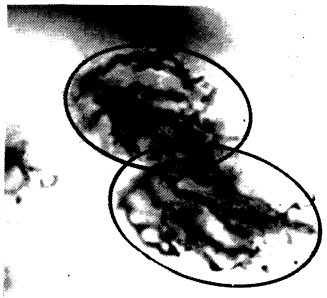

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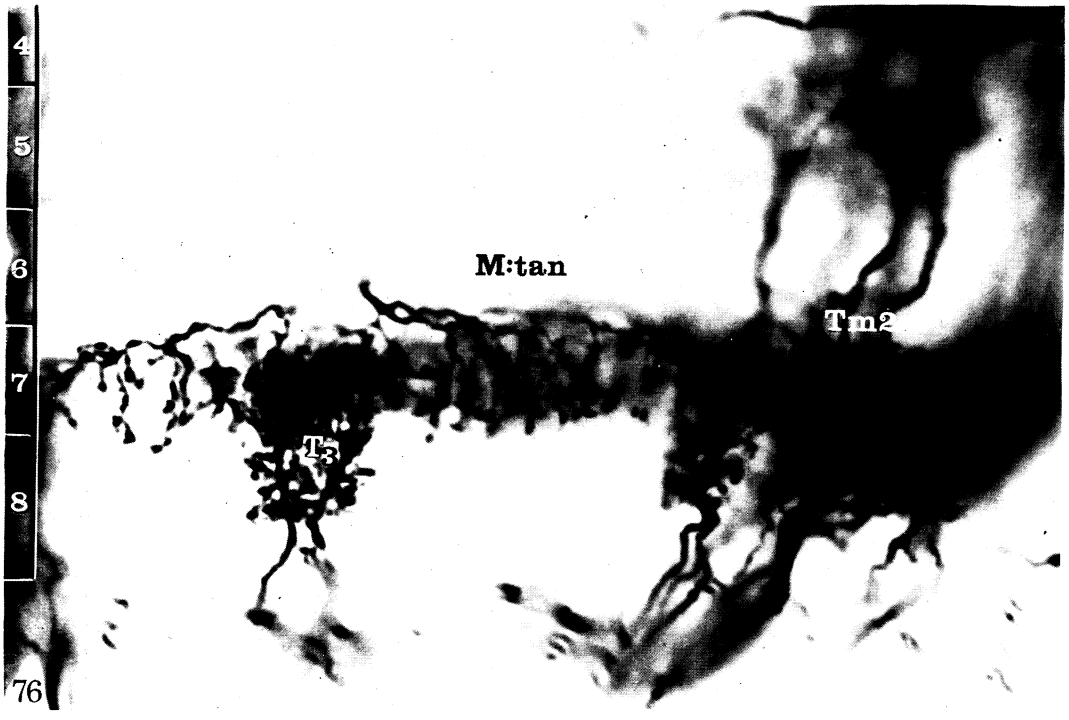

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lobula plate and multi-stratified endings in the lobula; these latter components have one or more lateral processes in the first stratum of the lobula and a second set restricted to the deepest lobula stratum. Y_2 cells have wide-field endings over the surface of the lobula plate and deep endings in the lobula. The three forms of Y-cells in *Calliphora* are shown in figures 62 and 79. There are four forms of Y-cells in the Syrphidae; their medulla and lobula complex components are shown in figures 80 and 81, respectively. Table 2 summarizes all the available information. Figures 140 and 141 show their endings in the lobula complex.

Class III cells in the medulla

Nine forms of amacrine cells have been identified in *Pieris* and four in *Sphinx*. There are at least 17 forms in the two species of *Calliphora* and many more in the Syrphidae. Although amacrine cells show a great variety of form they can, however, be grouped into four major categories. These are diffuse, wide-field, small-field and asymmetric amacrines. These cells are illustrated and summarized in figures 79 and 104, and figures 95–103, plate 22.

Amacrine cells are relatively infrequently impregnated. The small-field elements are particularly difficult to detect amongst other class I and II components. For example, the form of amacrine cell illustrated in figure 61 has only been seen in its entirety in one preparation of *C. erythrocephala* and *E. tenax*. But fragments of it have been detected in other species. This cell characteristically has a large field, equivalent to that of a large-field radial tangential element. When these two elements are impregnated together their fields lie directly over one another within the same stratum. The tuberous endings of the forked terminals of long visual fibres appear to be intimate with the parallel arrays of these amacrine cell processes. Each pool of amacrine cell processes may possibly be intimate with up to 30 long visual fibre endings arranged in two or three horizontal parallel strips.

Description of plate 19

The medulla

Figure 71. *C. erythrocephala*. This figure shows part of strata 7 and 8 of the medulla (M) and fibres in the second optic chiasma to the lobula plate (L.P.). Linking-fibres from the initial components of bushy T-cells (T_4i) in the medulla end in the lobula plate as characteristic terminals (T_4lp). The cell-body fibres (arrowed) run parallel to the linking-fibres and project through the lobula plate to their respective perikarya. Cell-body fibres of T_3 cells (arrowed) project along the inner face of the medulla to a position between it and the lobula plate. The initial components of lobula-lobula plate T-cells (T_5l) in the lobula are bushy. T_5 cells end in the lobula plate as a collection of between 5 and 6 tuberous processes (T_5lp). The cell-body fibres (arrowed) project through the lobula plate. Note the homotopic projection pattern of T_4 cells, via the second optic chiasma, and the T_5 cells, via the intra-complex tract (see also figure 114, plate 14).

Figure 72. *E. tenax*. Detail of initial components of bushy T-cells. The cell-body fibres (arrowed) are characteristically thin and blebbed.

Figure 73. *E. tenax*. A large form of bushy T-cell at the anterior median perimeter of the medulla which extends through $2\frac{1}{2}$ columns.

Figure 74. *E. tenax* (tangential section). The field shape of the initial component of a T_4 cell.

Figure 75. *E. tenax* (tangential section). Two vertically adjacent T_4 components in the medulla, showing the extent of dorsoventral overlap between them.

Figure 76. *C. vomitoria*. The perpendicular topographical relationship between the shallow T-cell (T_3), a small oval-field tangential (M: tan) and the inner processes of type 2 transmedullary cells.

Figure 77. *E. tenax* (tangential section). The overlapping fields in stata 1 to 3 of two type 2 transmedullary cells.

Figure 78. *E. tenax* (tangential section). The discrete fields of forked long visual fibre endings in stratum 5.
Scales: Figures 71 to 78, 25 μm.

TABLE 1. TRANSMEDULLARY CELLS

species and transmedullary cell type	medullary component: outer processes at the level of M	medullary component: outer processes at the level of LV	medullary component: inner processes at the level of T_3	medullary component: inner processes at the level of T_4	medullary component: middle processes in strata	lobula component: shallow endings (stratum 1)	lobula component: deep endings (strata 1 to 3)
Pieris							
Tm 1	+	–	+	+	.†	+	–
Sphinx							
Tm 1	+	–	+	–	.	+	–
Apis							
Tm 1	+	–	+	+	.	+	–
Tm 2	+	–	+	+	.	+	–
tristratified Tm cell	+	–	+	–	4 and 5, or 6	–	diffuse ending (2 and 3)
Automeris							
Tm 1	+	–	+	+	.	+	–
Locusta							
Tm 1	+	–	+	+	.	+	–
Tm 2	+	–	+	–	.	+	–
wide-field quadristratified	+	+	+	+	serpentine layer	–	multi-stratified (1, 2 and 3)
Musca‡							
Tm 1 (*a*)	+	–	+	+	.	?	?
Tm 1 (*b*)	+	–	–	–	5	?	?
wide-field tristratified (*a*)	+	–	+	+	.	?	?
wide-field tristratified (*b*)	+	–	–	–	5	?	?
Aeschna§						not traced	
diffuse Tm	+	?	+	+	all		
C. vomitoria							
Tm 1	+	–	+	+	.	+	–
Tm 2	+	–	+	–	.	+	2
Tm 3	+	+ (Lv3)	+	+	1–8	–	3
Tm 4	+	+	+	+	5, 6 and 7	?	?
Tm 5	+	+ (Lv3)	–	–	5	–	diffuse (1–inner face)
Tm 6	+	+	+	+	between 4 and 5	?	?
C. erythrocephala							
Tm 1	+	–	+	+	.	+	–
Tm 1b	+	+	+	+	6	+	–
Tm 2	+	–	+	–	.	+	2
Tm 3	+	+ (Lv3)	+	+	1–8	–	?
Tm 4	+	+	+	+	5, 6 and 7	–	?
Tm 5	+	+ (Lv3)	–	–	5 and 6	–	2 and 3
Tm 6	+	+	+	+	4 or 5	–	bistratified, (strata 1 and 3)
E. tenax							
Tm 1	+	+ (Lv3)	+	+	.	+	–
Tm 2	+	–	+	–	.	+	2
Tm 2a	+	–	–	–	outer half of 7 (inner processes)	–	?
Tm 2 (midget)	+	–	+	–	.	+	2
Tm 2c	+	+ (Lv3)	+	–	.	+	2

TABLE 1 (*cont.*)

species and transmedullary cell type	medullary component: outer processes at the level of M	medullary component: outer processes at the level of LV	medullary component: inner processes at the level of T_3	medullary component: inner processes at the level of T_4	medullary component: middle processes in strata	lobula component: shallow endings (stratum 1)	lobula component: deep endings (strata 1 to 3)
Tm 3	+	+	+	+	1–8 (inclusive)	–	bistratified (stratum 3)
Tm 4	+	+	+	+	5, 6 and 7	–	?
Tm 5	+	+	+	+	4 and 5	–	3(diffuse)
Tm 6	+	+	+	+	all	?	?
Tm 7, 7a	(7)+ (7a)+	(7)+ (7a)+	(7)– (7a)+	(7)– (7a)+	(7)6 (7a) 4, 5, 6	(7)+ (7a)+	2 (or 3) 2 (or 3)
Tm 8	+	–	+	–	.	+	2
Tm 9	+	–	+	+	.	+	2
S. vitripennis							
Tm 1	+	–	+	+	.	+	–
Tm 2	+	–	+	–	.	+	2
Tm 3	+	–	+	+	3, 6 and 7	–	3
Tm 4	+	+	+	+	5, 6 and 7	–	2 and 3 (diffuse)
Tm 5	+	+	–	–	4	–	?
Tm 6	+	+	+	+	4	?	?
Tm 8	+	–	+	–	.	?	?
Tm 9	+	+	+	+	.	–	3
S. elegans and *S. nitidicollis*							
Tm 1	+	–	+	+	.	+	–
Tm 2	+	–	+	–	.	+	2
Tm 2a	+	+	–	–	6	?	?
Tm 3	+	+	+	+	all strata	–	bistratified (stratum 3)
Tm 4	+	+	+	+	5, 6 and 7	?	?
Tm 5	+	+(Lv3)	+	–	5	–	3 (diffuse)
Tm 7	+	+	+	+	4, 5 and 6	–	3
Tm 8	–	+	+	–	.	–	2 and outer 3
Tm 9	+	–	+	–	.	?	?

† Spines in strata 3 and 7.
‡ From Cajal & Sanchez (1915).
§ From Zawarzin (1913).
+ = present; – = not seen; ? = questionable; M = monopolar cell terminals; Lv = long visual fibre terminals; T_3 = shallow T-cell; T_4 = bushy T-cell.

The line-amacrines are orientated dorsoventrally and horizontally at a characteristic level in the outer strata of the medulla just beneath the outer processes of the types 1 and 2 transmedullary cells (figure 79*b*). The line-amacrine in this figure illustrates the characteristic shape of these cells and the three distinct groups of lateral specializations derived from its tangentially directed process. Those nearest the cell-body fibre arise from a thick portion of the axis-fibre whose length is equivalent to that of a unilateral class I element (figure 103, plate 22). This latter cell-type projects through the strata of the medulla and the lobula to end, finally, in the optic tubercle (figures 101 to 103, plate 22 and figures 162 and 163, plate 33). These two cells together have an arrangement analogous to the line-tangential of *Pieris* (see part I).

The large-field radial amacrine cells are rarely impregnated in their entirety. Those that have been indicate that their field-sizes are equivalent to those of the small-field tangential

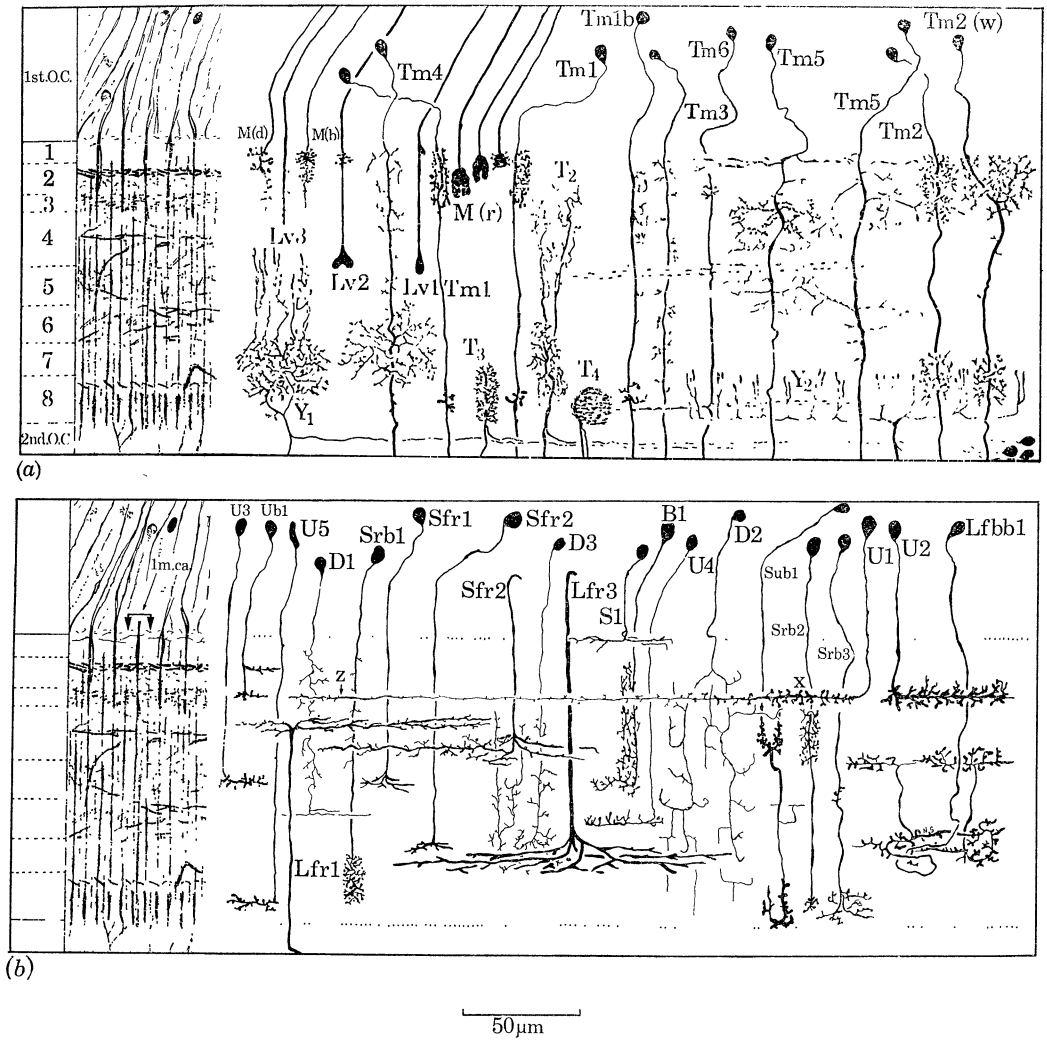

FIGURE 79 (*a*) and (*b*). The summary diagram of classes I and III elements in the medulla of *Calliphora*. These figures relate the stratification of the medulla from Holmes–Blest silver preparations (extreme left) with neuronal elements from Golgi preparation. The medulla is columnar. Each medullary column (lm.ca) consists of axis-fibres of a monopolar cell ending and long visual fibre ending (in strata 1 to 5) and at least two axis-fibres of transmedullary cells (through the whole medulla). Other perpendicular axis-fibres are detectable between column axes. These belong to other transmedullary cells (through the whole of the medulla) and T- and deep Y-cells through all or a portion of stratum 4 to the inner face of the medulla and some amacine cells (intrinsic to the medulla).

(*a*) Class I elements, excluding centrifugal cells.

(I) Inputs from the lamina: M(d) = shallow diffuse ending of a bilateral monopolar cell. M(b) = shallow radial ending of a unistratified radial monopolar cell. M(r) = three monopolar cell endings; from left to right these are: a deep and shallow lobed ending of two radial monopolar cells and a miniature surface ending of a midget monopolar cell. Lv1 = a long visual fibre club ending. Lv2 = a long visual fibre forked ending. Lv3 = a long visual fibre shallow ending.

(II) Transmedullary cells. Tml = type 1 transmedullary cell. Tmlb = a stratified-diffuse variant of Tml (seen only in *C. erythrocephala*). Tm2 = type 2 transmedullary cell. Tm2(w) = the wide-field variant of Tm2. Tm3 = the diffuse transmedullary cell. Its processes can extend through several columns. Tm4 = the stratified diffuse transmedullary cell. In the species of *Calliphora* its maximum extent is restricted to strata 6, 7 and 8. In the Syrphidae its maximum extent is in strata 2, 3 and part of 4. Tm5 = two wide-field tristratified transmedullary cells. The element on the left is drawn from *C. erythrocephala*. The right-hand cell is characteristic of *C. vomitoria*. The outermost processes in stratum 1 are oriented either dorsoventrally or antero-posteriorly and extend through between 8 and 10 columns. The two deeper groups of processes lie in strata 4 and part of 5 and 6, respectively. Their maximum extent is limited to five columns. Tm6 = a

elements lying at the same level. The forms and dispositions of amacrine cells are similar in the two species of *Calliphora*. These are illustrated in figure 79. Other elements characteristic of the Syrphidae are illustrated in figure 104 and are further described in the accompanying legends.

TABLE 2. OCCURRENCE OF T AND Y CELLS IN OPTIC LOBES

	Apis† *mellifica*	*Aeschna* (larva)‡	*Pieris brassicae*, *Sphinx ligustri*	*Musca*†	*Tabanus*†	*Calliphora erythrocephala*, *C. vomitoria*	*E. tenax*	*Syrphus elegans*, *S. vitripennis* *S. nitidicollis*
T_1	+	?	+ (w, s)	+	+	+	+	+
T_{1a}	?	?	–	?	?	+	+	–
T_2	+ (m)	?	+	?	+ (m)	+	+	+
T_3	?	?	+	?	+	+	+	+
T_4	+	+ (m)	+	+ (m)	+	+	+	+
T_5	(equiv.)	?	+	+	+	+	+	+
T_6	?	?	–	?	?	–	+	+
T_7	?	?	–	?	?	–	+	–
Y_1	+ (m)	+ (m)	+	+ (l)	+ (m, l)	+	+	+
$Y_{1a(3)}$	?	?	–	?	?	+	+	(f)
Y_2	?	?	+	?	?	+	+	+
Y_{2a}	?	?	–	?	?	–	+	(f)

+ = type present; – = not detected in the present preparations; ? = no data; (w, s) = various lateral extents; (m) = medullary component recognized; (l) = lobula complex component recognized; (equiv.) = possible amacrine cell equivalent; (f) = incomplete evidence.

† From Cajal & Sanchez's figures. ‡ From Zawarzin's figures.

FIGURE 79. Legend (*cont.*)

second form of wide-field transmedullary cell. The outer processes in stratum 2 are restricted to one column. The thin processes in strata 5 and 8 are arranged bilaterally from the axis-fibre and extend vertically through a maximum of 20 columns.

(III) T-cells and Y-cells (initial components). T_2 = deep bistratified T-cell to the lobula. T_3 = shallow unistratified T-cell to the lobula. T_4 = bushy T-cell to the lobula plate. Y_1 = the deep bistratified diffuse Y-cell. Y_2 = the tangential Y-cell. Its long axis may be oriented vertically or horizontally. The diffuse deep Y-cell (Y_3) is illustrated in figure 62. 1st O.C. = the inner segment of the first optic chiasma. 2nd O.C. = outer segment of second optic chiasma. The medullary strata are numbered 1 to 8.

(*b*) Amacrine cells of *Calliphora*.

(I) Unilateral amacrine cells. U1 = line amacrine. Note the three segments of specializations from the tangential fibre; x, y and z. The extent of x is equivalent to a unistratified class I element to the optic tubercle (figure 103, plate 22). U2 = unistratified amacrine cell in stratum 3. Its lateral extent is equivalent to that of segment x of U1. U3 to U5 = small unistratified amacrine cells. Ub1 = unilateral bistratified amacrine cell. Ub1 has only been seen in *C. vomitoria*. All the unilateral amacrines may be oriented vertically or horizontally.

(II) Small-field amacrine cells. Sfr 1 and 2 = small-field radial unistratified amacrine cells. Srb 1–3 = small-field bistratified amacrine cells. The outermost processes of Sub 1 have a characteristic U appearance. This is situated at the same level as the deepest lobed endings of monopolar cells (see figure 84, plate 20).

(III) Wide-field amacrine cells. Lfr 1, 2 and 3 = these elements characteristically have large disk-fields at two levels in stratum 4 and at stratum 7. Their lateral extents are equivalent to between 10 and 15 medullary columns. Their cell-bodies are situated in the cell-body cortex around the inner segment of the first optic chiasma and the outer segment of the second optic chiasma.

(IV) Large-field bilateral bistratified amacrine cells. Lfbbl = large-field bilateral bistratified amacrine cell (seen only in *C. vomitoria*) (Lfbl, in figure 61 = a large field bilateral unistratified amacrine cell).

(V) Diffuse amacrine cells. D1 = small-field diffuse amacrine cell. D2 = large-field diffuse amacrine cell. D3 = large-field recurrent diffuse amacrine cell. B1 = bent amacrine cell. This may be situated at any level between stratum 1 and the inner limit of stratum 7. S1 = surface amacrine cell. All the amacrine cells, except for Srbl and Lfbbl have been detected in the Syrphidae. However, these latter species have other forms of amacrine cells which have not been seen in the Calliphorinae. These are illustrated from *E. tenax* in figure 104 (*a*) and (*b*).

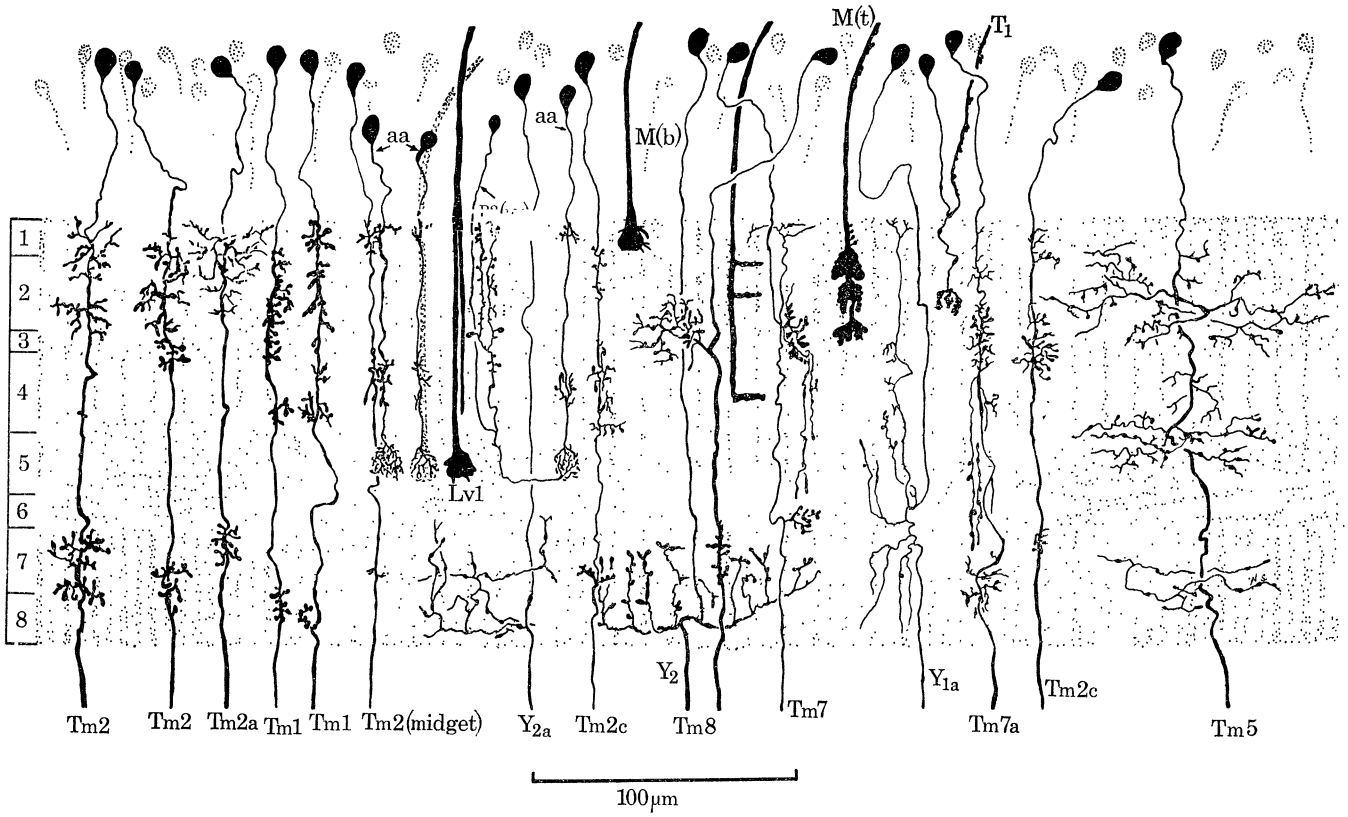

FIGURE 80. Transmedullary cell elements, long visual fibre and monopolar cell endings and some class III elements in the medulla of *E. tenax* (horizontal section). The camera lucida drawings of these cells are superimposed on medullary columns, that are recognized in phase contrast illumination, to indicate their different lateral extents.

(I) Tm1 = type 1 transmedullary cell. Tm2 = type 2 transmedullary cell. Tm2a = variant of Tm2. The outer processes are always much finer and are strictly limited to strata 1 and 2. Tm2 midget (b) = small form of Tm2. Tm2c = a small tristratified variant of Tm2. All Tm2 variants have the same characteristic terminals in strata 1 and 2 of the lobula. Tm3 (see figure 65, plate 18). Tm4 (see Tm9, figure 81). Tm5 = a tristratified wide-field transmedullary cell. This element is similar in all the present species of Syrphidae. It has three groups of processes which comprise disk-fields in strata 2, 3, 5 and part of 7 and 9, respectively. Tm6 (see figure 81). Tm7 and Tm7a. Stratified diffuse transmedullary cells. These are characteristic of the Syrphidae. They have lateral spreads equivalent to one column, horizontally, and two columns vertically. Their processes are extremely slender (usually less than 0.4 μm diameter) and are blebbed. Note the descendent processes from the outer group in strata 2 and 3. Tm8 = Eccentric bistratified transmedullary cell. Tuberous processes are derived from the axis-fibre in stratum 7. These are restricted to the column containing the axis-fibre. A unilateral branch projects from the axis-fibre in stratum 3 and the inner half of 2. This gives rise to processes which extend through the adjacent and sub-adjacent columns.

(II) The input from the lamina. Fibres from the lamina into the medullary columns are usually paired. However, this is not invariably the case. Some long visual fibre endings (Lv1; club ending) are accompanied by a shallow long visual fibre ending in the same column. Occasionally some preparations seem to have triplets of shallow endings M(t). These are composed of a bistratified lobed monopolar ending and an extremely shallow forked ending of a long visual fibre. This arrangement is rarely seen; it may represent another species of monopolar cell and long visual fibre or simply an unusual variant of the lobed and forked endings. T_1 = the initial component of a medulla-lamina T-cell. M(b) = a shallow ending of a midget monopolar cell.

(III) Three forms of amacrine cells have been seen which are characteristically associated with long visual fibre terminals. The narrow-field tristratified diffuse ending is illustrated in figure 96, plate 22. a = a tristratified narrow-field element. Its innermost processes have been seen wrapped around long visual fibre club endings (stippled), The outer processes seem to wrap around the outer swelling of a long visual fibre ending. The middle stratum of processes have not been related to another component. B2 (rec) = a recurrent 'bent' amacrine cell. The recurrent processes climb over Tm1 cell processes in the same column. The tangential component ends as a narrow-field group of processes which has been seen wrapped around a long visual fibre club or forked ending in a subadjacent column. It is not known if these associations represent synaptic contacts.

(IV) Y-cells. All Y-cells in *E. tenax* have their perikarya situated above the outer face of the medulla. Y_2 and Y_{2a} (tangential Y-cells) have smaller lateral extents than those of *Calliphora*. Their fields are invariably oriented horizontally. The Y_{1a} element has slender ascendant processes as far as the surface of the medulla and descendant processes as far as the inner face of this region. They are characteristically slender (less than 0.4 μm diameter) and difficult to resolve.

Some forms of narrow-field amacrine cells reflect the forms of groups or of single class I cells and thus appear to have very definable topographical relationships with them; these include, for example, a bistratified amacrine cell which has outer processes at the same levels as the long visual fibre endings and deeper processes at the level of bushy T-cells. Other forms may possibly have associations with adjacent long visual fibre endings (see figure 80 and figures 96 and 97, plate 22).

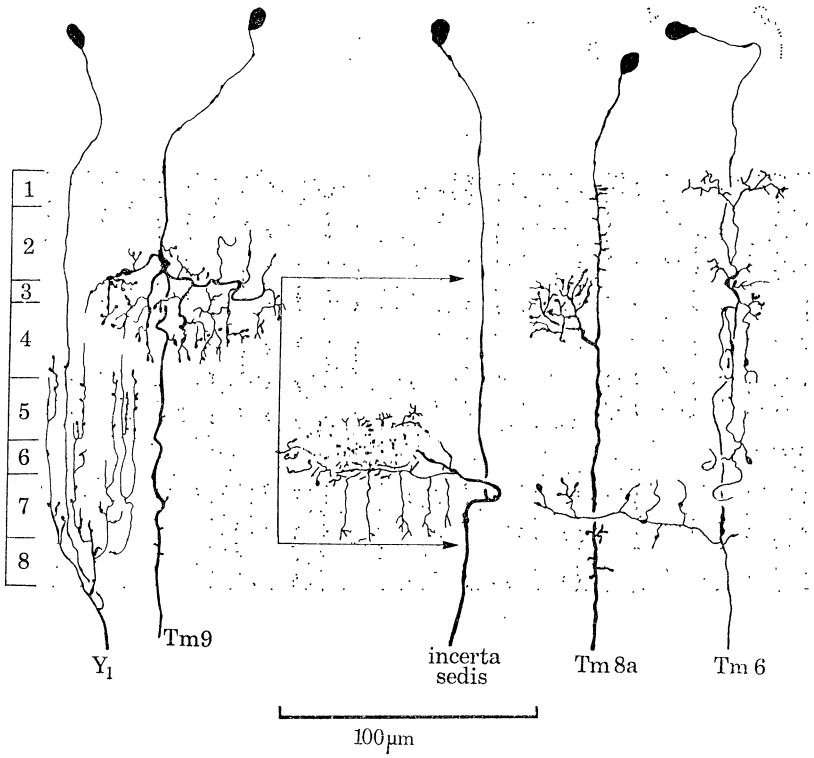

FIGURE 81. *E. tenax.* (Vertical section of the medulla). Y_1 = deep Y-cell. Tm 9 = stratified diffuse transmedullary cell. Tm 8a = tristratified eccentric transmedullary cell. Tm 6 = wide-field tristratified diffuse transmedullary cell. This form of element is complex, it cannot be illustrated in its entirety. Its axis-fibre gives rise to a recurrent branch in stratum 2; processes from this form an oval field in stratum 1. Other processes descend through strata 4 to 7 from stratum 3. Tangentially directed processes in stratum 3 extend bilaterally from the axis-fibre through a horizontal strip-field which is equivalent to between 6 and 10 medullary columns. Another branch extends unilaterally from the axis-fibre in stratum 7. Processes from this form a vertical strip-field, extending through between 5 and 8 columns. *Incerta sedis.* Only the medullary component of this element has been seen. Its unilaterally arranged group of processes may occur anywhere between strata 2 and 8. All the transmedullary cells have at least two separate groups of processes or diffuse processes in the strata of the medulla. The arrangement of Y-cell processes is either unistratified, bistratified diffuse, or diffuse; they arise from the same restricted portion of the axis-fibre. The element listed as *incerta sedis* is, in this respect, like a Y-cell. Its unilateral arrangement is also reminiscent of the unilateral class I element to the optic tubercle.

Asymmetric amacrine cells

These neurons require special consideration; they are unlike any other form of amacrine cell in the insects. The closest analogues, in shape, are some retinal amacrine cells described by Cajal in the pigeon retina (1888). These cells characteristically have two sets of processes, widely separated from one another, that are linked by a tangentially directed axis-fibre; one set is invariably unistratified and situated in, or just beneath, the serpentine layer. The other is multistratified or diffuse and extends either through the serpentine and outer layer of the medulla or through the serpentine and inner layer of this region.

The type 1 asymmetric amacrine cell (figure 104 and figure 95, plate 22)

Cell-bodies, below the inner face of the medulla give rise to extremely thin cell-body fibres which project as far as the middle of stratum 6. Each bifurcates in the medulla; one branch gives rise to a unistratified diffuse group of processes in the serpentine layer; the other gives rise to a stratified diffuse group which extends as far as the level of the long visual fibre endings. The two groups of processes are separated from one another by a distance of between 50 and 60 μm.

The type 2 and 3 asymmetric amacrine cells (figure 104)

These elements are enigmatic; in appearance they look like a hybrid between an amacrine cell and a component of a class II cell. Diffuse processes extend bilaterally from the distal end of a horizontally tangentially directed axis-fibre in the serpentine layer. These processes together form a strip-field which extends through about 20 to 30 medullary columns, in the horizontal plane, and four or five columns in the vertical plane. The axis-fibre has been traced as far as the anterior edge of the medulla where it becomes thin and blebbed: in appearance it is like a cell-body fibre, not a linking-fibre. There is evidence, in *Pieris*, that a similarly disposed blebbed fibre gives rise to a unistratified diffuse group of processes in the anteriormost part of the serpentine layer. It is likely that these elements, which are invariably seen in the horizontal mid-line of the medulla, are derived from the small cell-bodies located outside the anterior edge of this region.

The type 4 asymmetric amacrine cell

Recently a third form of amacrine cell has been reconstructed from serial sections of *Pieris*. This neuron consists of three groups of processes, widely separated from one another, at the level of the deepest long visual fibre endings. The three groups, together with their axis-fibre, form a right-angled arrangement as illustrated in figure 104*c*. This cell has not been detected in the present species of Diptera; however, its presence in this order cannot be yet discounted.

Class II elements in the medulla

Tangential elements in the medulla have been classified into strip-field, small-field and wide-field elements (part I). The former two have uni- or bistratified diffuse arrangements in

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DESCRIPTION OF PLATE 20

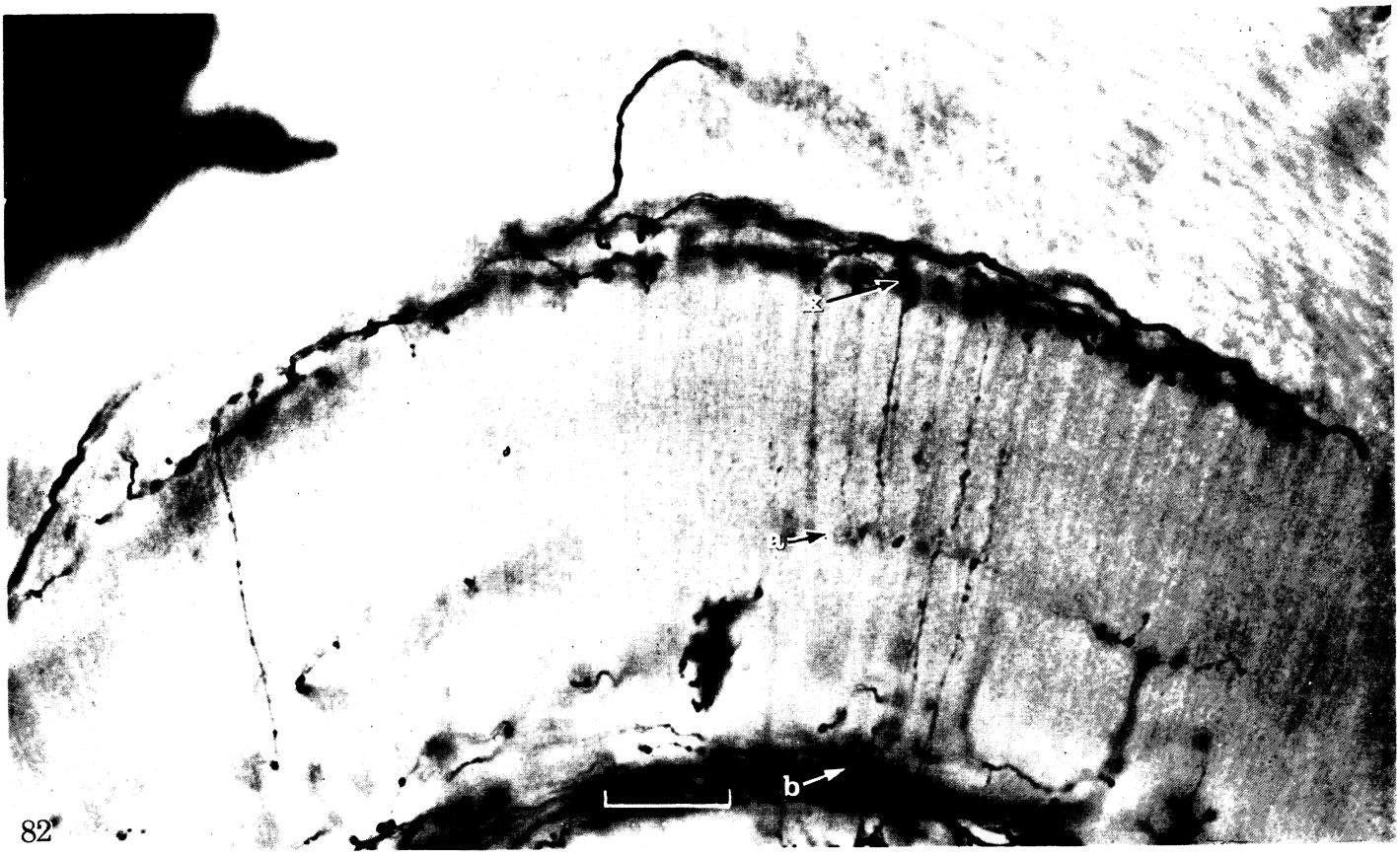
The medulla

FIGURE 82. *E. tenax*. The type 3 medullary tangential. Its surface field (x) has a lateral extent equivalent to at least 100 medullary columns. In the species of *Calliphora* and *Syrphus* this element is unistratified. In *E. tenax* the surface field gives rise to a slender descendent process in each medullary column. Only some have been impregnated in this section. Others were visible as unimpregnated ghosts but were not amenable to photography. Each of these processes gives rise to between 3 and 8 lateral branches in stratum 4 (a) and in the serpentine layer (b). The lateral extent of each group of branches at (a) is equivalent to a medullary column.

FIGURE 83. *E. tenax*. A tristratified tangential, characteristic of this species. Its processes are arranged at the same three levels as those of Med: tan 3.

FIGURE 84. *C. erythrocephala* (horizontal section). The type 12 medullary tangential (M: tan). This element is tristratified. Its ascendent processes branch in strata 4 and 2. Note the spatial relationship between the branches in stratum 4 and the outer processes of amacrine cell of Sub1 and the arrangement of the bushy T-cells (*en masse* impregnation) with the inner processes of this amacrine cell.

Scales: Figures 82 to 84, 25 μm.



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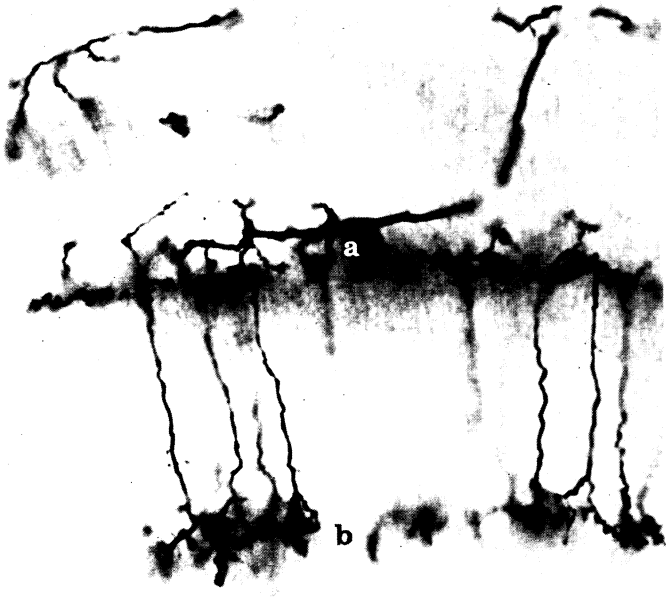

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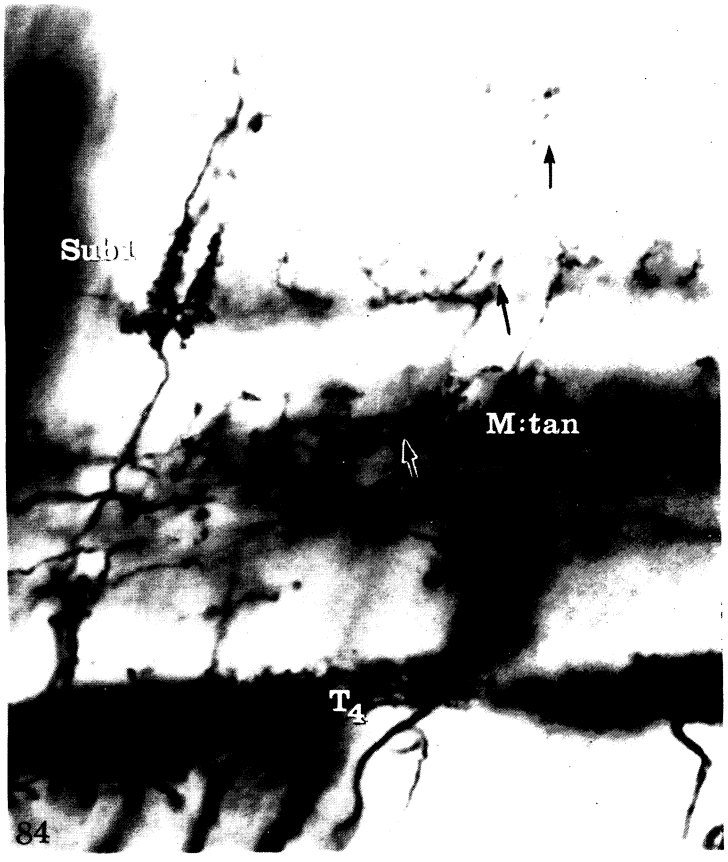

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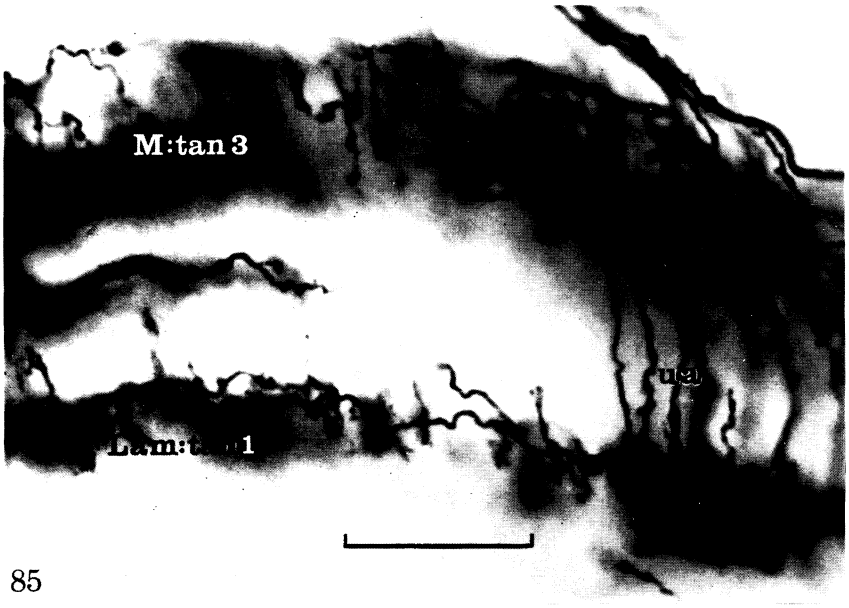
M:tan 3
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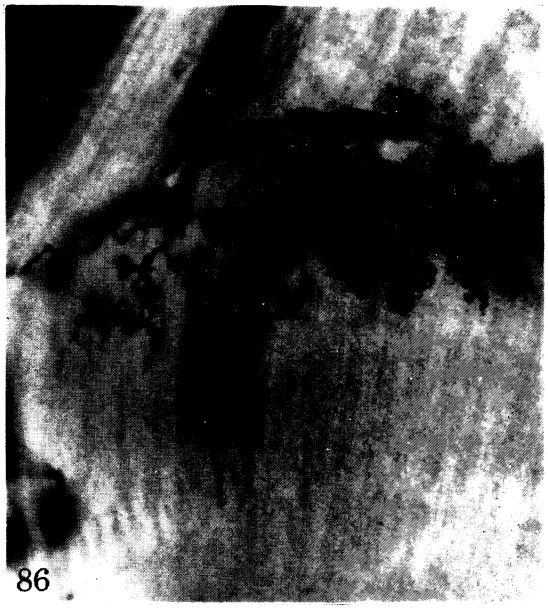
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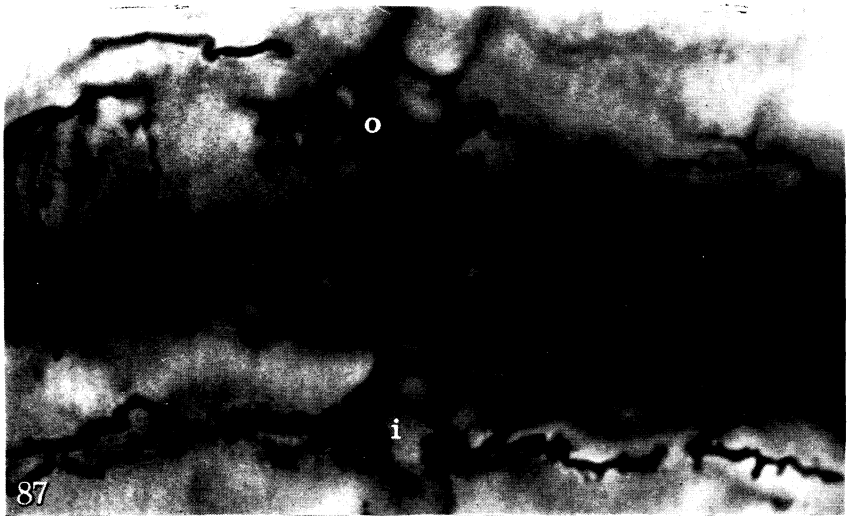
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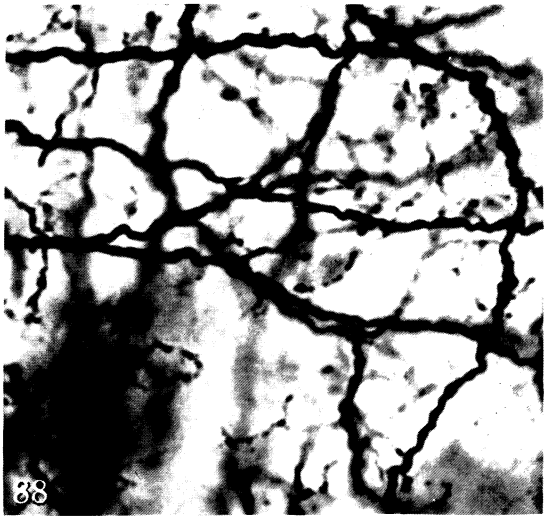
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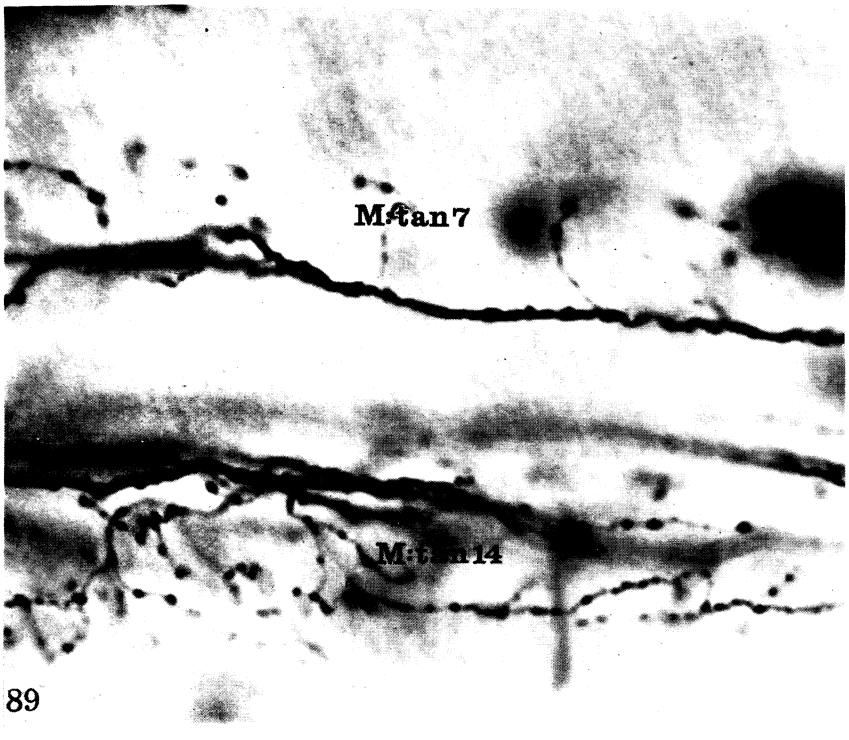
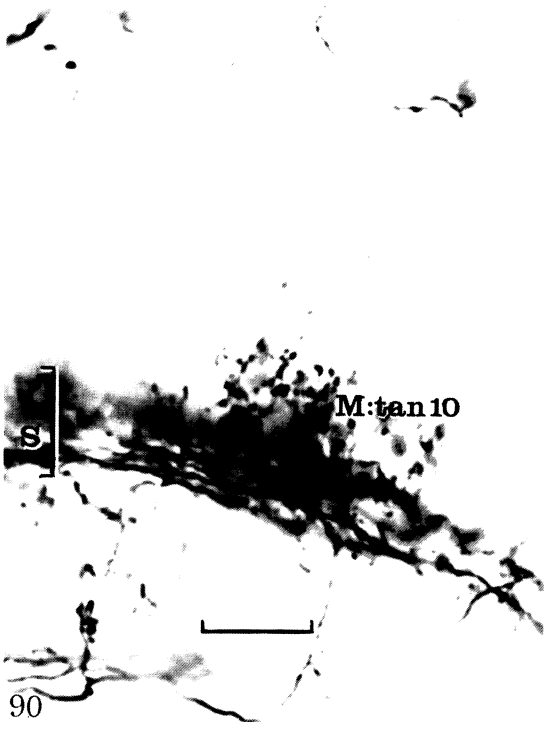

M:tan 7
89


M:tan 10
S
90

all the species of Diptera. The wide-field endings are either uni- or multistratified; these latter forms have distinct subfield components at two or three different levels. One subfield is invariably extremely large and discoid in shape and extends through an eighth or more of the stratum in which it lies. The others are derived from descendent perpendicularly directed fibres from the outermost subfield; each fibre gives rise to a small oval subfield which extends through between 1 and 12 columns, laterally. Strip-field endings are predominantly oriented vertically or horizontally. Small field endings have oval field-spreads directed in one of these planes. The former are unistratified, the latter uni- or bistratified diffuse.

Fifteen forms of tangential element have been detected in all the species of Diptera. They are illustrated in figures 91 to 94. Information about each is given in the accompanying figure text. There is, though, some variation between the forms of endings in different species. These deserve special consideration.

(i) *The giant optic lobe tangential.* This neuron enters the lobula plate, lobula and medulla of the optic lobes of the Lepidoptera and Diptera. There is also evidence for it in species with undivided lobulae (N. J. Strausfeld, unpublished). Its lobula plate component, which is remarkably similar in all the species of Diptera and Lepidoptera (part I), consists of a wide-field arborization of processes which spreads over the whole of the surface of this region.

Collaterals from the lobula plate subfield extend to the lobula via the intra-complex tract. Each terminates as a strip subfield which invades the outermost stratum of this region (and the outer half of stratum 2 in *E. tenax*). The lobula plate subfield gives rise to other prolongations which project as far as the inner face of the medulla via the second optic chiasma. The medullary subfields are made up of components which have a characteristic form in each species. For example, in *C. vomitoria* the oval subfields are contained within the innermost stratum at the same level as the bushy T-cells (figure 158, plate 32). However, in *C. erythrocephala* each medulla subfield is arranged as a strip-field component and has a perpendicular extent as far as the level of the deepest long visual fibre endings. Its lateral extent is between 20 and 30 medullary columns. The medullary subfields of *S. elegans* and *S. nitidicollis* are similar in form (figures 159 and 160, plate 32) but have slender ascending processes which extend outwards as far as the inner subfield of the type 1 lamina tangential ending in the medulla. Figure 94 shows a section of the complete form of this giant ending in three optic lobe regions of *E. tenax*. The medulla subfield is a strip-component restricted to the inner layer of this region. The lobula plate

Description of plate 21

The medulla

Figure 85. *C. vomitoria.* The topographical relationship between M: tan 3 and the deeper strata of processes of the medullary component of Lam: tan 1. Unilateral amacrine cell processes arborize at the same level.

Figure 86. *C. erythrocephala.* The unistratified surface tangential, M: tan 3.

Figure 87. *C. vomitoria.* The bistratified medullary component of Lam: tan 1. This component has been seen in all the present species (o = outer small field, i = inner large disk subfield). The wide-field element, M: tan 4 is situated between the outer and inner fields of these components.

Figure 88. *E. pertinax* (tangential section). The type 7 medullary tangential (M: tan 7) arborizes in stratum 5 to form a characteristic network of branches and blebbed processes.

Figure 89. *E. pertinax.* The same element (M: tan 7) in horizontal section. M: tan 14 has similar shaped processes which form an oval field in strata 7 and 8.

Figure 90. *S. nitidicollis.* The type 10 medullary tangential processes invest a small oval field of strata 5 and 6. s = serpentine layer.

Scales: Figures 85 to 89, 20 μm; figure 90, 20 μm.

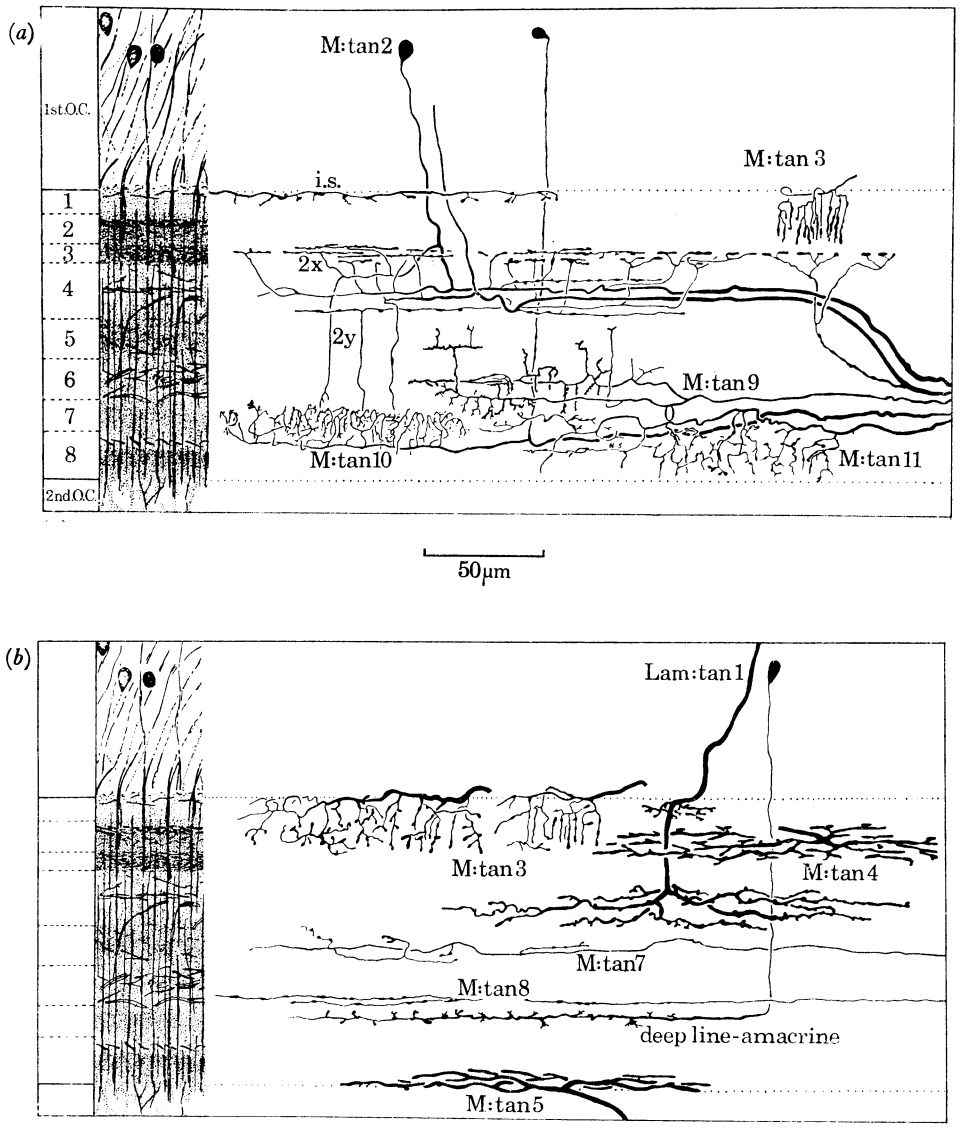


FIGURE 91. Summary diagram of the medulla (horizontal section); class II elements. The stratification of the medulla is shown to the left.

(*a*) M: tan 1 has not been positively identified in the Calliphorinae. It has, though, been seen in the Syrphidae and its equivalent has been seen in the Lepidoptera. Possibly the fibre at the surface of this region (i.s.) may be derived from M: tan 1. M: tan 2: in the Lepidoptera and Syrphidae the linking-fibre of this element projects to the contralateral medulla to give rise to M: tan 1. This figure illustrates the form of M: tan 2 in *C. vomitoria*; note the two levels of processes 2x and 2y and its cell-body above the medulla. Figure 154, plate 31, shows this element in *C. erythrocephala*; it has only one level of processes. Its cell-body is located at the anterior edge of the medulla. M: tan 3. A detail of the surface tangential of *C. erythrocephala*. M: tan 9, M: tan 10 and M: tan 11. Three small oval field components. Each field has a maximum extent through 15 columns antero-posteriorly, and about six columns dorsoventrally. The axis-fibres extend anteriorly (to the right of this figure) in the serpentine layer or stratum 7. The cell-bodies of M: tan 9 and 11 are located at the anterior edge of the medulla and above the anterior median perimeter of the medulla in the cell-body cortex. Each of these three tangential elements has characteristic forms of processes. They have a similar appearance in the present species. M: tan 10 elements are derived from cell-bodies above the outer face of the medulla amongst fibres of the first optic chiasma.

(*b*) M: tan 4 and M: tan 5 are large oval field tangential elements. They have not been seen in their entirety in the optic lobes. Golgi impregnated material gives the impression that they form a thin stratum of a plexus of fibres throughout the whole of strata 2 and 8, respectively. The processes of M: tan 7 also form a network of fibres throughout stratum 5 (see figure 88, plate 21). Thin blebbed fibres in the serpentine layer (M: tan 8) are apparently derived from a thicker tangential axis-fibre. However, they are rarely impregnated and have only been detected in *C. vomitoria*. The deep line amacrine is rarely seen. It is similar in form to the line amacrine, U 1 (see figure 79*b*), but it is not divided into three distinct 'segments'.

component is composed of strip-fields whose branches extend as far as the class IIS cells in the second stratum (figure 157, plate 32).

In *Pieris* the medullary element is bistratified. It consists of large over-lapping subfields at the deepest level of the medulla; these project ascendant processes as far as the level of the deepest monopolar cell endings where they end as discrete oval subfields with a lateral extent of between 2 and 4 columns. The medullary components of *Sphinx* have ascendent fibres as far as beneath the serpentine layer. The resultant subfields overlap marginally (see Collet 1970). Serial sections through pupal brains of *Pieris brassicae* show that giant optic lobe tangential elements are derived from a fibre that can first be detected posteriorly, deep in the suboesophageal ganglion.

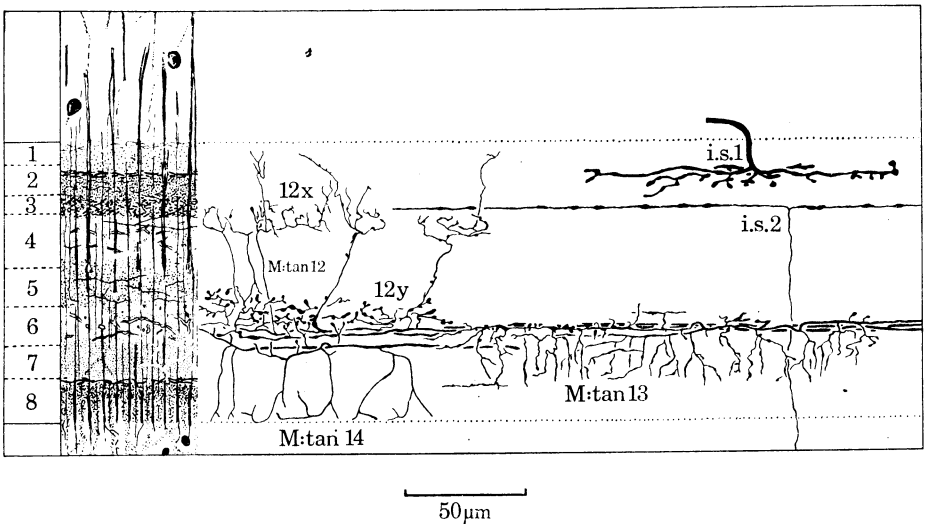


FIGURE 92. Summary diagram of class II elements in the medulla (*Calliphora*, vertical section). i.s.1. A wide disk-field element. It may possibly be derived from a class III cell-body. It has been seen only once, in *C. vomitoria* and is, at present, included as *incerta sedis*. i.s.2: this blebbed line fibre is derived from a thin (0.5 μm) ascendent process from the second optic chiasma. This arrangement has been frequently detected in the two species of *Calliphora* but not in the Syrphidae. Its origin and destination is unknown; it is included as *incerta sedis*. M: tan 12. The vertical small-field tristratified diffuse tangential. Varicose processes (12y) are derived from the axis-fibre in strata 6 and 5. These, in turn, give rise to ascendent processes which branch at two levels (12x) at the outer quarter of strata 4 and 3, and in stratum 1. The maximum vertical extents of the oval fields of these elements are equivalent to about 10 columns. Their horizontal extents are equivalent to less than five columns. M: tan 13. The processes of this element form a vertically oriented oval field in strata 7 and 8. Its maximum vertical extent is equivalent to about 12 columns; its horizontal extent is equivalent to about six columns. M: tan 14. Axis-fibres in the serpentine layer give rise to descendent branches through strata 7 and 8. The fields of this element are disk-shaped in the species of *Calliphora*, with a lateral extent through between 25 and 30 columns. In *E. tenax* the fields are oval, with the long axes oriented horizontally.

This fibre most probably ascends from the ventral nerve cord. Two thick linking-fibres are derived from it anteriorly in the suboesophageal region and at least one of them projects directly to the right-hand optic lobe. The other has not been traced in its entirety to the other side, but reconstructions from partially resolvable fragments suggest that both project to an optic lobe. They terminate in the characteristic species specific branching patterns described above. In addition, both of these linking-fibres have collaterals in the brain which arborize through an extensive volume of the regions of the medial tritocerebrum. The maximum width of the linking-fibres, at the oral edge of the lobula plate, are 5.0, 6.0 and 7.5 μm in *Calliphora*, *Syrphus elegans* and *E. tenax*, respectively. These are the widest diameter fibres yet observed in these preparations. At the same locality of *E. pertinax* this fibre-type exceeds 9.5 μm.

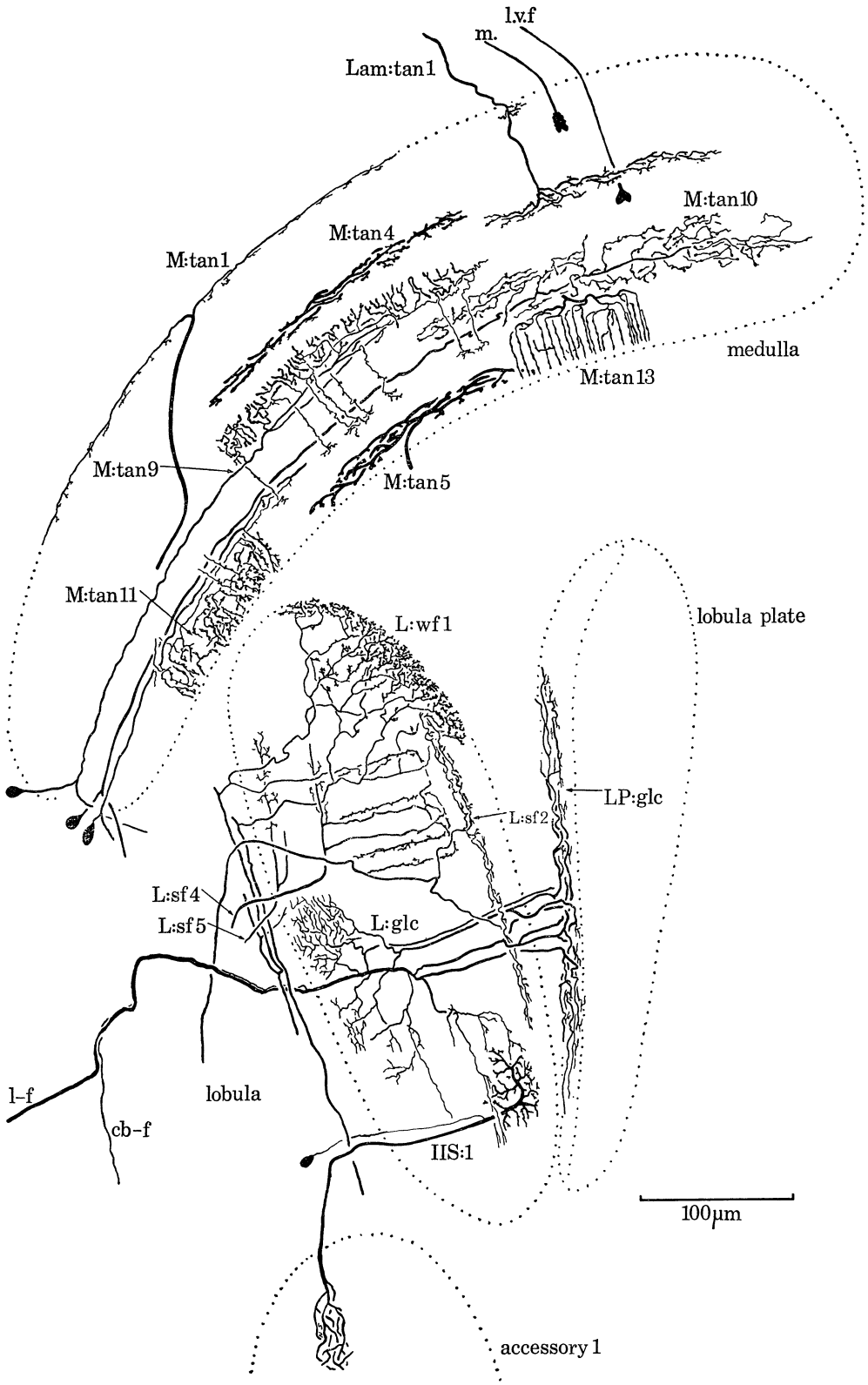


FIGURE 93. For legend see facing page.

(ii) There are two other important variations of class II elements between these species of Diptera. The surface tangential (M: tan 3) has a tri-stratified diffuse arrangement in *E. tenax* (figure 82, plate 20); in the other species there is only one stratum of processes (figure 86, plate 21). The descendent processes of the tristratified variant have distinct blebs and slender lateral branches at the levels of the deepest monopolar cell endings and in the serpentine layer. The processes at this latter level appear to wrap around the axis-fibres of other tangential elements.

The horizontal oriented strip-field tangential (M: tan 9) is unistratified diffuse in *Calliphora* and the species of *Syrphus*, but in *E. tenax* it has descendent processes to the serpentine layer (see figures 91*a* and 93, respectively). There is one oval-field element in all the present species which has been classified as *incerta sedis*; possibly this is a tangential element and not an amacrine cell, since its fibre from the outer surface of the medulla has the characteristics of a linking-fibre rather than a cell-body fibre. In the species of *Calliphora* this element is unistratified (figure 92), whereas in *S. elegans* it is bistratified and in *S. nitidicollis*, *S. vitripennis* and in *E. tenax* it is tristratified; there is a bilateral, horizontally oriented component at the surface of the medulla, a radial subfield in strata 2 and 3 and descendent processes from this which terminate in the serpentine layer (figure 94).

Apart from these few differences of shape the tangential elements in the medullae of different species of Diptera look extremely similar. However, there may be species-characteristic differences in their field-sizes; these must await further investigation. It is clear that the tangential elements M: tan 9, 10, 11, 12 and 13 all have small oval- or strip-fields. The former three are oriented horizontally, the latter two vertically. The maximum lateral extent of most of them does not exceed 20 medullary columns. The largest small-field detected (*S. elegans*) did not exceed 40 columns.

Tangential elements are illustrated in figures 76, plate 19 and 82–90, plates 20 and 21. Summary figures 91–94 show their perpendicular relationships and disposition in the medulla.

FIGURE 93. Summary diagram of the class II layer relationships in the medulla and lobula plate of *E. tenax*. (Figures 93 and 94 are derived from 3 horizontal sections at the same vertical level from three preparations.) M: tan 1 = surface wide-field tangential derived from an M: tan 2 cell-body in the contralateral lobe. M: tan 4 = wide-field element in stratum 3 and part of 4. M: tan 5 = wide-field element in stratum 8. M: tan 9 = bistratified small oval field element. This is unistratified in the species of *Calliphora*. Its long axis is oriented horizontally. M: tan 10 = small-field element in strata 6 and 7. Its long axis is oriented horizontally. M: tan 11 = small-field element in stratum 8. Its oval field is oriented horizontally. M: tan 13 = small-field element in strata 7 and 8. Its oval field is oriented vertically. Lam: tan 1 = the bistratified medullary component of the type 1 lamina tangential. m = radial monopolar cell ending. LvF = long visual fibre ending. Only one element of each type is figured. There are of course many of each type of element whose fields invade the whole of a stratum. The amount of overlap between the fields of the different elements in the medulla has not yet been determined. This tangential organization is still being investigated. L: wf 1 = the lobula surface wide-field element. L: sf 2 = the type 2 strip-field element (see text). L: sf 4 and 5 = the types 4 and 5 strip-field elements. Type 4 is oriented vertically (see text). IIS: 1 = the type 1 small-field sub-class IIS element. It has been seen in its entirety. Note the diffuse ending in the optic lobe accessory region 1 (accessory 1). The giant lobula complex cell (glc) has a strip sub-field in the lobula plate (LP: glc) and a bilateral bistratified diffuse sub-field in the lobula (L: glc). Its cell-body fibre (cb-f) arises from the linking-fibre (l-f) at the inner face of the lobula. The central ending is in the optic lobe accessory region 2 (see figure 156, plate 32).

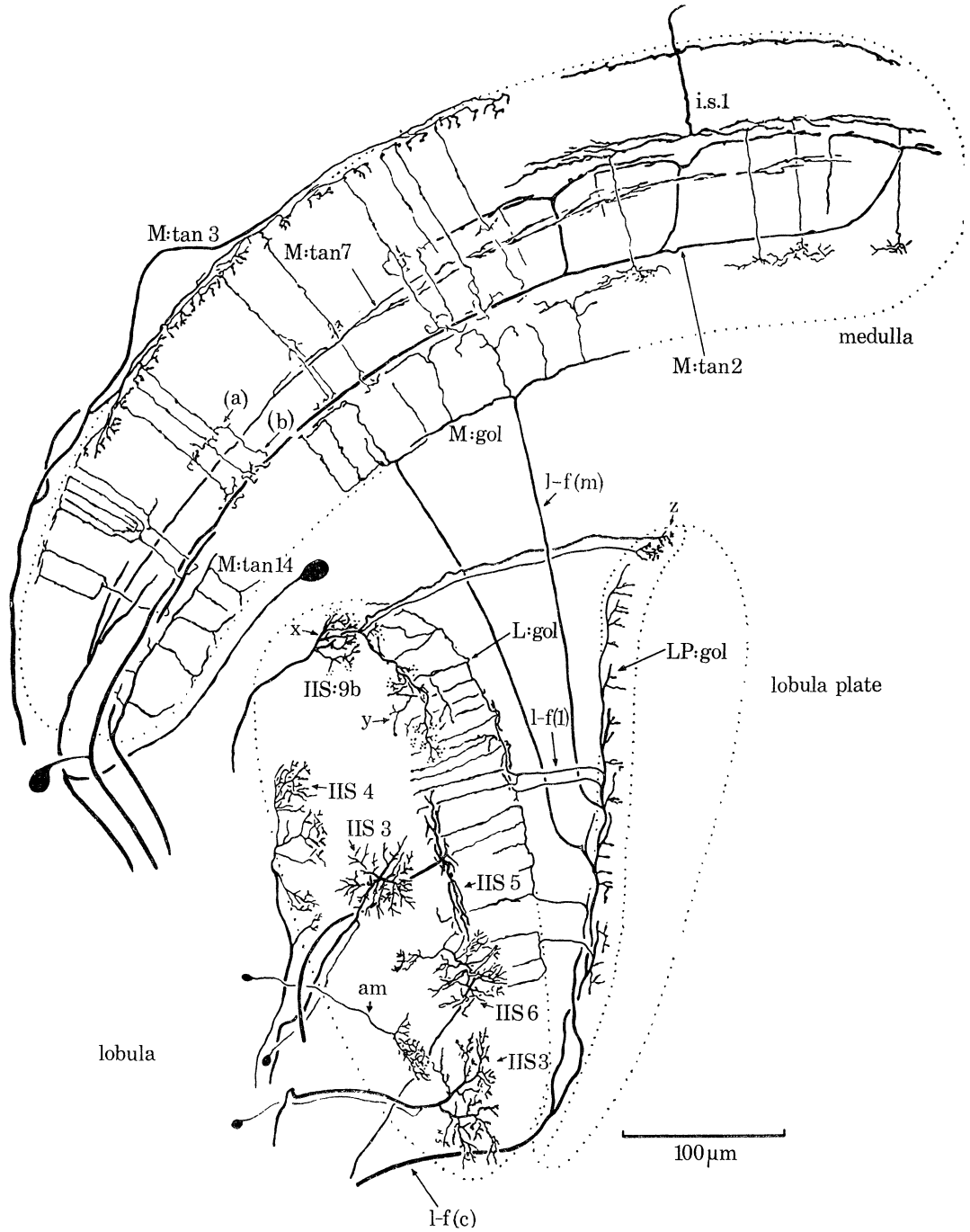
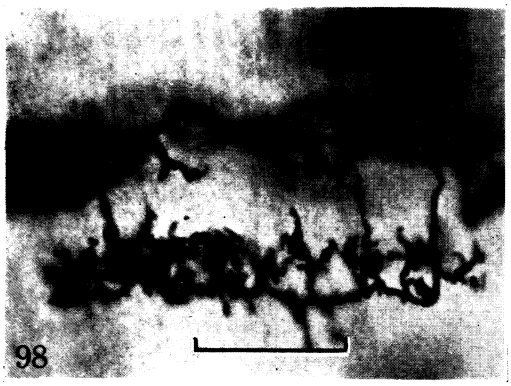
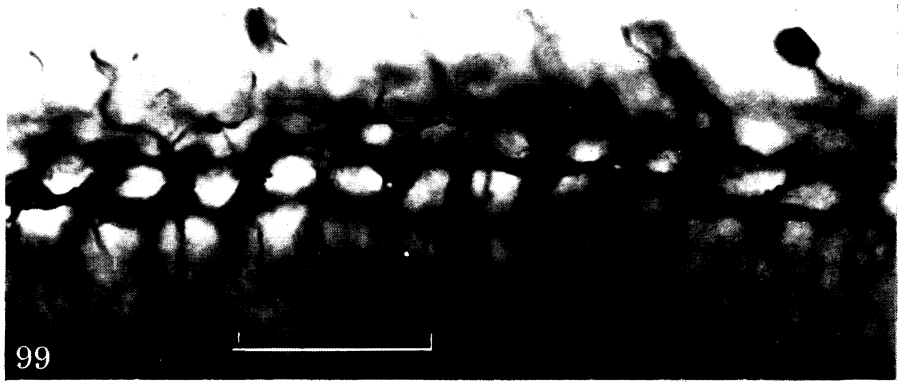
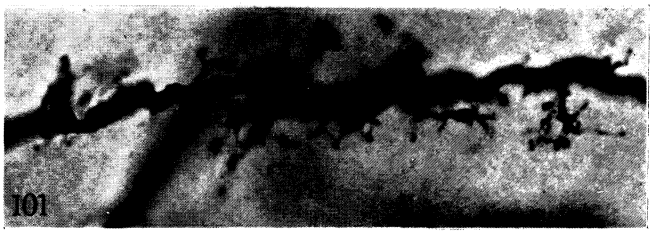
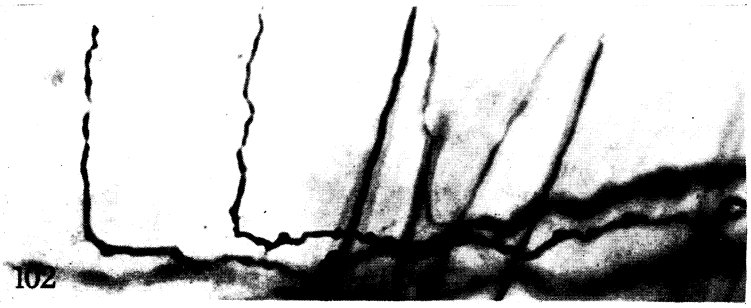


FIGURE 94. Summary diagram of the class II layer relationships in the medulla and lobula complex of *E. tenax* (continued). M: tan 3 = tristratified surface tangential. M: tan 2 = a unistratified wide-field tangential. The linking-fibre of this element extends to the contralateral medulla where it gives rise to M: tan 1 (see figure 93). M: tan 7 = unistratified tangential. Its processes form a network of fibres in stratum 5. Note the location of its cell-body between the medulla and lobula. M: tan 14 = a strip-field element in stratum 8. The same form of element invests an oval field in *Calliphora*. gol = the giant optic lobe tangential element. Note the dispersion of its fibres in the intra-complex tract and the second optic chiasma (l-f(l) and l-f(m), respectively), and from the oval edge of the lobula towards the mid-brain (l-f(c)). LP: gol = lobula plate subfield. L: gol = lobula strip subfield. M: gol = medulla subfield. Some class IIS elements are also shown. Note the lobula ocular edge variant of the IIS: 9 element (IIS: 9b). This has three groups of processes: two small sub-fields, x and z, and a strip subfield, y. am = type 4 lobula amacrine cell. See text for descriptions of IIS: 3–6.









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The lobula complex

Introduction

The lobulae of the Diptera and Lepidoptera share many topographical features. Some cell-types have been detected in both species of the Lepidoptera and the present species of Diptera. Others, which have not been seen in their entirety, seem homologous on the basis of the shape and disposition of their processes in these regions. An attempt has been made to make analogies between the components in different species of Diptera. But it must be realized that until their precise mid-brain destinations are known it is impossible to devise entirely satisfying criteria for establishing morphological homologies between these elements. The class II elements have been divided into two major groups. The first consists of tangential components which have lateral extents far exceeding their perpendicular spreads. Those in the second have sizes that are intermediate between the large-field class II cells and the class I elements. These cells must obviously interact with restricted groups of class I endings which probably relay small-field aggregates of the retinal mosaic to these regions. This second group has been classified under the heading of subclass IIS cells. They project exclusively to regions outside the ipsilateral optic lobe. Class I cells are contained exclusively within the optic lobe.

There are three main strata in the lobula. The outermost is distinctly striated and contains the endings of the type 1 trans-medullary cells and lobula-lobula plate T-cells (T_5). There are no subclass IIS endings at this level. The second and third strata cannot be distinguished from reduced silver preparations. Golgi-stained material reveals that the smallest field subclass IIS elements are restricted to a narrow stratum of neuropil directly beneath the outer layer. This second stratum also contains the endings of the shallow T-cell (T_3) from the medulla and the type 2 trans-medullary cells. The third stratum contains wide-field and strip-field class II elements, other subclass IIS components, endings of Y-cells, transmedullary cells (other than types Tm 1 and 2) and the endings of the deep T-cells (T_2).

Description of plate 22

The medulla

Figure 95. *E. tenax.* The type 1 asymmetric amacrine cell. Two groups of processes are joined by a tangential linking-fibre in the serpentine layer (arrowed). One group of processes is unistratified (su) the other has a tristratified diffuse arrangement (s1, s2, s3). T_4 = bushy T-cell.

Figure 96. *E. tenax.* Two narrow-field tristratified diffuse amacrine cells. Their lateral spreads are restricted to single medullary columns. The outer and inner groups of processes have been seen wrapped around the outer unilateral swellings and the inner club terminals of long visual fibre endings.

Figure 97. *E. tenax.* A tristratified amacrine cell. The outer most bilateral processes reflect the tristratified arrangement of bilateral processes of the wide-field long visual fibre endings. Arrows indicate the levels of stratification.

Figure 98. *E. tenax.* The terminal processes of a small-field unilateral amacrine cell.

Figure 99. *E. tenax.* Surface amacrine cell fibres form a network of processes over the outer face of the medulla. The 'gaps' between the meshes are equivalent, in width, to medullary columns and presumably allow space for axis-fibres and cell-body fibres into the neuropil.

Figure 100. *E. tenax.* The 'y' segments of line amacrine cells (see figure 79*b*).

Figure 101. *E. tenax.* High-power photomicrograph showing the lateral tubers and spines of the 'x' segment of a line amacrine cell.

Figure 102. *E. tenax.* Line amacrine cells: the characteristic L shapes of cell-body fibres and their tangential prolongations in stratum 3.

Figure 103. *E. tenax.* The unilateral branch of a class I element to the optic tubercle. Its extent is equivalent to the 'x' segment of the line amacrine cell.

Scales: Figures 95, 96, 100, 103, 20 μm; figure 97, 25 μm; figures 98, 101, 102, 10 μm; figure 99, 30 μm.

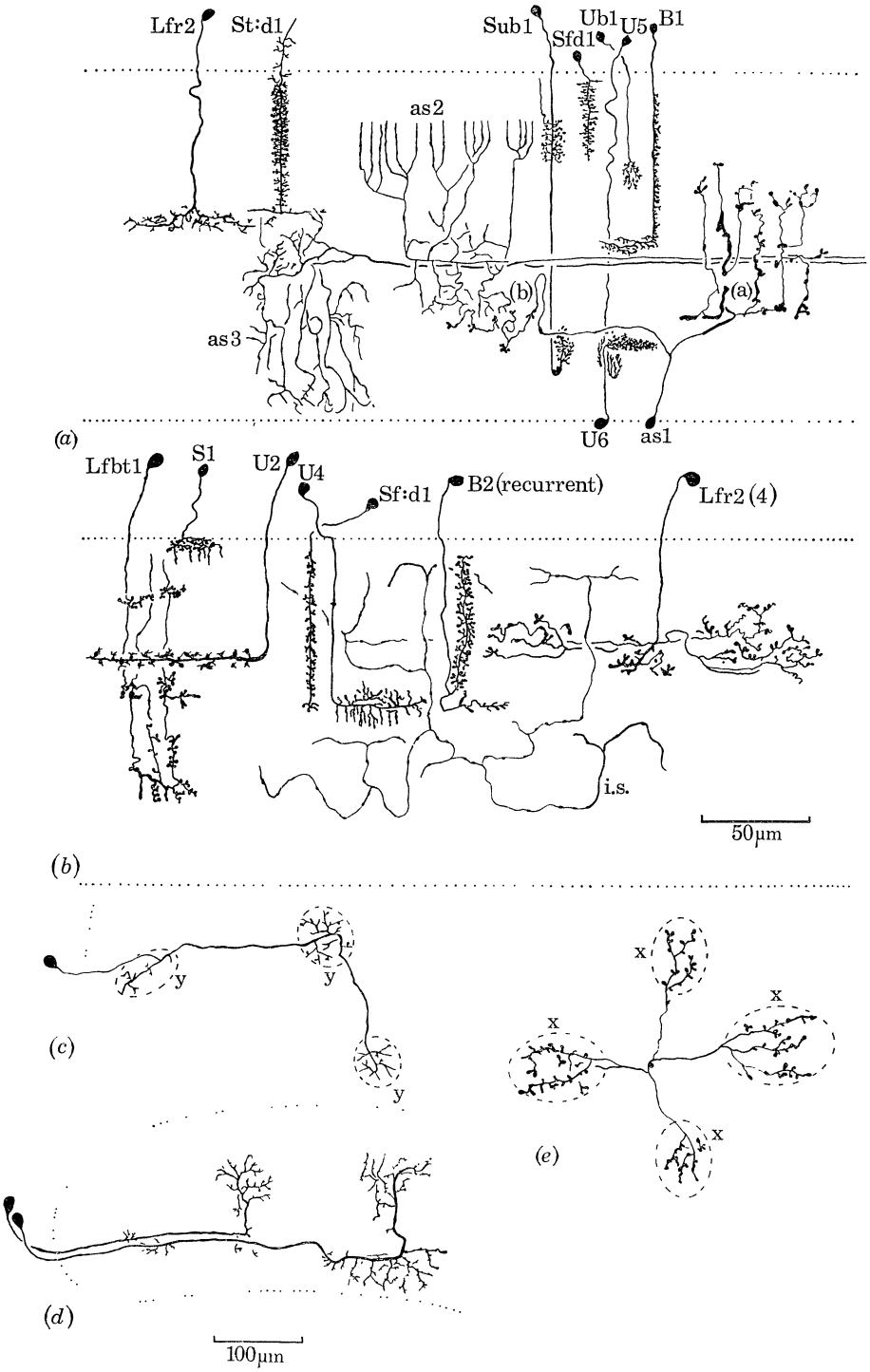

FIGURE 104. Species specific, and some common inter-specific forms of amacrine cells in the medulla of *E. tenax*; also two forms of asymmetric amacrine cells of *Pieris brassicae*. (*a*) Horizontal section of the medulla (posterior, left; anterior, right). Sub1 = small-field bilateral amacrine cell. Lfr2 = large-field radial amacrine cell. In *E. tenax* this element extends through only 6 columns. U6 = a sixth form of unistratified amacrine cell, derived from a cell-body below the medulla. Its processes are at the same level as U5. B1 = 'bent' amacrine cell. Sfd1 = a small-field diffuse amacrine cell, derived from clusters of cell-bodies in the first optic chiasma. Similarly located perikarya give rise to deeper forms of this element. Std1 = another form of small-field tristratified diffuse amacrine cell. Its outermost lateral processes are situated above the outer

Observations on class I elements in the lobula complex

Three forms of T-cells link the lobula to the lobula plate. They all have perikarya situated behind the posterior face of the lobula plate.

The bushy lobula T-cell (T_5). The initial (lobula) component is derived from a cell-body fibre which projects through the lobula plate to the outer face of the lobula (figure 114, plate 25). The arrangement of its processes is like that of the bushy T-cell (T_4) of the medulla; its field is compressed dorsoventrally and adjacent T-cells overlap in the horizontal (oral-ocular) plane. Each group of processes gives rise to a linking-fibre which ends as a simple bilateral tuberous ending in the lobula plate (figures 114 and 118, plate 25, and figures 140 and 141). The lateral extent of both the lobula and lobula plate component is between 8 and 10 μm in *Calliphora* and between 8 and 15 μm in *Eristalis*.

The diffuse lobula T-cell (T_6). This cell has only been detected in *E. tenax*, *E. pertinax* and *S. vitripennis*. Its lobula component consists of up to 40 thin blebbed processes which are arranged unilaterally with respect to the axis-fibre. They spread through between 35 and 40 μm as a horizontal strip-field (figures 115 and 116, plate 25) in strata 1 and 2. The lobula plate ending consists of one or two tuberous processes arranged unilaterally with respect to the axis-fibre and has a similar lateral extent (figure 117, plate 25).

The unistratified strip-field T-cell (T_7). This cell has only been detected in *E. tenax*. It is similar to the preceding type in all respects except that its lobula component is restricted to the outermost 10 to 15 μm of the outer stratum (figure 120, plate 25).

The diffuse translobula-plate cell (TRP 1). This neuron has been detected in *Pieris* and all the present species of Diptera. It has not been seen in *Sphinx* or *Automeris*. Perikarya posterior to the lobula plate give rise to cell-body fibres which project as far as the inner face of this region. Each bifurcates into two parallel axis-fibres which extend across the lobula complex tract as far as the second lobula stratum. Lateral processes extend from each in the lobula plate and second lobula stratum. The lateral extents vary within each species but never exceed 40 μm (figure 141).

FIGURE 104. Legend (*cont.*)

face of the medulla. as1 = the type 1 asymmetric amacrine cell. The tristratified component (*a*) is linked to the unistratified component (*b*) by a tangential fibre. The cell-body is situated below the medulla (see figure 95, plate 22). As 2 and as 3 = the type 2 and 3 asymmetric amacrine cells (terminal components). Note the characteristic bistratified diffuse arrangement of processes. The tangential fibres project to the anterior perimeter zone of the medulla via the serpentine layer where they give rise to a small group of processes in stratum 6.

(*b*) *E. tenax* medulla (vertical section). Lfbt1 = large-field bilateral tristratified-diffuse amacrine cell. The two deeper levels of processes are arranged at levels equivalent to the two strata of Lfbb1 in *Calliphora* (figure 79*b*). S1 = surface amacrine cell. U2 and U4 = two forms of unilateral unistratified amacrine cells. B2 (recurrent) = a second form of recurrent 'bent' amacrine cell (see figure 80). Lfr2 (4) = a large-field radial amacrine. Its cell-body fibre gives rise to four tangentially directed processes in stratum 3. Each of these terminates as a discrete oval subfield in strata 3 and 4. i.s. = *incerta sedis*. Extremely fine blebbed processes (between 0.8 and 0.2 μm diameter) have been seen arborizing throughout the medulla of *Eristalis*. Their origin and destination is unknown.

(*c*) The type 4 asymmetric amacrine cell of *P. brassicae*. This element has been reconstructed from horizontal serial sections; it is shown here mapped onto a tangential portion of the medulla. The cell-body, at the anterior edge of the medulla gives rise to an L-shaped tangential axis-fibre. Three groups of processes are derived from it at the same level as the deepest long visual fibre endings.

(*d*) The type 2 asymmetric amacrine cell, reconstructed from *Pieris*.

(*e*) A tangential view of Lfr2(4) showing the four subfields (x) from the cell-body fibre. The 50 μm scale of figure 104*b* is also applicable to 104*a* and *e*. The 100 μm scale of figure 104*d* is also applicable to 104*c*.

Observations on class I endings in the lobula complex derived from the medulla

Type 1 transmedullary cells have simple plug endings in the outermost stratum of the lobula. These components undoubtedly give this layer its striated appearance. There is evidence that these transmedullary cells end in groups of four or five; several type 1 cells, very close together in the medulla, can sometimes be traced to the lobula; their linking-fibres invariably converge together at the surface of this region (figure 113, plate 24). The type 2 transmedullary cells terminate as simple plug endings in the second stratum, and also have an additional swelling in the outermost layer. Shallow T-cells have simple radial tuberous endings in the second stratum (figure 123, plate 25). The diffuse transmedullary cells have sparsely branched uni-stratified endings deep in the third stratum. Other types of transmedullary cells end at various levels in the third stratum. These are illustrated in figure 140 and summarized in figure 141. The endings of the Y- and T-cells have been described in a previous section (see page 160). They are also illustrated in figures 140 and 141.

Class II elements in the lobula complex

Wide-field tangentials: lobula plate

This region is covered by two extensive arborizations. One of these components is derived from the lobula plate component of the giant optic lobe endings. The other is restricted to the lobula plate and consists of many dichotomous branches which are derived from a linking-fibre at its oral edge. These branches extend over the whole of the surface, roughly oriented in the oral-ocular plane (i.e. antero-posteriorly). Each branch gives rise to many bilateral clusters of baggy terminals (figure 136, plate 28). Reduced silver preparations indicate that there are probably about eight of these endings in each optic lobe. The linking-fibres have been traced anteriorly into the mid-brain and followed, through serial sections towards the contralateral lobula. Its corresponding contralateral component is at present not known.

Wide-field tangentials: lobula

A. *L.wf1.* Four or five linking-fibres, anterior to the inner face of this region give rise to many ascendent processes which project as far as the interface of strata 2 and 1. They branch

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DESCRIPTION OF PLATE 23

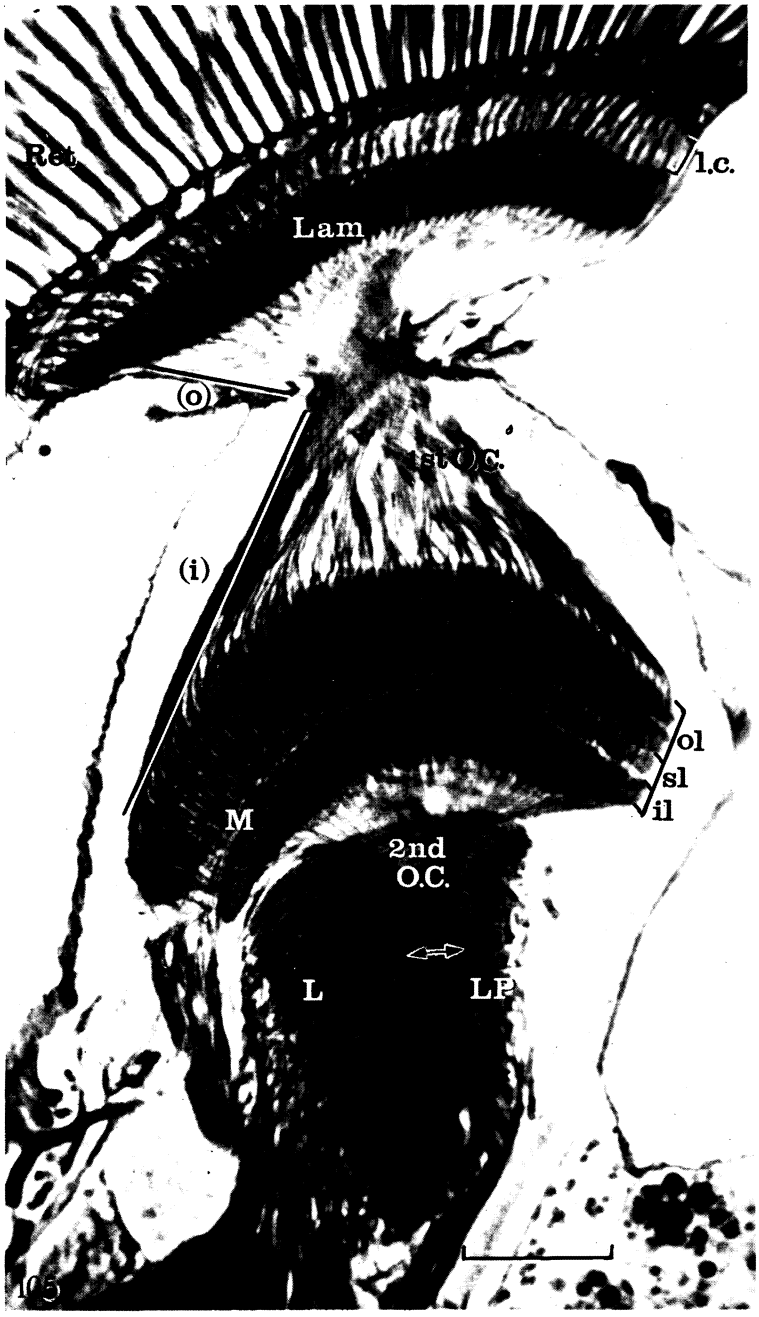
Optic chiasmata

FIGURE 105. *C. vomitoria.* (Holmes–Blest preparation). A horizontal section of the right-hand optic lobe. Ret = retina. l.c. = local chiasmata between retinula cells in the fenestration and cell-body layer of the lamina. Lam = lamina. 1st O.C. = first optic chiasma. (o) = outer segment of the first optic chiasma. (i) = inner segment of the first optic chiasma. M = medulla. ol = outer layer of the medulla. sl = serpentine layer of the medulla. il = inner layer of the medulla. L = (anterior) lobula. LP = (posterior) lobula plate. 2nd O.C. = second optic chiasma. (The intra-complex tract is indicated by a double-ended arrow.)

FIGURE 106. *P. brassicae.* The first optic chiasma (Golgi impregnation). Only a few of the total number of fibres have been impregnated. Two fibres from locus x in the lamina project to two widely separated points in the medulla (y and z). x is anterior to z. Fibre x-z follows the cross-over decussation pattern seen in non-selective preparations. The projection of x-y from an anterior position in the lamina to an anterior point in the medulla is atypical.

FIGURE 107. *C. erythrocephala* (Holmes–Blest preparation. Tangential section). Class I fibres leave the inner face of the medulla in horizontal strips. 8 = stratum 8.

FIGURE 108. *C. vomitoria* (Holmes–Blest preparation). The outer strata of part of the lobula (L; 1 and 2) and the lobula plate (LP). The type IIS: 2 elements are stained selectively by this method. Their regular distribution can be seen in stratum 2. *Scales:* Figure 105, 100 μm; figure 106, 25 μm; figure 107, 25 μm; figure 108, 20 μm.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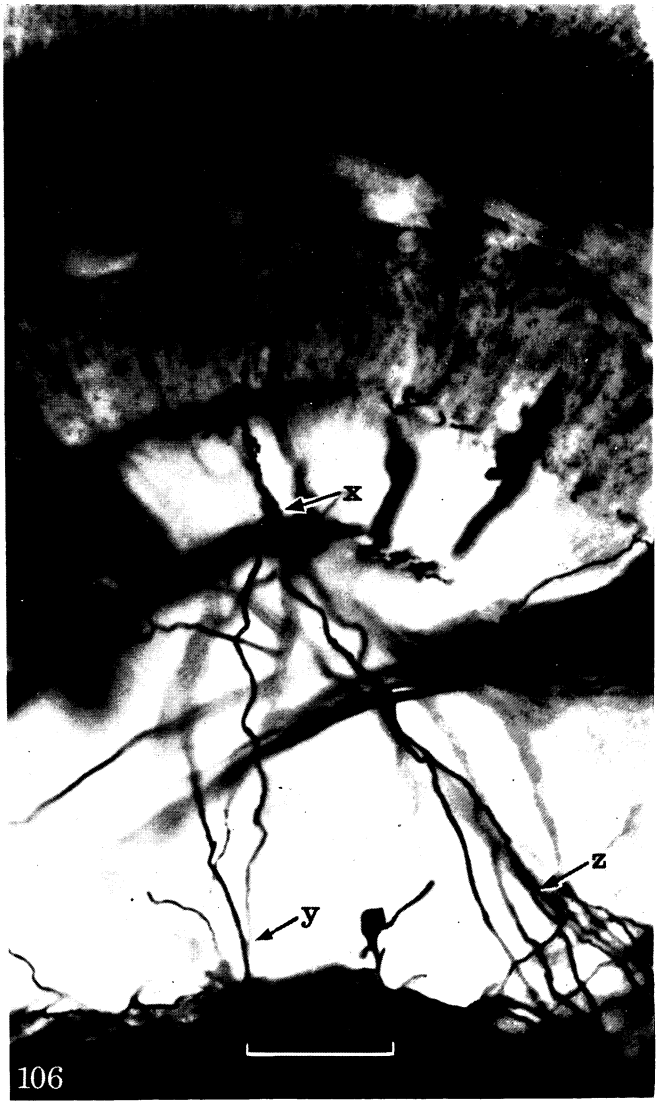
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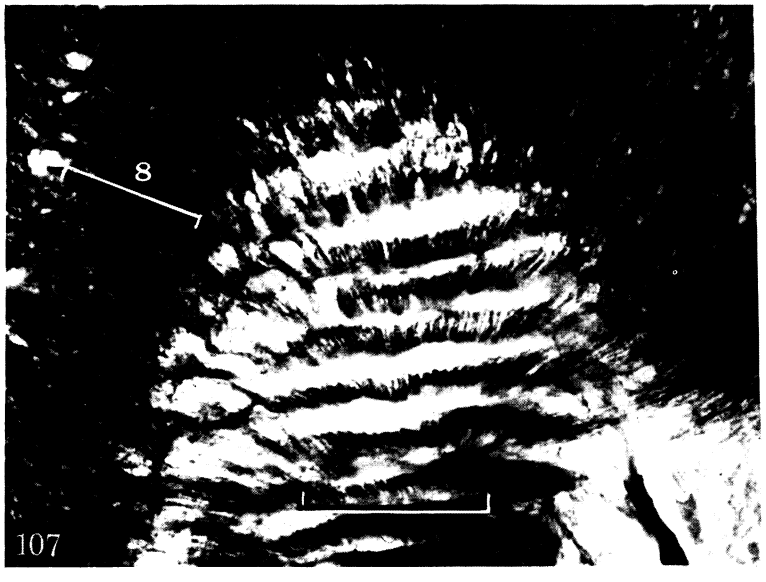
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IIS1
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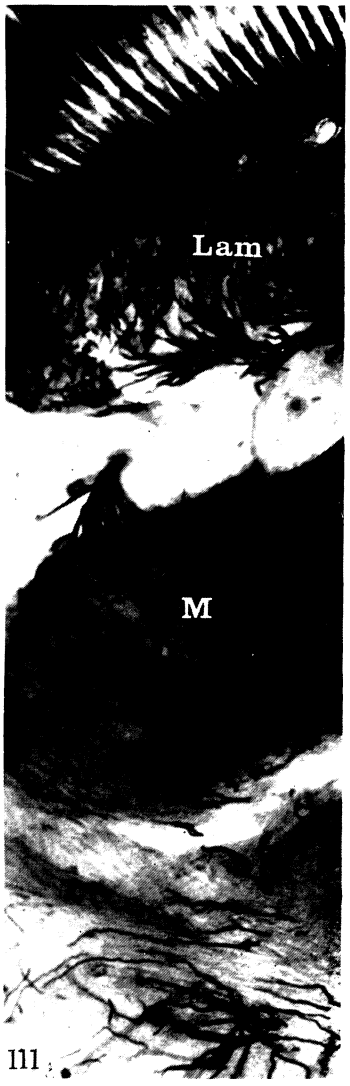

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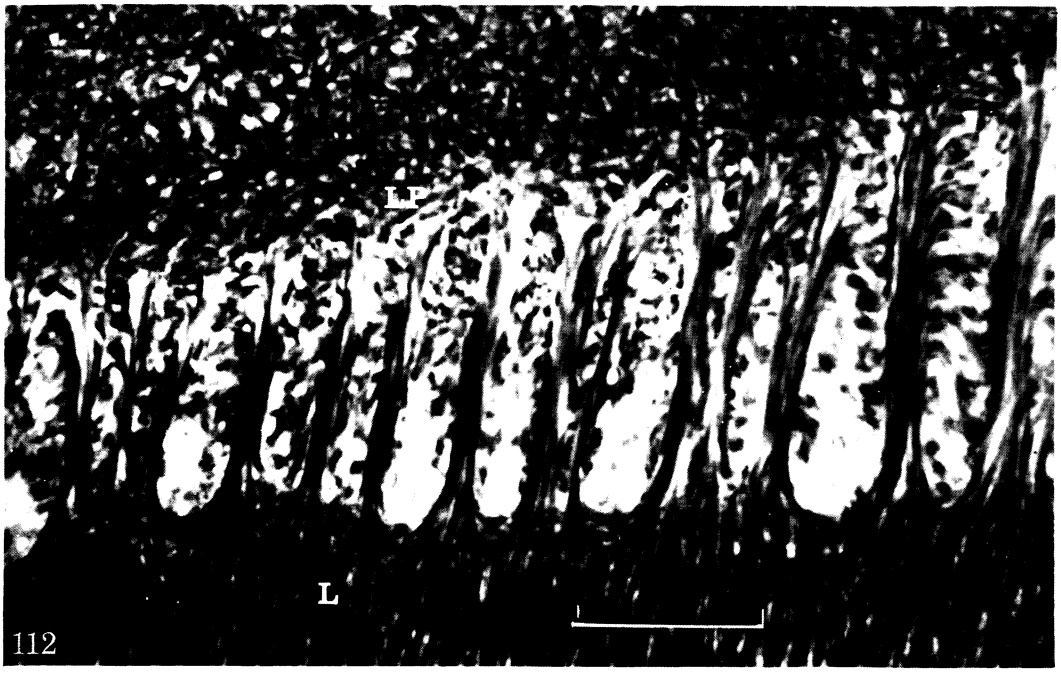

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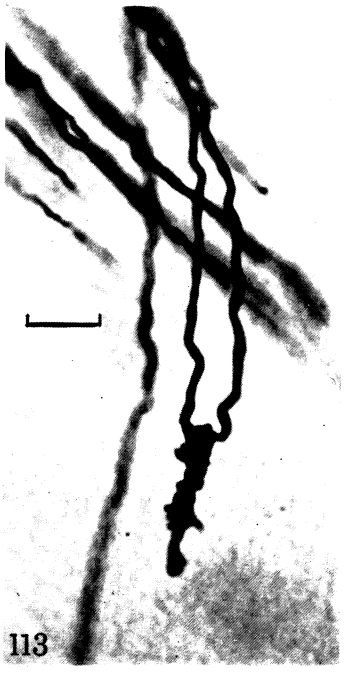
113

repeatedly within the outermost stratum; each branch finally terminates as a small subfield consisting of spiny processes. These subfields together cover the whole of the surface of this region (figure 149*b*, plate 30, and figure 93). Each linking-fibre gives rise to between 80 and 100 extremely small non-overlapping subfields which together cover about one-fifth of the region's surface. The linking-fibres have only been traced a short distance within the tract of the central commissure (Power's 1943*a* terminology).

B. *L.wf2.* This ending has been previously described from species of *Sphinx* and *Pieris* (part I). A similar form of element has been detected arborizing throughout the third stratum of the lobulae of the Diptera (figure 139, plate 28). Its processes are at the same level as the deepest endings of Y-, T- and transmedullary cells. Its linking-fibre has been traced for a short distance towards the mid-brain. A thin collateral derived from it near the inner face of the lobula has the characteristic form of a cell-body fibre, but it has not been possible to trace this to its cell-body.

C. *The ascendant diffuse tangential* (*L.wf3*). This ending is characteristic of the Diptera; there is no evidence for it in the Lepidoptera. A stout 2 to 3.5 μm linking-fibre, anterior to the inner face of the lobula gives rise to many ascendant processes which divide repeatedly within the innermost stratum. They subsequently terminate as tuberous swellings at a level just above the small field subclass IIS elements in stratum 2 (see figures 125, plate 26; figures 137 and 138, plate 28 and figures 133, plate 27 and 147, plate 29). The ascendent processes in all the species, except for *Syrphus elegans*, are tuberous. In this latter species they are smooth and end characteristically as several short varicose branches (figure 134, plate 27).

Incerta sedis. Figure 140 illustrates a diffuse element in the lobula plate of *E. tenax*. This element has not been detected in the other species of Diptera. It lies characteristically deep in this region and could only interact with the deepest Y-cell endings at the same level but not with other class I endings or the type 9 subclass IIS component in the lobula plate. This diffuse element extends between 200 and 300 μm in the oral-ocular plane and approximately 80 μm vertically. Possibly it is analogous to the type 2 strip-field ending in the lobula plate of the other species of Diptera.

Description of plate 24

Chiasmata and tracheation

Figure 109. *C. vomitoria* (osmium–potassium dichromate impregnation of late pupal animal). The trachea have been impregnated by this variant of the Golgi stain. M = medulla. L = lobula. L.P. = lobula plate.

Figure 110. *Pieris brassicae* (Holmes–Blest preparation). This illustration shows the parallel arrangement of fibres in the first optic chiasma revealed in sections which are cut parallel to the plane of cross-over. In this figure two groups of four fibres (aa) and (bb) leave two adjacent optic cartridges. Each group splits into two pairs near the surface of the medulla (a, a) and (b, b). However, groups of four fibres ('Quads') enter the medulla, regularly spaced from one another. Each quad contains two pairs of fibres from adjacent or sub-adjacent optic cartridges. In this instance one quad contains pair ab derived from group aa and bb. (This reorganization of pairs is shown schematically in figure 169.)

Figure 111. *C. vomitoria* (horizontal section, Colonnier impregnation). Tracheation in the lamina (Lam) and in the medulla (M).

Figure 112. *Sphinx ligustri* (Holmes–Blest preparation). A tangential section showing the homotopic projection of bundles of fibres in the intra-complex tract between the lobula and lobula plate.

Figure 113. *E. tenax.* Two convergant endings of type 1 transmedullary cells in stratum 1 of the lobula (see also figure 44, plate 7; part I).

Scales: Figures 109, 111, 50 μm; figures 110, 113, 10 μm; figure 112, 25 μm.

Strip-field tangential elements: lobula plate

The outermost stratum of the lobula and the unistratified lobula plate are invaded by narrow strip-field endings. These characteristically extend through the whole oral-ocular length of these levels. Their vertical extent is extremely narrow, usually less than between 10 and 15 μm.

A. *LP.sf1.* Linking-fibres connect the oral edge of the lobula plate to an ipsilateral region of the dorsal posterior proto-cerebrum at a point peripheral to the lobes of the corpora pendunculata. These linking-fibres run parallel to the inner face of the lobula plate (figure 147, plate 29) and their resultant prolongations (tangential axis-fibres) give rise to short unilateral branched processes along their length. These terminate as simple swellings. Each process penetrates the lobula plate neuropil only as far as the deepest extent of the T_4 and T_5 cell endings. The cell-body locations of these tangential cells have not yet been determined but are thought to be situated medially in the brain.

B. *LP.sf2.* A second form of strip-field tangential invades the lobula plate from its posterior face (figure 146, plate 29). The tangential axis-fibre of each gives rise to unilateral processes which terminate at the surface of this region as a cluster of short blebbed processes. The linking-fibres has not been traced any great distance towards the mid-brain and the cell-body location is unknown. This element has been seen in all the present species of Diptera, with the exception of *E. tenax.*

Strip-field tangential elements: lobula

A. *L.sf1.* A third form of strip-field tangential element invests the outer stratum of the lobula. However, each axis-fibre forms a subfield (between three and four axis-fibres are derived from a linking-fibre at the oral edge of the lobula). The arrangement of the unilateral processes is similar to that of LP.sf1. Each process consists of a bunch of tubers (figures 135 and 145, plates 28 and 29, respectively).

B. *The deep strip-field tangential (L.sf2).* This component has been seen in all the present

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Description of plate 25

The lobula complex

Figure 114. *C. vomitoria.* T_5 cells linking the lobula and the lobula plate (note homotopic projection pattern).

Figure 115. *E. tenax.* The initial component of a T_6 cell in the lobula.

Figure 116. *E. tenax* (tangential section). The lobula field spread of a T_6 cell.

Figure 117. *E. tenax.* The lobula plate ending of a T_6 cell.

Figure 118. *E. tenax* (tangential section). The field spread of a T_5 cell in the lobula.

Figure 119. *E. tenax* (tangential section). The field spread of two type 1 amacrine cells at the same level as the T_5 elements (stratum 1).

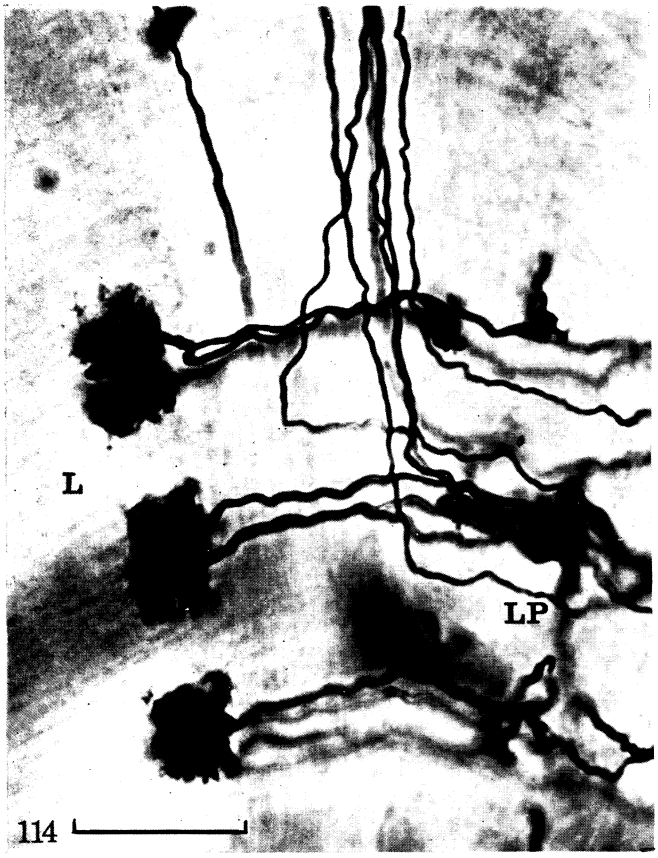
Figure 120. *E. tenax.* A T_7 cell. Note the thin cell-body fibre from the lobula component (L). L.P. = lobula plate ending.

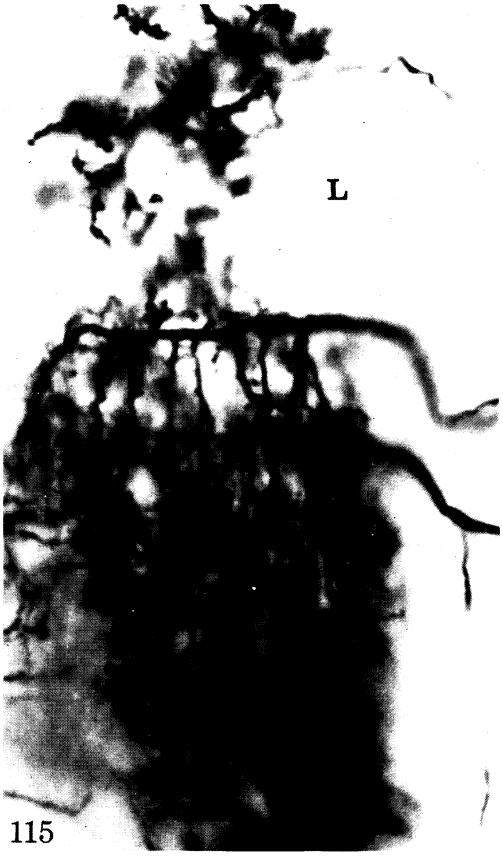
Figure 121. *C. erythrocephala.* A 'giant' lobula ending of a T_3 cell at the ocular edge of the lobula.

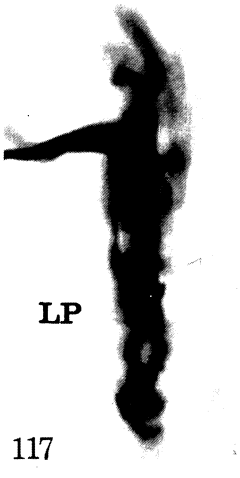
Figure 122. *S. nitidicollis.* Some endings of class I elements in the lobula complex derived from the medulla. Tm = type 1 transmedullary cell. Upper and lower Ys (arrowed) = respectively, the lobula plate and lobula branches of Y_1 cells. T = the sparsely branching tuberous ending of a T_2 cell. A deep ending of a Y_2 cell is indicated by an arrow.

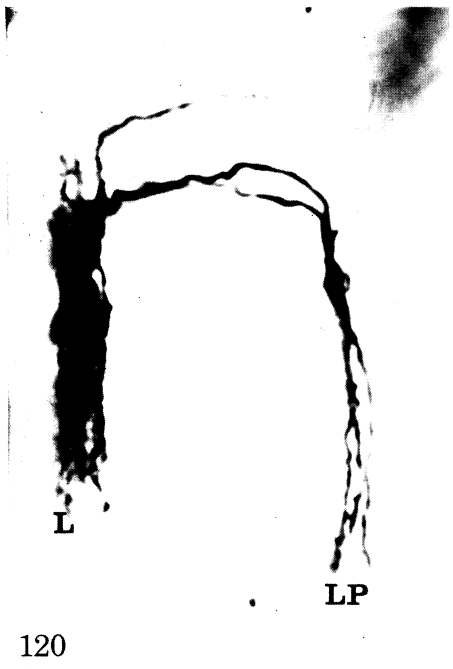
Figure 123. *E. tenax.* A T_3 ending in the lobula.

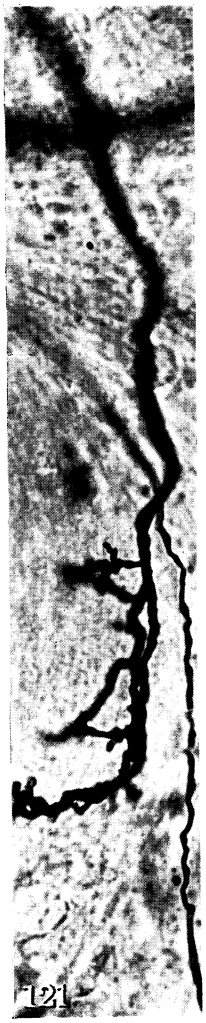
Scales: For figures 114 to 121 the scale on 114 = 25 μm; for figures 122 and 123 the scale on 122 = 25 μm.

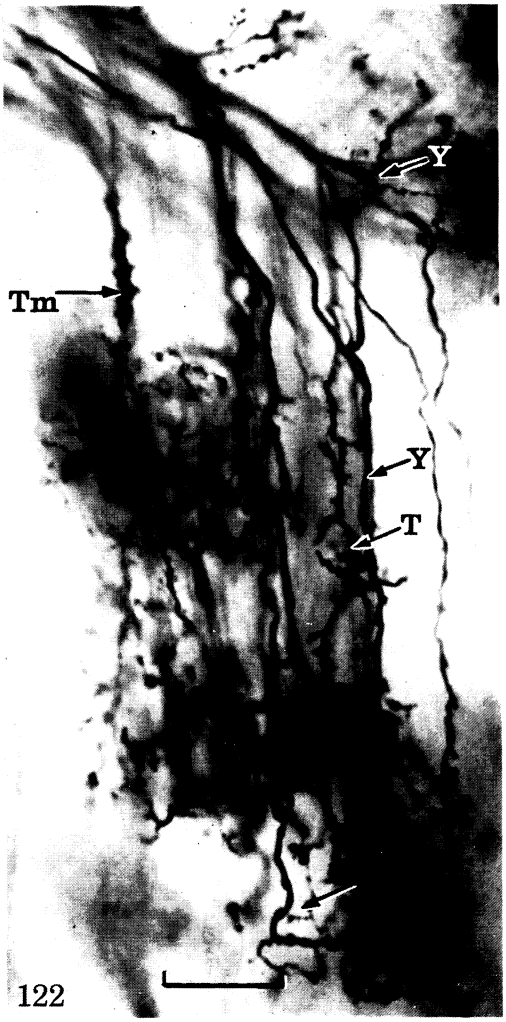


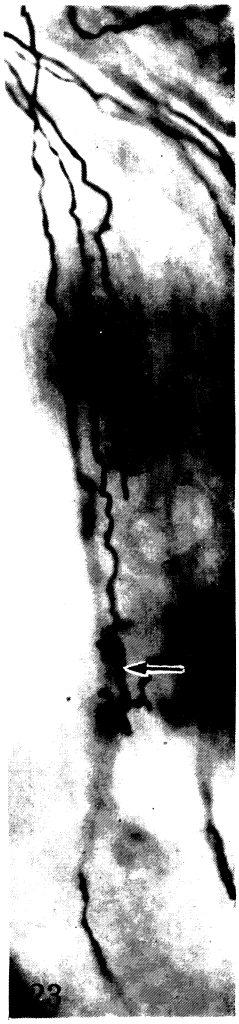












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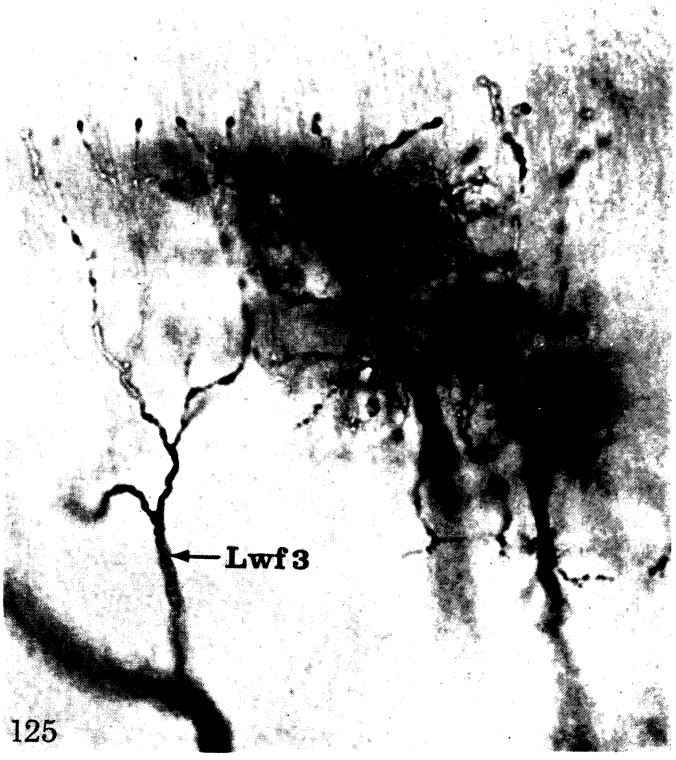

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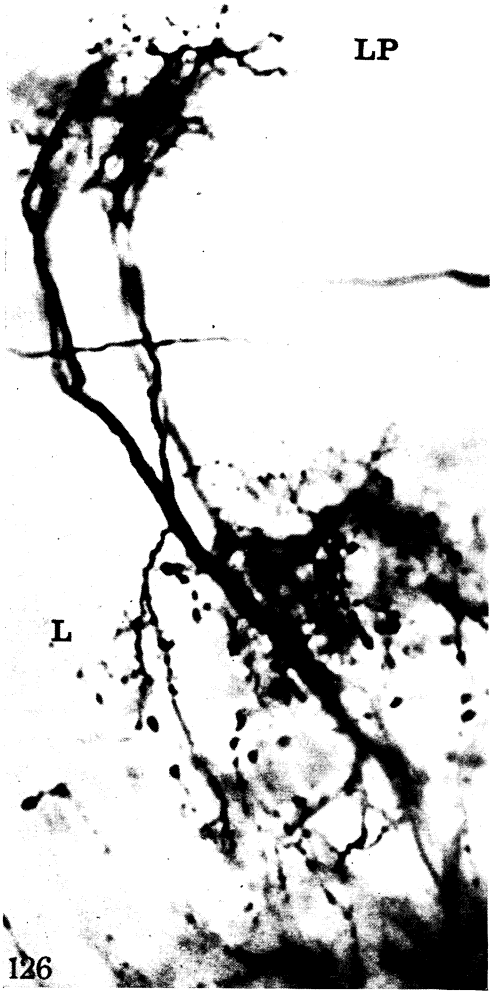

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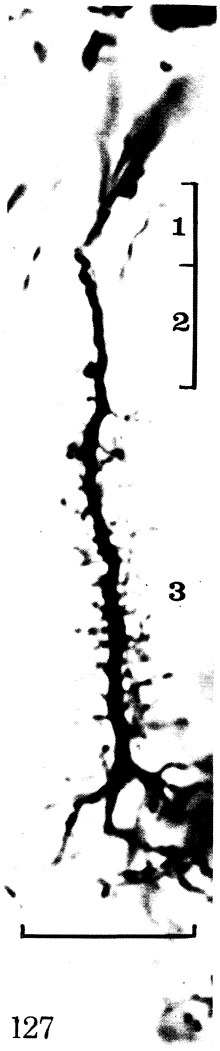

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species of Diptera, though it has a slightly different form in each. In *E. tenax* it consists of two pairs of tangentially directed terminal branches which extend through the whole of the oral-ocular length of stratum 2. These branches effectively divide this level into an outer and inner half. Short lateral processes arise bilaterally from each branch. The whole element has a dorsoventral lateral extent of less than 15 μm. Its perpendicular extent is small, less than 7 μm. Although this element has often been impregnated it has only been seen at the equatorial oral-ocular mid-line of the lobula, so dividing it into equal dorsal and ventral halves. The element is illustrated in figure 93 and figure 148, plate 29. Fragments of a similarly disposed tangential element have been detected in *Pieris* but not in *Sphinx*. The linking-fibre of this element projects towards the mid-brain but has not been traced to its destination. In the Diptera a cell-body fibre arises from the linking-fibre between the lobula and the margin of the protocerebral lobe. It has not been traced to its respective cell-body.

C. *L.sf3*. Dorsoventrally oriented strip-field elements have been detected near the inner face of the lobula, in the third stratum. They are impregnated infrequently and have not been seen in their entirety: each consists of a tangentially directed axis-fibre from which arise several disk-shaped subfields. These appear similar to the type 4 subclass IIS processes. The lateral extent, cell-body locations and projection patterns to other regions has not yet been determined.

D. *L.sf4* (*the ascendent-descendent strip-field tangential*). A bistratified tangential element with dorsoventrally oriented subfields has been described in detail from *Pieris* (see part I, figure 71). There is evidence of a similar element in the two species of *Calliphora* and it has been seen in part in *E. tenax*. However, it is either absent in the species of *Syrphus* or has not yet been impregnated.

As in the Lepidoptera this element is complex in shape. Ascendent fibres from a linking-fibre anterior to the lobula project perpendicularly as far as its second stratum. Each bends at right angles at this level and projects tangentially for about 100 μm. It bends again at right angles and descends as far as the inner face of this region. Fine blebbed processes are derived from the tangential component and from the descendent component in stratum 3. The field size of the whole element has not yet been determined; but each strip subfield has a lateral (oral-ocular) extent of less than 20 μm (see figure 93).

E. *The diffuse unistratified tangentials* (*L.sf5*). Fragments of class II elements have been detected

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Description of plate 26

The lobula complex

Figure 124. *E. tenax*. Type IIS: 2 elements. Note the bilateral processes (arrowed) beneath the junction between axis-fibres and cell-body fibres. One fibre in the intra-complex tract appears to project heterotopically (arrowed x, x).

Figure 125. *S. torvus*. Processes of the type 3 wide-field lobula tangential (Lwf3). They terminate at a level just above the outermost processes of type IIS: 2 elements in stratum 2.

Figure 126. *E. tenax*. The type IIS: 9 element. Two branches extend from the single axis-fibre in the lobula to the lobula plate. They give rise to two groups of processes. The two lobula plate subfields together have a lateral extent equivalent to the single subfield in the lobula.

Figure 127. *S. nitidicollis*. A bistratified diffuse element in stratum 3. This may possibly be the initial component of a centrifugal cell linking the lobula to the medulla (see text).

Figure 128. *E. tenax*. Two IIS: 3 elements in the lobula.

Figure 129. *E. pertinax*. The terminal component of an inter-lobula cell (IIS: 7).

Figure 130. *E. tenax*. A tristratified diffuse component in stratum 3 (*incerta sedis*).

Scales: For figures 124 to 126, 129 and 130 the scale on 124 = 40 μm; figure 127, 40 μm.

in the third stratum of the lobula near its inner face. These have the form of long narrow brush-like endings which are directed in both the oral-ocular and dorsoventral plane (figure 141). Similar elements have been seen in *Sphinx* and *Pieris*. These are derived from a linking-fibre near the oral, posterior edge of the lobula in a tract which links this region with an accessory region of the ipsilateral protocerebrum. The precise destination of this fibre is not known.

The giant lobula complex cell

This cell has been detected in its entirety in *E. tenax* (figure 93 and figures 155 and 156, plate 32). It links the lobula and lobula plate with an anterior region in the protocerebrum. This cell has not been described by other authors, although Cajal & Sanchez did figure and describe asymmetrically shaped small-field tangential elements in both lobula regions of *Tabanus*. However, these elements are clearly homologous to similar small-field subclass IIS cells in the present species which are described in the next section. The lobula complex component of this giant cell is divided into two parts, one in each region. The axis-fibre enters the lobula at the mid-point of its anterior face; it projects as far as the interface between strata 3 and 2 where it bends at right angles. The straight portion of the axis-fibre gives rise to two sets of processes; one extends, unilaterally, from the axis-fibre through the ocular half of the inner half of stratum 3; the other also extends unilaterally from the axis-fibre through the oral outer half of the same stratum. Several perpendicular processes extend from the curved portion of the axis-fibre, at the edge of stratum 2, across to the outer face of the lobula plate. There they give rise to a tangled plexus of processes which extend through the whole oral-ocular arc.

Both lobula and lobula plate components form a narrow horizontal strip-field at the oral-ocular equator of these regions. The lobula component is especially remarkable in that its field is divided into two distinct levels which are separate from one another. The protocerebral ending has the form of a large brush-shaped terminal in accessory region 2 (figure 156, plate 32). This region, hitherto undescribed, is linked to the central body by another large-field component (N. J. Strausfeld, unpublished).

There is good evidence that a giant lobula complex cell is present in *C. erythrocephala* (figure 149*b*, plate 30). However, its linking-fibre has only been traced as far as the perimeter of the optic lobe accessory region 2. The cell-body fibre of this cell in *Eristalis* is derived from the linking-fibre at the anterior edge of the lobula; it has not been seen in *Calliphora*. There is a large-field lobula-lobula plate element in *C. vomitoria* (figure 144). Its lobula component consists of a wide, diffuse subfield of spiny processes in strata 2 and 3. Collaterals from the axis-fibre extend into the lobula plate where they end among the Y_1 cell endings. The axis-

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DESCRIPTION OF PLATE 27

The lobula complex

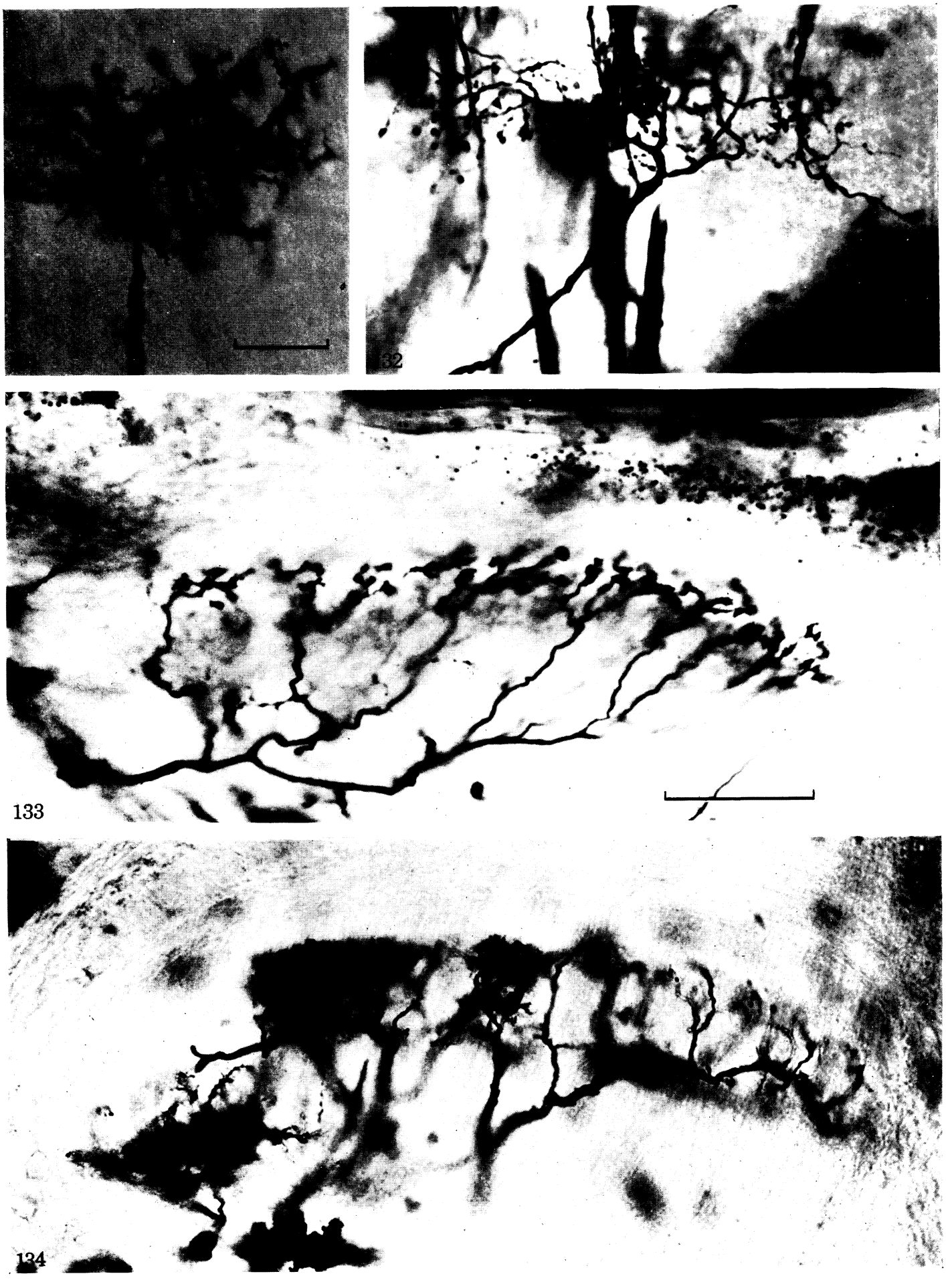
FIGURE 131. *S. vitripennis*. A large-field IIS: 3 element in lobula stratum 2.

FIGURE 132. *E. tenax*. An oval-field IIS: 4 element in lobula stratum 2.

FIGURE 133. *S. vitripennis*. The type 3 wide-field lobula tangential element (Lwf3) extends through the whole oral-ocular arc of the region.

FIGURE 134. *S. elegans*. Lwf3. The wide-field element in this species has the same dispersion of branches as in others. However, its terminal processes in stratum 2 have a different branching pattern (see text). Some IIS: 1 elements have also been impregnated.

Scales: Figures 131, 132, 25 μm; figures 133, 134, 50 μm.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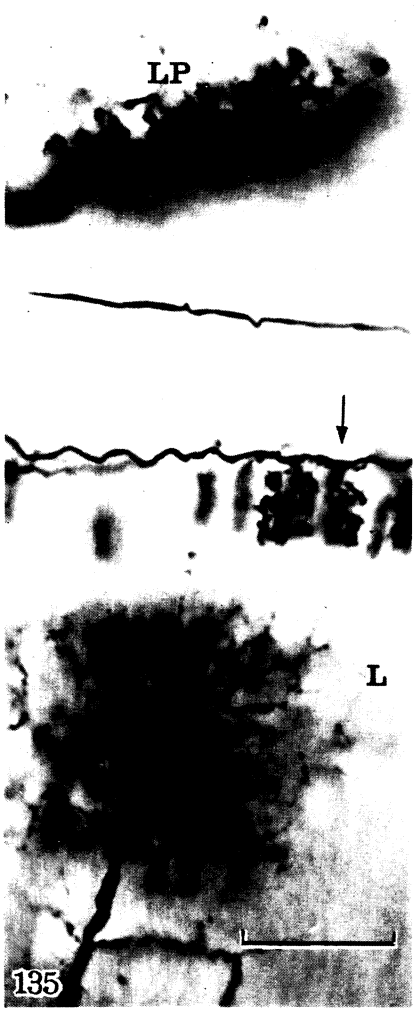
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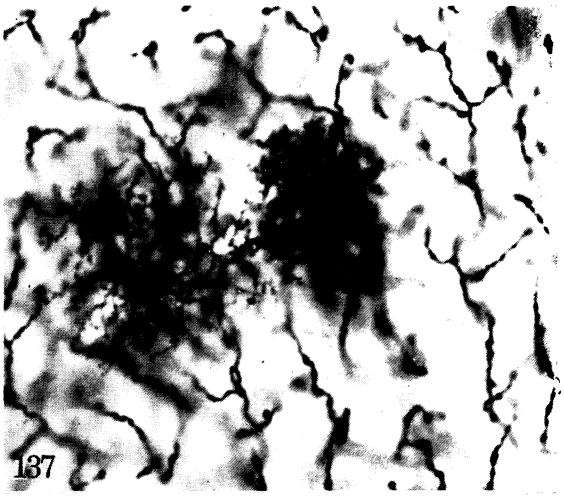
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fibre has been traced from the inner face of the lobula towards the protocerebrum. However, its mid-brain ending is not known.

If these last two elements in the two species of *Calliphora* are derived from the giant lobula complex cell, then this neuron, like the giant optic lobe tangential, seems to have both shape and field-characteristics which are different in the optic lobes of each species.

Subclass IIS cells

The Spanish authors described and figured various forms of small-field elements in the lobulae of *Tabanus* which projected towards the mid-brain. The components of these elements are uni-, bi- or tristratified in the single lobulae of *Apis* and *Libellula* and uni- or bistratified in the divided lobula of *Tabanus*. Subclass IIS cells have been further subdivided into three groups. Those of the first have uni- or bistratified components derived from cell-bodies situated near the anterior edge of the ipsilateral lobula. Their optic lobe components invest this region only. Their cell-body fibres project into the lobula neuropil where they all give rise to an outer set of processes and a subsequent perpendicular fibre below it; this extends as a linking-fibre from the lobula's inner face towards the mid-brain. The second group consists of unistratified or diffuse endings derived from the mid-brain or contralateral lobe. None of them appear to have cell-bodies in the vicinity of the ipsilateral lobula which they invest. Those of the first group invariably have smooth or spiny processes. Those of the second are invariably blebbed, varicose or tuberous. Other elements have small-field groups of processes in both the lobula and lobula plate; these have been categorized under group 3.

Group 1

IIS 1 and IIS 2. Both these forms of cells have their outermost processes situated exclusively in lobula stratum 2. The type 1 cell has a stout axis-fibre (between 2 and 4 μm in diameter) surmounted by thick spiny branches. These form an oval field whose long axis extends obliquely from an antero-dorsal to a postero-ventral position (figure 142). There is a second bilateral group of processes in stratum 3 derived from the axis-fibre just below its junction with the cell-body fibre. These cells can be clearly seen in the Holmes–Blest preparations (figure 108, plate 23). They are distributed in the lobula so that there is only marginal overlap between adjacent fields. Densely impregnated Golgi preparations reveal the same spatial relationship.

Description of plate 28

The lobula complex

Figure 135. *E. tenax.* A small portion of the wide-field lobula plate component of the giant optic lobe tangential element. The lobula type 1 strip-field element invests stratum 1 (arrowed). IIS: 2 elements are restricted to stratum 2. L = lobula. LP = lobula plate.

Figure 136. *E. tenax* (vertical section). The characteristic branching pattern of the wide-field element over the lobula plate surface.

Figure 137. *E. tenax* (tangential section). This section has cut through the curved surface of stratum 2 to reveal the terminal processes of Lwf3 and two small disk-field elements at a level just below them. These have been identified as a IIS: 2 element (the larger of the two fields) and a type 5 lobula amacrine cell.

Figure. 138. *E. tenax.* Part of the section shown in figure 137 was cut horizontally to show the layer relationships between a plug ending of a type 1 transmedullary cell, the outermost processes of Lwf3 and just visible below them, the outermost processes of a IIS: 2 element.

Figure 139. *C. erythrocephala* (methylene blue prefixation–Golgi Colonnier). The type 2 wide-field lobula element (Lwf2). This extends throughout the whole of stratum 3.

Scales: Figures 135 to 139, 25 μm.

The portion of the protocerebral lobe that flanks the optic lobe is divided into at least four discrete regions, two of which are known to receive endings from the ipsilateral lobula complex. These have been termed optic lobe accessory regions 1 and 2. The former receives the endings of the IIS: 1 cells (figure 153, plate 31); the latter receives the ending of the giant lobula complex cell.

The IIS: 2 cells have the same bistratified arrangement of processes as the preceding type. The outer processes lie within stratum 2. The most densely impregnated Golgi preparations show that adjacent fields overlap by as much as one-quarter of their total lateral extent (figure 124, plate 26). The bilateral processes lie at the outer margin of stratum 3. Those of adjacent cells have frequently been detected closely applied to one another.

IIS: 3 cells. These elements appear similar to the type IIS: 2 cells (figure 131, plate 27). However, they lack the bilateral processes below the axis-fibre cell-body fibre junction and have larger field spreads. The extent of their disk-fields range from 35 to 60 μm (figure 128, plate 26). The largest can overlap by as much as three-fifths of their total lateral extent. The processes of these cells lie either in the lower half of stratum 2 and the outer half of 3 or exclusively at various levels in stratum 3.

IIS: 4 cells. The processes of these elements form large oval fields at any level between the outer margin of stratum 2 and the inner face of the lobula (figure 132, plate 27). In *Eristalis* their long, oval fields are oriented both dorsoventrally or antero-posteriorly. In the species of *Calliphora* they have only been seen oriented dorsoventrally.

Group 2

The monostratified ending; IIS: 5 (figure 140). This element is situated at the interface between strata 1 and 2. It consists of between four and seven dichotomous branches which together form an oval or disk-field just above the level of the type IIS: 1 and 2 cells. Each branch is varicose and sparsely populated with short lateral projections.

The diffuse ending; IIS: 6. This ending has only been positively identified in *E. tenax* and *S. elegans*. It consists of fine blebbed processes which arise from a curved axis-fibre in stratum 3. They spread through this and stratum 2 to form characteristically oval field-spreads which are oriented dorsoventrally. Although these endings have not been seen in the two species of *Calliphora* there is a type of diffuse ending, characteristic of these two species, which may be analogous to the IIS: 6 ending of the Syrphidae. These (IIS: 10 endings) have oval fields of various sizes which are sparsely populated by thin blebbed fibres that stem from an axis-fibre in the outer half of stratum 3 and in stratum 2. These are illustrated in figures 151 and 152, plate 31).

The inter-lobula cell; IIS: 7. This element has been identified in *Eristalis*, *S. torvus* and in *S. elegans*. There is only fragmentary evidence for it in *Calliphora*. It consists of a small disk-field formed by varicose processes within the outer half of stratum 3 and the whole of stratum 2 (figure 129, plate 26). The axis-fibre extends as a linking fibre from the inner face of the lobula, across the brain to the contralateral lobula. Its corresponding contralateral component has not been seen. However, the axis-fibres from the ocular edge of stratum 3 of the ipsilateral lobula project to a corresponding position in the contralateral region. It seems that this projection pattern is invariably homotopic.

The lobula-optic tubercle cell; IIS: 8. Two elements invest the optic tubercle from the optic lobes (see part I). One of these is a small-field component in stratum 3 of the lobula (figure 140).

Its processes are short and varicose in the Diptera. The precise cell-body location is at present unknown although a fine collateral has been detected from the linking-fibre near the optic tubercle which has the characteristic beaded appearance of a cell-body fibre.

Group 3

IIS: 9 and 9a. Both these elements have groups of processes in the second stratum of the lobula and in the lobula plate. The type IIS: 9 element has been detected in all the Diptera; its shape is characteristic. A thick (3 to 4 μm diameter) axis-fibre extends as far as the outer margin of stratum 2 where it bifurcates twice, eventually giving rise to four fibres that cross the intra-complex tract to the lobula plate. Two groups of processes, with the same field sizes, are situated in the lobula plate and second lobula stratum (figure 126, plate 26). The type IIS: 9a cell has only been detected in *E. tenax* and *S. nitidicollis*. Its axis-fibre bifurcates only once in stratum 1. The subsequent pair of fibres terminates in the lobula as two characteristically bistratified endings (figure 149*b*, plate 30). The lobula processes of IIS: 9 are situated in stratum 2; those of 9a are in the outer half of 2 and the inner half of 1. Both types are shown together in figure 140.

Incerta sedis. Figure 130, plate 26, shows a tristratified diffuse element in stratum 3 of the *Eristalis* lobula. Similar shaped elements have been detected in the other species of Syrphidae but have never been seen in the species of *Calliphora*. They have oval fields which are usually oriented dorsoventrally, and have three sets of processes, one of which is invariably varicose and the others spiny. Its axis-fibre has only been traced as far as the inner margin of the lobula and it is not known whether this extends further as a linking-fibre to another region or as a cell-body fibre to a perikaryon anterior to this region. This element is one candidate for the initial component of the cell that terminates contralaterally as IIS: 7.

Observation on class III cells in the lobula complex

Two elements in the lobula of *Pieris* are most probably derived from amacrine cell-bodies (see part I). Four forms of amacrine cells have been seen in their entirety in the present species of Diptera. The unistratified small-field amacrine cell in the outermost lobula stratum is common to each species. Narrow-field diffuse amacrines invade strata 2 and 3 from cell-bodies situated anterior to the lobula. These too have been detected in these species of Diptera. The other forms, which enter the lobula from perikarya behind the lobula plate, have different shapes in each species. In all the Diptera they spread diffusely through strata 1 to 3 or lie at the same level as the lobula-lobula plate T-cell (T_5) and, if they are present, T_6 and T_7.

Lobula amacrine cells are included in figures 140 and 141 from *E. tenax* and *Calliphora vomitoria* respectively.

Centrifugal class I cells between the lobula complex and the medulla

Centrifugal cells link the medulla to the lamina. However, there is only fragmentary evidence that similar elements link the lobula to the medulla. Cajal & Sanchez classified one perpendicular component in the medulla of *Tabanus* as centrifugal; this entered the region from its inner face. They did not, though, trace the axis-fibre to its respective destination in another region or to a cell-body. At present the evidence for this element being an amacrine cell or a class I cell is equivocal. A similar ending has been detected in *Eristalis*. Its linking-fibre was followed only a short distance into the second optic chiasma where it seemed to project antero-

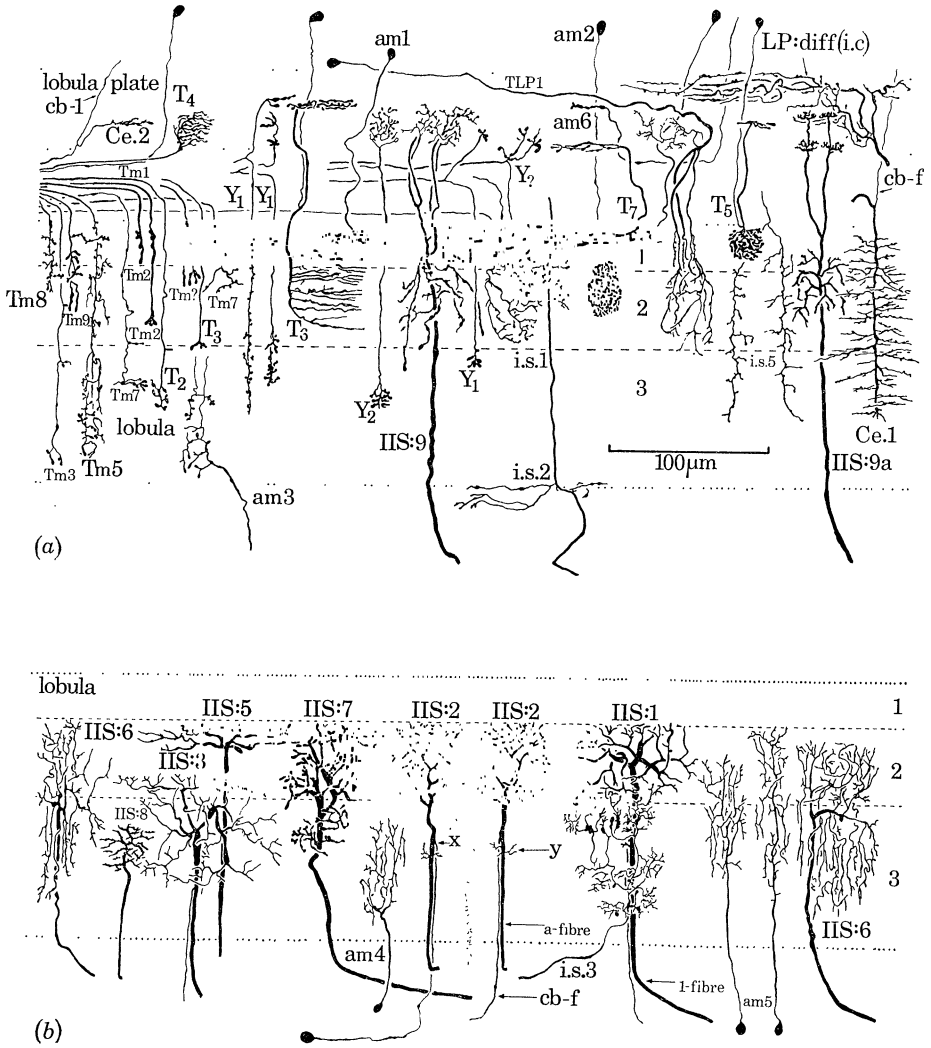

FIGURE 140. Summary diagram of the lobula complex (*E. tenax*, horizontal plan).

(*a*) The layer relationships in the lobula complex between class I inputs from the medulla, class I elements between the lobula and lobula plate, amacrine cells, and the IIS: 9 elements.

(*b*) The layer relationships in the lobula between subclass IIS elements and amacrine cells. Both figures *a* and *b* are drawn to the same scale.

Tm 1–3, 5 and 7–9 = transmedullary cell endings (see figures 80 and 81). Tm 4 and Tm 6 have not been traced in their entirety. However, four endings in the lobula may be derived from them; the transmedullary cell ending, Tm ? and i.s. 1, 4 and 5 which are derived from very slender fibres in the intra-complex tract and second optic chiasma (between 0.2 and 1.0 μm diameter). i.s 1 has diffuse processes in strata 1 and 2; i.s. 5 extends through strata 1, 2 and the outer half of 3. T_5, T_6, T_7 = the three forms of lobula-lobula plate T-cell. T_4 = the lobula plate ending of the bushy T-cell. Y_1 = three variants of Y_1 endings. Y_2 = the tangential Y-cell ending. $Y_?$ = this may be the Y-ending of the Y_{2a} variant in the medulla or possibly of the element listed as *incerta sedis*, figure 81. IIS: 9 = the lobula-lobula plate IIS component. IIS: 9a = the narrow-field variant of IIS: 9. am 1 and 2 = the two amacrine cell elements in stratum 1 and stratum 2, respectively. am 6 = the lobula plate amacrine cell (amacrine cells have not been seen in the lobula plate of other species). Ce. 1 = an initial component in the lobula. The linking-fibre may project to the medulla, giving this element the status of a morphological lobula-medulla centrifugal cell (see text). Ce. 2 = an initial component in the lobula plate. The linking-fibre may project to the medulla giving this element the status of a morphological lobula plate-medulla centrifugal cell. Cb-f = cell-body fibres. TLP 1 = translobula plate cell. am 3 = type 3 amacrine cell. LP: diff (i.c.) = tangential element close to the posterior face of the lobula plate. This has been listed as *incerta sedis*; it may, however, be analogous to the type 2 lobula plate strip-field tangential (LPsf 2) which has been seen in all the present species with the exception of *E. tenax*. i.s. 2 = a medium diameter fibre (about 2 μm diameter) from the second optic chiasma. Note the blebbed processes from this

ventrally from an antero-dorsal position in the medulla; i.e. in the opposite plane to the general pattern of decussation of other centripetal class I elements in this chiasma.

Some lobula elements, derived from cell-bodies behind the lobula plate, give rise to linking-fibres (between 0.5 and 1.5 μm diameter) which project from the outer face of the lobula into the second optic chiasma. Some of them seem to pass tangentially over the lobula's surface in a ventral or dorsal direction. Others project towards the medulla. These latter fibres have been traced from the medial oral surface of the lobula towards the posterior inner surface of the medulla. This again is in the opposite direction to the decussation of other class I fibres from the medulla to the lobula complex regions.

There are two other forms of elements in the lobula which may belong to lobula-medulla centrifugal cells. These are illustrated in figure 127, plate 26, and in figure 140. They have only been seen in *E. tenax* and *S. nitidicollis*. Studies of serial sections suggest two possible courses for their linking-fibres.

(*a*) Linking-fibres from ocular-ventral locations in the lobula project towards antero-dorsal positions in the medulla. Likewise, those from oral-dorsal locations project towards postero-ventral positions in the medulla. Thus they could form a vertical chiasma between these two regions.

(*b*) One alternative to this arrangement could be that dorsal elements in the lobula project to ventral endings in the same region and vice versa (via an arced fibre-course that runs at right-angles to centripetal class I fibres from the medulla and lobula plate). Thus they would not be centrifugal at all but have the status of an intrinsic cell of the lobula, composed of two widely separated components linked by tangentially directed fibres that pass vertically over the face of this region. The only evidence for these similar shaped arborizations being both initial and terminal components is that some have clearly resoluble cell-body fibres and others either lack them or are not stainable with them.

Thus, at present the whole question of centrifugal elements between the lobula complex and other outer regions remains enigmatic. A third, less probable, possibility is that these elements project either dorsally or ventrally over the lobula face to twin dorsal and ventral tracts which project towards the mid-brain.

A small plug-element has been seen in the lobula plate (figure 140), derived from a cell-body fibre behind this region, which gives rise to a thicker fibre that passes towards the medulla. This has not been traced any great distance into the second optic chiasma and at present must be included as *incerta sedis*.

The optic tubercle

Two endings in the optic tubercle are derived from the medulla and lobula, respectively. A third is derived from the ipsilateral protocerebrum. In *Pieris* the line tangential in the medulla gives rise to linking-fibres which project through the lobula, into the dorsal branch of the

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FIGURE 140. Legend (*cont.*)

element at the inner face of the lobula. Similar fibres have been traced into the ventral branch of the anterior optic tract; possibly they may be derived from a class II element in the medulla. At present, however, they have been listed as *incerta sedis*. IIS: 1 to 3, 5 to 8 = subclass IIS elements in the lobula. Descriptions of these are in the text. IIS: 4 elements (stippled) have wide-fields at any level between the inner margin of stratum 1 and the inner face of the lobula. Note the origins of cell-body (cb-f) fibres from IIS: 1, 2 and 3 (x), and side branches (y). IIS: 4 elements are also derived from cell-bodies near the ipsilateral lobula. am 4 = type 4 amacrine. am 5 = two levels of type 5 amacrines. IIS: 7 is derived from the contralateral lobula. IIS: 8 links the lobula to the optic tubercle. Numbers 1, 2, 3 indicate lobula strata 1 to 3.

naterior optic tract, to end, finally in the optic tubercle. A small-field lobula component in stratum 3 projects into the same tract to end over the surface of this region.

There is no homologous line tangential in the Diptera. However, there is a network of line amacrine cells at the equivalent level. These may be intimate with a unilateral class I cell in the same stratum (figures 100 to 103, plate 22). These latter cells project through the medulla

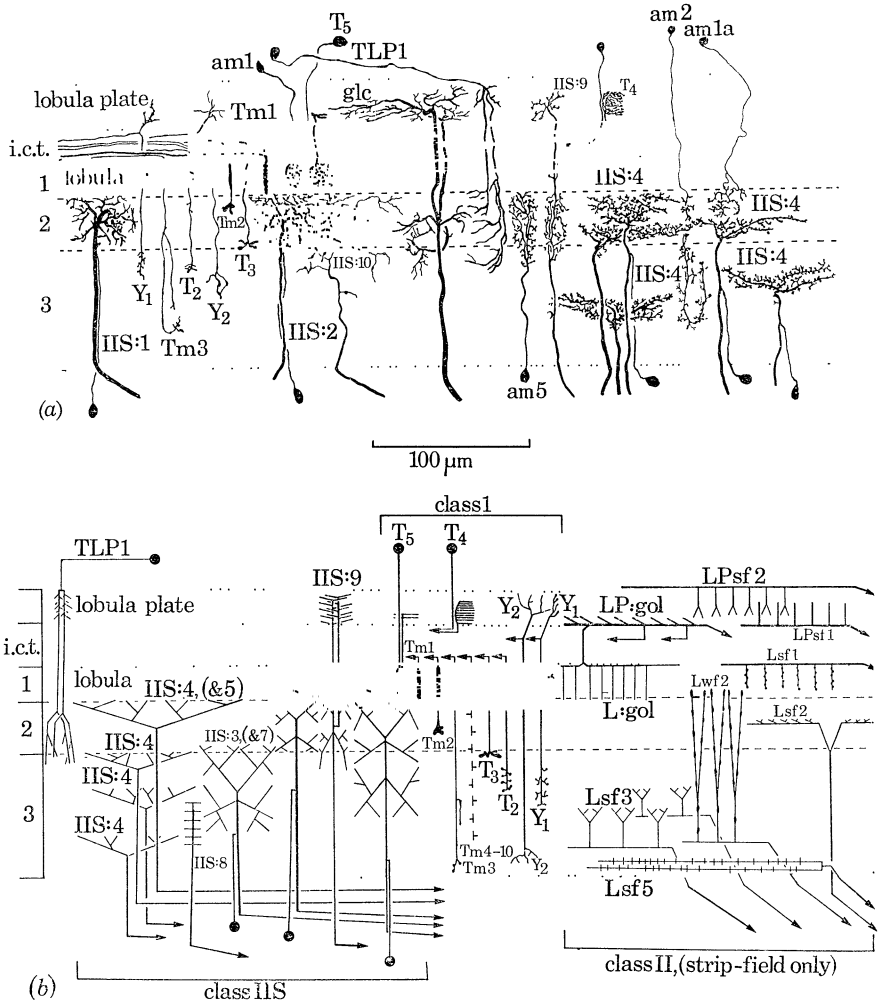


FIGURE 141. Summary diagram of the lobula complex (horizontal plan). The same forms of elements are present in both species of *Calliphora*.

(*a*) The layer relationships in the lobula complex between class II elements, amacrine cells and subclass IIS elements.

(*b*) The fundamental plan of lobula complex layer relationships in the Diptera. The wide-field type 2 element (Lwf2) has been included, in this instance, with the strip-field elements. IIS: 10 in figure 141*a* has only been detected in the species of *Calliphora*. The lateral spreads of its processes vary (see figures 151 and 152, plate 31). It may possibly be analogous to IIS: 6 in the Syrphidae. Several IIS: 4 elements are shown at various levels. In *Calliphora* these have long axes oriented dorsoventrally (see figure 142). glc = the lobula complex component of the giant lobula complex cell. IIS: 5, 6 and 7 have not been seen in the species of *Calliphora*. IIS: 3 is not figured. IIS: 8 has only been seen in part and is not figured. Two variants of amacrine cells have been seen in the outer lobula stratum, am 1 and am 1a. The strip-field tangential relationships in figure 141*b* are applicable to all the present species with the exception of *E. tenax*. This species does not have the characteristic form of LPsf2. LP: gol and L: gol = the lobula plate and lobula components of the giant optic lobe tangential element. LP: gol is a wide subfield. L: gol is a strip subfield. The linking-fibres to other regions are indicated as arrows. These do not imply direction of transmission.

and the lobula into the anterior optic tract. In all other respects the arrangement of the optic tubercle of the Diptera is the same as that of *Pieris* (figures 162 and 163, plate 33). The same arrangement of line amacrines has been seen in *Locusta* and *Apis* (N. J. Strausfeld, unpublished).

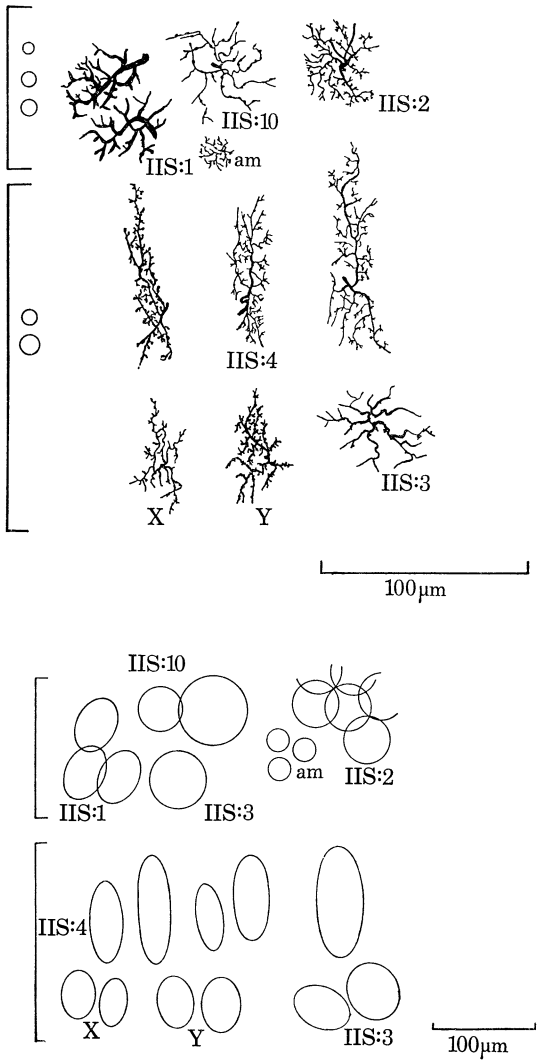


FIGURE 142. The fields of subclass IIS elements (*C. erythrocephala*). Camera lucida drawings of the fields from tangential sections of the lobula. Upper bracket = IIS elements and am 5 in stratum 1. The closed circles represent the lateral extents of class I endings from the medulla and lobula. Second bracket = IIS elements in stratum 3. Closed circles represent the lateral extents of class I endings. Lower brackets = schematized field shapes of the IIS elements. X and Y are variants of IIS: 4 elements. They are distinguished only by their smaller oval fields. Note the overlapping fields of IIS: 1 and 2 cells, and the exclusively vertical orientation of the IIS: 3 cells.

DIVIDED AND UNDIVIDED LOBULAE

The earlier authors considered the lobula plate of the Diptera to be homologous to the outermost stratum of the undivided lobula of the Hymenoptera and Orthoptera. But there are some analogies between these two types of lobula complex which suggest that the lobula plate of the Lepidoptera and Diptera is equivalent to the fourth stratum of the undivided lobula of some

other orders. In the Diptera and Lepidoptera the type 1 transmedullary cells, T_5 cells and unistratified lobula amacrine cells have endings or components in stratum 1 of the lobula. If, as Cajal & Sanchez suggested, the outermost stratum of the bee's lobula was equivalent to the lobula plate of the Diptera then it would be expected that these cell-types would be detectable in the second stratum of the bee lobula. However, this is not the case; type I transmedullary cells and unistratified lobula amacrine cells invariably end in the outermost stratum of both types of lobula complex. There are no T_5 cells in the bee or locust; however, there is a bistratified

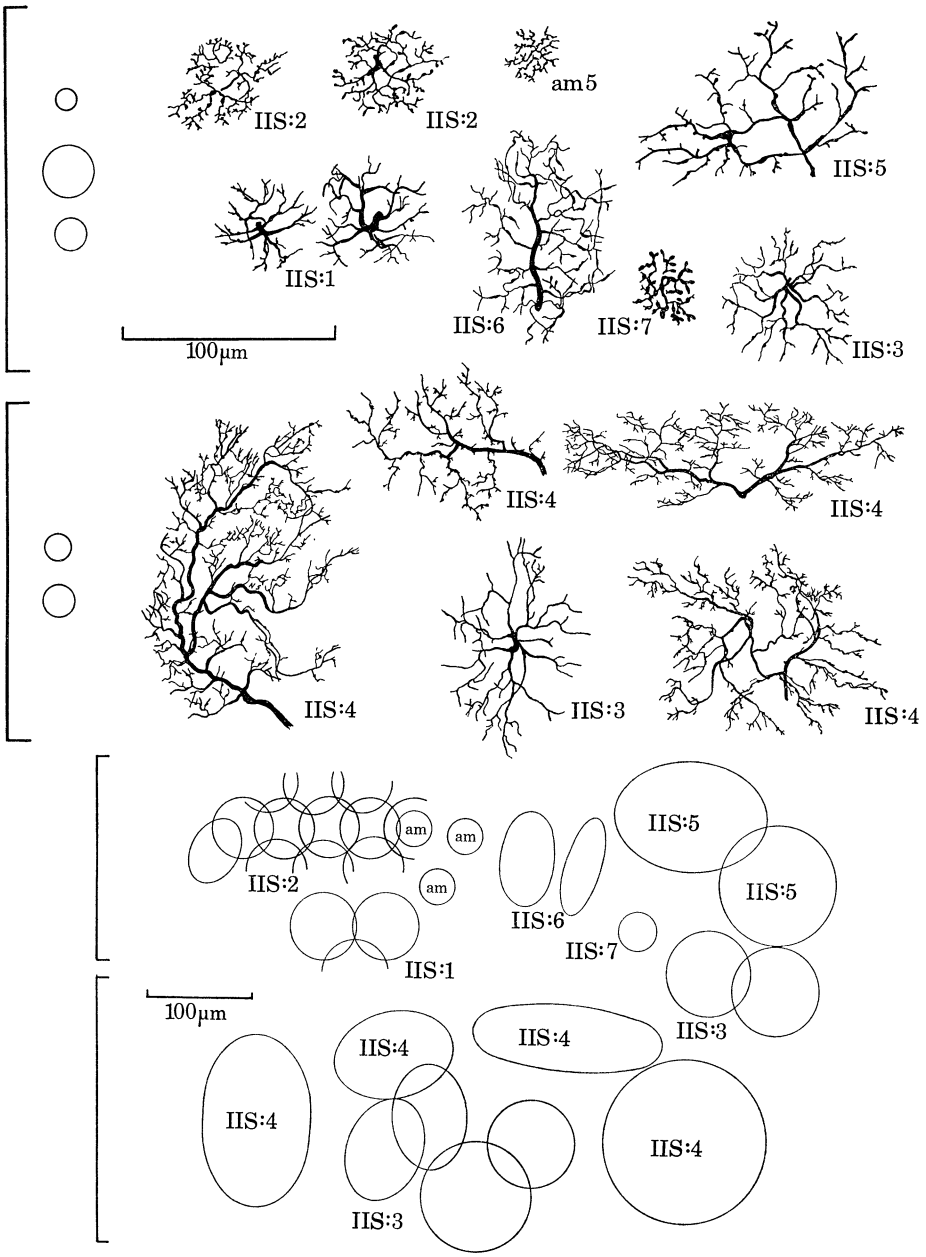


FIGURE 143. The fields of subclass IIS elements (*E. tenax*). Upper brackets = the class I fields in the lobula (closed circles) are larger than those of *Calliphora*. The fields of IIS: 1, 2 and 3 and am5 elements are correspondingly larger. However, the fields of the largest deep IIS: 3 and 4 cells are relatively very much greater than those in *Calliphora*. Lower brackets. Note the vertical orientation of IIS: 6 fields, and the vertical and horizontal orientations of IIS: 4 fields. Some IIS: 4 fields are circular.

amacrine cell which invests strata 1 and 4. Its outermost processes look exactly the same as those of the initial component of the T_5 cells in Diptera and Lepidoptera, and the inner processes look exactly like those of the T_5 ending in the lobula plate.

Similarly, the same forms of strip-field tangentials of the lobula plate are situated in stratum 4 of the undivided lobula. The lobulae of Diptera, Lepidoptera, Hymenoptera and Orthoptera also have the same form of strip-field tangential which lies in the oral-ocular extent of stratum 1. Further analogies can be made between the type IIS: 9 element of the Diptera and a IIS cell of the Hymenoptera. In this latter order a bistratified small-field element invades stratum 2 and also gives rise to a recurrent collateral, from this level, which descends as far as stratum 4.

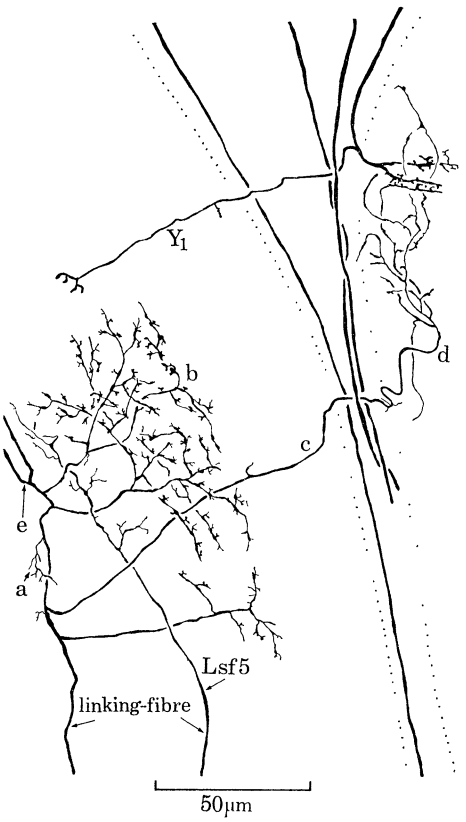


FIGURE 144. A camera lucida drawing of a giant lobula complex element in *C. vomitoria*. e = tangential axis-fibre. a = recurrent processes near the inner face of the lobula. b = wide-field in stratum 2. c = collateral branch to lobula plate. d = lobula plate processes. Some of these appear closely applied against the lobula plate components of Y_1 cells. Also shown is the type 5 strip-field tangential in the lobula (Lsf5).

The 1st, 2nd and 3rd strata of the undivided lobulae are separated from the 4th by a serpentine layer of fibres derived from the axis-fibres of subclass IIS cells which invade strata 2 and 3. This arrangement is similar to that of the medulla where strata 1 to 5 are separated from 7 and 8 by the serpentine layer (stratum 6). Fragments of the giant optic lobe ending have been seen in *Apis*. Significantly they invade strata 4 and 1: fibres in the outermost stratum are derived from those in 4. Further prolongations extend to the inner face of the medulla.

There is a 5th stratum in *Apis* which has not yet been analyzed. It consists of a tangle of processes, some of which are derived from axis-fibres of subclass IIS cells in stratum 2. There is no equivalent in the lobula of the Diptera and Lepidoptera. These findings are summarized in figure 150.

Distributions of cells and variations of field-sizes in the medulla and lobula complex

The likelihood of a neuron being impregnated in one part of a region rather than another cannot be predicted with the Golgi stain. Neurons are rarely or frequently impregnated at any point through a geographical region. Reduced silver preparations give the impression that the four main geographical regions are each homogeneously organized, vertically and horizontally, across their disks (the medulla and lobula of the locust is an exception). On the other hand, Golgi preparations give the impression that some elements may have specific horizontal and vertical locations in the medulla and that others may have characteristic variations of field-size also at particular horizontal and vertical locations.

The medulla can be divided into two concentric zones. The middle zone is formed by medullary columns whose widths, in the horizontal plane, do not exceed 9 μm (*Calliphora*). The perimeter zone is composed of wider columns which vary between 11 and 15 μm in width. The columns at the extreme edge of the medulla are less than 7 μm in width.

The lateral spreads of the processes of the types 1 and 2 transmedullary cells and T_3 and T_4 cells have simply been plotted on to a map of their respective strata. Figure 167 is a correlation diagram of the variations of their lateral extents through a median horizontal section of the medulla of *Calliphora*. The extents of the type 1 transmedullary cells are wider in the perimeter zone than in the middle zone. These variations reflect the different lateral extents of the medullary columns. The maximum and minimum extents of the outer processes as of the type 2 transmedullary cells have been similarly plotted. The minimal extents reflect the variations of columnar widths; however, the maximum extents are 2 to 3 times greater near, and at the perimeter, than they are in the central zone. The inner processes of both types of transmedullary cells have similar extents irrespective of their horizontal or vertical location in strata 7 and 8. Similarly, the lateral extents of T_5 and T_4 cells show little or no variation. The Y_1 and T_2 cells are less frequently impregnated than the preceding types. However, it seems that both show little variation of their lateral extents in the inner layer of the medulla. Any variations in the outer strata reflect those of the medullary columns. The T_1 components in stratum 2 lie between pairs or triplets of fibres derived from the lamina; i.e. they lie between the axes of medullary columns. They show no marked variations in lateral extent. The deep T_{1a} components in the medulla have only been detected in the perimeter zone of the two species of *Calliphora* and in the dorsal perimeter zone of *E. tenax*. They have not been detected in the species of *Syrphus*. Similarly, their corresponding endings in the lamina have only been detected at the perimeter of this region (figure 168).

Description of plate 29

The lobula complex (ocular edge to the left)

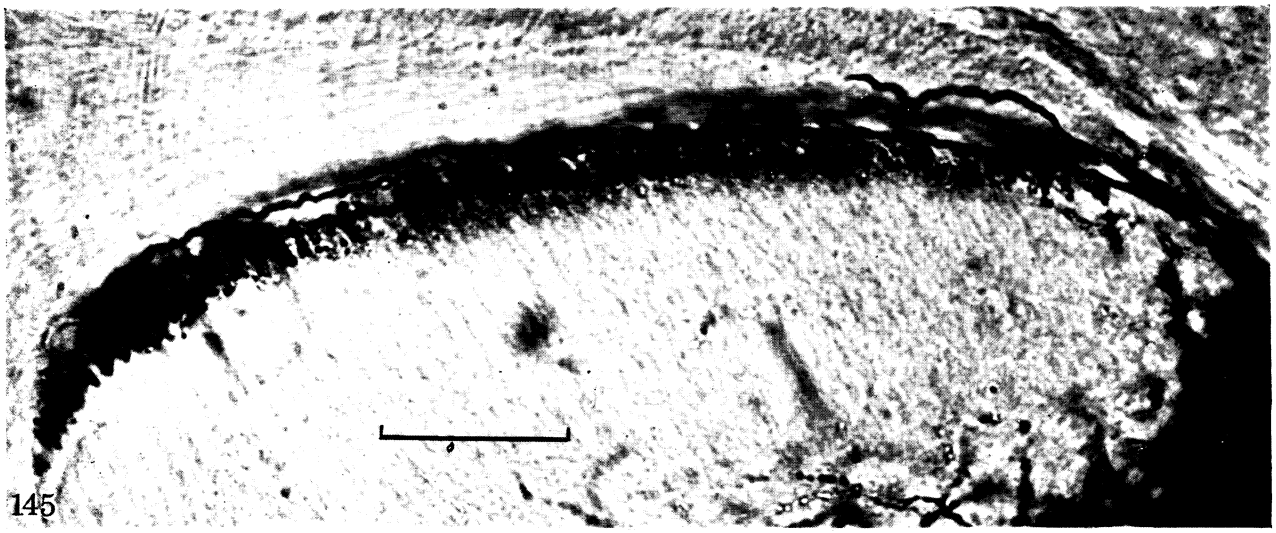
Figure 145. *C. vomitoria*. The type 1 lobula strip-field tangential element (Lsf1). The strip subfield extends through the whole oral-ocular arc of stratum 1.

Figure 146. *C. vomitoria*. The type 2 lobula plate strip-field tangential element (LP.sf2). Each field extends through the oral-ocular length of this region.

Figure 147. *E. tenax*. The type 1 lobula plate strip-field tangential element (LP.sf1). Its field extends through the oral-ocular extent of the lobula plate. The layer relationships between IIS: 2 elements and Lwf3 processes can be seen in the lobula (L).

Figure 148. *E. tenax*. The type 2 lobula strip-field tangential (Lsf2) in stratum 2 (see text).

Scales: Figures 145, 146, scale on 145 = 50 μm; figure 147, 50 μm; figure 148, 50 μm.



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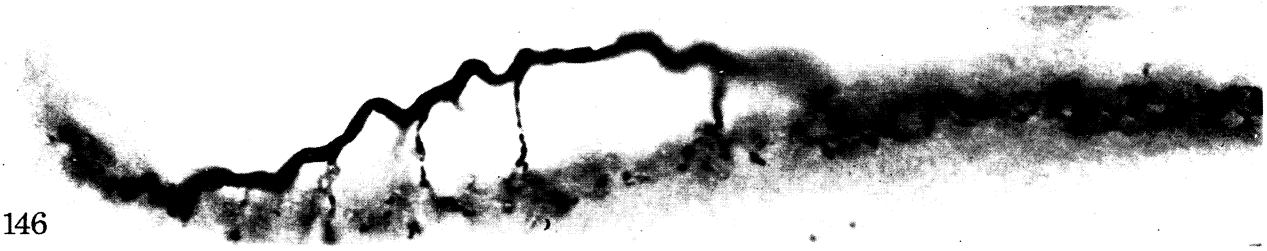

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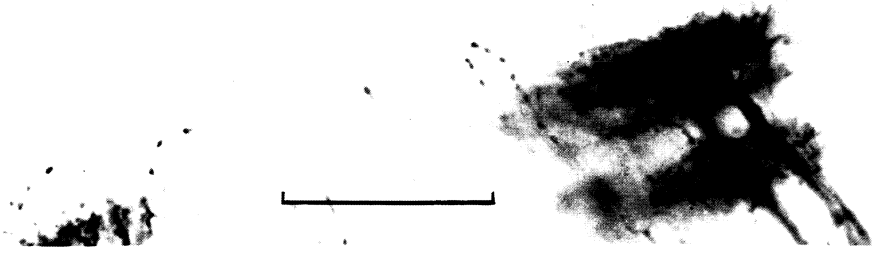

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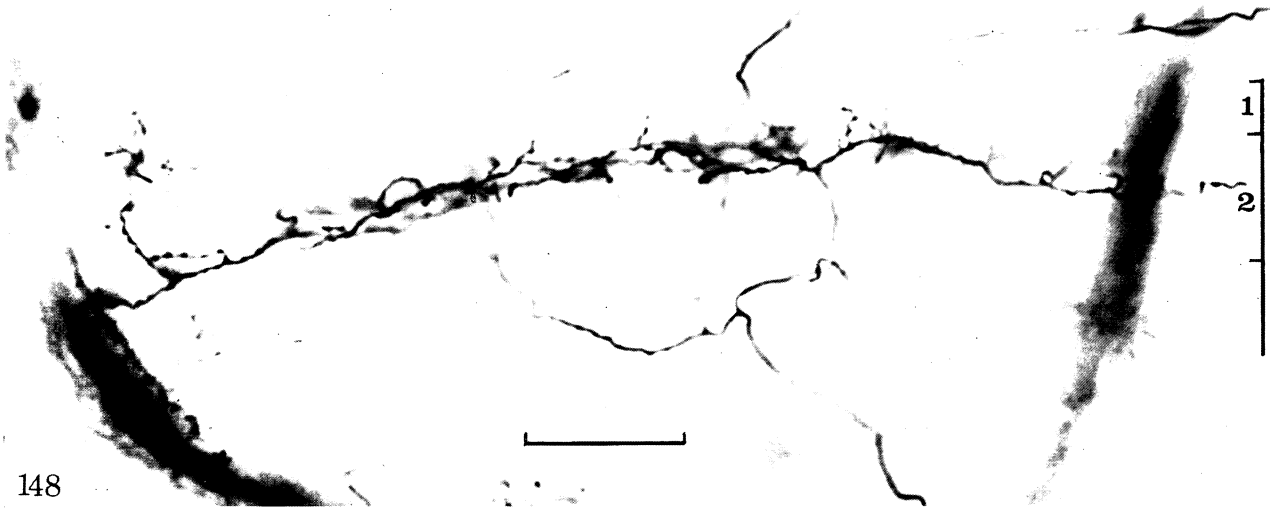

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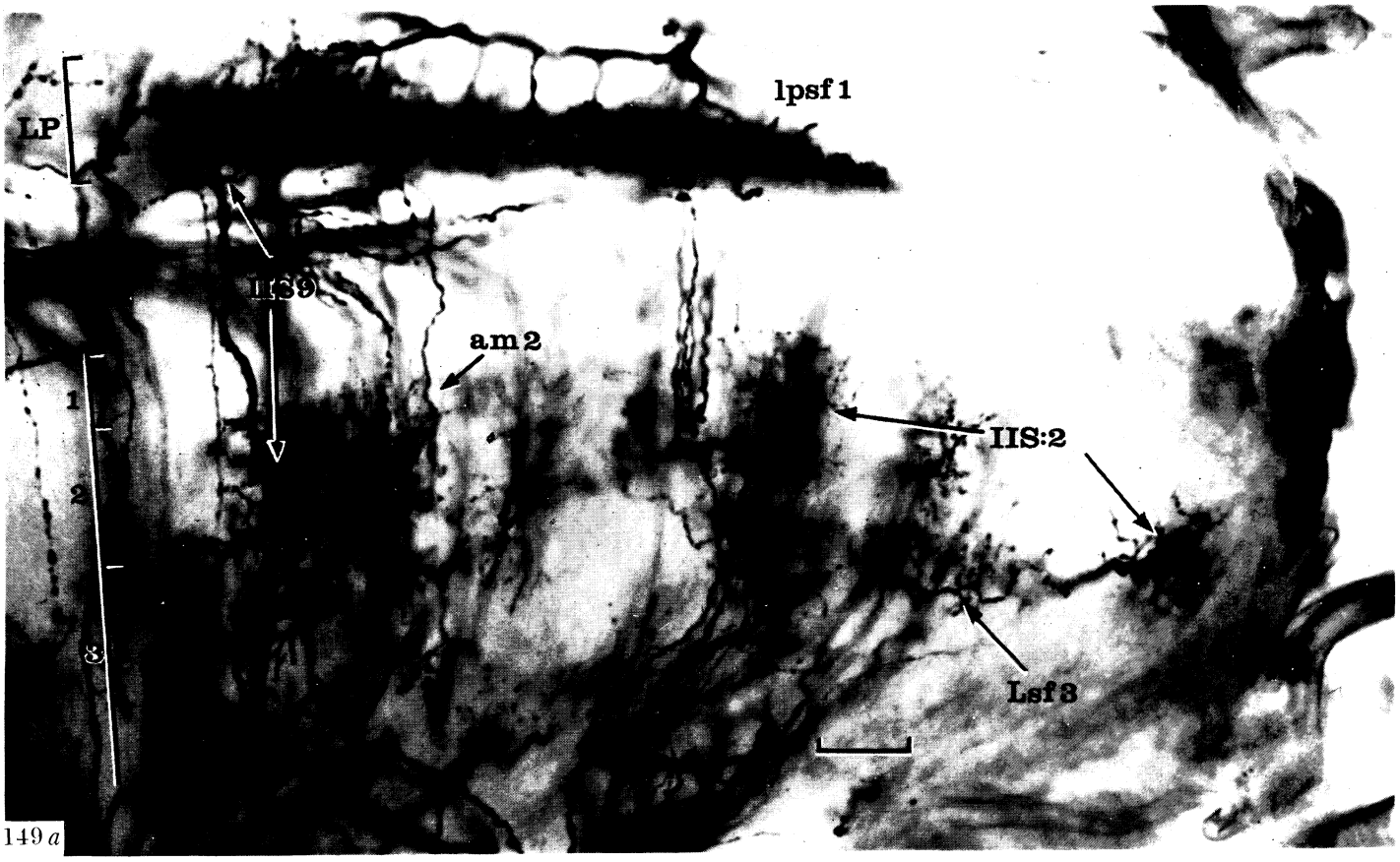


149 *a*

149 *b*

Type IIS: 1 and 2 cells in the lobula have similar lateral extents, irrespective of their location in stratum 2. Those of the type IIS: 3 and IIS: 4 cells vary considerably (figure 161), but this variation has no particular pattern in the lobula. Class I endings in the lobula also have characteristically similar lateral extents throughout their respective strata. With the exception of one element (see below) there is no detectable localization of particular endings nor is there any kind of perimeter variation in this region like that of the type 2 transmedullary cells in the medulla. The only exception is one giant form of T_3 cell that has been detected once in the posterior median perimeter of the medulla of *Eristalis*. Similarly, a giant lobula T-cell ending has been seen at an equivalent position in the lobula of *C. erythrocephala* (figure 121, plate 25). However, these two components have not been seen joined together by a linking-fibre and may possibly represent two different cell types.

Preliminary counts indicate that each type of class 1 cell in the medulla has a characteristic number of processes from the axis-fibre at its various levels of branching. Similarly, the IIS: 1 and 2 cells, in the lobula, each have characteristic densities of processes and spines per unit area of their field throughout stratum 2. But the IIS: 3 and 4 cells show variations both in the number of processes per unit area, the density of processes per unit area and the number of spines on a unit length of process. Amacrine cells show little or no variation of this sort. This study is still in progress, but it may be necessary to reclassify some of the IIS cells into morphologically simple and complex elements on the basis of these variations. Electron-microscopy is also needed to determine what structures, seen by light microscopy, are synaptic specializations.

The T_{1a} cells are the only elements which can be definitely localized to particular parts of the medulla. However, some other elements have variations in form at the anterior and posterior perimeter zone of the medulla. These include the tangential variant of the Y_1 cell in *Pieris* and the ascendent component of a strip-field tangential in strata 7 and 8 of this species (see part I, figures 40 and 57). Similarly, the type 2 and 3 asymmetric amacrine cells seem to be invariably asymmetrical in one direction only; their unilateral processes in the serpentine layer are characteristically disposed at a position anterior to their diffuse processes which extend through strata 3 to 8. It is not clear whether any of the class II elements of the Diptera have a similar polarity. Usually many are impregnated together, if at all, and the methylene-blue variant of the Golgi stain cannot clarify this position (see part I, p. 86) since it does not give a good suppression of staining in this order. Some ascendent processes have been detected near the anterior margin of the medulla disk which may possibly be derived from a tangential

Description of plate 30

The lobula complex (ocular edge to the left)

Figure 149*a*. *S. nitidicollis*. This illustration shows the characteristic appearance of Golgi stained material treated with buffered prefixation solution. Several elements can be seen together in the same region and their layer relationships determined. IIS: 9; this element has processes in the second lobula stratum and in the lobula plate. The element shown here is a narrow-field variant. LPsf2; the type 2 lobula plate strip-field element. Branches arranged unilaterally from the tangential axis-fibre project through the posterior face of this region to give rise to the groups of terminal processes at the same level as the IIS: 9 ending and T_4 and T_5 components. IIS: 2 elements have similar extents irrespective of their location in stratum 2. Amacrine cells have also been impregnated (am2). Lsf3 = processes of the type 3 lobula strip-field tangential.

Figure 149*b*. *C. erythrocephala*. The axis-fibres of type 1 wide-field elements give rise to many processes at the inner face of the lobula. These project to the outer surface. The small subfields from them cover the face of the lobula. glc = the lobula plate (LP) component of the giant lobula complex cell. IIS: 1 = a type 1 sub-class IIS element.

Scales: Figure 149*a*, 30 μm; figure 149*b*, 20 μm.

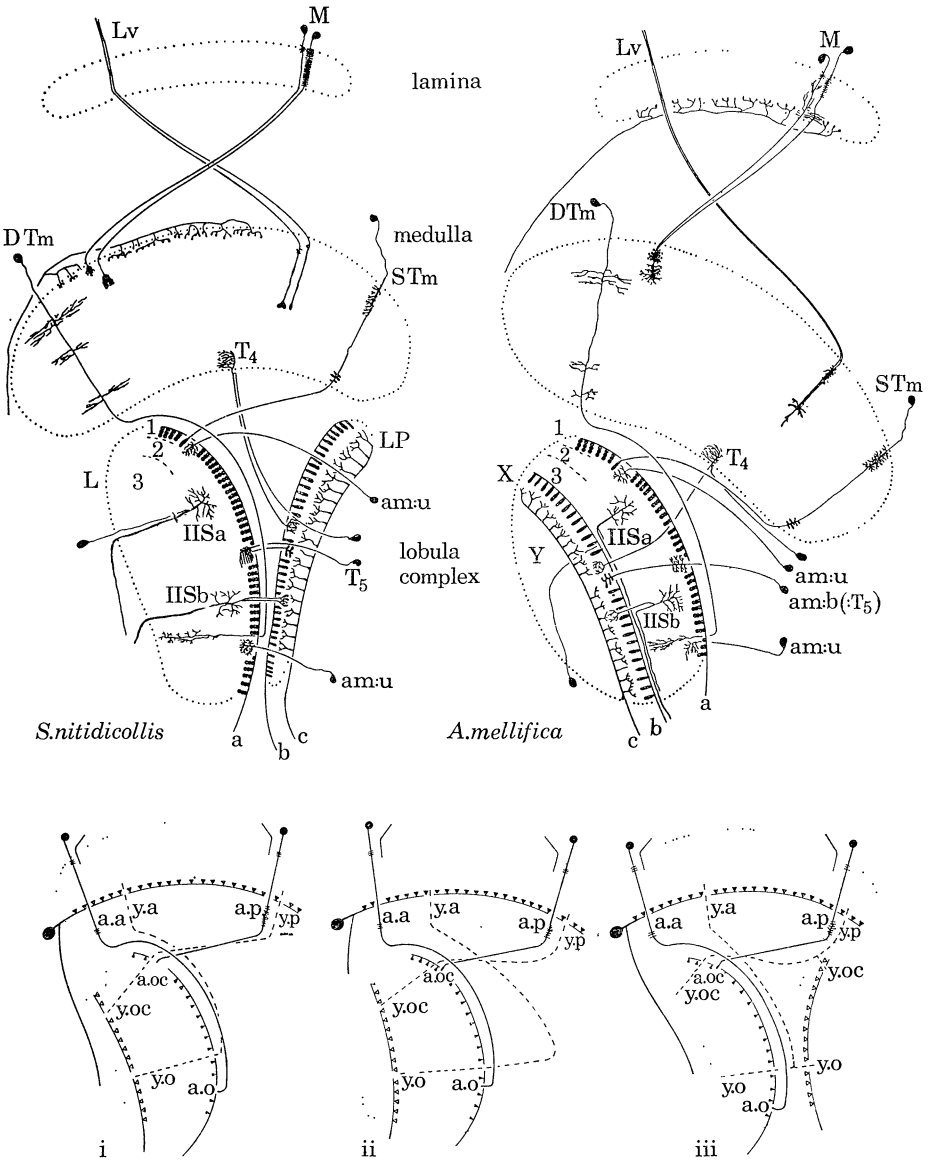


FIGURE 150. A schematized comparison between the stratification of Hymenoptera and Diptera lobulae. Lobula strata 1 to 3 of *S. nitidicollis* are equivalent to 1 to 3 of *A. mellifica* in that they contain analogous strip-field and small-field (IIS) elements. The lobula plate of *S. nitidicollis* is most probably equivalent to stratum X in *A. mellifica* in that both contain analogous class II strip-field elements. a = Lsf1. b = LPsf1 (Diptera) and b in stratum in *Apis* lobula. c = LPsf2 (Diptera) and stratum in *Apis* lobula. IISb = IIS: 9 in the Diptera and the recurrent IISb in the Hymenoptera. IISa invests lobula stratum 2 in both species. The narrow-field transmedullary cells (STm) end in the outermost stratum of both species. The unistratified amacrine (am: u) also invests stratum 1 of both species. The deep endings of the wide-field transmedullary cells (DTm) are disposed in strata 2 and 3 of both species. The bushy T-cell (T_4) ends in stratum 1 of *S. nitidicollis* and stratum X of *A. mellifica*. The lobula-lobula plate T-cell (T_5) of the Diptera is probably equivalent to the bistratified amacrine cell (am: b) of *A. mellifica*. Note the positions of the IIS linking-fibre in *A. mellifica* in a serpentine layer between stratum 3 and X. The analogous fibres in the Diptera leave the inner face of the lobula. A surface tangential (M: tan 3) in the Diptera has a similar appearance to a wide-field tangential over the inner face of the lamina of the bee. Long visual fibre and monopolar cell endings are arranged in pairs in the medulla of *Apis* (as they are in the Lepidoptera) and singly in the Diptera.

Figure 150. (i) The second optic chiasma of *Apis*. (ii) The second optic chiasma of *Libellula*. (iii) The second optic chiasma of the Diptera and Lepidoptera. Anterior class I cells in the medulla (a.a and y.a) end orally (posterior) in the lobula complex (a.o and y.o). Posterior class I cells in the medulla (a.p and y.p) end ocularly in the lobula complex (a.oc and y.oc). The second optic chiasma reverses the lateral topographical relationships in the same way in both divided and undivided lobulae.

element localized to this part of the medulla neuropil. Fragments of a tangential element seem to arborize over the edge of this region. However, there is as good evidence that they may belong to an anterior component of one or two types of horizontal oriented strip-field elements. One variant of a subclass IIS cell has been detected at the ocular margin of the lobula complex. This cell-type looks, in most respects, like a type IIS: 9 cell; however, its lobula component in stratum 2 gives rise to a tangential process which extends horizontally for between 20 and 40 μm towards the oral edge in stratum 2 (IIS: 9b, in figure 94).

DISCUSSION

Perpendicular pathways: the first optic chiasma and neuronal density in the medulla

The columnar arrangement of the lamina is a common feature of the Diptera (see, for example, Power 1943*a*; Melamed & Trujillo-Cenoz 1967; Larsen 1966; Braitenberg 1967). A similar arrangement has been detected in some species of diurnal Lepidoptera (part I), but is not apparent in the nocturnal moths *Sphinx* and *Automeris*. These last species have laminae in which groups of between six and eight retinula cells terminate in close proximity to two or three giant monopolar cells, but do not surround them to form discrete optic cartridges. There are, nevertheless, characteristic similarities between the optic chiasmata of the species described in this and the previous account.

The spatial relationships between the optic lobe regions are not symmetrical; the dorsoventral mid-line of the medulla is usually displaced anteriorly with respect to that of the lamina. Likewise the vertical and oral-ocular mid-lines of the lobula complex are displaced antero-dorsally with respect to the vertical and horizontal mid-lines of the medulla. The surfaces of all these regions are curved and fibres between them can only be traced out with some difficulty. Reconstructions of their projection patterns is also complicated by the different affinities of some of these fibres for reduced silver stains: fibres in the outer segment of the first optic chiasma near the lamina are particularly prone to mediocre impregnation. The fibres of the first optic chiasma cannot all cross-over at the same point between the lamina and medulla since there is not room for them to do so. Thus they may appear whorled around one another (figure 105, plate 23) or together may seem to form more than one chiasma between these two regions (figure 169). Vertical sections which cut the chiasma at right angles show that fragments of fibres appear to interdigitate with one another, especially within the outer segment near the lamina. This gives the appearance of many brush-like endings. The somewhat dubious centrifugal endings described by Larsen (1966) from reduced silver preparations appear extremely similar to these artefacts of sectioning. Golgi-impregnated material shows that the great majority of fibres in both Lepidoptera and Diptera are involved in a simple horizontal cross-over. Anterior fibres from the lamina project posteriorly to the medulla and posterior ones project anteriorly. Thus in the horizontal plane a linear array of fibres in the lamina is simply reversed in the medulla. But some exceptions to this form of decussation have been detected; figure 106, plate 23, shows two fibres derived from the same point in the lamina of *Pieris*, which project to two widely separated points in the medulla. The cell-type involved in this divergence is not yet known, but it is most probably derived from a tangential component in the lamina. Similarly, there is also evidence for an anterior lamina to anterior medulla projecting class II fibre (see p. 146).

The precise projection patterns of the fibres from the lamina to the medulla are still obscure. Optic cartridges are arranged, more or less, in vertical strips and each gives rise to a minimal group of four fibres. When the chiasma is cut obliquely, parallel to the plane of cross-over, dorsoventral arrays of these groups look like a flat sheet of fibres. In *Pieris* these arrays can be followed along their entire length (figure 110, plate 24). It can be seen that the bundles retain their dorsoventral lateral relationships from lamina to medulla. There is no apparent cross-over in this plane. But the four components of a quad in the medulla are not all derived from a single group from the same optic cartridge. Two are derived from a cartridge either posterior or anterior to that which gives rise to the other pair. There is thus a convergence and divergence of groups of fibres in the horizontal plane. Although this arrangement is not easily detectable in *Sphinx* dorsoventral displacement of lateral relationships in the first optic chiasma are similarly taking place very close to the medulla's surface.

In the present species of Diptera each medullary column usually contains a pair of fibres which are derived from the retina and lamina. But occasional exceptions have been detected where there are pairs of long visual fibres and a monopolar cell ending in very close proximity to one another (figure 61). Each lamina column gives rise to at least two monopolar cell fibres from the axis of a cartridge and two long visual fibres which lie satellite adjacent to it. Dorsoventral arrays of these groups of four fibres project into the optic chiasma in the same way as do those of *Pieris*. However, the curvature of these bundles is such that obliquely cut chiasmata cannot include their entire length on the same section. It is though, possible to trace some of the groups of four fibres in horizontal sections; the double pairing is detectable from the lamina as far as between 20 and 40 μm from the outer face of the medulla (figure 36, plate 15). From this point the two pairs are separate and project individually into the medulla so that most seem displaced obliquely dorsoventrally with respect to one another (figure 37, plate 15). This arrangement of pair-dispersion may not necessarily be the rule for all the fibre-bundles between the two regions but it is certainly apparent that there is no cross-over in the dorsoventral plane. Four endings in the medulla which are derived from the same optic cartridge end close to one another, irespective of their displacement or pair or triplet arrangement (figure 169).

Apart from a few exceptions estimations of the total number of neurons in the optic lobes cannot be determined by the simple procedure of cell-body counts (see p. 139). Some elements can, however, be recognized by Holmes–Blest procedures. These include the retinula cells, long

Description of plate 31

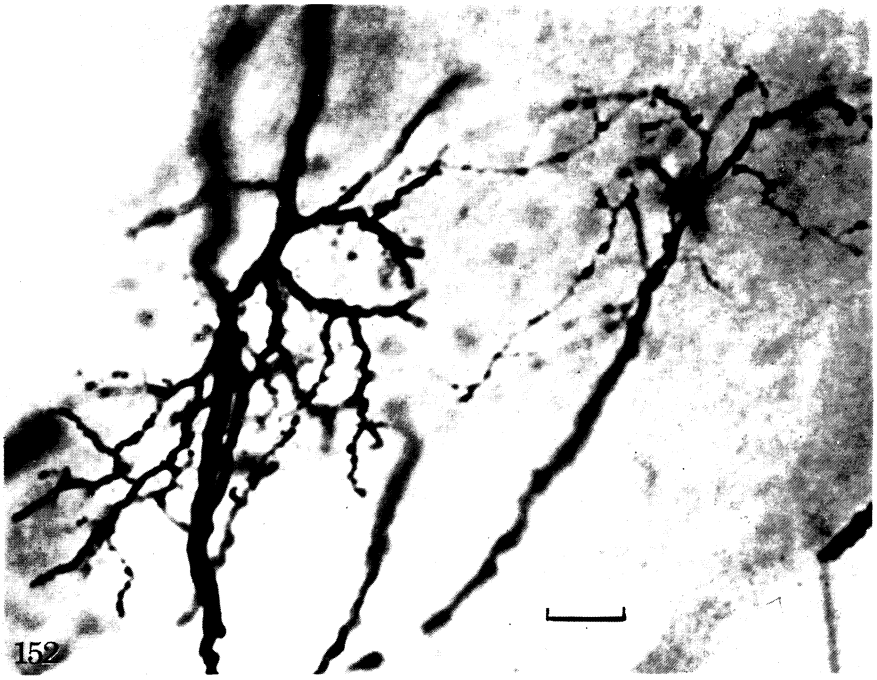
Figure 151. *C. erythrocephala*. Type 5 amacrine cells processes (am) and a small-field IIS: 10 element in stratum 2 of the lobula.

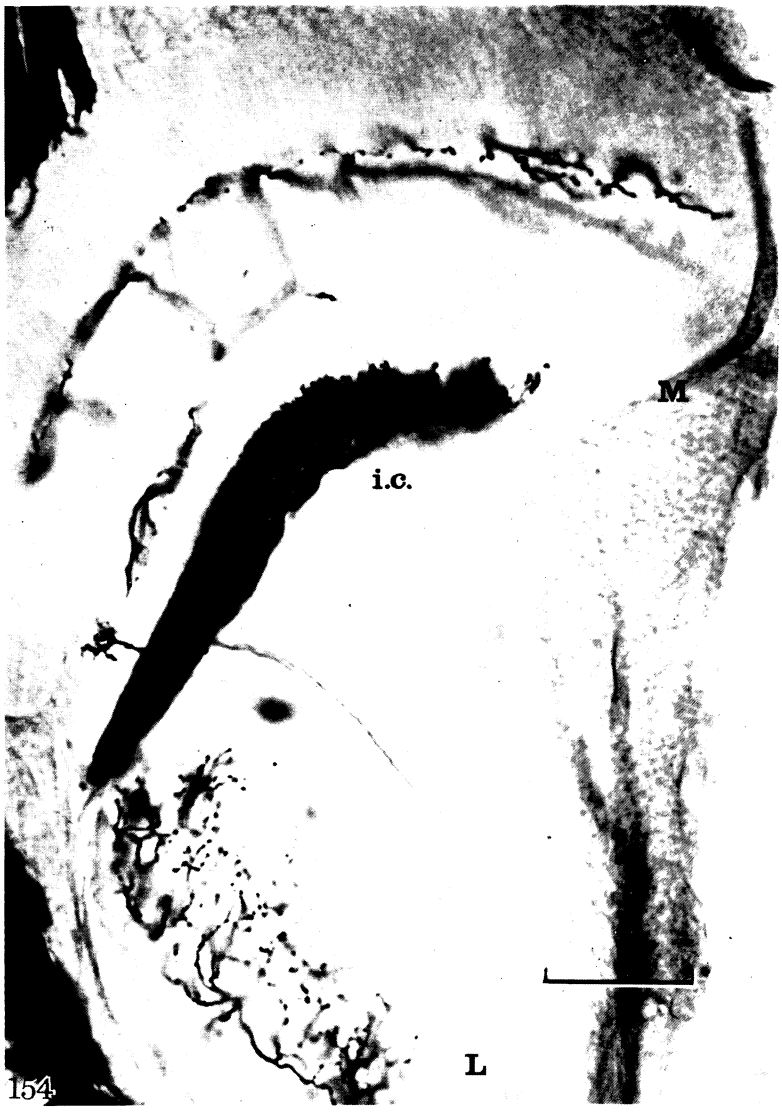
Figure 152. *C. erythrocephala*. A large field IIS: 10 element and the lobula processes of the giant lobula complex cell. Note the characteristic blebbed processes of IIS: 10.

Figure 153. *E. tenax*. IIS: 1 elements in the lobula (L) send linking-fibres to optic lobe accessory region 1 (AR1) where they terminate as a tangle of processes.

Figure 154. *C. erythrocephala* ('chalky' mutant). This preparation shows remarkable features. There is only a vestigial lobula plate, and the lobula (lower left) is much reduced. Lwf3 processes have been impregnated in it, but look abnormal in that they terminate in a tangle of fibres located deep in stratum 2. The medulla's (M) maximum depth exceeds 160 μm. Other preparations show the maximum medullary depth ranging from between 120 and 130 μm. Two components have been impregnated. The outer is the M: tan 2 tangential element. The inner component (i.c.) looks very like the type 1 lobula strip-field tangential. Its axis-fibre is atypically oriented postero-anteriorly; i.e. the linking-fibre (out of section) is derived from it posteriorly.

Scales: Figures 151, 152, 15 μm; figure 153, 40 μm; figure 154, 50 μm.





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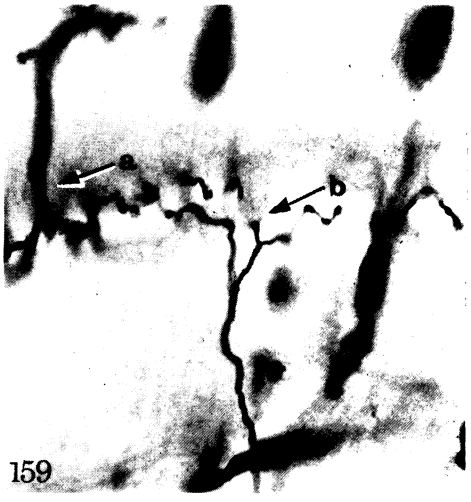

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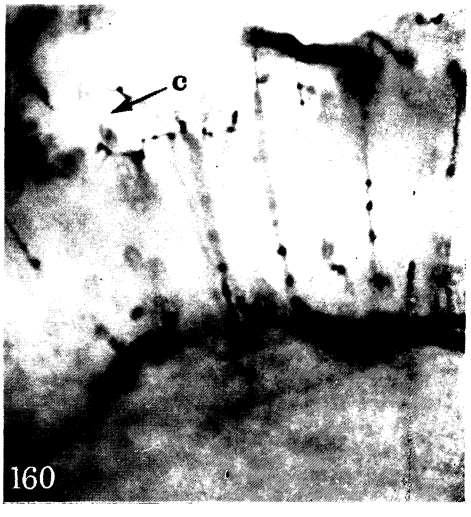

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visual fibres and monopolar cell components in the lamina. But with few exceptions their characteristic shapes which are detectable in Golgi preparations cannot be distinguished. Only the type 1 subclass IIS elements in the lobula can be displayed by both the Golgi and the Holmes–Blest methods; the packing of these cells in Golgi-stained material can be compared with that in reduced silver sections (figure 108, plate 23). The packing of other elements must be derived by indirect methods which rely, in part, on circumstantial evidence.

Reduced silver stained material reveals axis-fibres that extend completely through the medulla from its outer face into the second optic chiasma: these can only be the axis-fibres of transmedullary cells. Axis-fibres that can be traced through only the inner and serpentine layers of the medulla, and which enter the second optic chiasma belong to the deep and shallow T-cells. The bushy T-cells and the medullary components of the Y-cells do not have perpendicular axis-fibres of sufficient length to be recognized. The cell-body fibres of most class I cells are not displayed by Holmes–Blest silver techniques, however, those of both the bushy and shallow T-cells are exceptions and aid in the identification of these cell-types. On the other hand, there are no components of the centrifugal cells to the lamina from the medulla detectable in either Holmes–Blest or Fraser Rowell preparations.

In the medulla pairs of axis-fibres are clearly associated with each pair of endings from the lamina. These together define the axis of a medullary column. The axis-fibres of class I cells have been counted at successive levels in reduced silver sections of the medullae of *C. vomitoria*. Each medullary column contains the axis-fibres of a pair of transmedullary cells. The number of linking-fibres derived from the inner face of each column to the second optic chiasma is an average of 4.8 (these results are summarized in table 3). The number of fibres derived from an area of inner surface of this region, equivalent to a strip of 10 adjacent columns is 54. Narrow-field stratified amacrine cells have axis-fibres that extend perpendicularly through the medulla but not outside it. These have not been counted and are at present excluded from these calculations.

Golgi stained preparations sometimes reveal the *en masse* impregnation of one or two types of neuronal components within a small volume of a geographical region. It seems that on these occasions, all the components of only one or two cell-types have been selectively stained within a small portion of the region. However, this is only a subjective assessment and cannot yet be confirmed by other light microscopy methods. The densest packing of cell-types observed in

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Description of plate 32

Giant elements in the optic lobes

Figure 155. *E. tenax*. The lobula complex components of the giant lobula complex cell. LP = lobula plate. L = lobula.

Figure 156. *E. tenax*. The central ending of the giant lobula complex cell in optic lobe accessory region 2 (AR 2).

Figure 157. *E. tenax*. The wide-field lobula plate (LP) component of the giant optic lobe tangential element gives rise to branches to the medulla and to the lobula (L). These latter fibres give rise to strip sub-fields which invade lobula strata 1 and 2.

Figure 158. *C. vomitoria*. The wide-field lobula plate component of the giant optic lobe tangential (LP) and its processes in the medulla (M). Processes derived from the ocular margin of the lobula plate project to the posterior inner face of the medulla.

Figures 159, 160. *S. nitidicollis*. The medullary component of the giant optic lobe tangential. Its ascendent processes terminate at the outer margin of stratum 7 (c) and also at stratum (b) at the same level as the deep oval subfields of the medullary component of Lam: tan 1 (a).

Scales: Figure 155, 50 μm; figure 156, 100 μm; figures 157 to 159, 25 μm.

such Golgi preparations is summarized in table 4. The packing per 10 columns computed from these figures is an average of 50 elements, compared with the average of 55 detected in reduced silver preparations. The maximum number of fibres detected as leaving an inner face area equivalent to 10 columns, in these latter preparations, was 63. It is suggested that each column

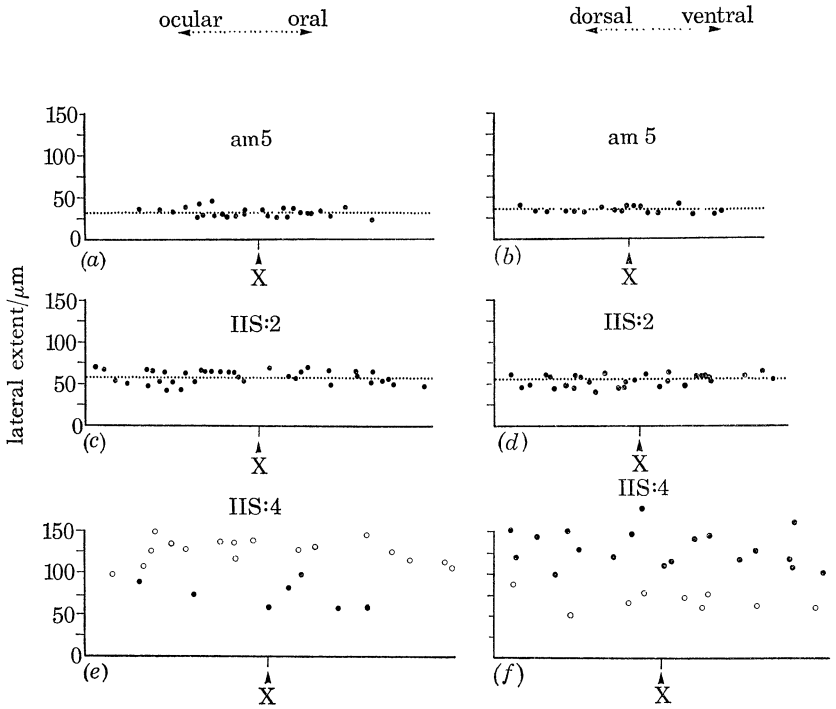


FIGURE 161. An example of a correlation diagram showing the lateral extents of some subclass IIS fields (derived from 30 sections of *E. tenax* containing similar horizontal lengths of lobula). *a*, *c* and *e* are oral-ocular extents. *b*, *d* and *f* are dorsoventral extents. Elements located and plotted from the lobula section mid-point, X. (*e* and *f*; open circles represent horizontally oval fields, closed circles represent vertically oval fields.)

DESCRIPTION OF PLATE 33

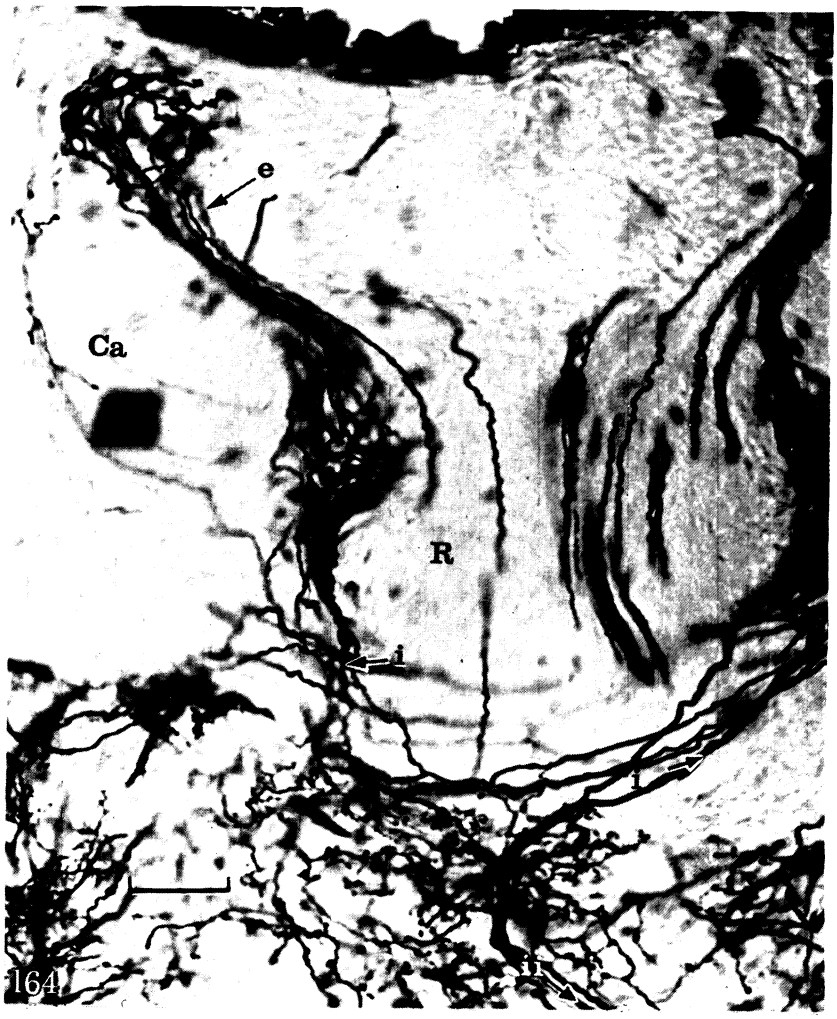
FIGURE 162. *S. vitripennis*. The dorsal branch of the anterior optic tract. The optic tubercle contains two components, derived from the lobula and medulla (a and b, respectively).

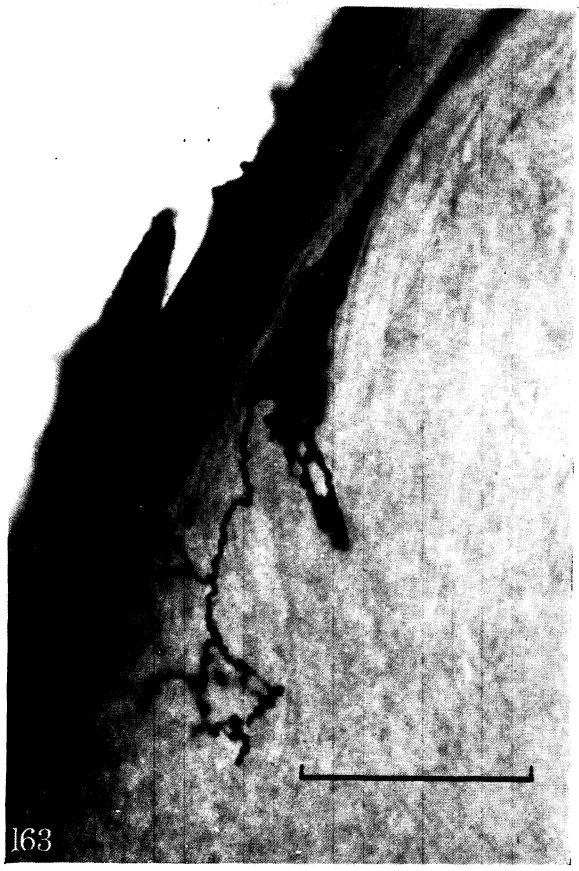
FIGURE 163. *S. vitripennis*. The characteristic branching patterns of a and b. These are similar in both the Lepidoptera and Diptera.

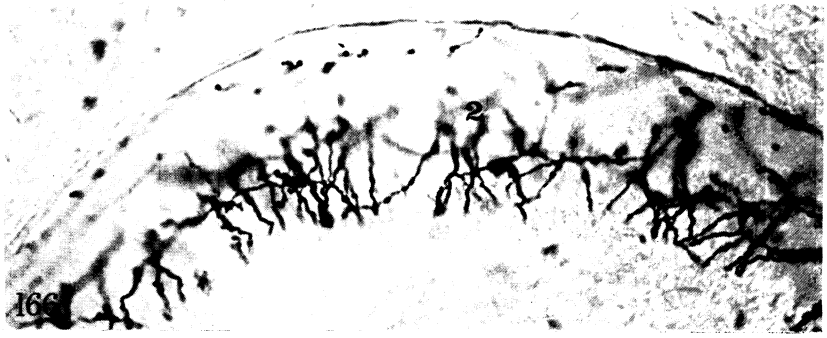
FIGURE 164. *Apis mellifica* (vertical section). A calyx of the left mushroom body. Bundles of fibres (ii) derived from sensory regions, including the lobula, project to the ipsi- and contralateral pairs of calyces. Each bundle (i) gives rise to clusters of blebbed processes (e).

FIGURES 165 and 166. *A. mellifica* (vertical sections). The types of elements in the calyces: 1 = pseudo-purkinje cells. 2 = afferent fibres from sensory regions. 3 = circum-tangential cells. The pseudo-purkinje cells are equivalent to the types 1 a–b and II, III and IV cells described by Goll (1967) from *Formica*. In the bee these elements have minor variants categorized by their branching patterns. Their lateral extents are equivalent to the bundles of afferent terminal processes (e, in figure 164). The synaptic relationships described by Steiger (1967) are most likely representative of functional relationships between these two types of elements. The circum-tangential elements have strip-fields arranged parallel to the circumference of the calyx in which they lie. The structure of the corpora pedunculata is complex. Pseudo-purkinje cells give rise to different types of processes which extend into the α- and β-lobes. Their dispersion, in the bee, is complicated and is at present under investigation. Golgi impregnated material also shows the calyces as having particular zonations of afferent bundles. Histochemical investigations have revealed stratifications in the corpora pedunculata which are not yet detectable by the Golgi procedure (see Frontali 1968).

Scales: Figure 162, 100 μm; figure 163, 100 μm; figures 164 to 166, 25 μm.







(*Facing p.* 198)

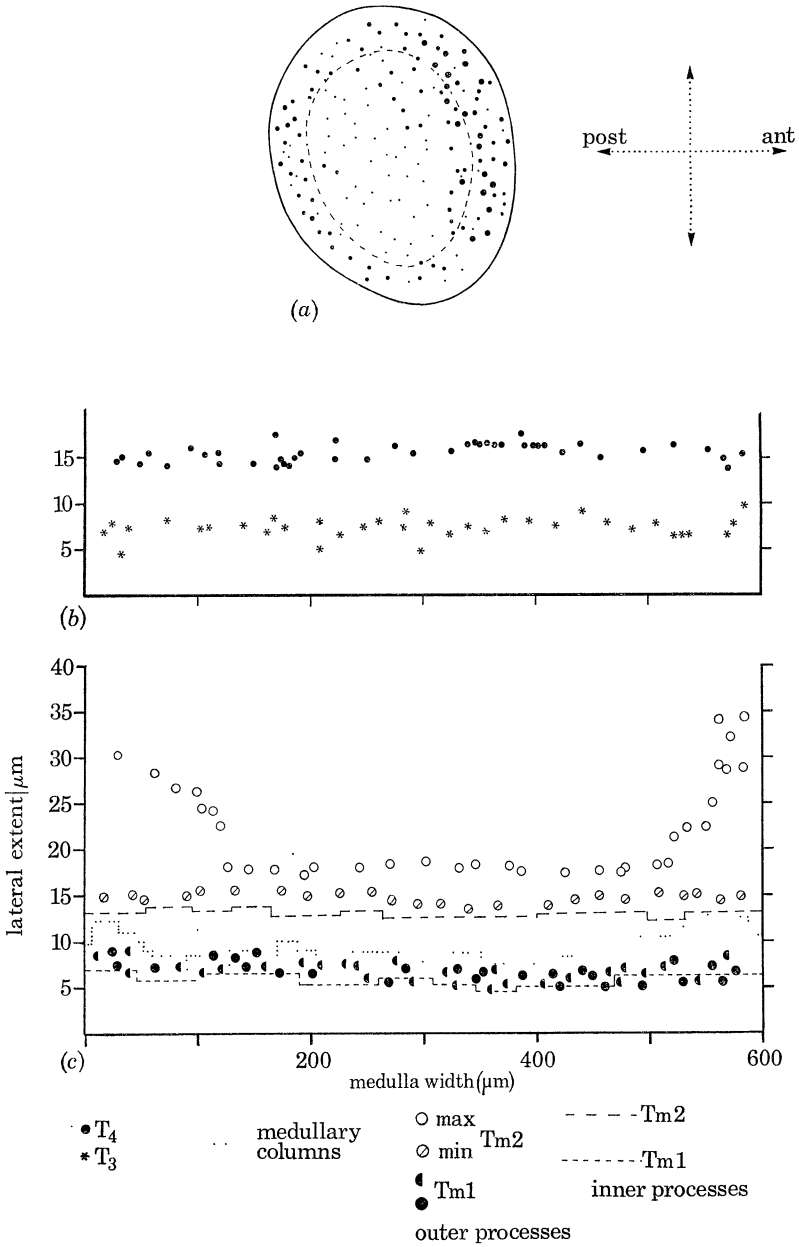


FIGURE 167. Correlation diagrams of class I elements. Field sizes and their locations in the medulla (horizontal plane).

(*a*) (*Calliphora*). This diagram shows the lateral extents covered by the outer processes of type 2 transmedullary cells. Their extents have been measured from 20 preparations and their locations plotted onto a surface map of the region (from serial sections). Dashed lines indicate the inner limit of the perimeter zone (see also figure 64 and 66, plate 18). Largest points = lateral extents exceeding 30 μm. Smallest points = lateral extents between 15 and 20 μm. Other points = intermediate extents. The widest fields seem to be located in the anterior perimeter zone.

(*b*) The lateral extents of T_3 and T_4 cell initial components plotted against a 600 μm maximum median horizontal extent of the medulla (strata 7 and 8) of *C. vomitoria*.

(*c*) The lateral extents of medullary columns and outer and inner processes of Tm1 and Tm2 cells plotted against a 600 μm extent of the medulla. The points for figure 167*b* and *c* have been derived from 100 preparations containing horizontal lengths of the medulla that exceed 600 μm (curved outer face). Elements were located with respect to the medulla's horizontal mid-point and plotted with respect to the 300 μm mid-point of the diagram.

Note: these diagrams do not indicate neuronal populations.

contains two small-field transmedullary cells (types 1 and 2, see p. 158) and, in addition, one shallow and one bushy T-cell. A column also contains the pair of elements from the lamina in the outer layer of the medulla. Deep T-cells and Y_1 cells may relay aggregates of two or three columns. Other types of transmedullary cells are probably more scattered through the medulla or conversely may have very particular localized horizontal or vertical distributions. At present too few of these have been impregnated to allow an assessment of their distribution. However, the lobula endings have been detected throughout all of the horizontal and vertical extent of stratum 3. Medullary components of centrifugal elements to the lamina are also stained relatively frequently in Golgi preparations. The medulla lamina T-cell endings are disposed between adjacent pairs of endings from the lamina in the horizontal plane. Types 2 or 3 centrifugal cells are associated with each column in the medulla (see p. 155), however, Golgi stains have never shown more than one of either of these two forms in the same column.

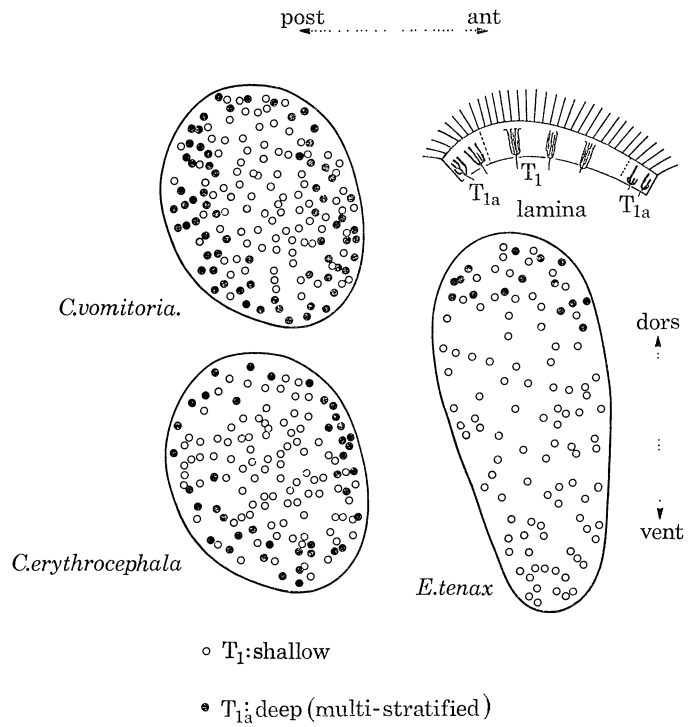


FIGURE 168. The locations of some T_1 and T_{1a} initial components have been derived from horizontal and vertical serial sections of the medullae of *C. vomitoria*, *C. erythrocephala*, *E. tenax*, *S. nitidicollis* and *S. elegans*. Their locations were plotted onto a surface map of the medulla. This figure shows the T_{1a} components restricted to the whole perimeter zone in the two species of *Calliphora* and to the dorsal perimeter zone in *Eristalis*. The corresponding lamina endings have only been detected near the edge of the lamina disk in the species of *Calliphora*. They have only been seen near the dorsal edge of the lamina of *Eristalis*. No T_{1a} components have been impregnated in the species of *Syrphus*. Note that T_1 components are not restricted to the middle zone of the medulla.

The stippling of the medulla in Golgi stained material allows some reconstruction of the field spreads of lamina input pairs and the outer components of transmedullary cells. These are summarized in figure 170. Figures 170*a* and *b* show the reconstruction of the class I components common to each medullary column, and figures 170*a* and *c* show the small-field class II components at their respective levels across arrays of medullary columns. The type 1 transmedullary cells have circular fields which can extend, maximally, through up to six columns.

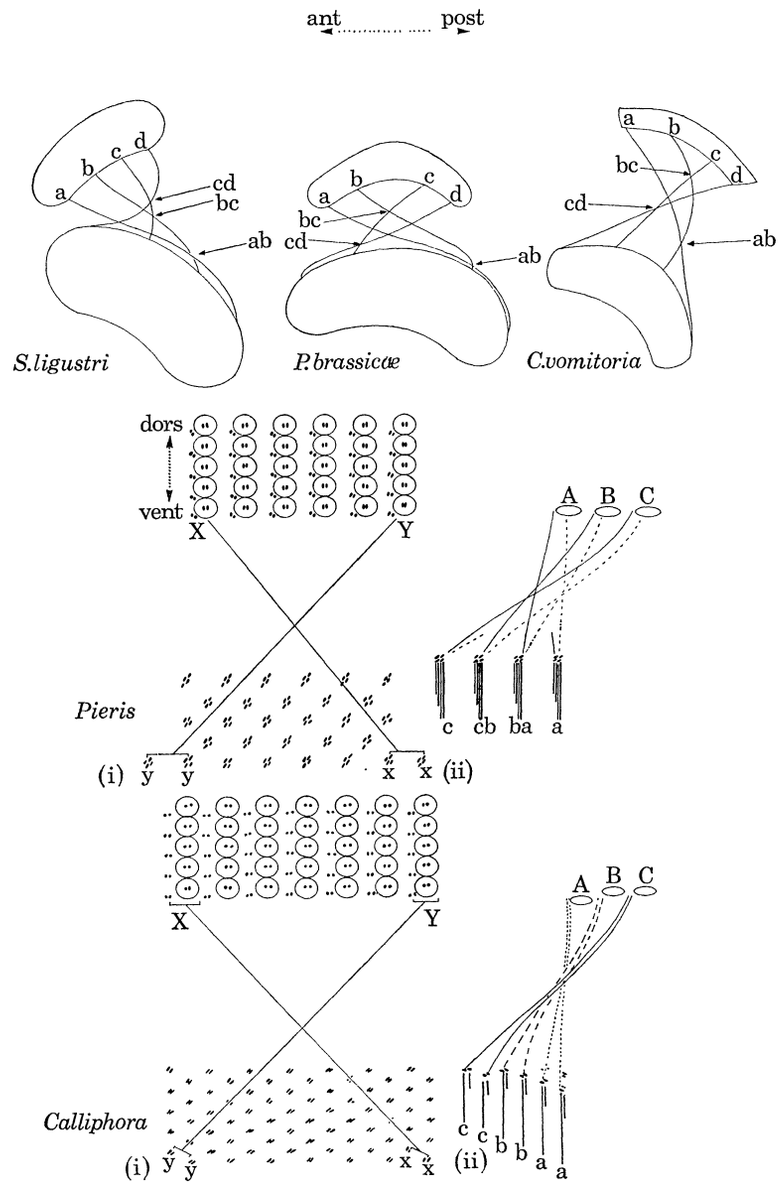


FIGURE 169. Projection patterns of class I efferent fibres to the medulla from the lamina.

Upper diagrams: first optic chiasma cross-overs. Anterior fibres from the lamina project posteriorly to the medulla and vice versa. A horizontal array of fibres between the two regions appears to form several cross-over points between the outer and inner segments of the chiasma.

Lower diagrams: *Pieris* (i). Arrays of optic cartridges (closed rings) contain pairs of monopolar cell axis-fibres. Pairs of long visual cell fibres are satellite to the cartridges. The axes of medullary columns are primarily formed from four perpendicular fibres from the lamina. Medullary columns x and x, y and y have components derived from cartridges X and Y, respectively. (ii). This diagram shows the projection patterns from three optic cartridges A, B and C, which contribute to four medullary columns. There is a recombination of the double pair arrangement, near the medulla, by an apparent horizontal displacement. Broken lines = pairs of monopolar cell linking-fibres. Continuous lines = pairs of long visual cell fibres.

Calliphora (i). As in *Pieris* the optic cartridges contain two monopolar cell axis-fibres. Pairs of long visual cells are satellite to the cartridges. The medullary columns have axes which are primarily composed of two fibres from the lamina. However, the pairs of fibres from an optic cartridge project to columns close to one another in the medulla. (ii). A pair of long visual fibres, beside optic cartridge A, projects to two adjacent medullary columns, a and a. Likewise, pairs of long visual fibres from B and C (dashed and unbroken lines, respectively) project to medullary columns, bb and cc, respectively. Each long visual fibre is accompanied by a monopolar cell linking-fibre from the cartridge next to it.

TABLE 3. MEDULLARY COLUMNS (AXIS-FIBRES)

class I axis-fibres in the medulla (reduced silver)	numbers of axis-fibres in 100 columns	average numbers of axis-fibres per column	types of class I cell axis-fibres in medullary strata (Golgi preparations)
axis-fibres from outer face of medulla through all strata into second optic chiasma	231	2.31	transmedullary cell axis-fibres extend from the outer face of medulla into the second optic chiasma. Monopolar cells terminate in strata 1 and 2
axis-fibres from first optic chiasma as far as stratum 3 (outer limit)	120	1.20	
axis-fibres from first optic chiasma as far as the inner limit of stratum 5	99	0.99	long visual fibres terminate in strata 3 to 5
axis-fibres from second optic chiasma as far as the middle of stratum 7	161	1.61	T_3 cells have axis-fibres in stratum 8 and part of 7. T_2 cells have unbranched axis-fibres in both 8 and 7. Some extend into the serpentine layer (stratum 6)
axis-fibre and cell-body fibre junctions recognizable at the inner face of the medulla. The axis-fibres extend as far as the mid-point of stratum 7 or are traceable only a short way into stratum 8	213	2.13	T_3 and T_4 cells have corresponding extents of axis-fibre penetration into the medulla
axis-fibres from inner face of columns	480	4.80	transmedullary cells, T-cells and Y-cells leave the inner face of the medulla

Number of fibres from an area of the inner face of the medulla equivalent to 10 columns = 54 (av. 5.4 per column).

Maximum number of fibres counted from 10 adjacent columns = 63 (av. 6.3 per column).

TABLE 4. MEDULLARY COLUMNS (PACKING OF ELEMENTS)

	maximum number of elements in adjacent columns		
cell type	number of adjacent columns sampled	number of elements counted	average number of elements in 10 columns
Tm 1	6	6	10.0
Tm 2	15	15	10.0
long visual fibre ending	25	27	10.8
monopolar ce'l ending	14	15	10.7
T_2 (initial component)	10	6	6.0
T_3 (initial component)	18	18	10.0
T_4 (initial component)	38	38	10.0
Y_1 (medullary component)	10	4	4.0

Average number of elements which contribute to the second optic chiasma (from 10 columns) = 50 (5 per column).

Average number of axis-fibres in 10 adjacent columns (from 12 Holmes–Blest preparations: counts at stratum 8) = 55 (5.5 per column).

Maximum number of class I fibres from the inner faces of 10 adjacent columns (from Holmes–Blest preparations) = 63 (6.3 per column).

Maximum number of class I fibres from the inner faces of 10 adjacent columns (from *en masse* impregnated Golgi–Colonnier material) = 57 (5.7 per column).

The maximum number of class I fibres seen from a column into the second optic chiasma (from *en masse* impregnated Golgi–Colonnier preparations) = 7 fibres.

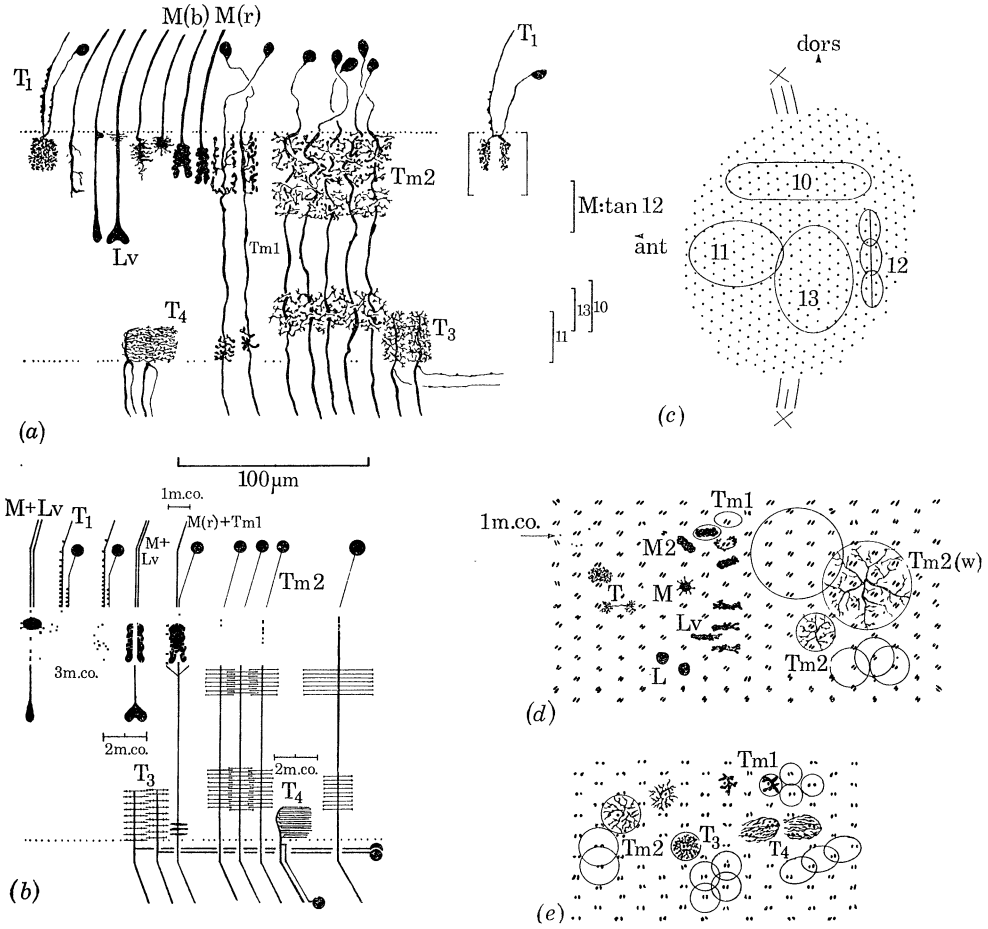


FIGURE 170. The components of medullary columns.

(*a*) This diagram shows the closest packing of elements seen in Golgi-preparations (camera lucida drawings from two preparations of *Calliphora* which showed *en masse* impregnation). Note that the lateral spreads of the type 1 transmedullary cells do not overlap. The initial components of T_1 cells are included to show their relative depths of penetration.

(*b*) A schematic representation of column components. 1m.co. = the lateral extent of 1 medullary column. 2 and 3 m.co. = the lateral extents of 2 and 3 adjacent medullary columns. Note the paired arrangement of the lamina inputs and the hypothesized lateral topographical relationship between the type 1 transmedullary cell and the lobed ending of a bilateral monopolar cell. Note also that the T_1 components are situated between column axes. The lobed monopolar cell endings and long visual fibre endings have non-overlapping fields at their respective levels (the club endings in figure 55, plate 17, are exceptions).

(*c*) A schematic plan of the medulla relating the fields of four small-field class II elements to medullary column axes (each dot represents one axis). Medullary tangential fields of M: tan 10, 11, 12 and 13 have characteristically oriented fields at characteristic levels. These are shown in figure 170*a*. Note also the curved arrays of columns. The linking-fibres from the medulla to the lobula complex leave the inner face of the medulla as thin sheets of fibres for the second optic chiasma.

(*d*) Strata 1, 2 and 3 of the medulla (tangential section). Column axes are represented by pairs of dots (lamina input pairs). Some fields of type 1 and 2 transmedullary cells have been related to columns from phase-contrast microscopy of Golgi-impregnated material. Reduced silver preparations show that two transmedullary cell axis-fibres contribute to the axis of a column. Golgi-preparations give the impression that a Tm 1 and a Tm 2 cell are topographically associated with each column. The fields of the Tm 2 cells overlap. The widest field variants of Tm 1, at the perimeter zone of the medulla, spread through many medullary columns. Note the location of the initial components of T_1 cells in relation to column axes. Phase-contrast microscopy of osmium-fixed material shows lozenge-shaped delineations of medullary columns (1m.co.)

(*e*) Strata 7 and 8 of the medulla (tangential section). The inner groups of processes of Tm 2 cells have overlapping fields. The initial components of T_3 cells have marginally overlapping fields. Note the extents of overlap of the initial components of T_4 cells (see also figure 75, plate 19). The inner fields of Tm 1 cells have lateral extents restricted to medullary columns. (*Legend continued on following page*)

The unilateral type 1a Tm cells clearly embrace the endings of bilateral monopolar cells in their own column. The deep T-cells and Y_1 cells extend through between 1 and 3 columns laterally in both the horizontal and vertical planes and their fields overlap. The bushy T-cells have fields which overlap one another by about one-quarter to one-half of their extent in the horizontal plane. The shallow T-cells are restricted to single columns and their fields overlap only marginally.

The proportions of different class I cell-types estimated above may possibly be a conservative value. Neither selective nor reduced silver procedures can give wholly accurate data. The former is capricious and, in vertebrates at least, the latter may not show up fibres which lack neurofibrillae (Boycott, Gray & Guillery 1961; Gray & Guillery 1966). If the thinnest have only a few widely separated fibrillae in the fibre then these also may not be resoluble with the light microscope. Counts of fibres can be made most accurately from electron-micrographs. This technique has been successfully applied to crustacean nerve tracts (Nunnemacher 1966), but in insects, cell-body fibres often project in parallel with their linking-fibres (for example, the cell-body and axis-fibres of bushy T-cells). There should be morphological criteria for distinguishing these two fibre-types in cross section.

In summary, the retinal mosaic pattern of the ommatidia is preserved in the lamina by both the retinula cells and long visual fibres. This lamina mosaic is projected to the outer face of the medulla by discrete groups of long visual fibres and monopolar cells. The projection pattern is basically a homotopic one which is apparently doubly represented in the medullae of these species of Diptera (figure 169). In the Lepidoptera the medullary mosaic may possibly reflect homotopic and heterotopic projections of the lamina mosaic. The medullary mosaic at the outer face is projected homotopically to the inner face. At least four parallel relays project each column to the lobula complex. Thus in these species of Diptera, the retinal mosaic of ommatidia could possibly be morphologically relayed to the lobula complex by a successively increasing number of parallel pathways. Each ommatidium is most probably structurally represented in the regions of the lobula complex by at least eight small-field class I cells. The projection pattern of the fibres between the lobula and lobula plate is apparently homotopic (figure 112, plate 24), but occasionally fibres do appear to have unusual courses (figure 124, plate 26). Golgi preparations suggest that the projection patterns of some elements between the medulla and the lobula complex preserve the medulla/lamina mosaic, while others may permutate it. The type 1 and 1a transmedullary cells converge at the lobula (figure 113, plate 24) and horizontally adjacent Y_1 elements in the medulla are displaced dorsoventrally by their corresponding endings in the lobula complex. The shallow and bushy T-cell components in the medulla

FIGURE 170. Legend (*cont.*)

Notations

170*a*, *b*. M(b) = endings of bilateral and midget monopolar cells. M(r) = endings of radial monopolar cells. L.v. = long visual fibre endings. M+L.v. = input pairs to a column composed of one monopolar cell ending and one long visual fibre ending. Tm1 = type 1 (narrow field) transmedullary cells. Tm2 = type 2 (overlapping fields) transmedullary cells. T_3 = initial component of a shallow T-cell to the lobula. T_4 = initial component of a bushy T-cell to the lobula plate. 170*d*. Tm1 = fields of type 1 transmedullary cells in relation to column axis (see figure 42, plate 15) and a radial monopolar cell ending (M2). M = field of a radial ending of a midget monopolar cell. Lv and L = fields of lobed and club endings of long visual fibres. Tm2 and Tm2(w) = fields of small and giant variants of the type 2 transmedullary cells. 170*e*. Tm1 = inner fields of type 1 transmedullary cells. Tm2 = inner fields of both small and giant variants of the type 2 transmedullary cells. T_3 = fields of initial components of shallow T-cells. T_4 = fields of initial components of bushy T-cells.

preserve their spatial relationships with one another in the lobula and lobula plate, respectively. The deep T-cells, wide-field T-cells and Y_2 cells may possibly relay aggregates of the retina mosaic, but their precise projection patterns have not yet been determined. In his studies of *Drosophila* Power (1943*a*) disputes the term chiasma being applied to the dispersion of fibres between the medulla and the lobula complex. However, there is a true decussation between the medulla and lobula which was recognized by the Spanish authors in both the Diptera and Lepidoptera (Cajal & Sanchez 1915; Sanchez 1915, 1918, 1919). Anterior fibres which leave the medulla (see figure 107, plate 23) end orally in the lobula and posterior fibres end ocularly (figure 150). In some orders of insect, for example the Hymenoptera and Orthoptera, there is an obvious cross-over between the medulla and undivided lobula (figure 150). It has been suggested earlier in this account that the lobula plate of the Diptera and Lepidoptera might be homologous with an inner stratum of the undivided lobulae of other orders. If the lateral relationships of analogous class I elements, in divided and undivided lobulae, must be preserved in the same geometry between the strata of the former and the two regions of the latter there should obviously be no chiasma between the medulla and lobula plate. Fibres which project directly to the lobula via the second optic chiasma and those which project via the lobula plate (for example, Y-cells) are both following the same pattern of chiasmal decussation (figure 150).

The functional significance of these chiasmata is not known. Similar decussations are a characteristic feature of the optic lobes of many Crustacea (Hanström 1924, 1928): usually their plane of cross-over is predominantly horizontal, but some may be vertically orientated. These structures need further study; the atypical projection patterns of some fibres may project small aggregates of the relayed retinal mosaic to a deeper level where both anterior and posterior aggregates may interact at the same level and locus in a region. There is also some evidence that at least one class II linking-fibre leaves the anterior edge of the medulla, and enters the ocular edge of the lobula, but it has not been possible to detect the corresponding arborizations from Golgi preparations.

Tangential pathways: morphological considerations

There is little physiological data about individual cell-types at levels other than the lamina, although some electrophysiological investigations have been attempted deeper in the optic lobes. Horridge *et al.* (1965) have detected numerous responses in the optic lobes of locusts, including a cell-type which registers tactile stimulation of the abdomen and thorax. Burtt & Catton (1959) have assessed rough figures for transmission times and synaptic delays in successive neuropil layers. Bishop & Kheen (1966), Bishop, Kheen & McCann (1968) and Collett & Blest (1966) have recorded from movement detectors, probably at the level of the lobula, in the Diptera and Lepidoptera, respectively.

None of these studies were able to demonstrate precisely which neurons were responsible for various discharges; also it is unlikely that any of these results were derived from the individual small-field class I cells: these elements exist at all levels in the optic lobes but their axis-fibres and linking-fibres have extremely small diameters in the species of Diptera and in *Locusta*. In *Sphinx*, however, the transmedullary cells may be amenable to recording since they have relatively large diameter axis-fibres near the surface of the medulla and in the second optic chiasma (see table 5; fibre diameters, and table 1, part I).

TABLE 5. FIBRE DIAMETERS (AXIS-FIBRES IN REGIONS, LINKING-FIBRES OUTSIDE REGIONS: FROM GOLGI-PREPARATIONS)

		fibre diameters (μm)			
		Calliphora (both species)		*E. tenax*	
cell type	location of measurement	max.	min.	max.	min.
retinula cell fibres	external plexiform layer	2.0	1.2	2.2	1.2
smooth long visual fibre	lamina	1.7	1.0	1.5	1.2
	first optic chiasma	1.5	1.0	1.5	1.0
spiny long visual fibre	lamina	1.6	1.0	1.7	1.0
	first optic chiasma	1.2	1.0	1.2	0.9
wide-field long visvul fibre	lamina	–	–	1.5	1.0
	first optic chiasma	–	–	1.5	1.0
midget monopolar cell	ext. plexiform	1.0	0.5	1.2	0.7
	first optic chiasma	0.8	0.5	1.0	0.7
radial monopolar cell	ext. plexiform	1.2	0.7	1.2	0.7
	first optic chiasma	1.0	0.7	1.2	0.7
bilateral diffuse monopolar cell	ext. plexiform layer	2.0	1.5	2.2	1.5
	first optic chiasma	1.0	0.5	1.8	1.2
bilateral bistratified monopolar cell	ext. plexiform layer	1.5	0.8	2.6	1.7
	first optic chiasma	1.0	0.5	2.0	0.9
unistratified bilateral monopolar cell	ext. plexiform and fenestration layer	–	–	2.0	1.5
	first optic chiasma	–	–	1.7	1.5
T_1	first optic chiasma	0.75	0.3	0.8	0.5
T_{1a}	first optic chiasma	1.0	0.3	0.8	0.5
C_2	ext. plexiform	0.4	0.3	1.0	0.6
	first optic chiasma	0.3	0.2	0.5	0.4
	medulla (axis-fibre)	2.3	2.2	2.0	1.9
C_3	ext. plexiform	0.2	0.2	0.4	0.2
	first optic chiasma	0.3	0.2	0.4	0.2
	medulla (axis-fibre)	2.1	1.7	2.0	1.5
Lam Tan 1	first optic chiasma	2.2	2.1	2.3	2.3
	medulla	3.4	3.0	3.2	3.0
Tm 1	medulla (axis-fibre)	1.5	0.4	1.6	0.3
	second optic chiasma	1.3	1.0	1.2	1.0
Tm 2	medulla (axis-fibre)	1.5	0.6	2.3	0.3
	second optic chiasma	1.0	1.0	2.0	1.0
Tm 3	medulla (axis-fibre)	1.0	1.0	1.0	1.0
	second optic chiasma	1.0	1.0	1.0	1.0
Tm 4	medulla (axis-fibre)	1.1	0.8	–	–
	second optic chiasma	1.0	1.0	–	–
Tm 5	medulla (axis-fibre)	2.0	0.8	2.2	0.7
	second optic chiasma	1.1	1.0	1.0	0.9
Tm 6	medulla (axis-fibre)	1.0	0.5	2.3	0.3
	second optic chiasma	1.0	0.4	1.0	0.4
Tm 7	medulla (axis-fibre)	–	–	0.7	0.3
	second optic chiasma	–	–	0.4	0.3
Tm 8	medulla (axis-fibre)	–	–	1.9	0.7
	second optic chiasma	–	–	1.0	1.0
Tm 9	medulla (axis-fibre)	–	–	3.5	1.0
	second optic chiasma	–	–	1.0	0.8
T_2	second optic chiasma	1.0	0.6	1.1	0.6
T_3	second optic chiasma	0.8	0.7	0.8	0.8
T_4	second optic chiasma	1.1	0.6	1.2	1.0
T_5	intra-complex tract	1.1	0.7	1.0	1.0
T_6	intra-complex tract	–	–	1.2	0.7
T_7	intra-complex tract	–	–	1.0	0.5
Y_1	second optic chiasma	0.8	0.5	0.6	0.4

TABLE 5 (*cont.*)

cell type	location of measurement	fibre diameters (μm) *Calliphora* (both species) max.	*Calliphora* (both species) min.	*E. tenax* max.	*E. tenax* min.
Y_{1a}	second optic chiasma	0.6	0.3	0.6	0.3
Y_2	second optic chiasma	1.2	1.0	1.0	0.8
Y_{2a}	second optic chiasma	–	–	1.0	0.7
translobula plate cell	intra-complex tract	1.5	0.7	1.2	0.5
M. tan 1	medulla (inner face)	3.8	3.5	4.0	3.8
M. tan 2	medulla (ant: edge)	2.7	2.5	3.0	2.5
M. tan 3	medulla (ant: edge)	2.5	1.0	2.8	1.2
M. tan 4	medulla (stratum 2)	1.7	?	2.0	?
M. tan 5	medulla (inner face)	2.5	2.4	2.5	2.5
M. tan 6(?) (i.c 2)	medulla (inner face)	0.4	0.3	–	–
M. tan 7	medulla (ant: edge)	0.6	0.3	3.8	3.5
	medulla (serpentine layer)	0.4	0.3	3.4	2.0
M. tan 8	medulla (serpentine layer)	0.5	0.2	–	–
M. tan 9	medulla (ant: edge)	1.4	1.0	2.5	1.7
M. tan 10	medulla (serpentine layer)	0.3	2.8	0.7	2.8
	medulla (ant: edge)	2.6	4.0	2.9	3.8
M. tan 11	medulla (serpentine layer)	3.0	0.8	1.3	2.0
	medulla (ant: edge)	3.5	2.5	3.5	2.2
M. tan 12	medulla (serpentine layer)	1.6	0.9	1.5	1.0
	medulla (inner face)	2.0	1.0	2.0	1.4
M. tan 13	medulla (serpentine layer)	2.5	1.6	3.0	1.8
	medulla (inner face)	4.0	3.2	4.1	3.2
M. tan 14	medulla (serpentine layer)	3.1	1.5	3.5	2.0
	medulla (inner face)	3.0	2.3	4.4	3.7
giant optic lobe element	linking-fibre (second optic chiasma)	2.0	1.9	2.4	2.0
	linking-fibre (intracomplex tract)	2.0	1.5	2.0	1.0
	linking-fibre (to mid-brain)	5.0	2.7	7.5	4.0
LP. wf 1	inner face of lobula plate	3.8	3.6	4.0	4.0
LP. sf 1	lobula plate (oral edge)	1.9	1.5	2.0	1.5
LP. sf 2	lobula plate (oral edge)	2.0	1.5	3.0	2.0
L. wf 1	lobula (inner face)	2.3	2.0	2.3	2.0
L. wf 2	lobula (inner face)	2.5	2.0	2.4	2.2
L. sf 1	lobula (oral edge)	3.0	2.4	3.5	2.0
L. sf 2	lobula (stratum 3)	4.0	2.1	2.8	2.5
	lobula (inner face)	2.7	2.5	3.0	3.0
L. sf 3	lobula (oral inner face)	2.5	0.8	3.0	1.4
L. sf 4	lobula (inner face)	?	?	2.9	1.5
L. sf 5	lobula (oral edge)	2.1	0.8	2.0	1.0
IIS: 1	lobula (stratum 2)	4.8	–†	5.8	–†
	(stratum 3)	4.0	–†	4.3	–†
	(inner face)	3.5	2.4	3.5	3.0
IIS: 2	lobula (stratum 2)	3.0	–†	3.8	–†
	(stratum 3)	2.6	–†	2.6	–†
	(inner face)	3.0	1.2	1.9	1.5
IIS: 3	lobula (stratum 3)	3.8	–†	5.6	–†
	(inner face)	2.8	2.0	3.9	2.5
IIS: 4	lobula (stratum 2)	2.8	–†	5.8	–†
	(stratum 3)	2.7	–†	4.9	–†
	(inner face)	1.7	1.5	1.9	1.5
IIS: 5	lobula (strata 1–3)	?	?	4.0	3.9
	(inner face)	?	?	4.0	2.7
IIS: 6	lobula (strata 2–3)	–	–	3.4	2.0
	(inner face)	–	–	3.0	0.7
IIS: 7	lobula (strata 2–3)	–	–	6.3	–†
	(inner face)	–	–	4.0	2.0

TABLE 5 (*cont.*)

cell type	location of measurement	fibre diameters (μm) *Calliphora* (both species) max.	*Calliphora* (both species) min.	*E. tenax* max.	*E. tenax* min.
IIS: 8	lobula (stratum 3)	1.7	1.5	2.0	1.5
	(inner face)	1.0	1.0	1.7	1.2
	(ant. opt. tract)	2.0	1.3	2.7	1.8
IIS: 9, 9a	intra-complex tract	2.0	1.5	2.0	1.8
	lobula (stratum 2)	2.0	1.7	3.9	2.8
	(inner face)	1.8	1.3	2.0	1.3
IIS: 10	lobula (stratum 3)	2.5	1.7	–	–
	(inner face)	1.6	1.0	–	–
giant lobula complex element	intra-complex tract	2.9	2.0	3.1	2.0
	lobula (strata 1–3)	2.8	1.0	4.0	2.6
	linking-fibre	2.7	2.0	2.7	2.6

– = not seen; –† = minimum diameters not measured; ? = no data.

There are morphological elements at all levels of the optic lobes whose field sizes suggest a physiological relationship between them and particular shapes of aggregates of the relayed retinal mosaic. In the Lepidoptera and the Diptera the largest fields of class II elements are situated at four successive layers in the medulla and lobula complex. There are two large-field tangentials over the whole of the medulla's surface and a third at the same level as the deepest monopolar cell endings (this and one surface component, M: tan 2 and 1, respectively, are derived from the same cell-body; see p. 113). Other smaller large-field elements have been seen at strata deeper in the medulla (figures 88, 89, plate 21, figure 77, plate 19 and figures 91 to 94). In addition, there is the medullary component of the giant optic lobe tangential which invests the whole of the medulla disk at its various levels of branching and the whole of the lobula plate's surface. It also sends strip-field collaterals into the entire volume of the outermost stratum of the lobula. Another large-field class II component is situated in the deepest lobula stratum and there are also many small subfields (figure 93, 149*b*, plate 30), derived from about four linking-fibres anterior to the lobula, which cover the regions surface. Yet another large-field element covers the lobula plate surface (figure 136, plate 28). To these extremely large morphological units one must add the type 1 lamina-medulla tangential cells; in the Diptera each cell is organized into discrete strip subfields in the plexiform layer of the lamina which invest, together, about one-fifth to one-quarter of its area. Each subfield sends collaterals to the medulla where they terminate as bistratified wide-field endings. A second tangential cell has been seen in the Syrphidae which also enters both these regions but its projection patterns are still obscure.

Strip-field tangentials have been found in the outer and inner layers of the medulla, lobula and lobula plate. Only those in the latter regions invade a horizontal extent equivalent to the whole oral-ocular strip of the relayed retinal mosaic. The others in the medulla can only interact, by virtue of their lateral extent, with relatively small fractions of the mosaic. They are found at the same levels as the lateral processes of small-field class I elements of medullary columns (see figure 170).

The lobulae of the Diptera have a fundamental plan of class II element stratification (figure 141*b*). Apart from the strip- and wide-field components there are small oval and circular field elements (subclass II: S cells) which are derived from, or project to, the mid-brain. At least one

of them links the ipsi- and contralateral lobula (see p. 184). Likewise the tangential forms in the medullae of these Diptera are remarkably similar even though some interspecific variants are detectable (for instance, the type 3 surface tangential of *E. tenax* and *C. erythrocephala*, see figures 82, plate 20 and 86, plate 21, respectively). Characteristic variants of form between species of the same order are detectable in the class I cell compliments (see figures 79*a*, 80 and 81). However, the main variations of field-size, form and stratification are detectable between the amacrine cells of the medullae of all the species described in both accounts.

Perhaps the neurons most amenable for testing correlations between field-shapes and function are the small-field tangentials in the medulla and the strip-field and subclass IIS cells in the lobula complex. They have relatively wide-diameter linking-fibres, compared to those of class I cells, disposed in discrete tracts. Their field-sizes can be measured from sections cut obliquely and tangentially to the lobula surface. Some of the subclass IIS cell fields are shown in figures 142 and 143; it is apparent that in both species, *C. erythrocephala* and *E. tenax*, the fields in stratum 2 of the lobula are circular whereas the greater proportion of those at deeper levels are oval. In *Calliphora* their long axes extend predominantly in the vertical plane: in *Eristalis* their axes are both horizontal or vertical. There is evidence from Golgi preparations that some elements which comprise part of the class I input to these levels preserve the topography of the relayed medulla mosaic. If the medulla mosaic is a homotopic representation of the retina-lamina mosaic, then it might be proposed that at least some of these small-field elements, with particular field sizes and orientations, are interacting with similar shaped fields of the relayed retinal mosaic. Conversely, the shape of some of these fields may only reflect variations in the embryonic outgrowth of processes. These may have to make extensive lateral excursions to make contact with parallel class I endings which possibly relay permutated aggragates or fractions of the mosaic arrangement.

The pathways of class II linking-fibres from the optic lobes to other regions are scarcely understood and are still being investigated. There is also very little information about the precise physiological roles of the mid-brain regions to which most of them project. One of the characteristic features of these elements is that those in the medulla project directly to the mid-brain and by-pass the lobula complex and its associate regions *en route*. It could be speculated that these elements serve to decrease the latency between the recognition of certain distinctive features of the visual environment, and a subsequent mid-brain or effector response, without the involvement of several stages of integration in the deeper optic lobe levels. Some tangentials may also be derived from the mid-brain and serve to interact with whole aggragates of mosaic elements in their stratum. Some multistratified tangentials invest more than one stratum in one or more optic lobe regions.

Light and electron microscopy of vertebrate neural tissue has revealed that spines from neurons, such as the Purkinje cells in the cerebellum and pyramidal cells in the cerebral cortex, are usually postsynaptic and that baggy or varicose specializations are predominantly presynaptic (see, for example, Gray & Guillery 1966; Eccles *et al.* 1967). Some pre- and postsynaptic specializations in the octopus have similar differences in form (Gray & Young 1964). Electron microscopy studies by Trujillo-Cenoz & Melamed (1966) and Melamed & Trujillo-Cenoz (1967) on the lamina of Diptera and by Steiger (1967) on the calyces of the corpora pedunculata of ants also indicate similar morphological differences of synaptic apparatuses. Golgi studies of these regions show that presynaptic retinula cell endings are baggy or are simple plugs and the monopolar cells post-synaptic to them are spiny (figures 8 to 11 and 22

to 25, plates 12 and 14). The two main components of the calyces of *Apis* have spiny or baggy specializations (figures 164 to 166, plate 33). A great deal more study is needed to correlate apparent synaptic apparatuses seen by light microscopy with those detected by electron microscopy. But it is noteworthy that the most complexly branched tangential cells (the giant optic lobe neuron, for example) and amacrine cells have several different types of specializations at the same or different levels. Possibly some of the most complex forms of tangentials may require extremely specific spatio-temporal presynaptic performances by other cells before a response is elicited from them. Or, on the other hand, they may have complexities of responses equal to that of some other neurons recognized in arthropods (see, for example, Bullock 1959; Tauc & Hughes 1963; Kennedy & Mellon 1964).

Perpendicular and tangential pathways: general considerations

Essentially, the 'Mosaic' theory of insect vision (Müller 1826) postulates that discrete areas of the visual field are represented by individual ommatidia: these areas correspond to the geometrical projections of the ommatidia on to the visual field. Until recently it seemed that the ommatidia were the smallest receptive components of the compound eye with respect to resolution in space. The visual acuity of some insects had been shown to correspond to the minimal ommatidial angles (Baumgärtner 1928) or angles greater or smaller than would be expected from these (Hecht & Wolf 1929; Wolf 1933; Hecht & Wald 1934); it had also been suggested that ommatidia work in groups in eyes whose acuity is less than would be expected from the values of the ommatidial angles (Von Buddenbrock & Schulz 1933). However, it was proposed that independent action of the retinula cells may explain perception of an angle smaller than that subtended by adjacent ommatidia. The sensory cells in a dipterian ommatidium do not share a common axis. It has been shown that individual retinula cells are sensitive to light only from a specific position in the total visual field (de Vries & Kuiper 1958; Autrum & Wiedemann 1962; Wiedemann 1965; see also, Burkhardt, de la Motte & Seitz 1966). It is known that in *Musca domestica* six retinula cells in six different ommatidia, all of which are 'looking' at the same point in the visual field, converge to the same optic cartridge in the lamina (Trujillo-Cenoz & Melamed 1966; Melamed & Trujillo-Cenoz 1967; Braitenberg 1967; Kirschfeld 1965, 1967; Kirschfeld & Franceschini 1968). Scholes (1969) has demonstrated that lamina units (possibly monopolar cells), which receive an input from six receptors convergent to one optic cartridge, show angular acceptance curves that are barely different from those of single receptors.

In summary then, it can be fairly well assumed that in some Diptera, if not all of them, about six different receptors, in six different ommatidia, sharing the same optical axis (with respect to the axis of the eye) converge on to the same second order neuron in the lamina which, in turn, projects to the outer or second stratum of the medulla. Golgi preparations of the two species of *Calliphora* and the species of Syrphidae bear out the scheme of retinula cell projections derived from electron-microscopy (Trujillo-Cenoz & Melamed 1966; Melamed & Trujillo-Cenoz 1967) and from light microscopy by Braitenburg (1967). But there are some other important features of lamina organization that are detectable in Golgi preparations but do not seem compatible with previous electron-microscopy studies.

There are at least three forms of long visual fibres in the Syrphidae (figures 4 to 6, plate 11) and two forms in the species of *Calliphora*. Similarly, in the Lepidoptera there are three distinct forms.

These light microscopy studies confirm electron-microscopy evidence that the long visual fibres pass as pairs through the lamina outside the confines of an optic cartridge. However, they are difficult to trace into the first optic chiasma (in reduced silver preparations), since they lose some of their affinity to these stains just below the inner face of the lamina. They are, though, detectable elsewhere in the optic chiasma and in the medulla. Melamed & Trujillo-Cenoz (1967) do not describe any synaptic specializations on these elements in the lamina. However, Golgi preparations show that the pairs of long visual fibres are sometimes composed of two smooth types or other combinations (see p. 141). Possibly those with lateral spines or lateral processes (the spiny and wide-field types, respectively) may have synaptic intimacy with other components in this region (figure 20, plate 13). But it must be remembered that these variants may not necessarily be present in all species of Diptera. It is also largely a matter of chance that they will be in a section taken for electron-microscopy.

Trujillo-Cenoz (1965) has shown that there are usually two presynaptic elements associated with each retinula ending in an optic cartridge, and that these processes may also give rise to further lateral prolongations that are eventually presynaptic to a first-order interneuron fibre. This author suggests the possibility that these elements may be derived from two separate centrifugal systems, since the fibres do not seem to arise from a common source within the external plexiform layer. In *C. erythrocephala* and *C. vomotoria* Golgi preparations show that each basket ending of the type 1 centrifugal cell is composed ultimately of between 10 and 14 perpendicular processes which surround the six retinula cell-endings and also enclose the monopolar cell pairs (figure 7, plate 11 and figure 26, plate 14). These branches are often derived from their parent linking-fibre at a point just beneath the margin of the external plexiform layer (figure 13, plate 12) or even as far as 10 and 15 μm from this border. They also have short lateral processes with knobs or tubers between 0.5 and 1.0 μm long which are directed inwards towards the centre of a cartridge. In the Syrphidae there are between six and eight of these terminal processes which have a similar arrangement of short lateral processes. It would be interesting to see whether electron-microscopy indicates that correspondingly fewer fibres are associated with the retinula cell endings. Trujillo-Cenoz (1965) also points out that there is no clear distinction of ultrastructure between the two sets of efferent processes. The branches comprising the basket-endings could be interpreted as two sets of centrifugal components derived from the same linking-fibre which invest each retinula cell ending in such a way that all of these, under the electron-microscope, seem to have separate origins.

This discussion does not suggest that there is only one physiological centrifugal ending in the lamina, for this is most probably not the case. It has already been shown that there are at least three types of class I cells which may morphologically fulfil the requirements needed for a centrifugal input to this region from deeper levels (see p. 143). On the other hand, all of these elements have characteristics that would seem to make them separately identifiable, in outline, under the electron-microscope in serial sections. The mass of inter-cartridge processes from amacrine and tangential cells in the lamina may, though, confuse such a high-powered picture of this region. However, the processes of the former are relatively thick, up to 1 μm in diameter, and the processes of tangential cells, within the external plexiform layer, are either thin and smooth with an occasional bleb, or are characteristically tuberous at the margin between the external plexiform layer and the cell-body layer. Also some processes seem to have a special relationship with midget monopolar cells (figures 31 to 33, plate 14).

The types 2 and 3 centrifugal endings in the lamina have few lateral branches; those that are

present are *either* at the inner and outer margins of the external plexiform layer *or* are arranged unilaterally up the whole of the perpendicular fibre in the external plexiform layer (figures 14 to 16, plate 12). There is evidence that perpendicular components of the type 2 centrifugal endings are always situated outside the confines of optic cartridges and that the type 3 ending may also have a particular association with the midget monopolar cell. There is no indication that more than one of these narrow-field centrifugal cells is associated with each optic cartridge. Possibly some cartridges may not have them at all.

Some of the type 1 T-cell endings (basket endings) have perpendicular processes which are curved at the outer limit of the external plexiform layer (figures 34 and 35). These tangentially directed extensions are characteristically blebbed and extend part of the way over an adjacent optic cartridge. Amacrine cells in the lamina have processes that ramify between cartridges but in *Calliphora* rarely have a lateral extent greater than one or two cartridges in any plane (figure 34). The dispersion of class II processes in the lamina is not completely understood, but it is likely that they invest the optic cartridges themselves and the volumes between them which contain the satellite long visual fibre elements (figure 34). Thus it seems that the lamina may have many more components in its the synaptic arrangement than has been previously indicated.

Studies of the anatomical organization of the visual system naturally provoke the questions 'How does it work?' and 'What roles do the various species of neuron play in visual integration?'. These can, at most, be suggested only in part from the study of Golgi stained material, and there should be some physiological information to provide a frame of reference even for speculation. However, as it was pointed out earlier, there is little of this evidence from insects compared with the amount from studies on vertebrate visual systems.

In the vertebrates correlations have been made between anatomical studies of ganglion cells and their physiologically receptive fields (Brown & Major 1968). Knowledge of the structure of the vertebrate retina has allowed sensible speculation about the anatomical basis of integration at the ganglion cell level, and at the outer plexiform level (see, for example, Barlow, Hill & Levick 1965; Maturana, Lettvin, McCulloch & Pitts 1960; Maturana & Frenck 1963; Dowling & Boycott 1966; Dowling 1968). The relative abundance of physiological data has also enabled extremely successful studies of visual analysis at the level of the visual cortex and lateral geniculate body (Hubel & Wiesel 1965). There are, however, few physiological and electron-microscopical parameters, which enable us to recognize individual species of neuron in the insect visual system as being equipped to perform specific roles in visual analysis. It is tempting to make analogies between the perpendicular and tangential pathways of the insect optic lobes with the vertical and horizontal pathways of the vertebrate visual system. Such analogies do not originate here (see Cajal 1910, 1917; Cajal & Sanchez 1915; Zawarzin 1925; Maynard 1967) and must, anyway, be speculative. Nevertheless, they may give some indication of which morphological features are common to two types of visual systems and what physiological features are likely to be shared by them.

It has already been pointed out that there is good evidence that one monopolar cell is relaying information from the majority, if not all, of the retinula cells in an optic cartridge (see p. 210). But apart from the probable candidate for this (the radial monopolar cell, figure 9, plate 12) there are several other forms of first-order interneurons in the lamina and just as many forms of their endings in the medulla. Bilaterally diffuse monopolar cells are possibly intimate with only between two and four retinula cells in an optic cartridge (figures 23 to 25, plate 14), and

midget monopolar cells may perhaps be intimate with only one. The widest processes of some diffuse monopolar cells, above the outer margin of the external plexiform layer, could interact with one or two retinula cells to adjacent cartridges at the level of their local decussations. No more than two dissimilar monopolar cells have ever been detected in the same cartridge (figure 34*a*). Possibly the different forms of monopolar cells perform different abstracting functions and may be equivalent to the different species of cone bipolars of the vertebrates (Polyak 1941; Boycott & Dowling 1969; Kolb, Boycott & Dowling 1969). If two separate abstraction processes are occurring in the optic cartridges, then it would seem that the tight junction detected by Trujillo-Cenoz & Melamed (1966) between pairs of monopolars would prevent any separation of the two parallel pathways if it had the role of an electrical synapse. However, in insects the mode of function of this structure at this level is entirely unknown. Possibly monopolars could act in pairs, and various pair combinations in the cartridges provide different types of independent pathways. There is good evidence that insects have colour vision (Von Frisch 1914, 1965; Daumer 1956; Fingerman & Brown 1952; Autrum & Burkhardt 1961; Mazokhin-Porshnyakov 1966; Swihart 1964; see also Burkhardt 1964; Langer & Thorell 1966; Langer 1967*b*; Burkhardt & Hoffman 1962), even if the evidence for a red receptor in the Diptera is somewhat doubtful and the peak sensitivity at 620 nm may be an artefact caused by the filtering effect of the screening pigments on short wavelengths (see Autrum 1955; Burkhardt 1962, 1964; Goldsmith 1965). If there are discrete colour coded receptors between receptor cells 1 to 6 it would be expected that first-order interneurons would similarly provide discrete colour-coded channels to deeper regions, and that some cell-types in the medulla may have receptive fields excited or inhibited by colour-coded inputs.

There is both evidence for and against separate photopic and scotopic elements in insects. A Purkinje shift has been reported for *Drosophila* (Fingerman & Brown 1952, 1953) yet this phenomenon has not been found in some other species (Walther 1958; Goldsmith 1961). However, behavioural and electro-physiological evidence does show a shift of maximum sensitivity in *Calliphora* from 540 to 480 nm when the light intensity is decreased (Schneider 1956). If such elements are present in some insects then, as Cajal (1937) pointed out with reference to vertebrate scotopic and photopic vision, two discrete first order interneuron pathways ought to exist for them (unless the long visual fibres are providing one of them by a direct first-order receptor pathway to the medulla).

Bees are receptive to polarized light (Von Frisch 1949, 1965). Dichroic pigments have been postulated to be present in insect retinae (Dethier 1963; Stockhammer 1956) and Langer & Thorell (1966) have provided evidence for dichroism in one of the seven rhabdomeres in the ommatidia of *C. erythrocephala*. Experiments on this species have shown some retinula cells to be sensitive to the plane of polarized light (Burkhardt & Wendler 1960): the arguments for such a detector mechanism being present in the Diptera have recently been discussed by Goldsmith (1964). Melamed & Trujillo-Cenoz (1967) have postulated that the two long visual fibres of the Diptera have their microvilli arranged at right angles to one another so that they could fulfil the role of the polarized light analyzer. The rhabdomeres of these two cells in an ommatidium are separate, and each gives rise to a prolongation which projects through the lamina (outside the optic cartridges in *Lucilia*, *Phormia* and the present species of Diptera), to end finally in the medulla. Some pairs of long visual fibres have been traced the entire distance from lamina to medulla in *Pieris brassicae*, where they could separately make contact with two sets of wide-field tangentials to the mid-brain. In the Diptera it is rare to detect pairs of long visual fibres ending

in the medulla. As a rule they terminate singly at two levels. The three distinct forms of these elements in the Syrphidae suggest that some of them may have other than just the paired function of a polarized light analyzer.

There is evidence that insects can discriminate between differences of contour, shape and pattern (see accounts by Jander & Voss 1963; Jander 1963; Voss 1967) and shapes of contrasting colours (Von Frisch 1965; Daumer 1958). But as yet there is no physiological evidence to suggest that certain types of cell are associated with particular form abstracting functions. However, some speculation about the neural architecture of the medulla and lobula may provide some relevant analogies with vertebrate visual systems. The stratification of the vertebrate lateral geniculate body has been suggested by some authors to be correlated with the abstraction of colour information, on, on-off and off responses (de Valois, Smith, Karoly & Katai 1958) and similarly, the strata of the inner plexiform layer for on, on–off and intermediate responses (Maturana *et al.* 1960; Schiperheyn 1965). Such speculation could just as well be applied to the strata of the medulla with as little real evidence. However, it is certain that in the visual cortex of the cat discrete layers and columns delineate groups of neurons with specific integrating functions. The histological demonstrations of the precise architectural arrangement of pyramidal and stellate cells (Sholl 1953; Ramon-Moliner 1961, I and II) could not have revealed their functional significance without the elegant physiological studies of other workers (Hubel & Wiesel 1962, 1963, 1965).

Compared with the lobula, the lamina and medulla of the Diptera are histologically relatively simple. This may seem a strange statement considering the number of different species of neurons in the two former regions, as compared with the latter: but it is apparent that the lateral spreads within individual sets of medulla class I cell processes show little variation of size or vertical location. The only definable variations that have been detected are those of the outer group of processes of the type 1 transmedullary cells; these are greater at the perimeter of the medulla than elsewhere. One type of T-cell component, which gives rise to a process to the lamina, is also restricted to this zone in *Calliphora*. Preliminary investigation indicates that the lateral processes of small-field class I cells are characteristic of each cell type, and that there is little variation of the lateral spreads of the same types in different columns. Likewise the field sizes of tangential cell processes in the medulla are characteristically similar, irrespective of their horizontal and vertical location in a stratum. It must be stressed that these measurements are by no means complete but they do, at first sight, point to a standardization of the processes of individual types of class II cells in this region. The small-field subclass IIS neurons in the lobulae are characterized by their branching patterns and by the appearance of their processes (figures 140 and 143). But it is difficult to relate any of the components to discrete columns from Holmes–Blest procedures or phase-contrast microscopy. Reduced silver preparations show only that the subclass IIS: 1 cells are regularly spaced throughout this region (figure 108, plate 23); the Golgi stain also indicates a regular dispersion of IIS: 2 cells (figure 124, plate 26). Although the axis-fibres of other cell-types in this subclass are irregularly spaced, the sets of processes derived from several of them close together are arranged as tiers, one under the other. The lateral processes that make up adjacent tiers must, of course, interdigitate but nevertheless this does mean that there are structural, if not functional neuropil columns.

Only the outermost stratum of the lobula is clearly definable by techniques other than the Golgi method. The mosaic of the medulla seems to be superimposed by most class I endings in the three strata of the lobula. Golgi preparations indicate that many of these carry a fairly

exact replication of the medulla map, except that it is reversed by the second optic chiasma. This mosaic superimposition is architecturally essentially similar to the central replication of the retinal map in some vertebrates (Talbot & Marshall 1941; Hamdi & Whitteridge 1954). The lateral extents of these class I endings in the lobula are similar irrespective of their horizontal or vertical location, but those of most of the subclass II S cells are not. Initial measurements indicate that the type II S: 1 and II S: 2 cells have field-spreads that are standard throughout their level. Others have various orientations, variable numbers of processes and lateral extents (Strausfeld, unpublished). Some subclass II S components are morphological centrifugal endings derived from the mid-brain, and one of them is derived from a component in the contralateral lobula, so providing an anatomical basis for direct inter-lobula interaction by a small-field unit. Other II S cells have groups of processes which are derived from a perpendicular axis-fibre just above its junction to a cell-body fibre (figure 140). These processes are invariably spiny or knobbed, their linking-fibres project to ipsilateral mid-brain regions and some may conceivably project to the suboesophageal ganglion. At least one bundle of fibres from the lobula projects to the calyces of the corpora pendunculata where it ends in a characteristic dispersion similar to that of other insects such as the Hymenoptera (figures 164 to 166, plate 33). The diameters of these linking-fibres are comparable to those of some subclass II S cells. The topography of the lobula's architecture (in so far as the class I inputs from the medulla, the subclass II S cells and amacrine cells are concerned) shares some features of the arrangement of neurons in the mammalian visual cortex. However, it is not known if these lobula elements each take part in a similar sequence of integrations within the columns they define. It could be speculated that differences between II S cells might be correlated by their different synaptic, dendritic and interposing internuncial populations and arrangement. It would be useful to know these aspects as well as to determine variations of inputs to the different levels of the lobula from the medulla. It was pointed out earlier that the axis-fibres of II S cells are wider than most in thel obula neuropil and that they also contribute to definable tracts towards the mid-brain. Perhaps electrophysiological and sophisticated anatomical correlations may indicate the function of their forms.

An analogy can possibly be drawn between the medulla and inner plexiform layer of the vertebrates on the basis of its disposition with respect to the lamina and retina, and that it must receive first-order, and contain second-order interneurons. There are also some similarities between the gross shapes and disposition of the amacrine cell processes of the outer layer of the medulla, and those of the inner plexiform layer of primate (Boycott & Dowling 1968) and the pigeon retinae (Cajal 1888). But if this analogy is made then all but the amacrine cells of the medulla ought to be equated with ganglion cells. This would include all types of class I cells that project to the lobula and lobula plate, and at least some of the class II cells that relay visual information centrally. The morphological relays of class I cells can be divided into three categories: (*a*) those that end in the outermost stratum of the lobula or in the lobula plate, (*b*) those that end deeply in the lobula amongst the subclass II S cells, and (*c*) those that invest both lobula and lobula plate. All the elements that can be included under category (*a*) have small-fields restricted to only one, or at most one and a fraction of the adjacent columns in the medulla (the exceptions to this are the exceptionally wide-field elements at the perimeter of the medulla). All those cells in the other two classes, with the exception of the T_3 and Y_2 cells, have processes at the same level as the monopolar cell endings, or extend up as far as the level of the long visual fibre endings. It could be speculated that the small-field elements of group

(*a*) project strip-field information to the ocular-orally orientated strip-field tangentials in the outermost layer of the lobula and in the lobula plate. The others in groups (*b*) and (*c*) project to the level of the oval and circular field subclass IIS cells and wider field class II cells with which they are presumably intimate, either directly or via amacrine cell relays. This speculative scheme does not include the wide-field tangentials which cover the surfaces of these regions, nor the smaller field tangential components in the medulla. These may, as has been pointed out earlier, have functions which are special to insect visual systems. However, if any component was involved in inhibiting or being influenced by, the whole relayed mosaic, or sampling any part of its activity, the wide-field elements at the surfaces of the regions would be the most likely candidates for this. They could interact with all the fibres to or from other regions.

The visual-fields of the eyes of some insects overlap to some degree; prey location and fixation by *Aeschna* sp. (Baldus 1926) and by *Mantis* (Rilling, Mittlestaedt & Roeder 1959; Maldonada, Levin & Pita 1967) seems to indicate the use of the overlapping visual fields of both eyes. True binocular vision, which is the coordinated use of both eyes to produce a single impression (Adler 1965) occurs in vertebrates. In insects only one small-field element has yet been seen that projects directly from one optic lobe region to the other (figure 129, plate 26) and this has only been positively detected in the Syrphidae. As yet no other mosaic pathways have been demonstrated which can be traced to a centre receiving a similar input from the contralateral eye. Nevertheless, some pattern discrimination responses imply that some interaction between the two eyes is occurring. Electrophysiological experiments support this (Blest & Collett 1965*a*, *b*; Collett & Blest 1966; McCann & Dill 1969). Wallace (1960) has proposed that *Schistocerca* does not perceive depth by binocular interaction even though lesions in the mid-brain connectives, dorsal to an antennal lobe, result in an increased tendency by the animal to respond to objects at greater distances than normal. Possibly insects can use monocular clues such as convergence lines and vanishing points for distance perception. The peering behaviour of locusts described by Kennedy (1945) and Wallace (1958, 1959) may be overt expressions of this kind of depth perception. There may be no need for a direct binocular input into a common centre; bilateral relays from the class II endings responsible for the type of pattern position separation mechanism proposed by Maynard (1967), could project the relevant information about the two monocular visual fields into separate centres in the mid-brain. Objects either side of the animal would become relatively larger or smaller as it moved towards or away from them. If a change of pattern size was also registered between these centres then a crude form of depth perception by parallax could be achieved, although it would give only the relative, rather than the actual distances of one object from the other. Jander & Barry (1968) have recently postulated bilateral optic lobe-ocellar interaction for the phototatic responses of *Locusta migratoria* and *Gryllus bimaculatus*. There is evidence for an appropriate fibre tract for such an interaction in the bee (see p. 147), and in *Locusta* (N. J. Strausfeld, unpublished). However, this cannot be regarded as true binocular vision.

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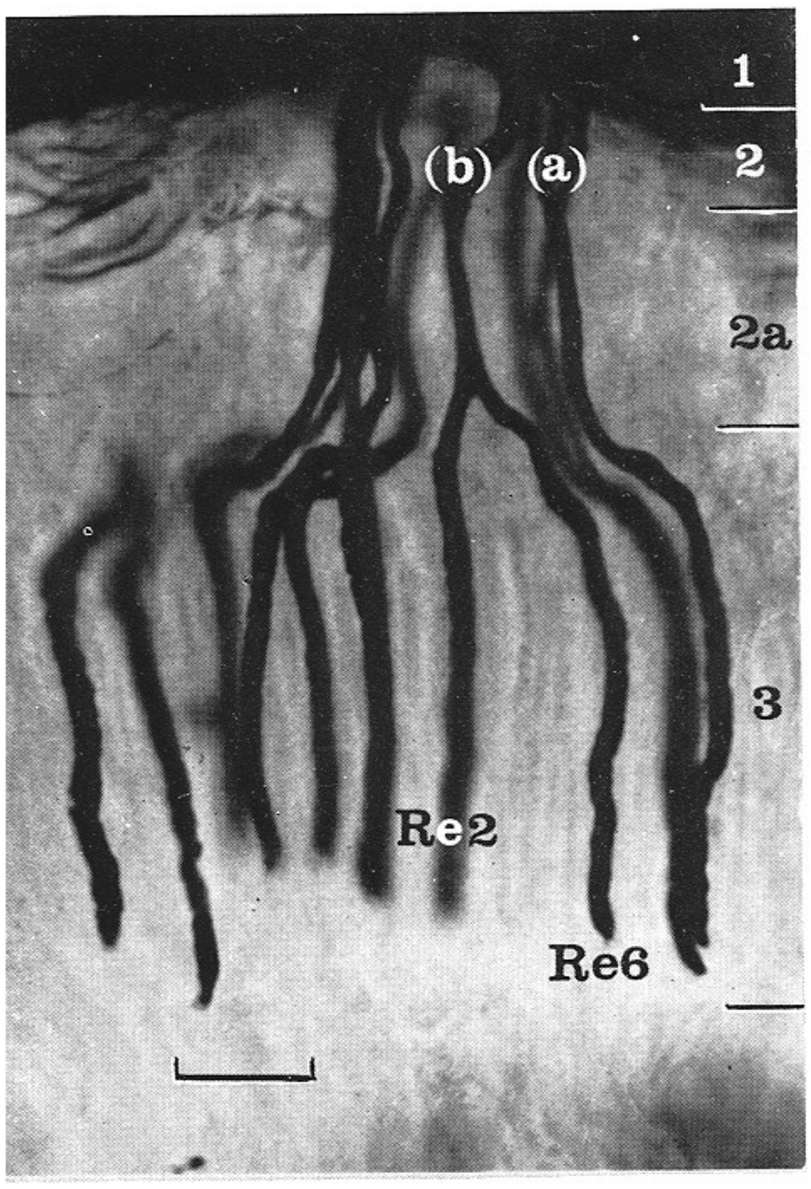
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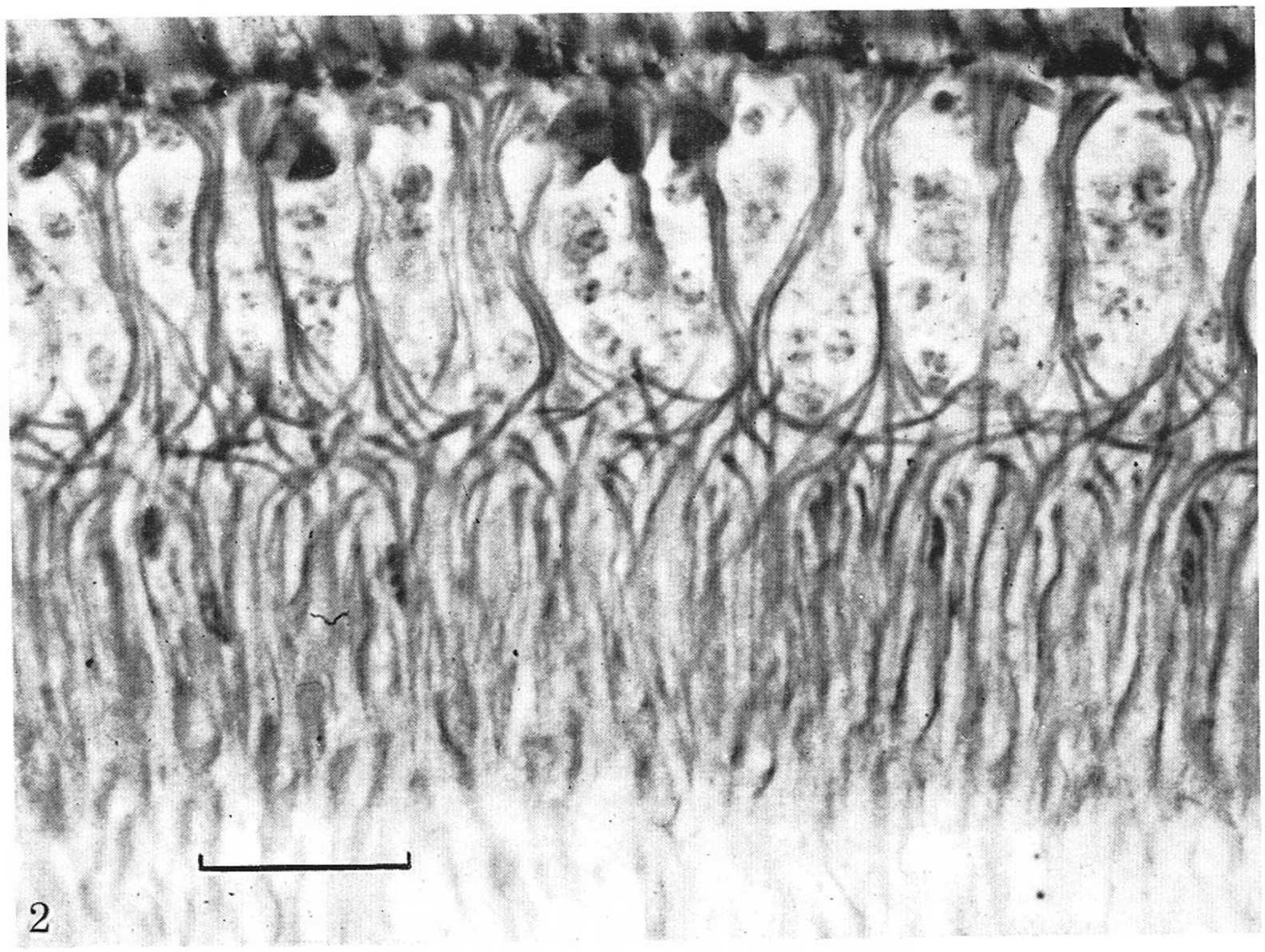
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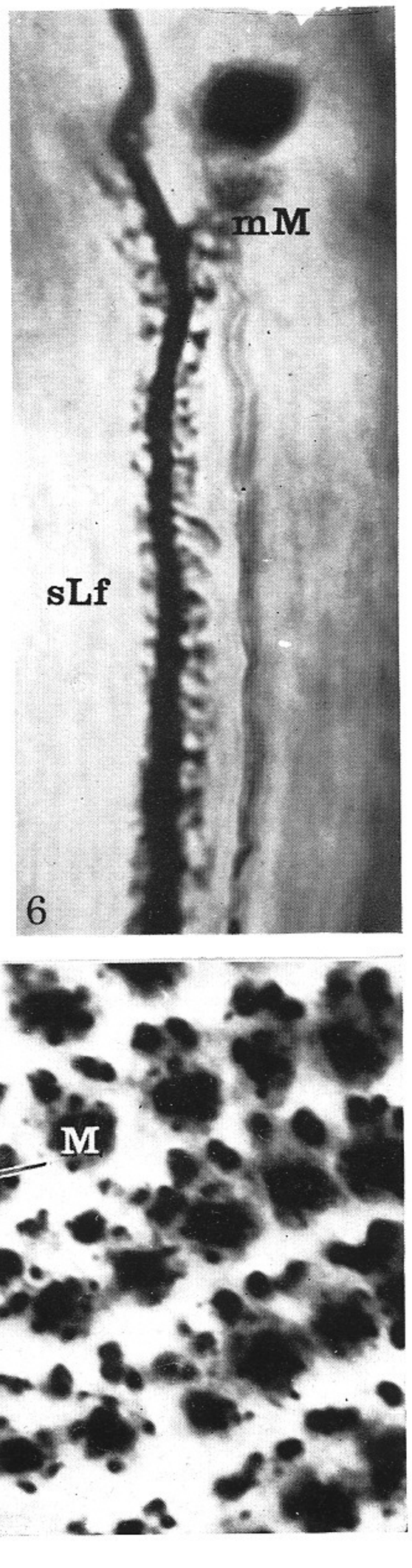
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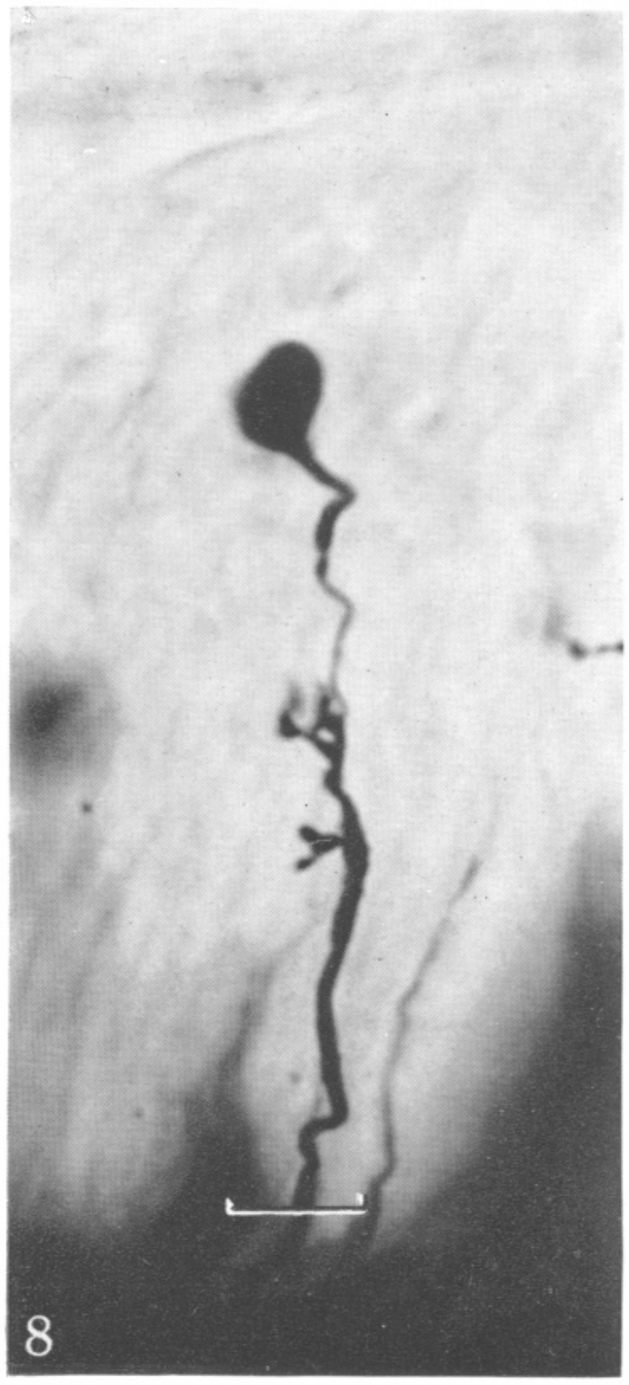

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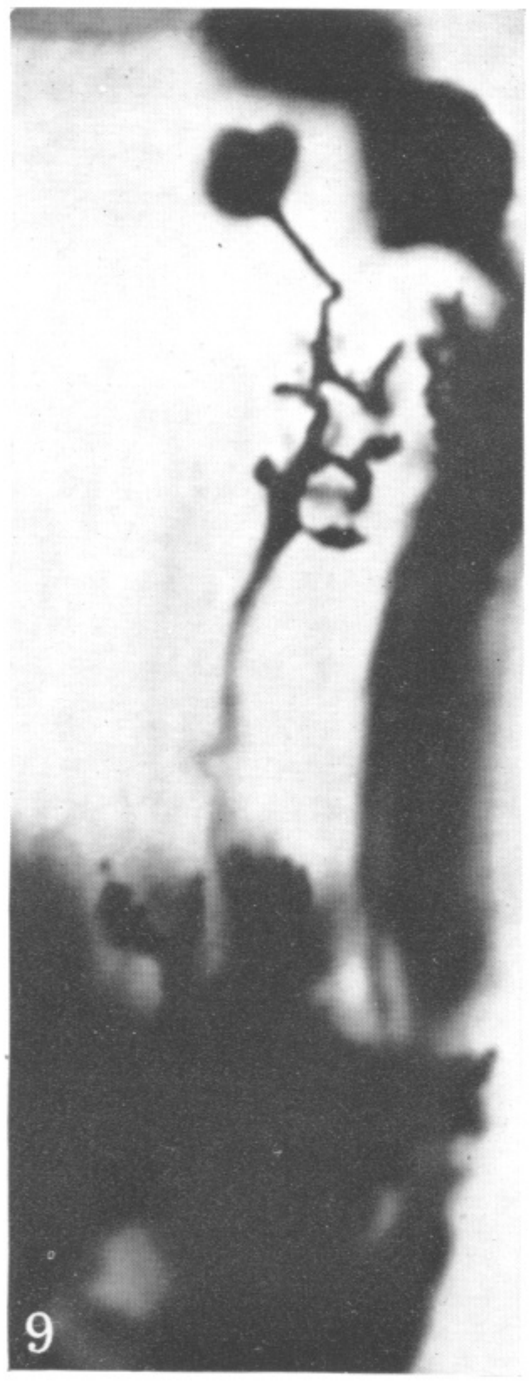

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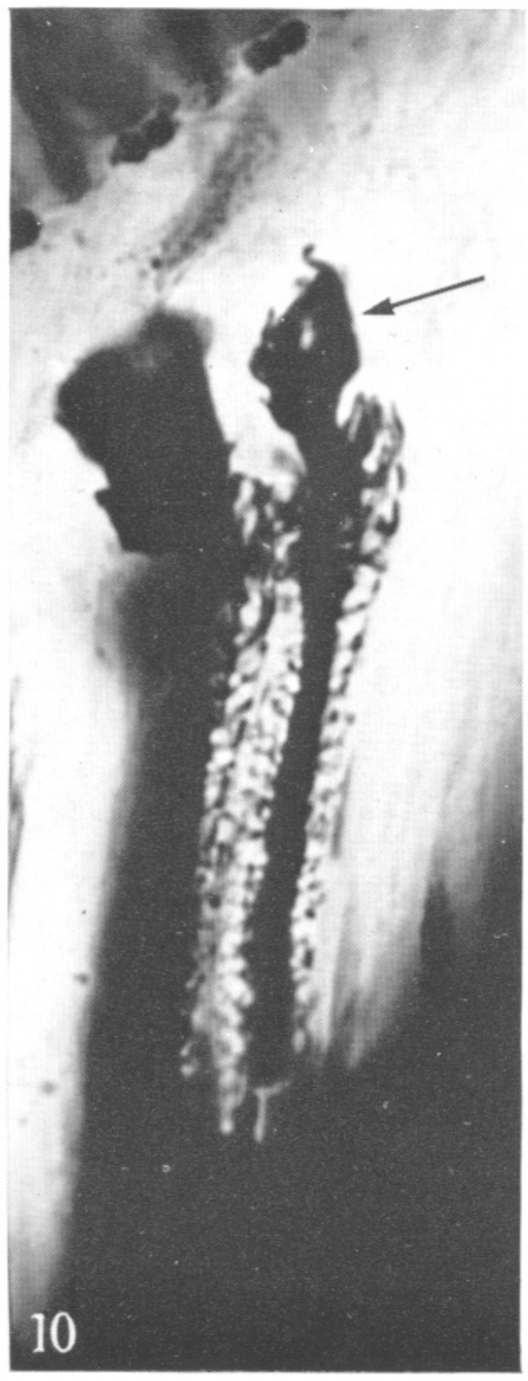

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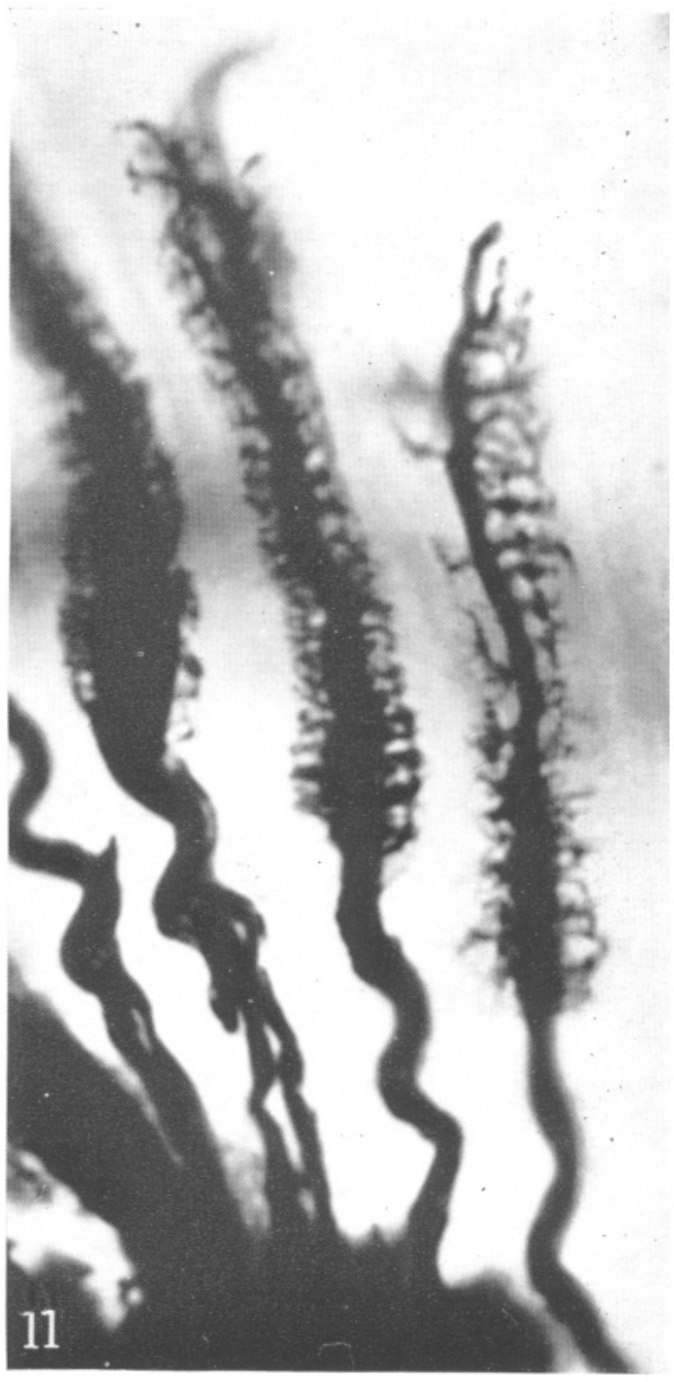

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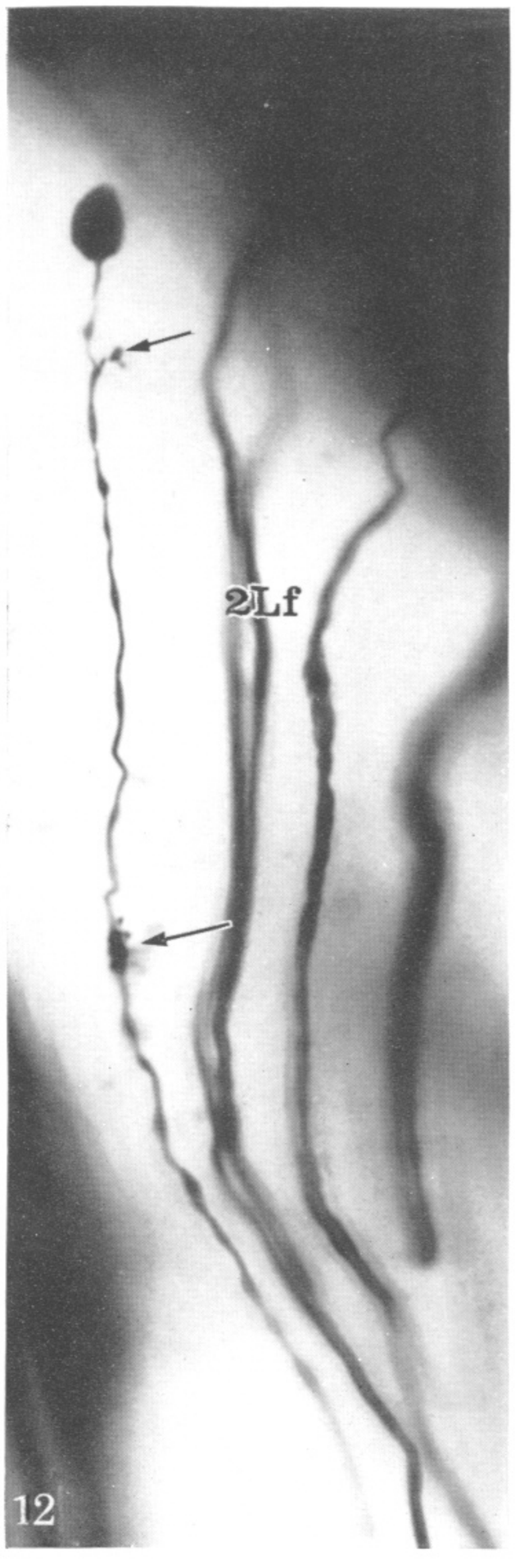

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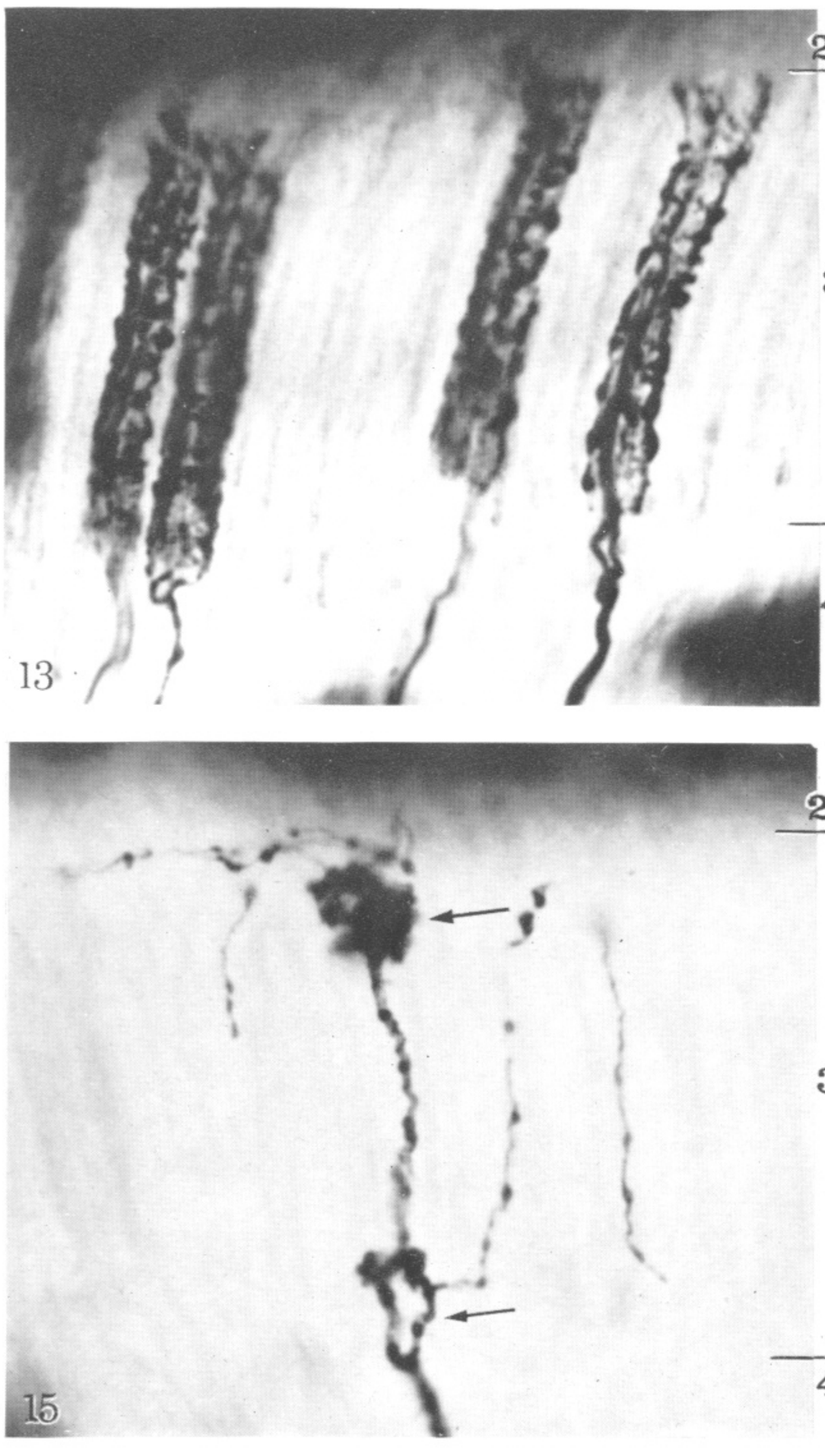

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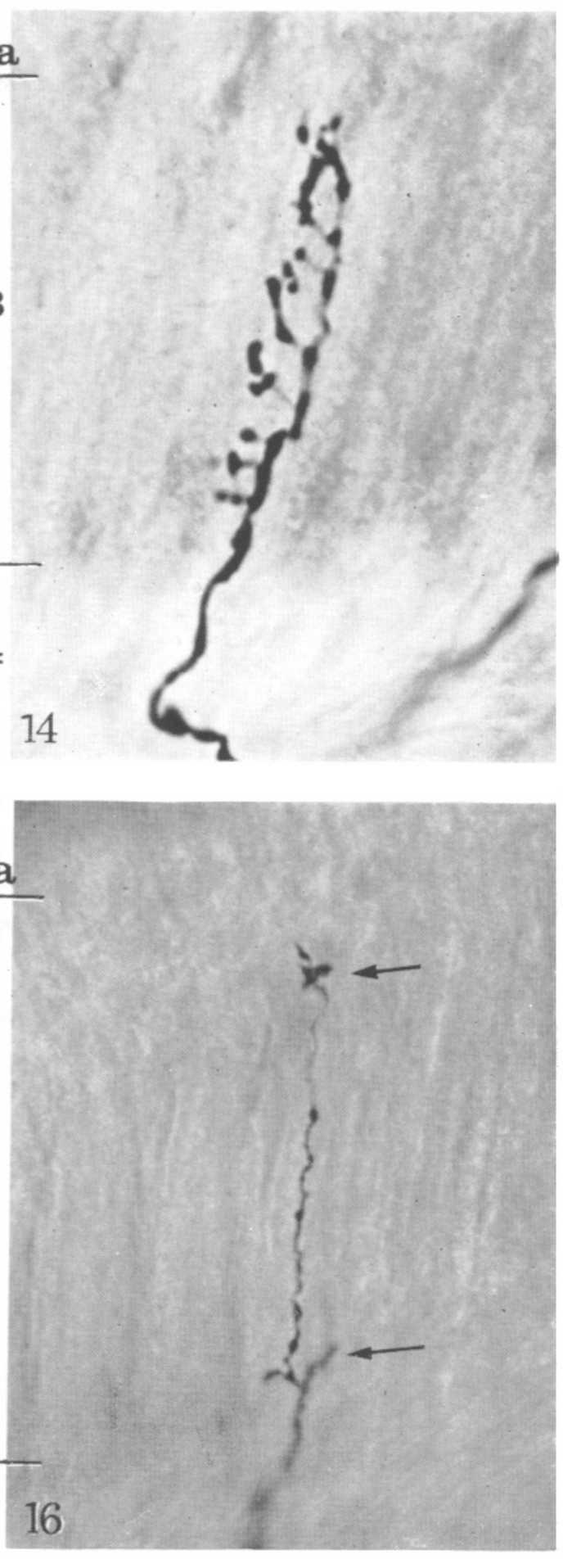

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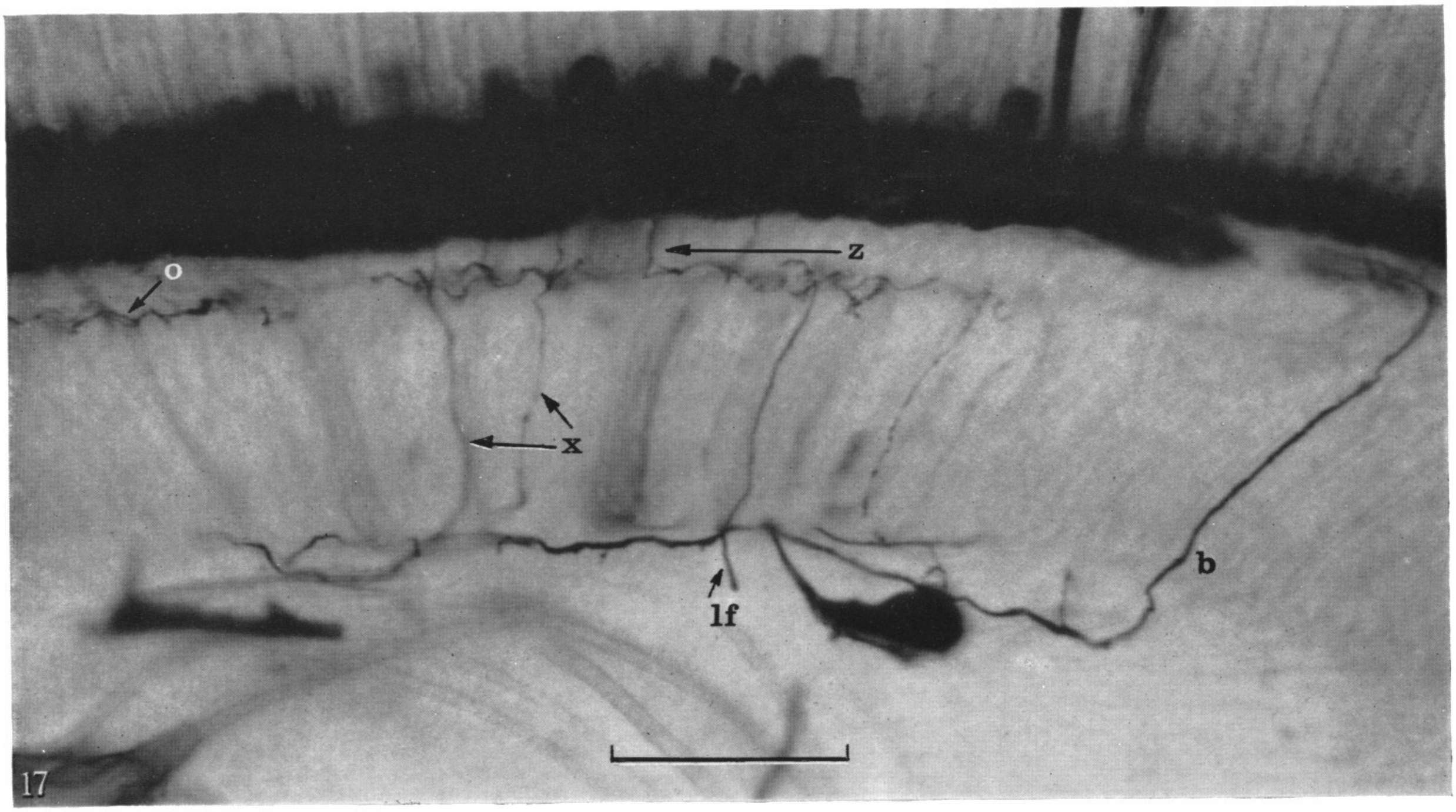

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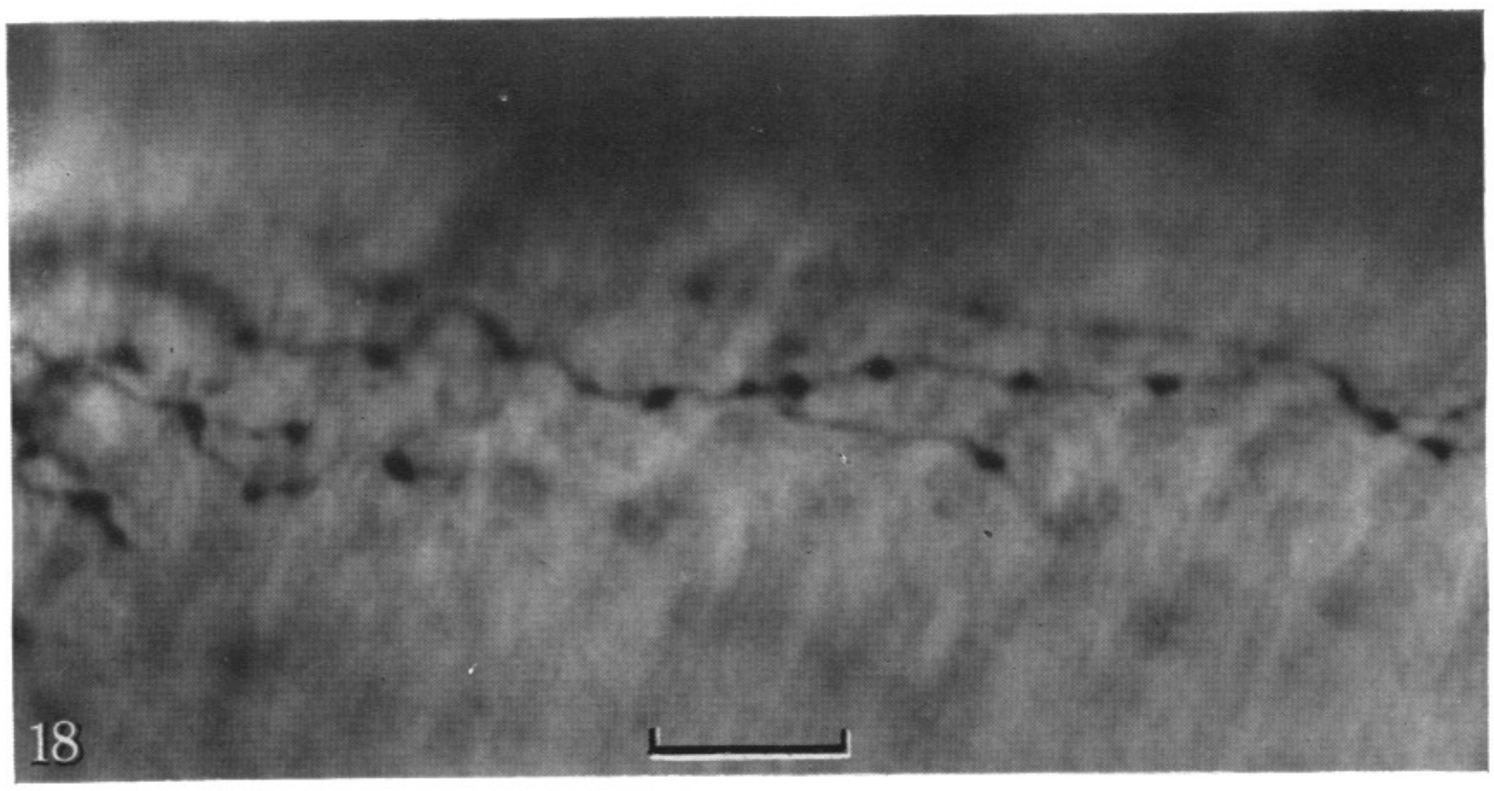

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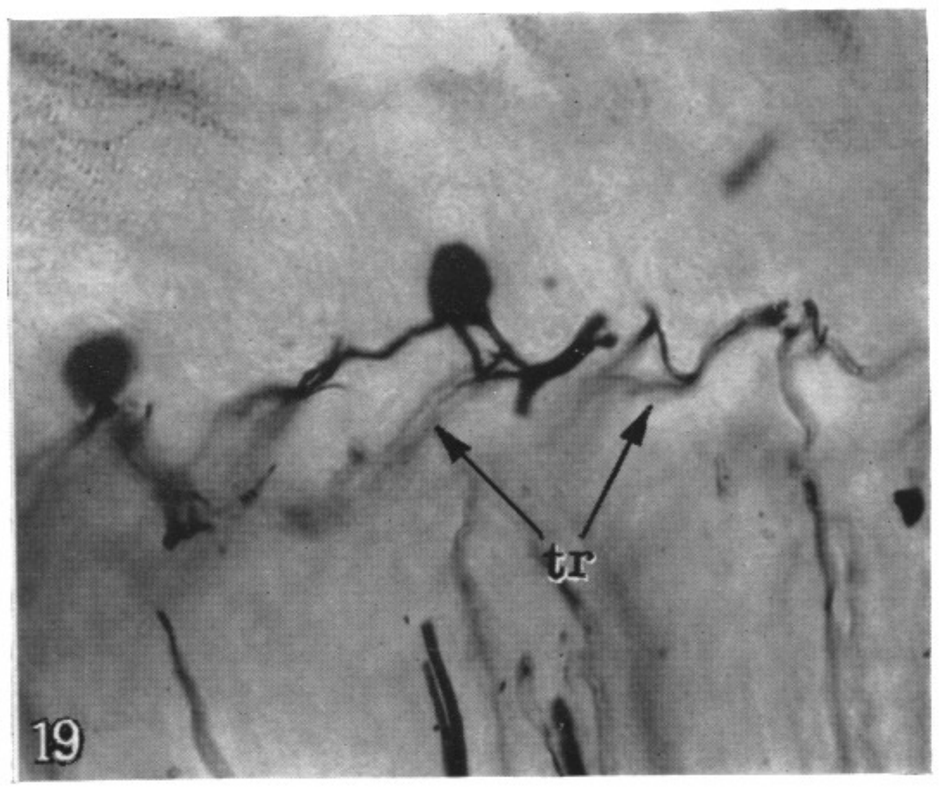

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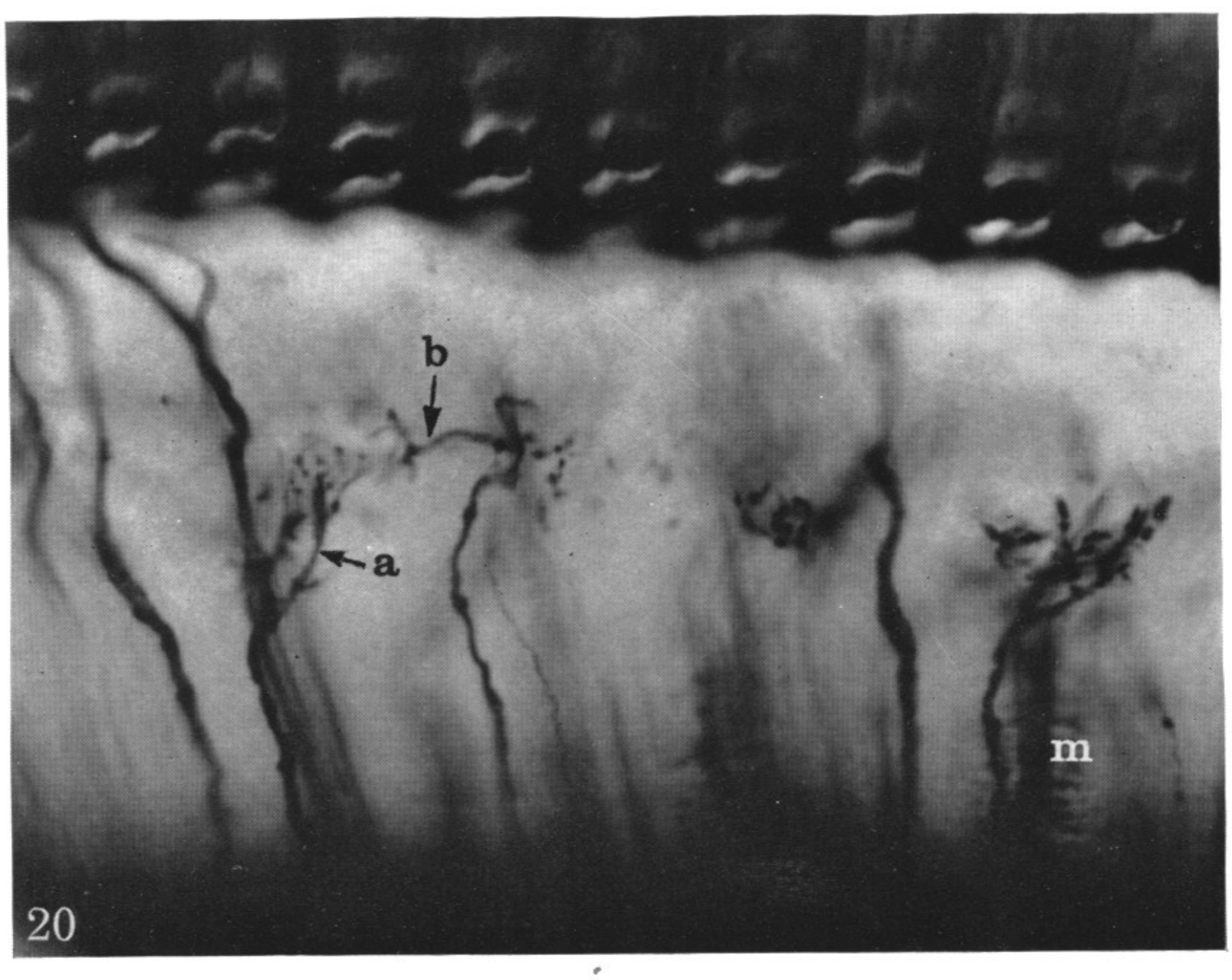

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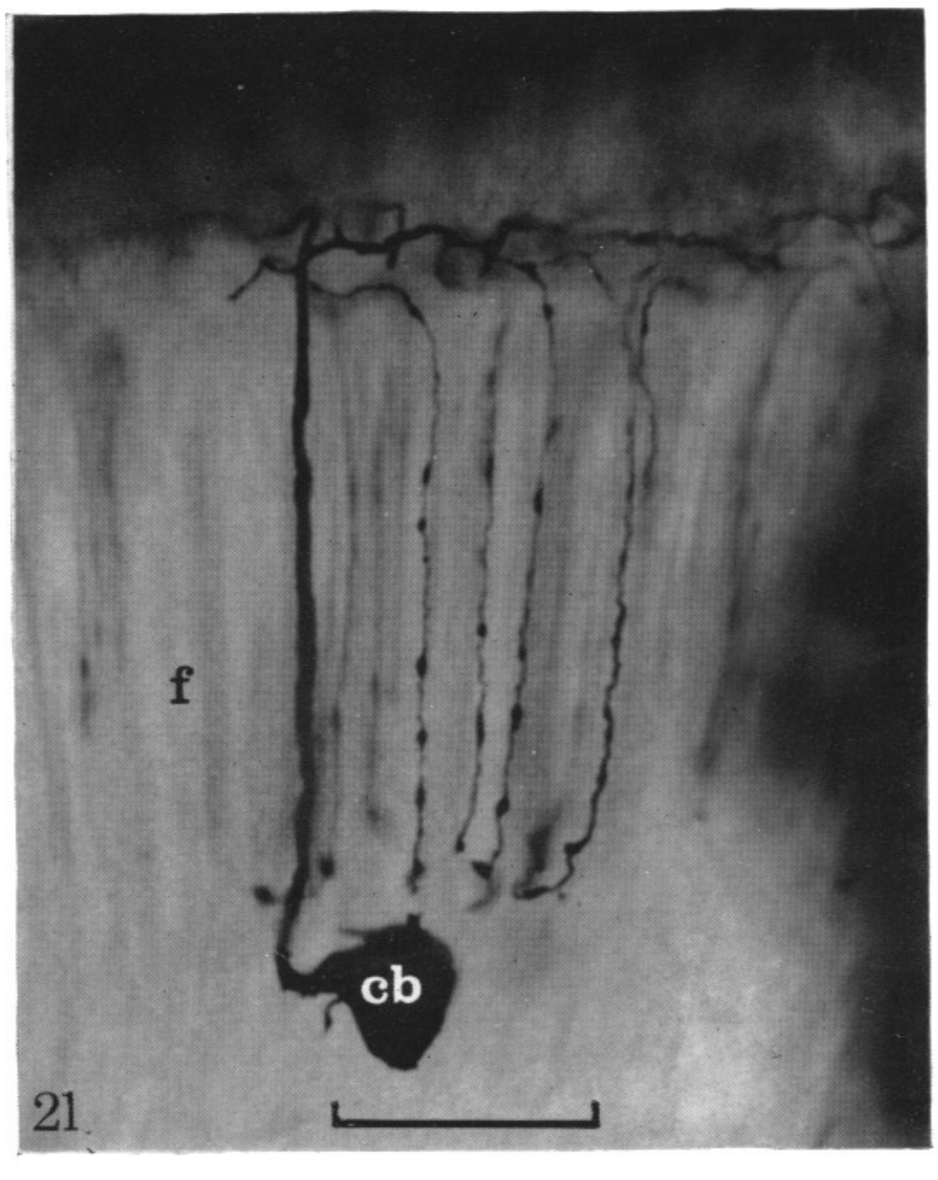

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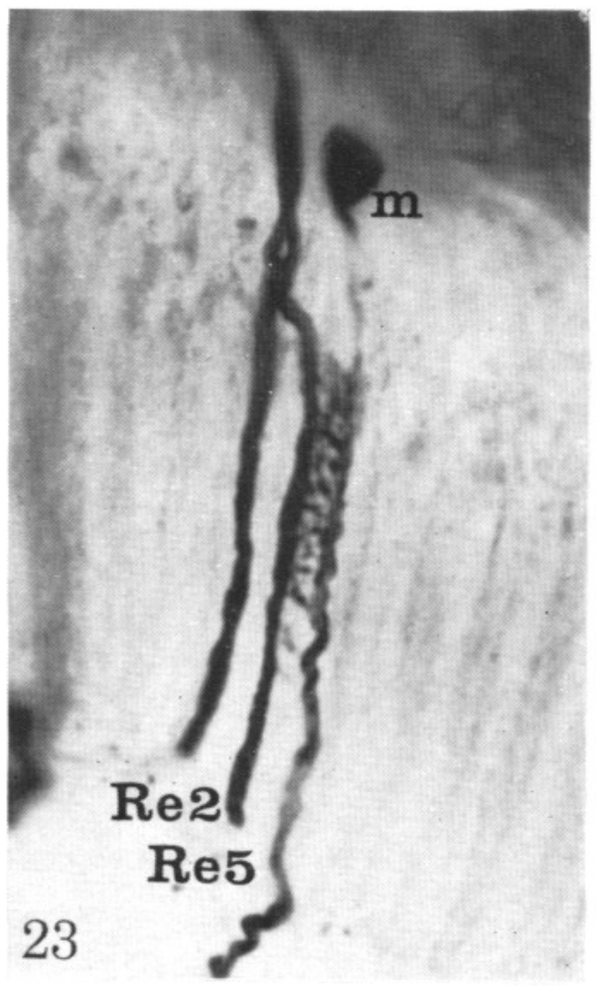

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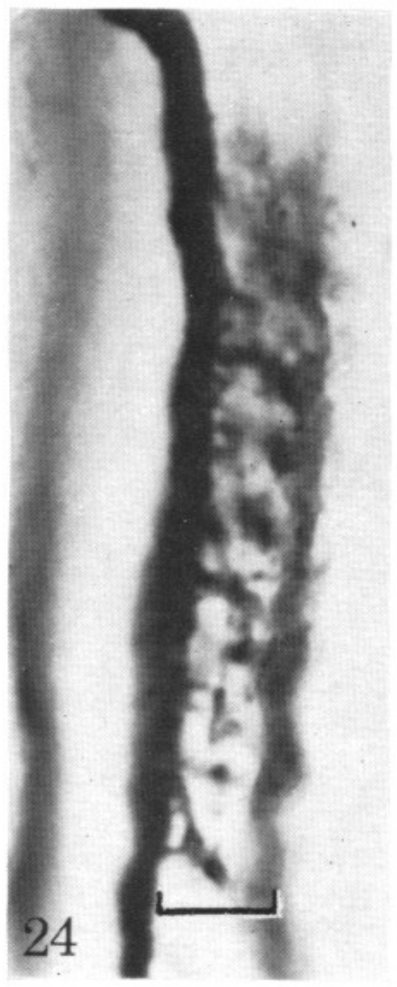

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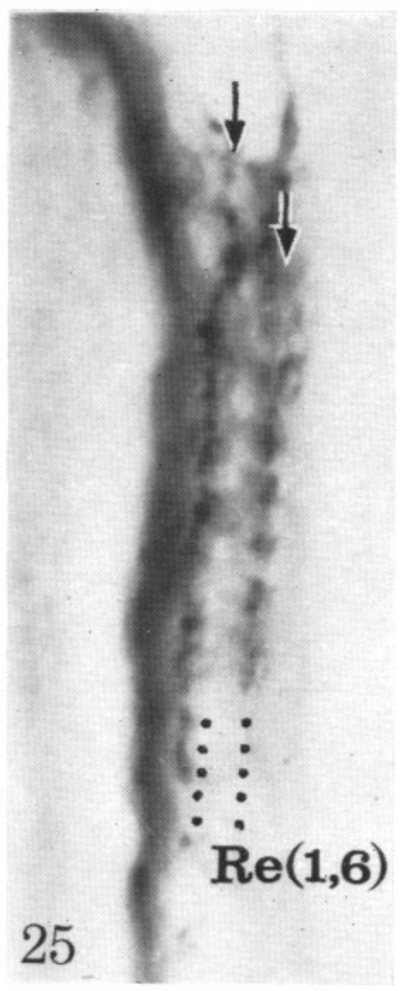

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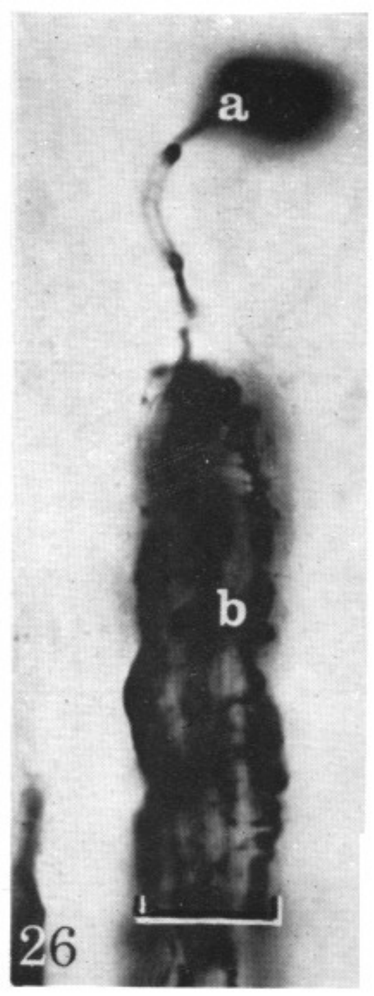

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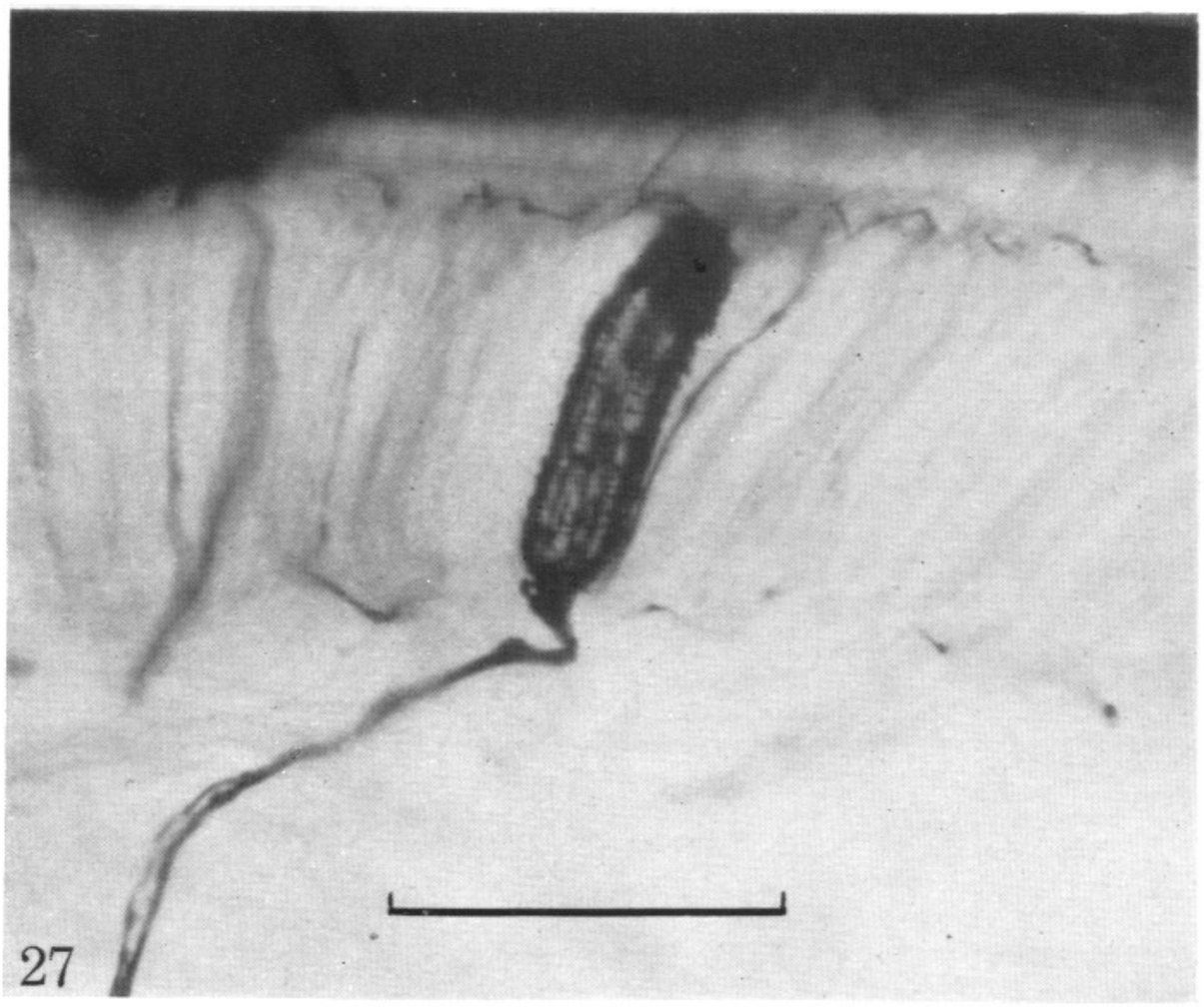

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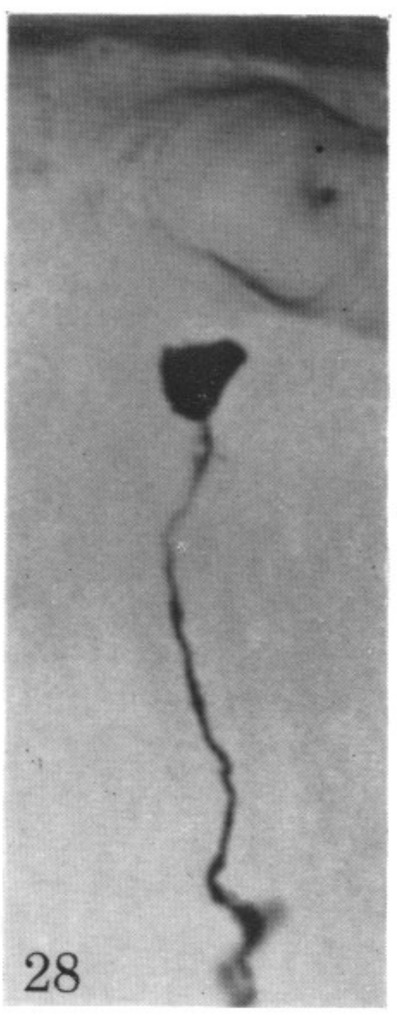

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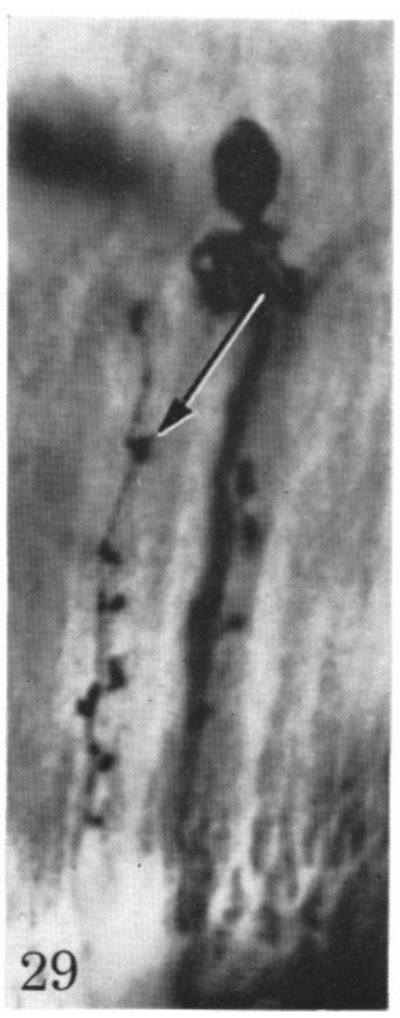

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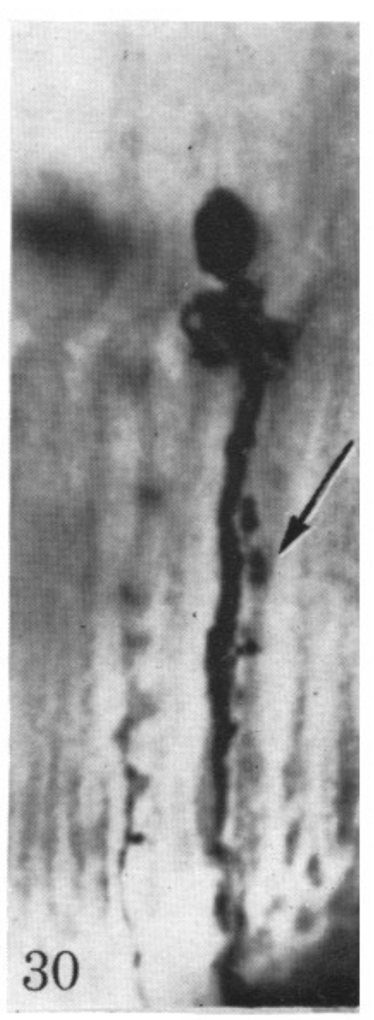

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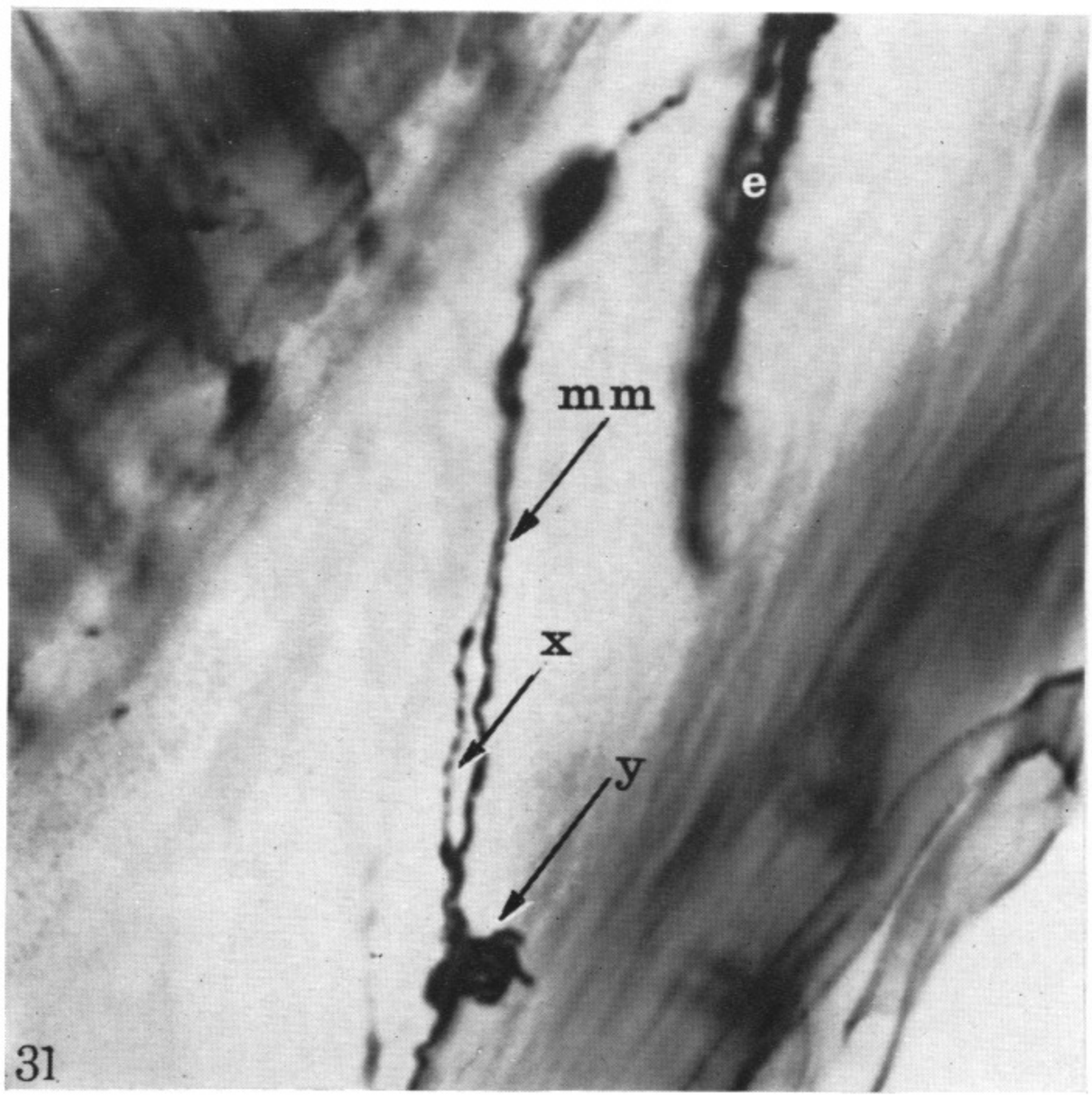

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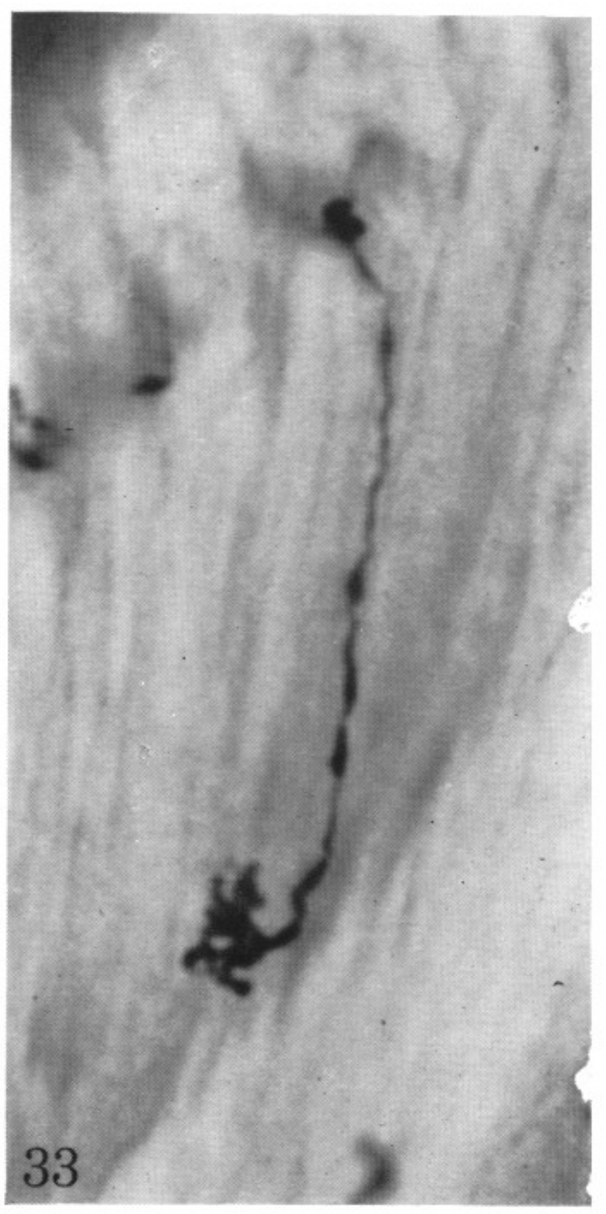

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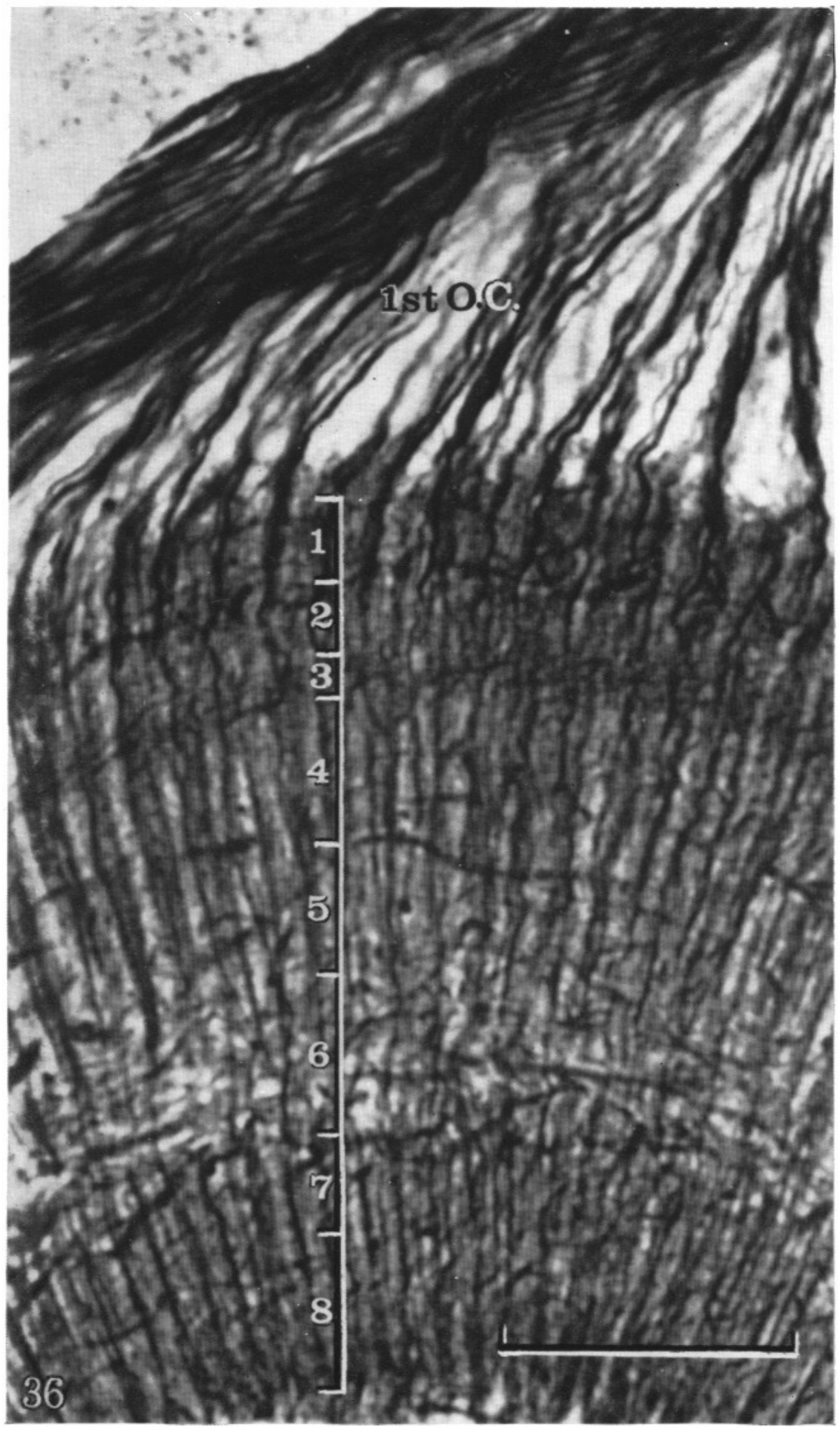

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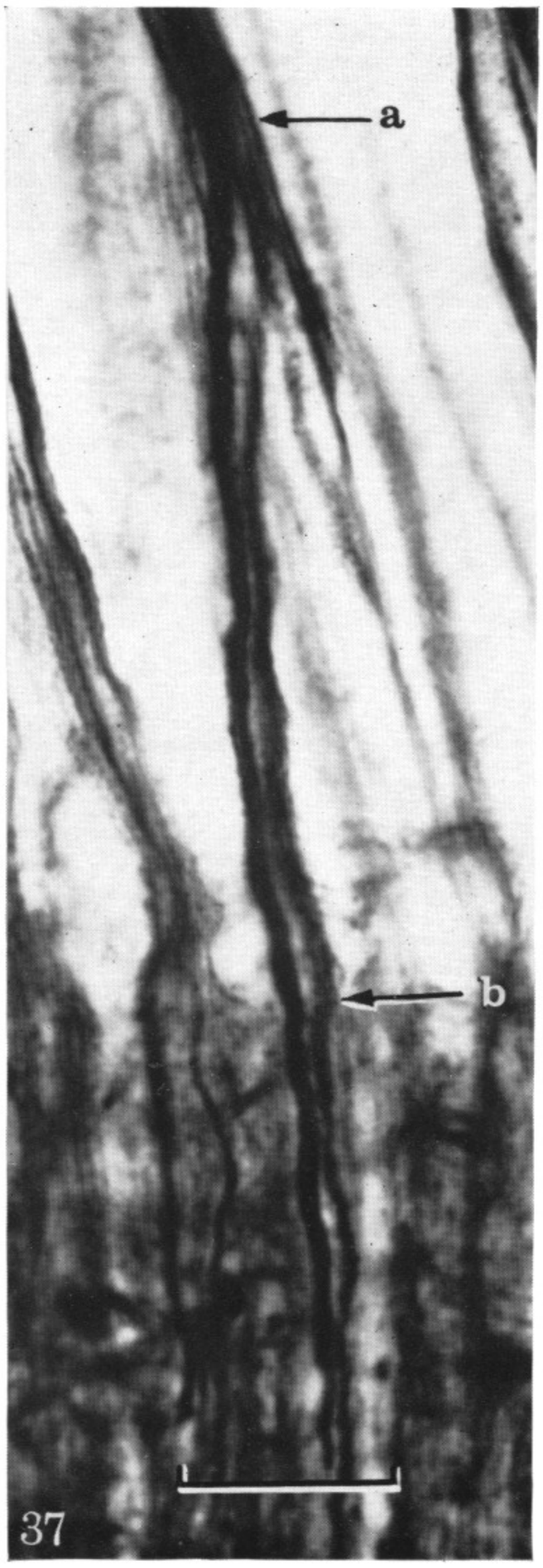

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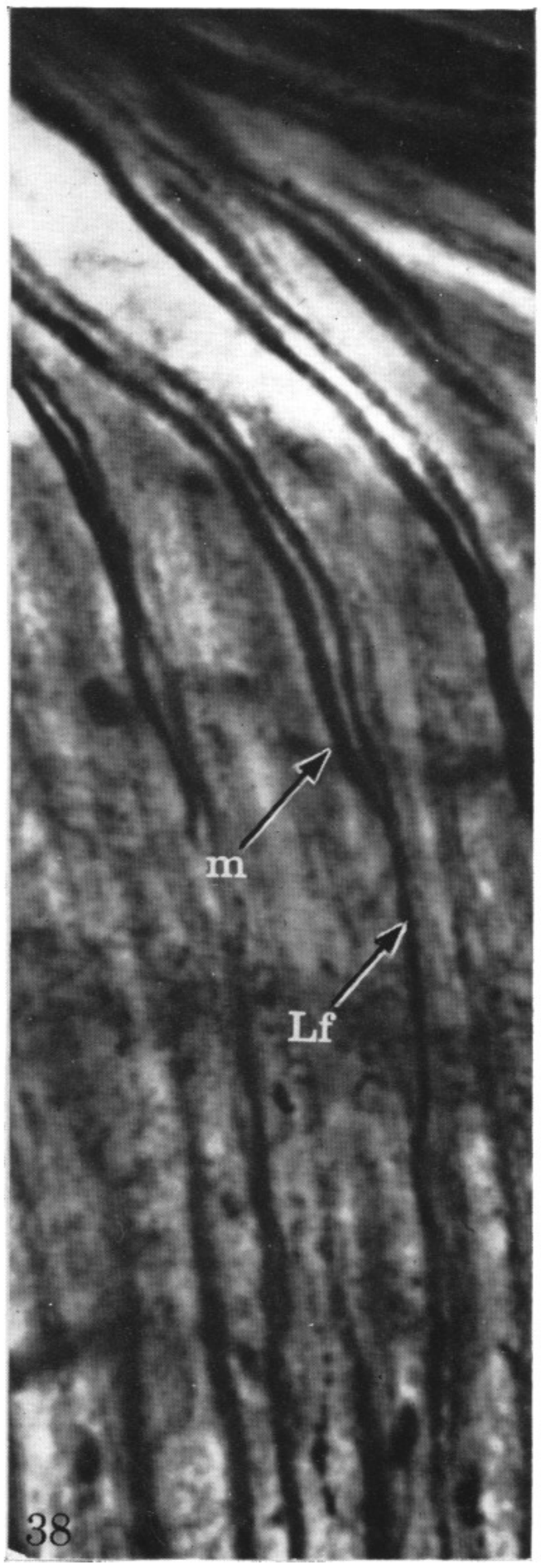

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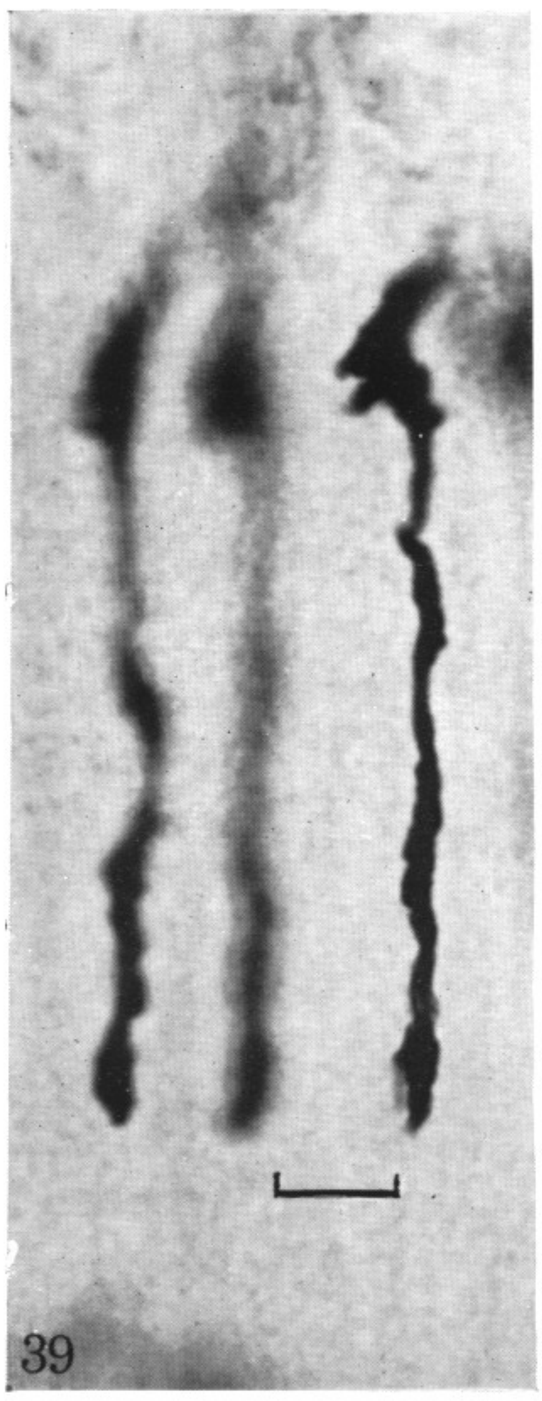

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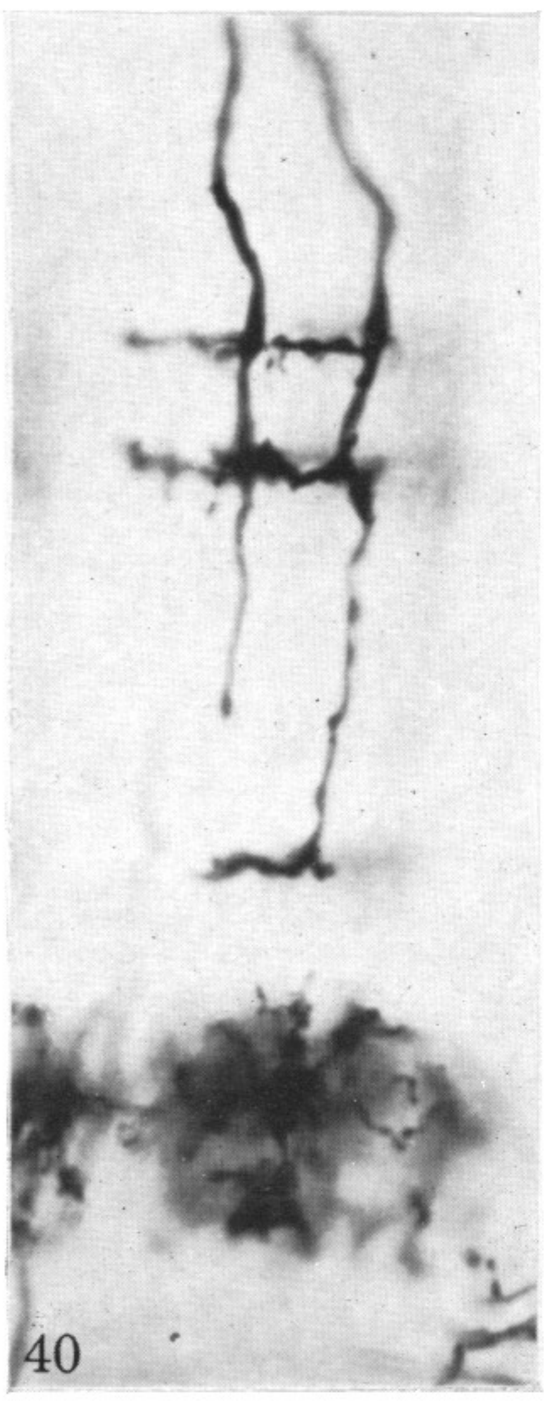

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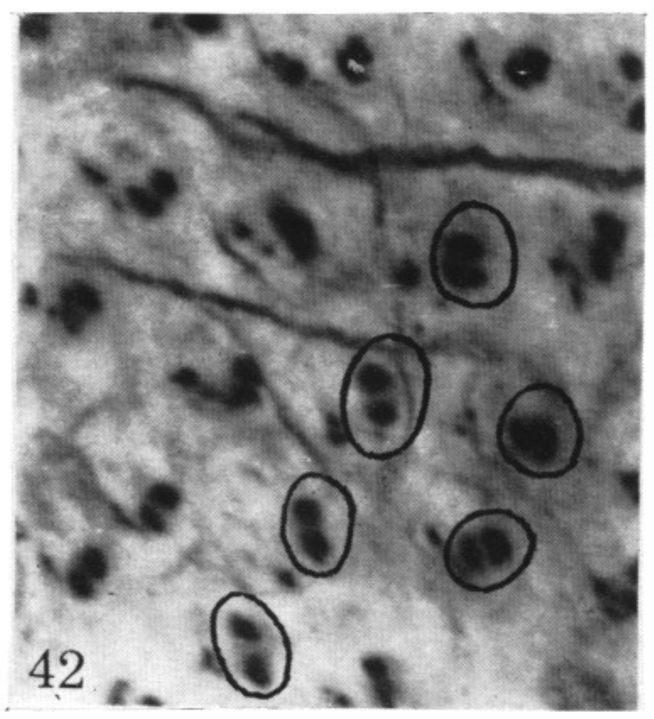

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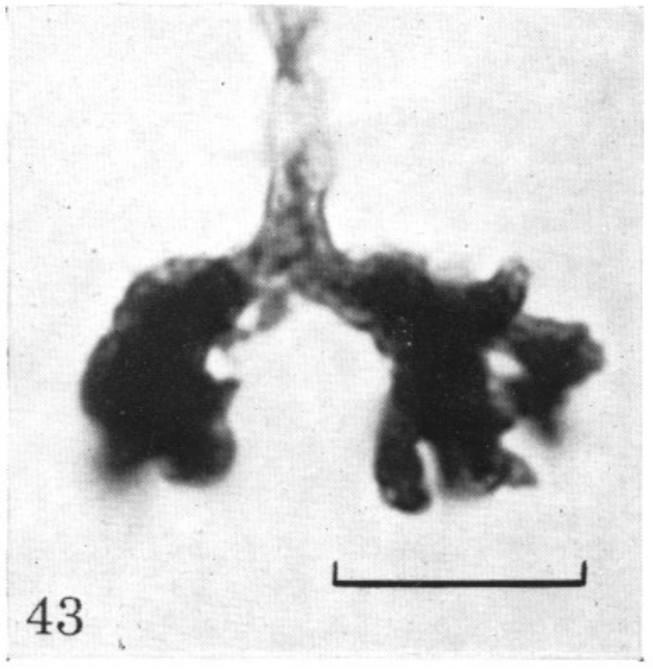

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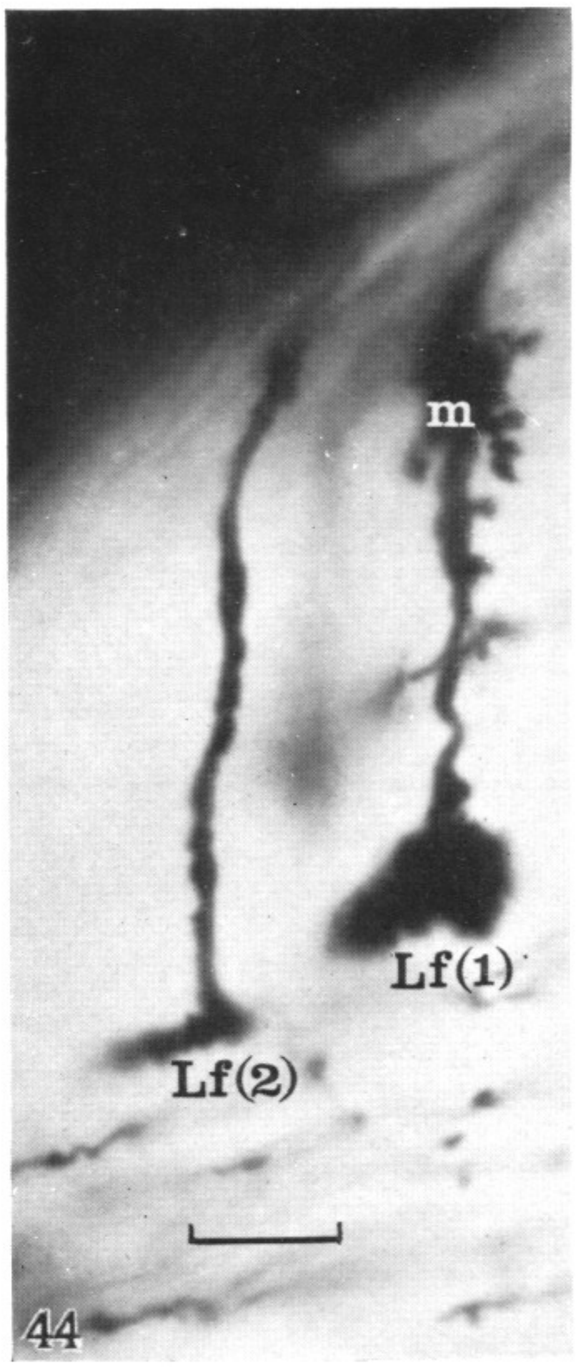

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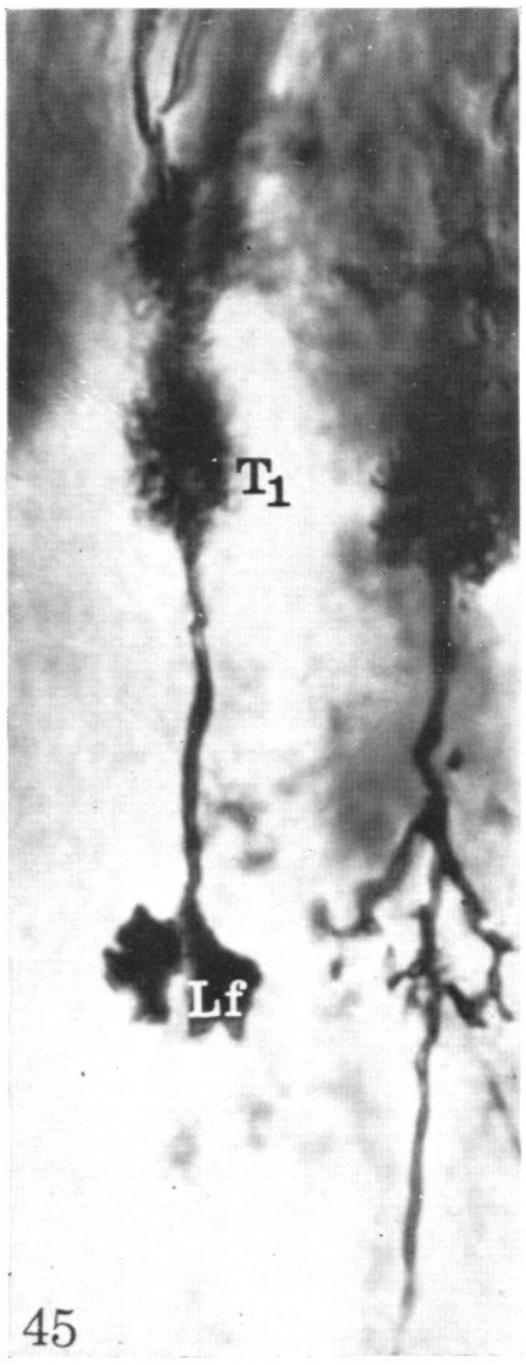

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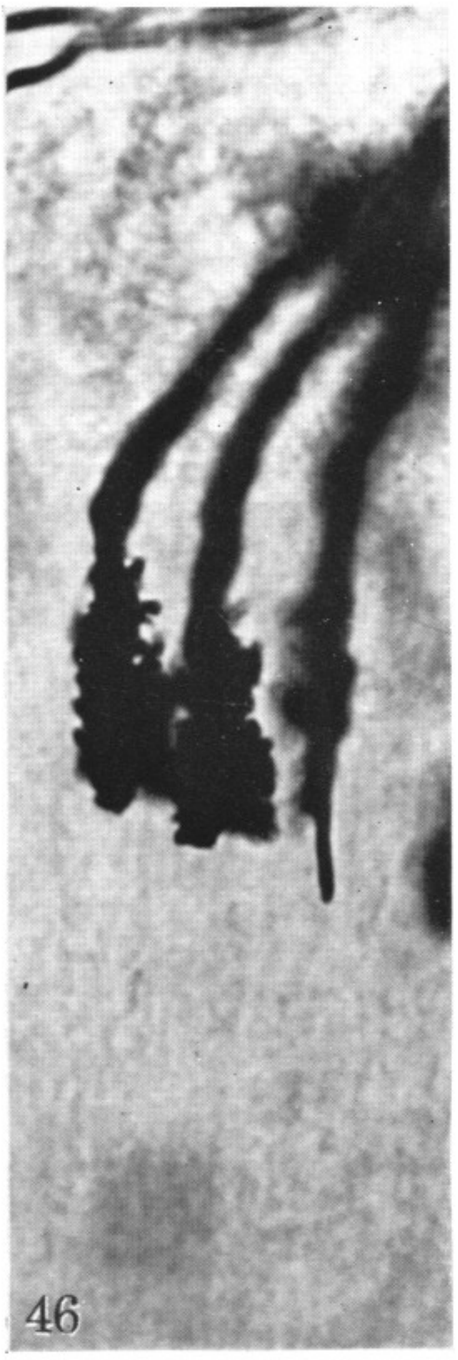

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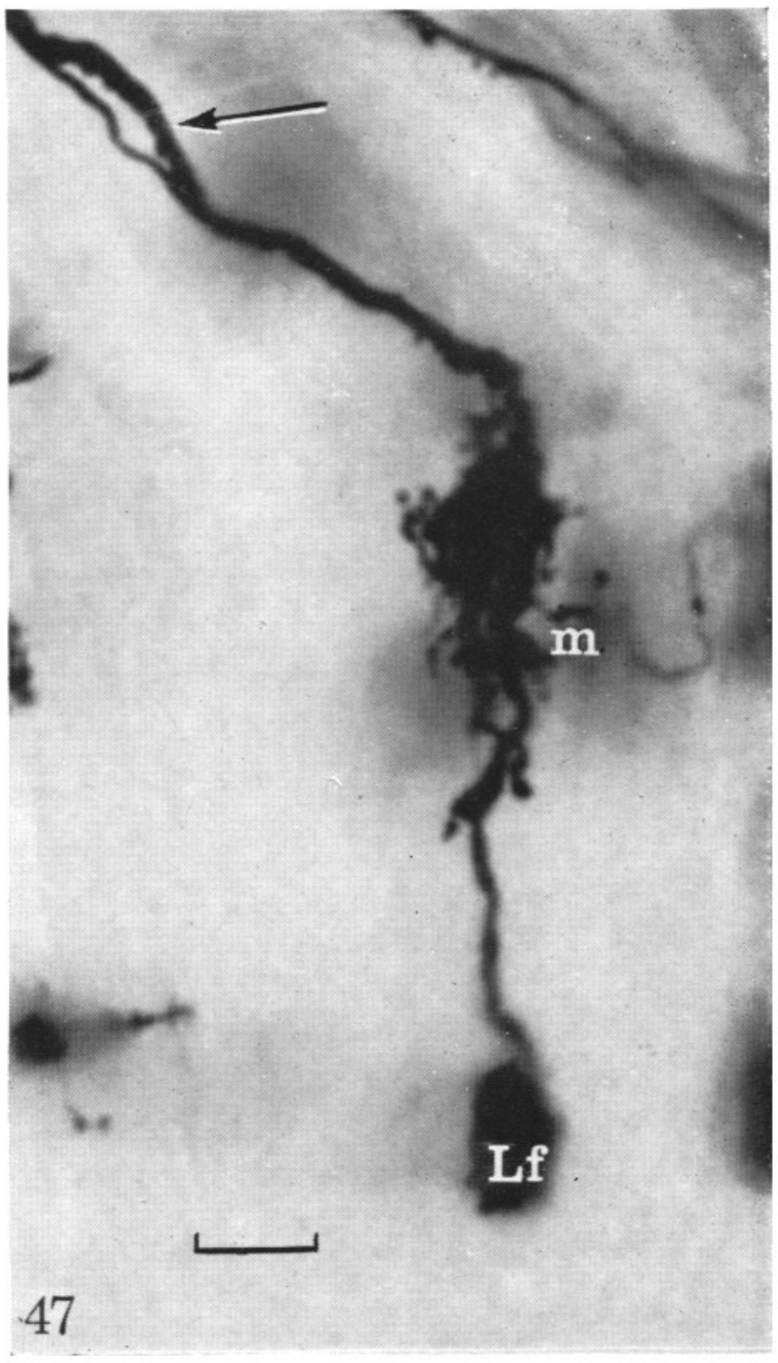

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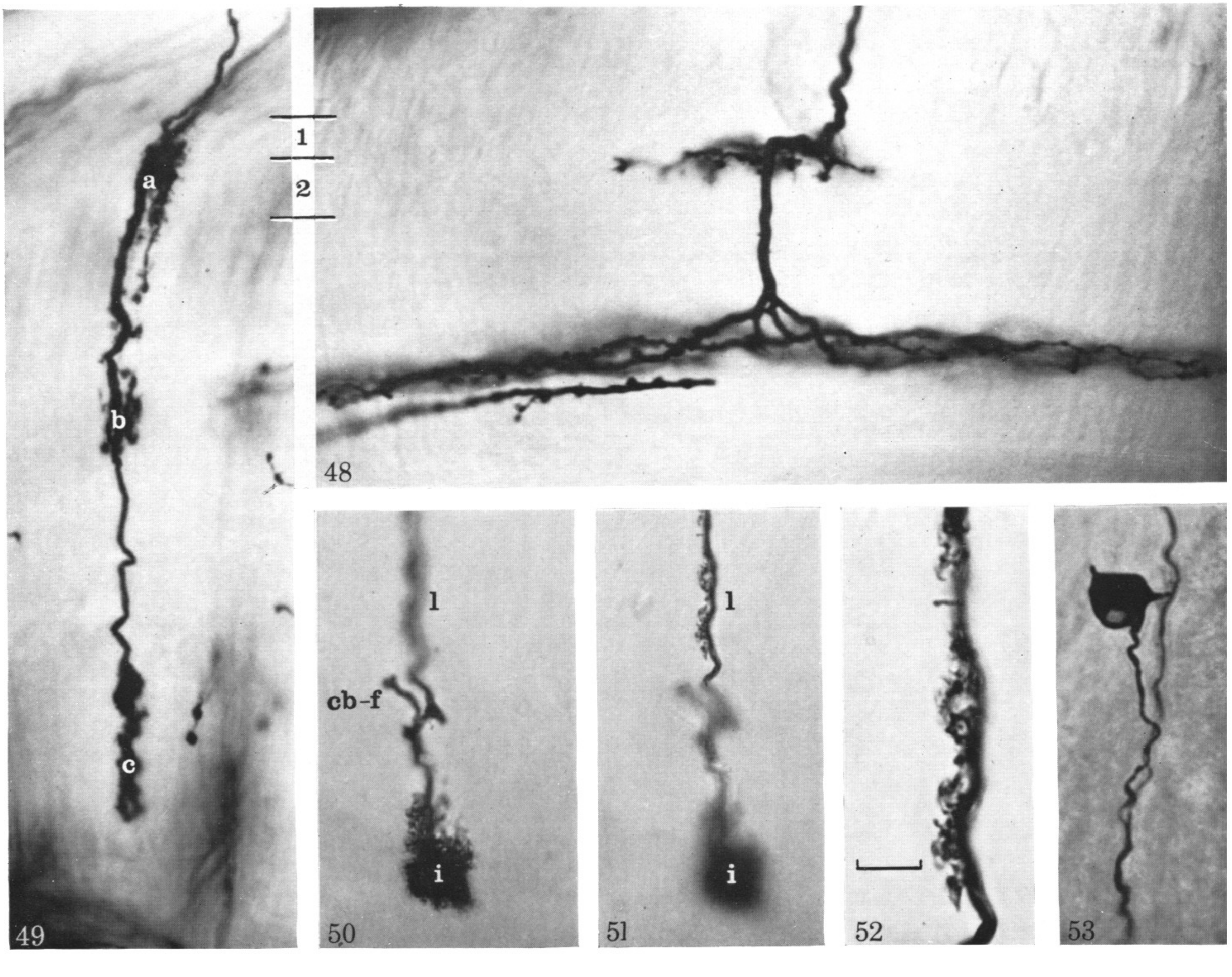

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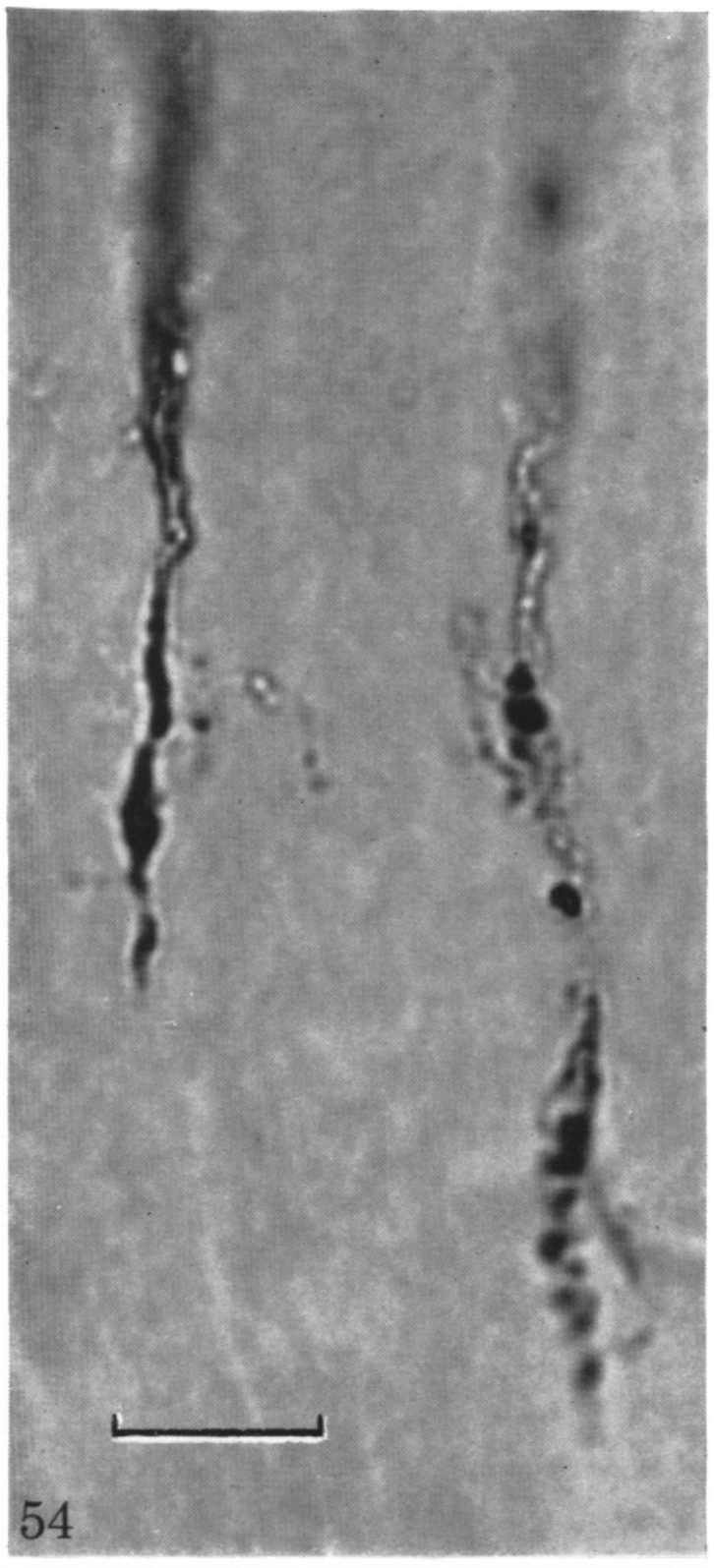

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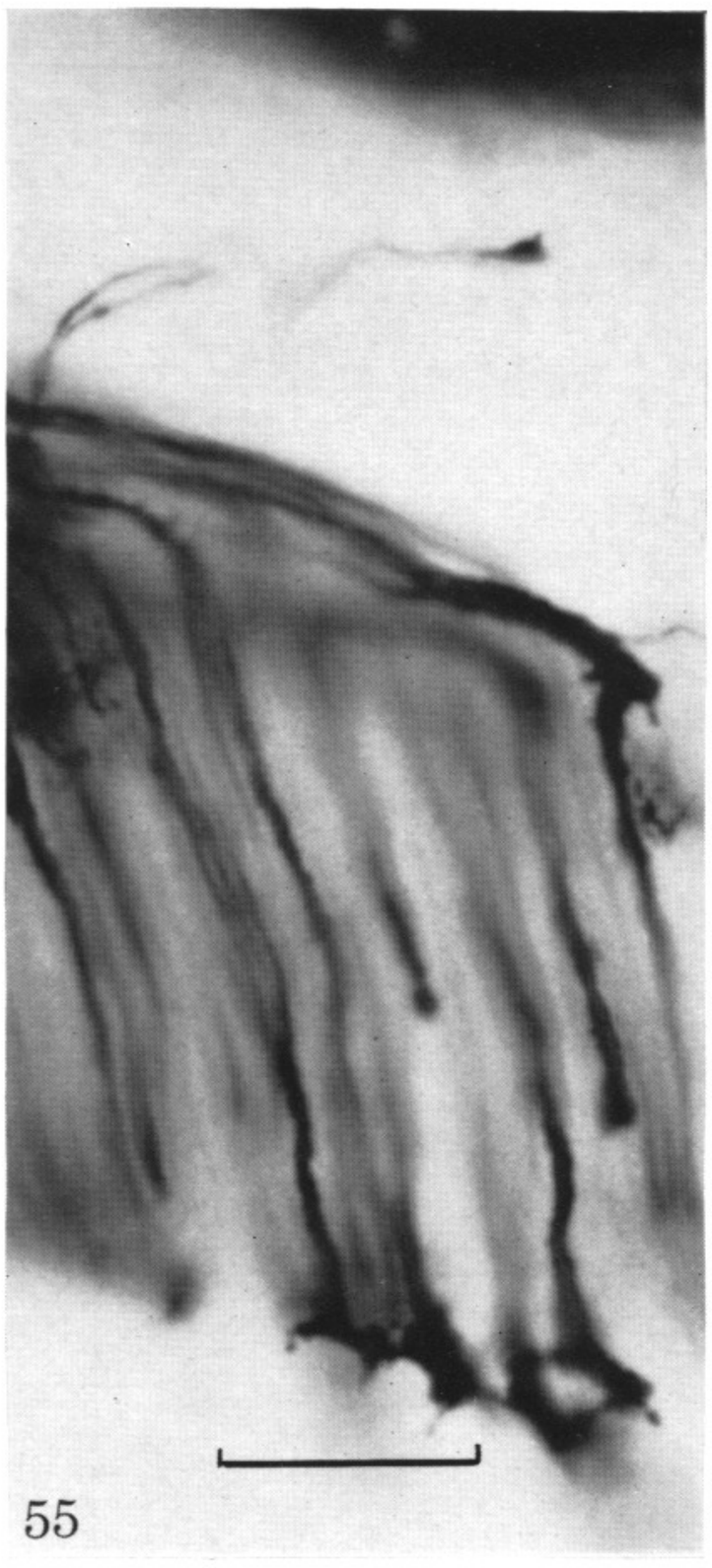

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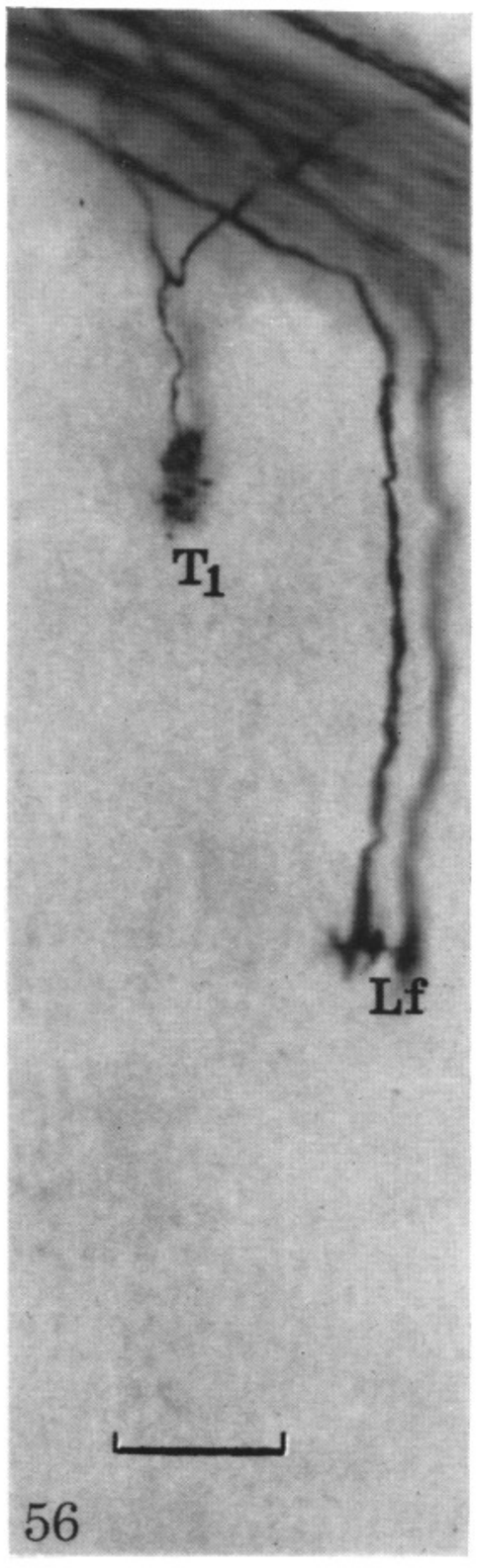

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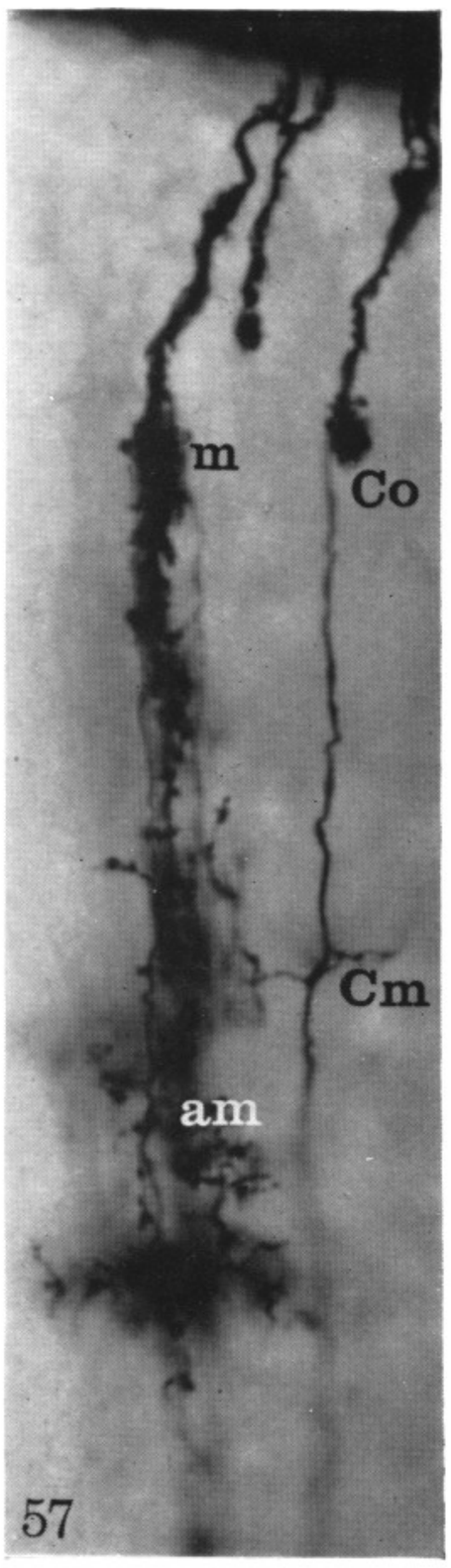

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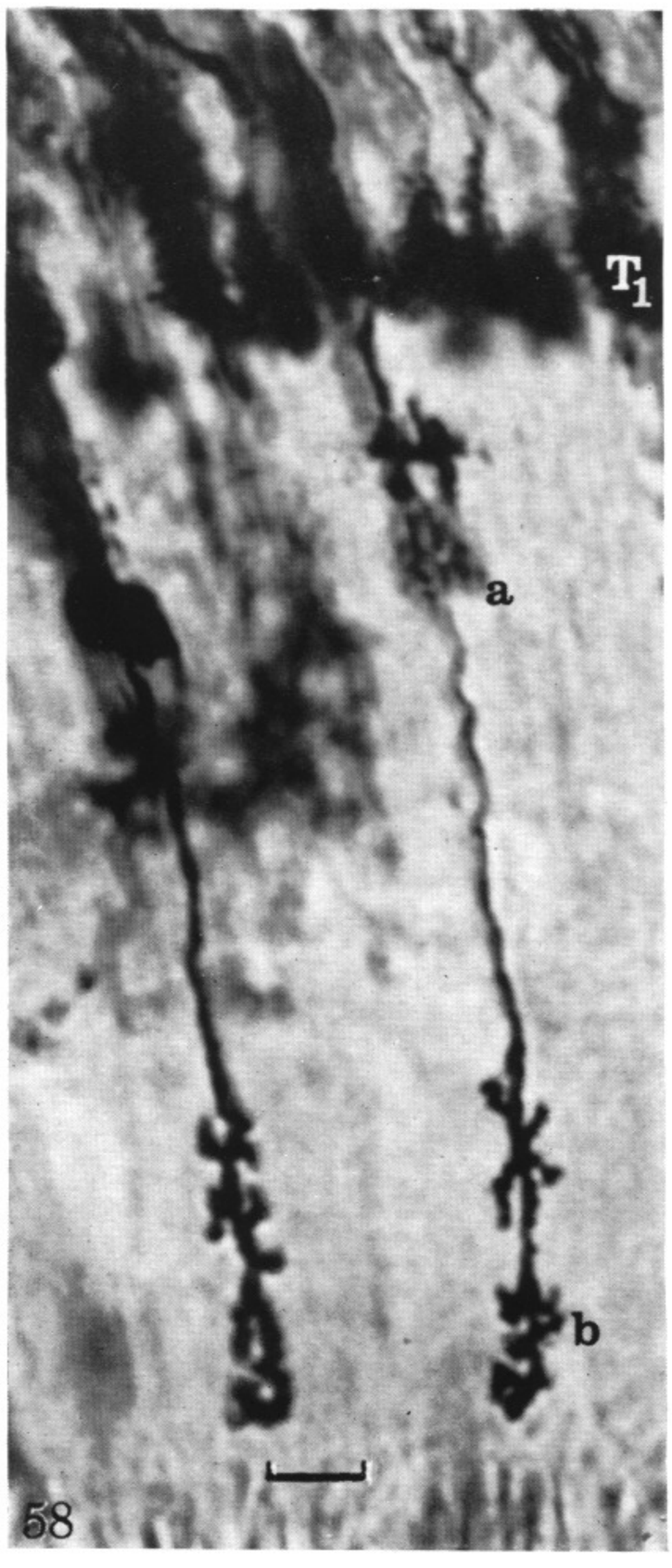

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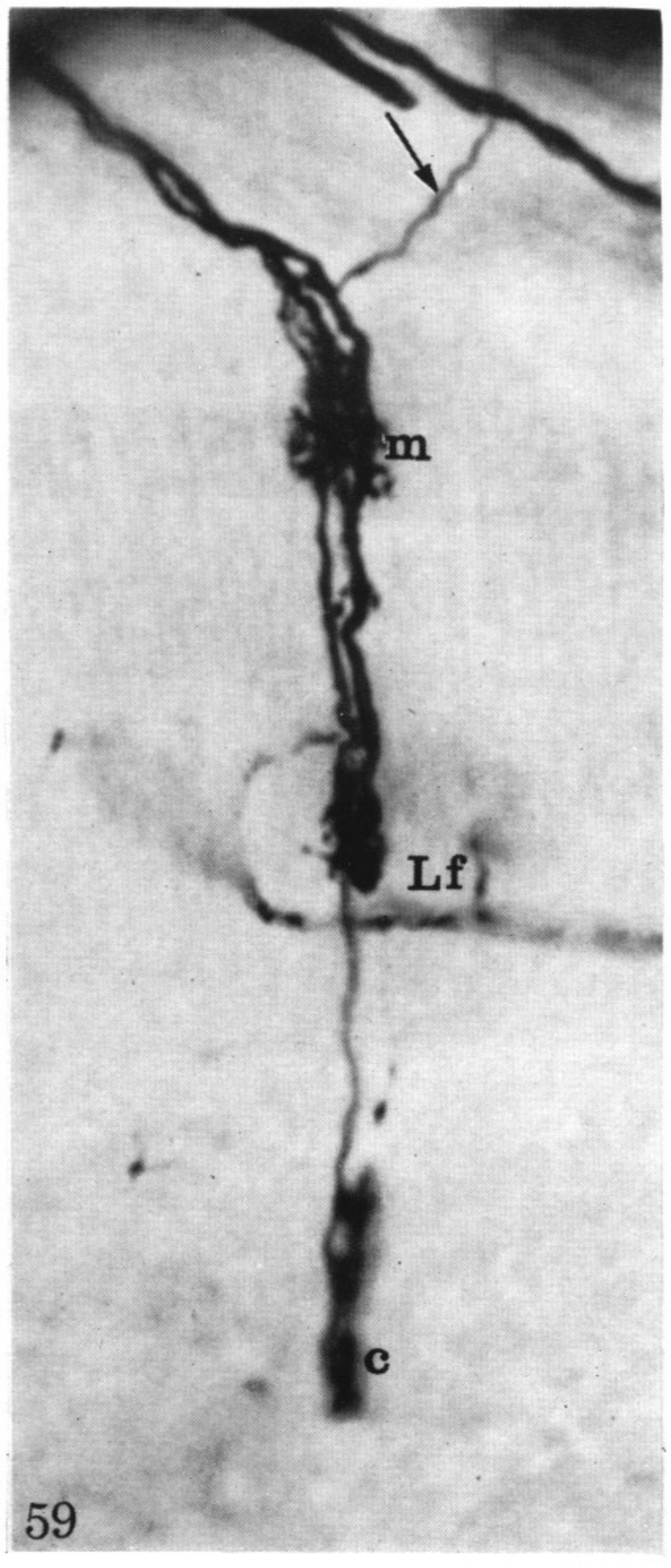

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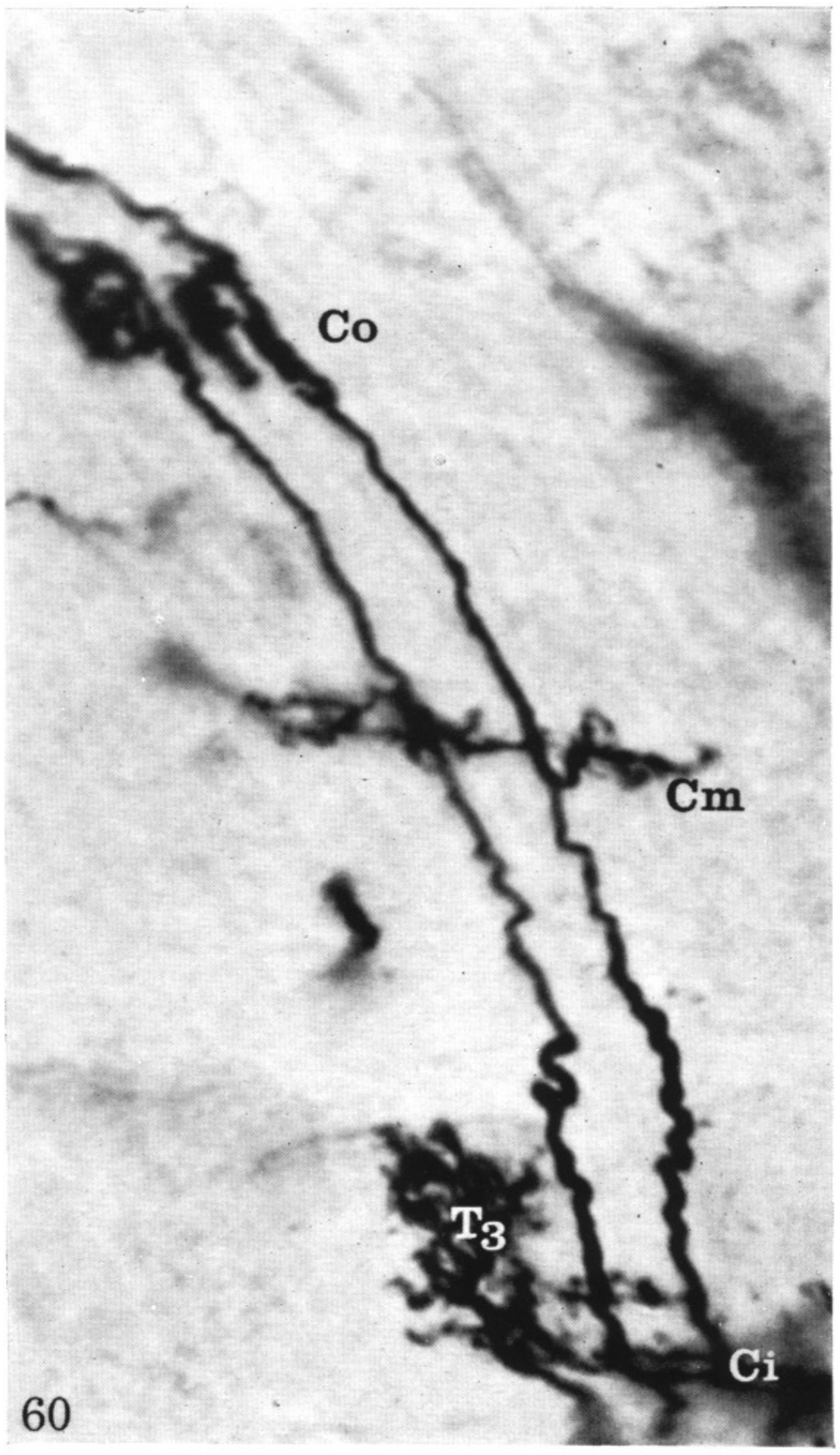

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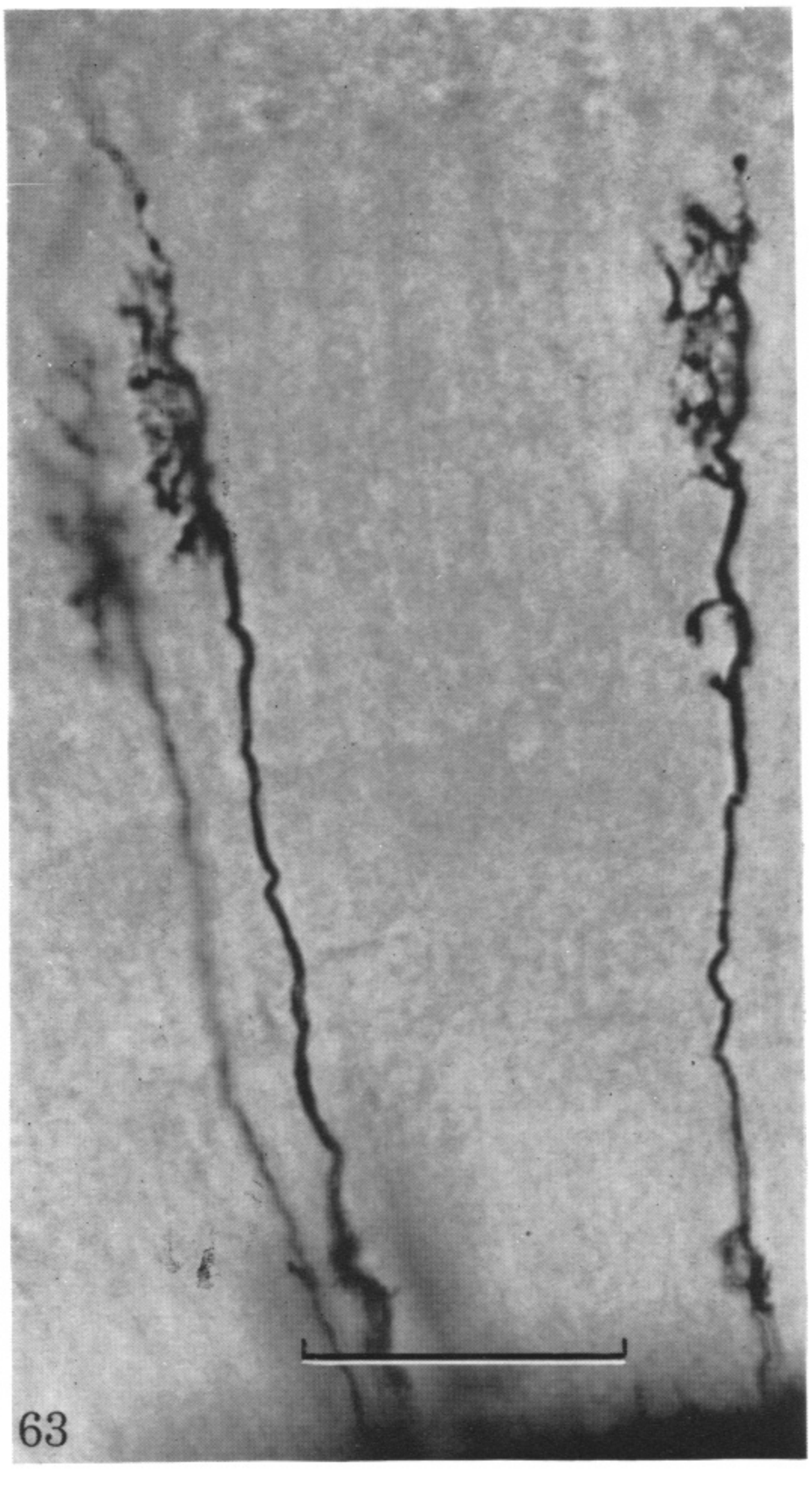

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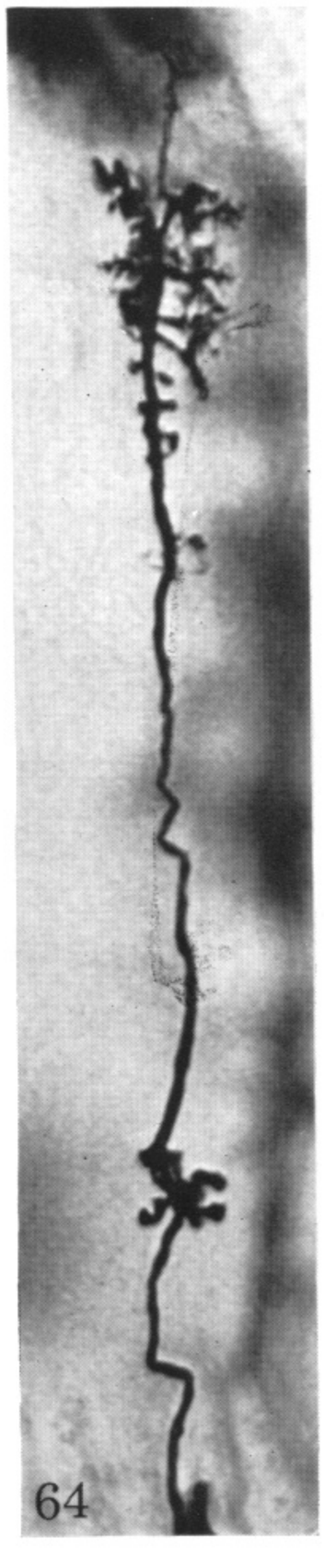

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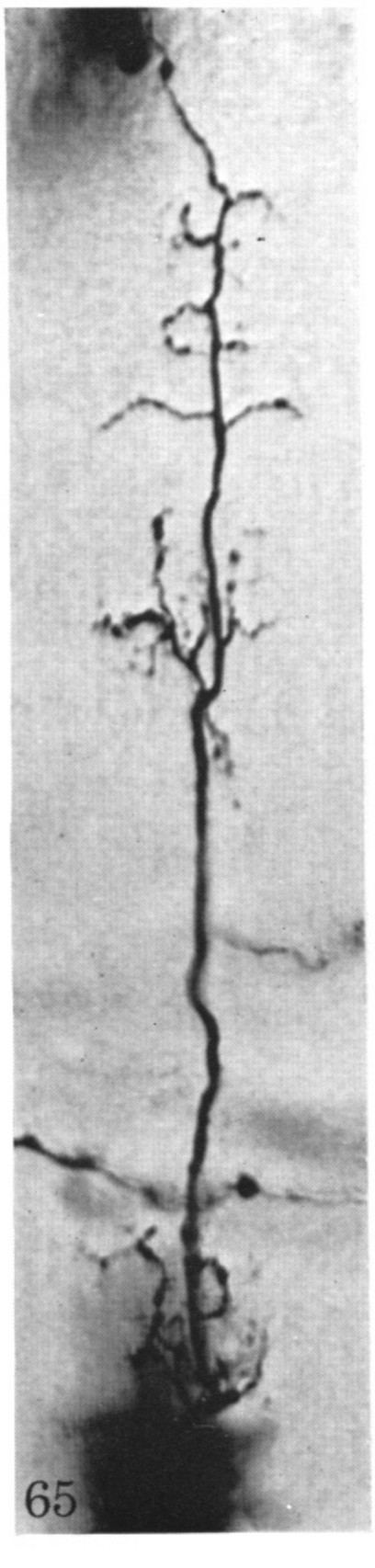

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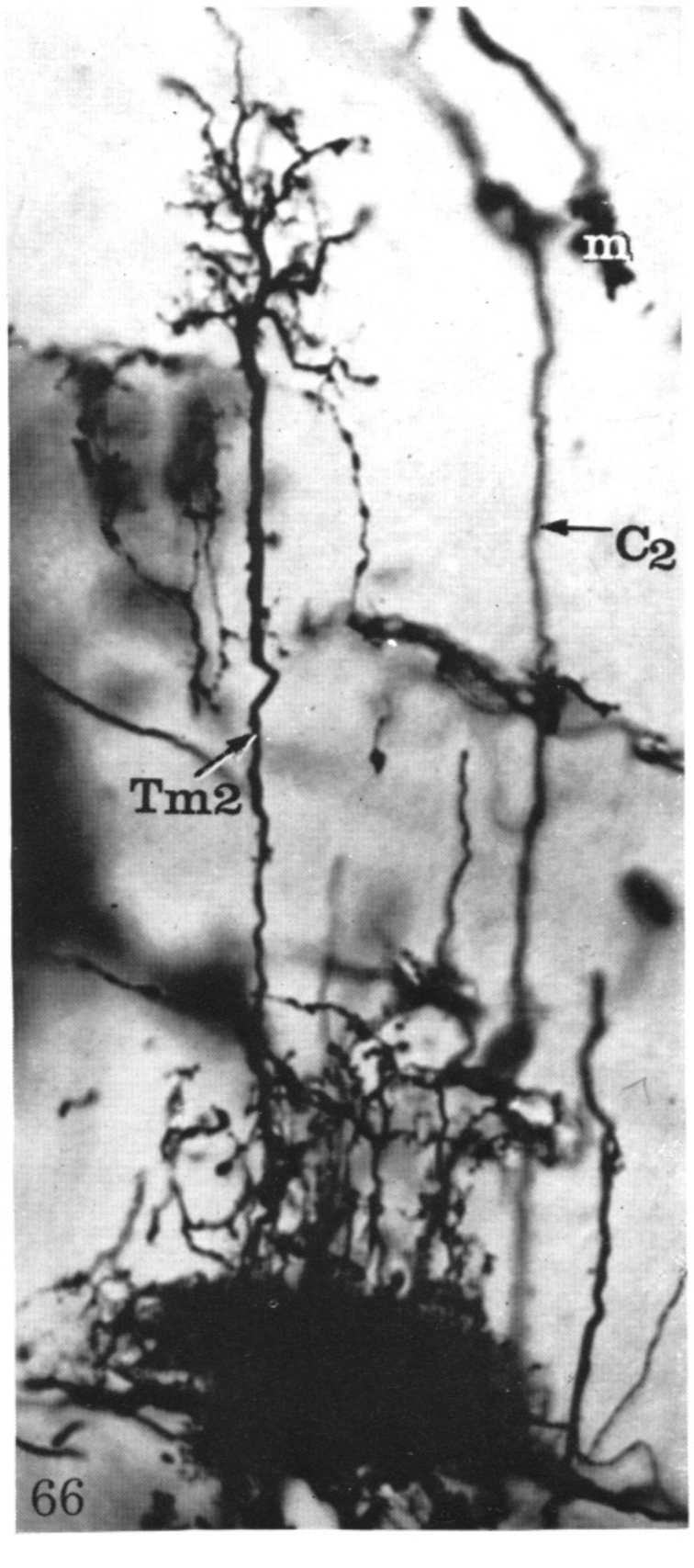

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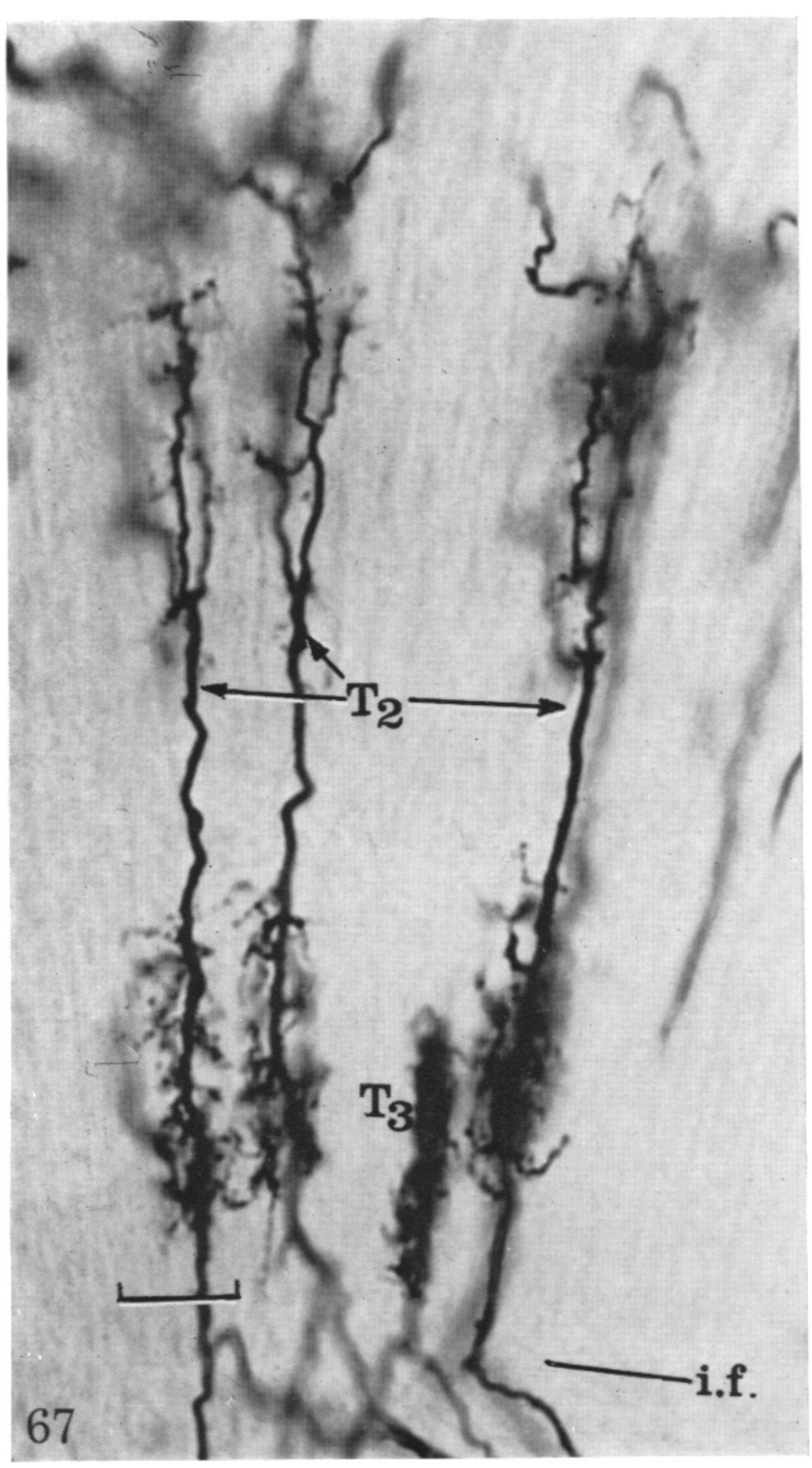

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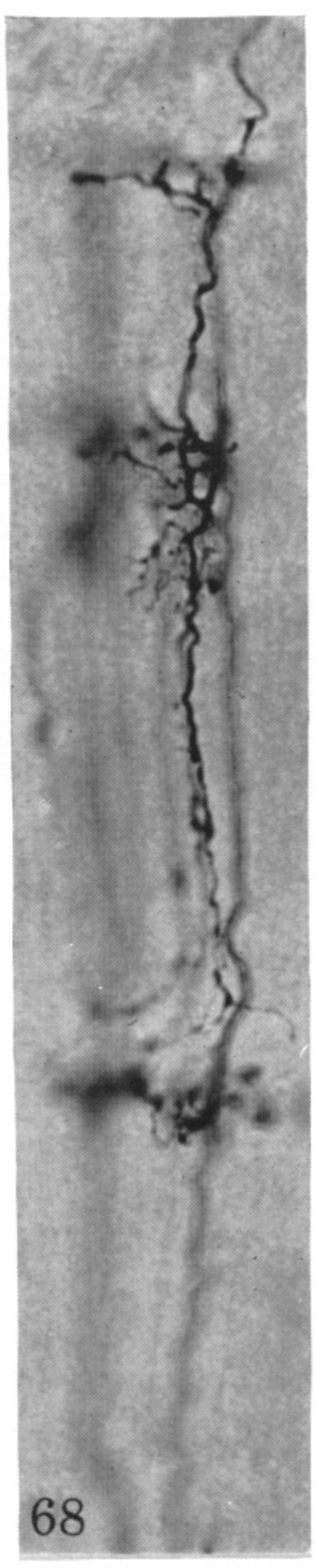

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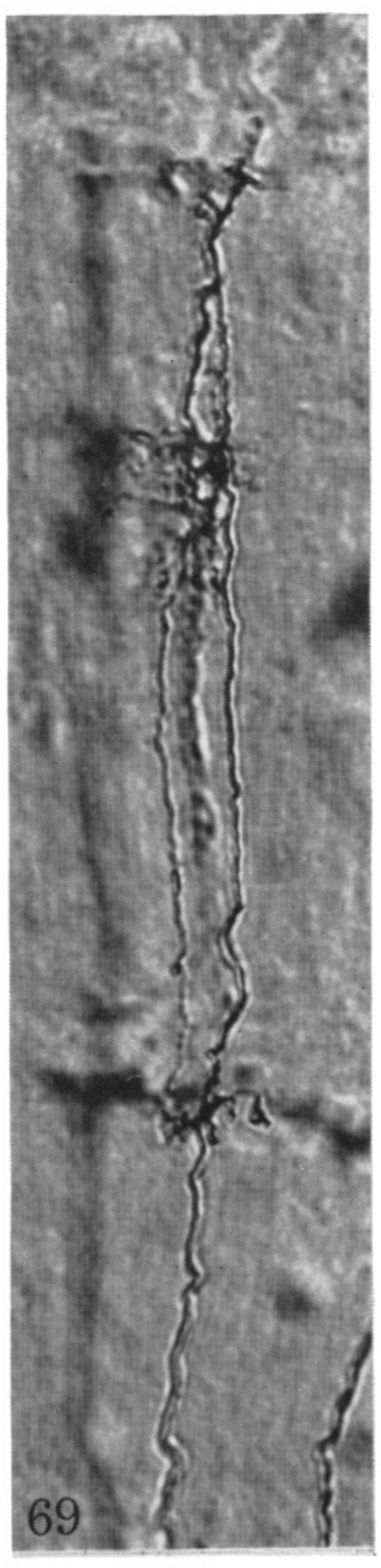

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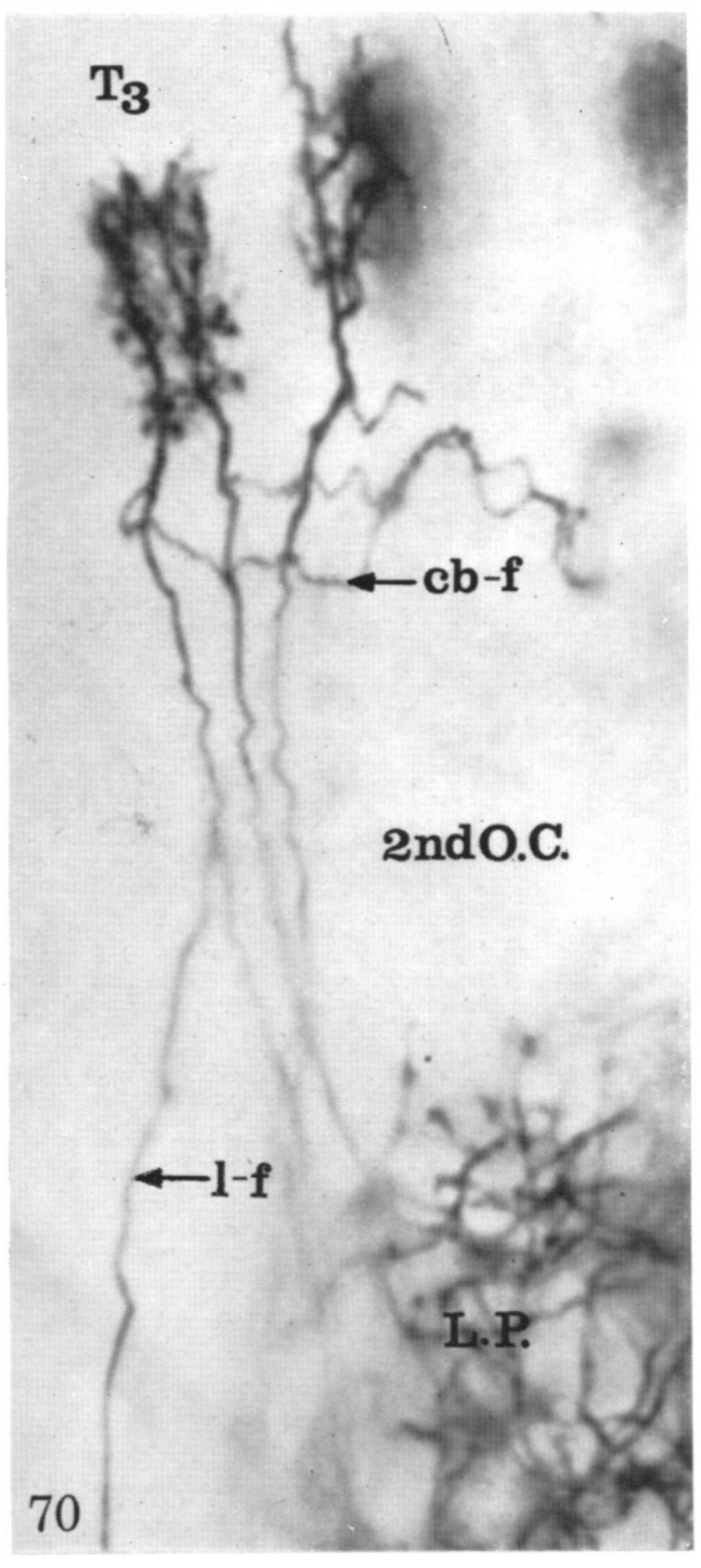

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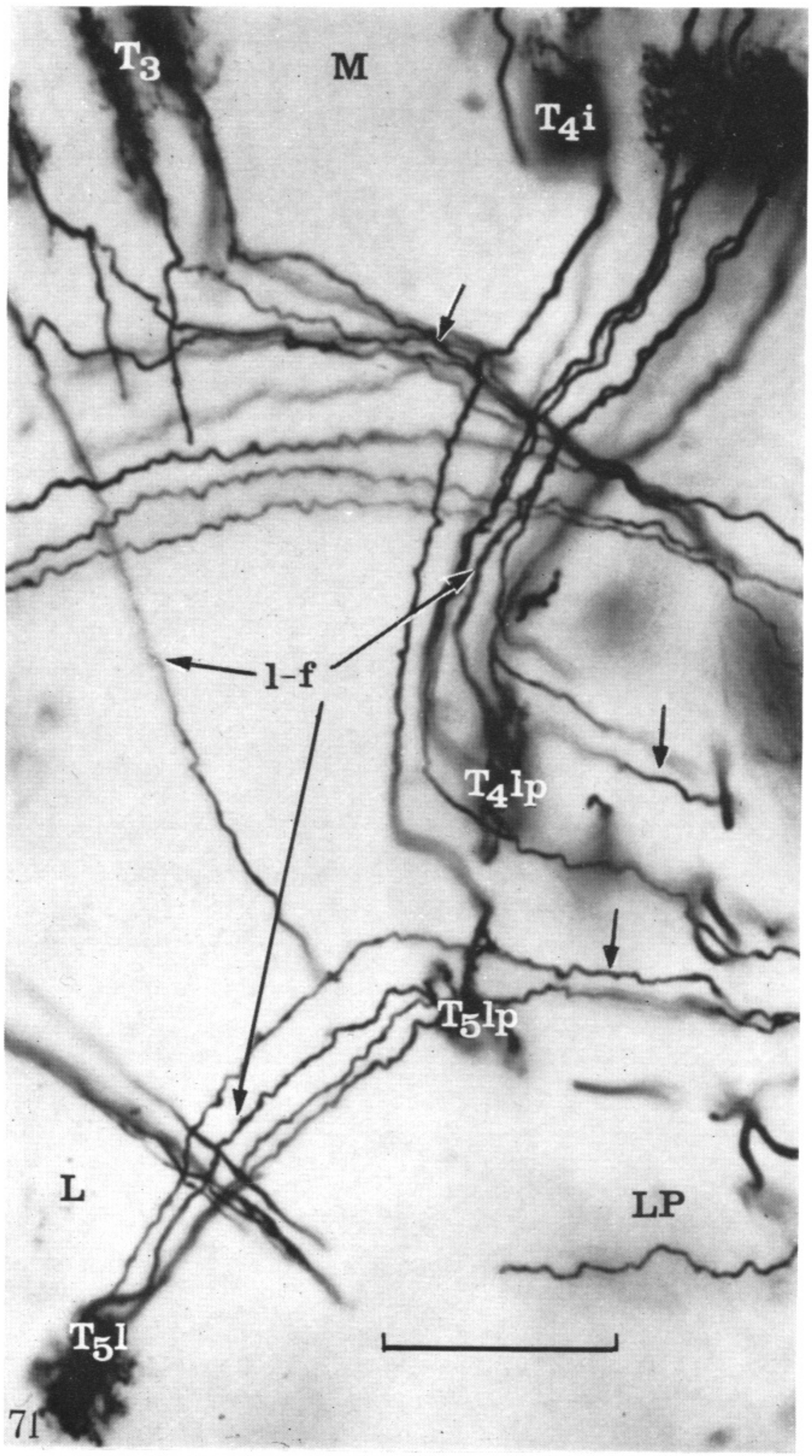

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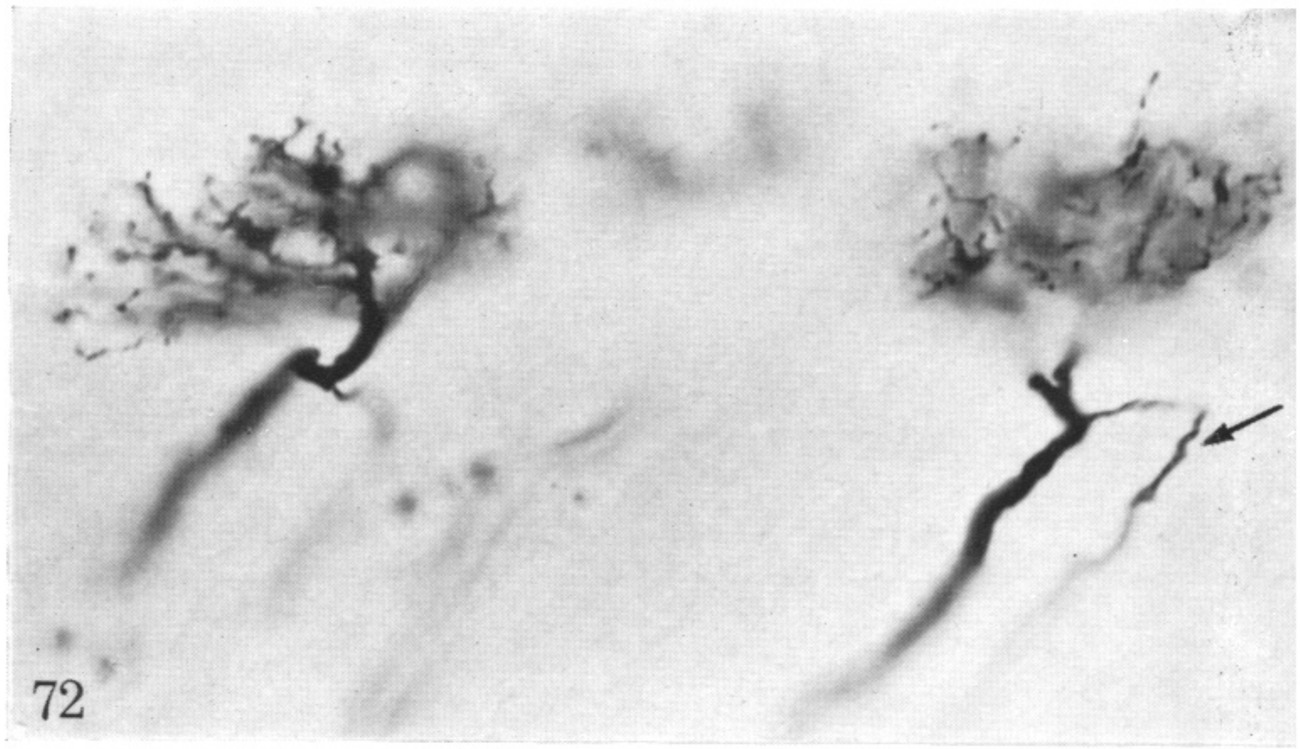

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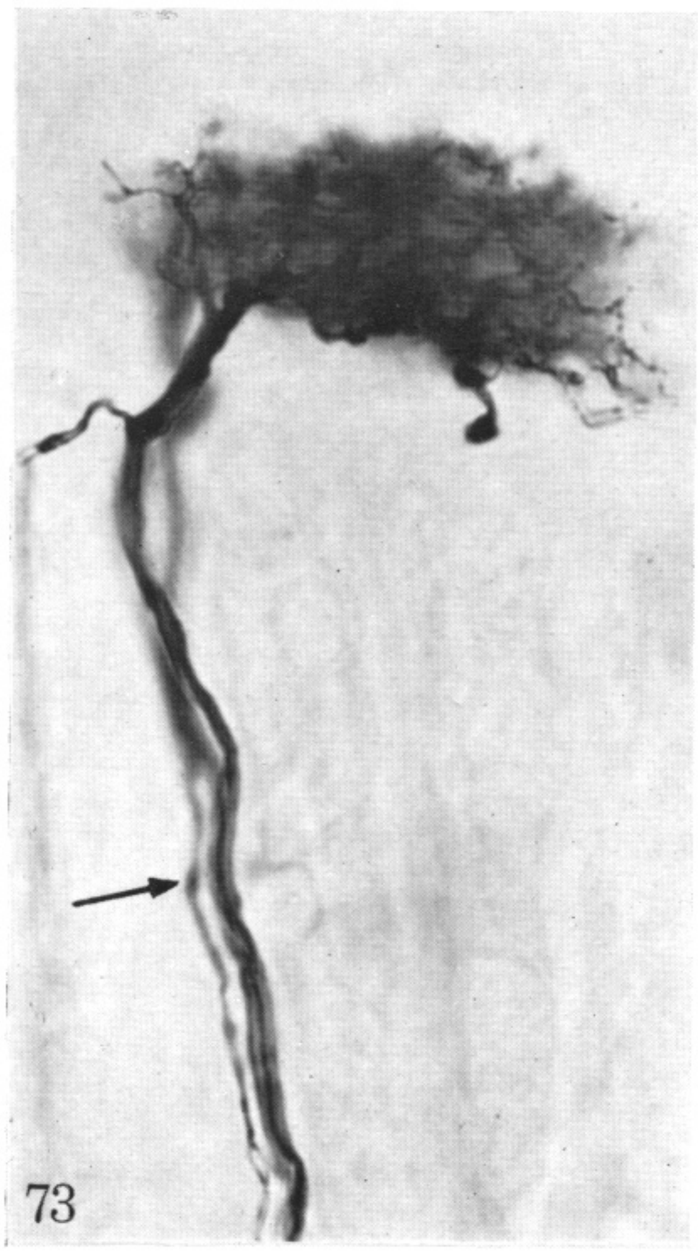

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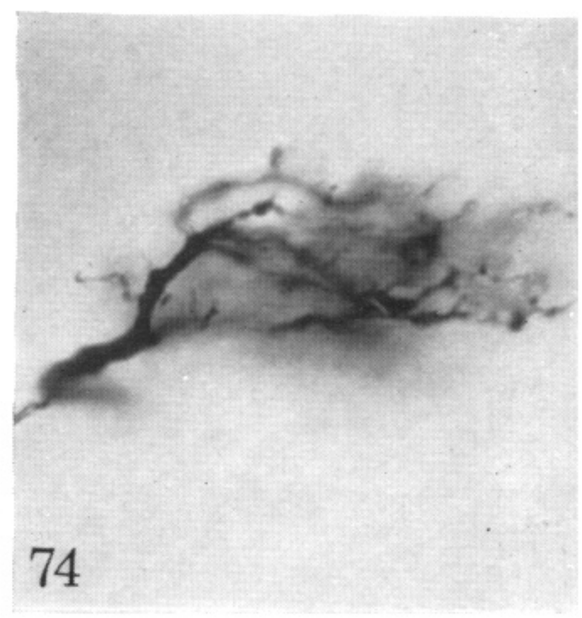

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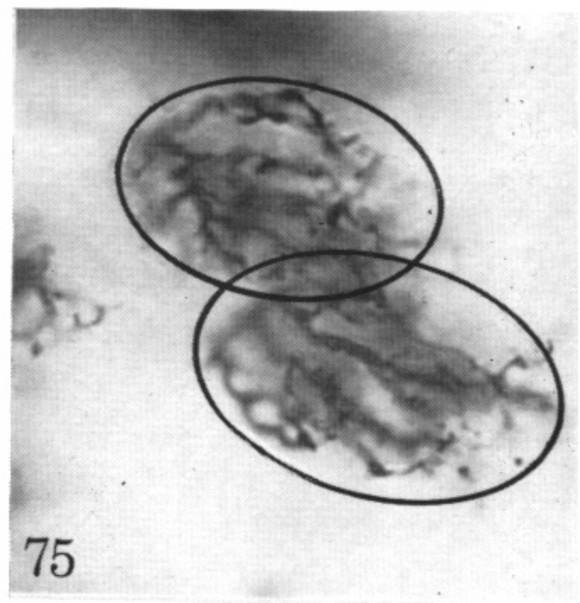

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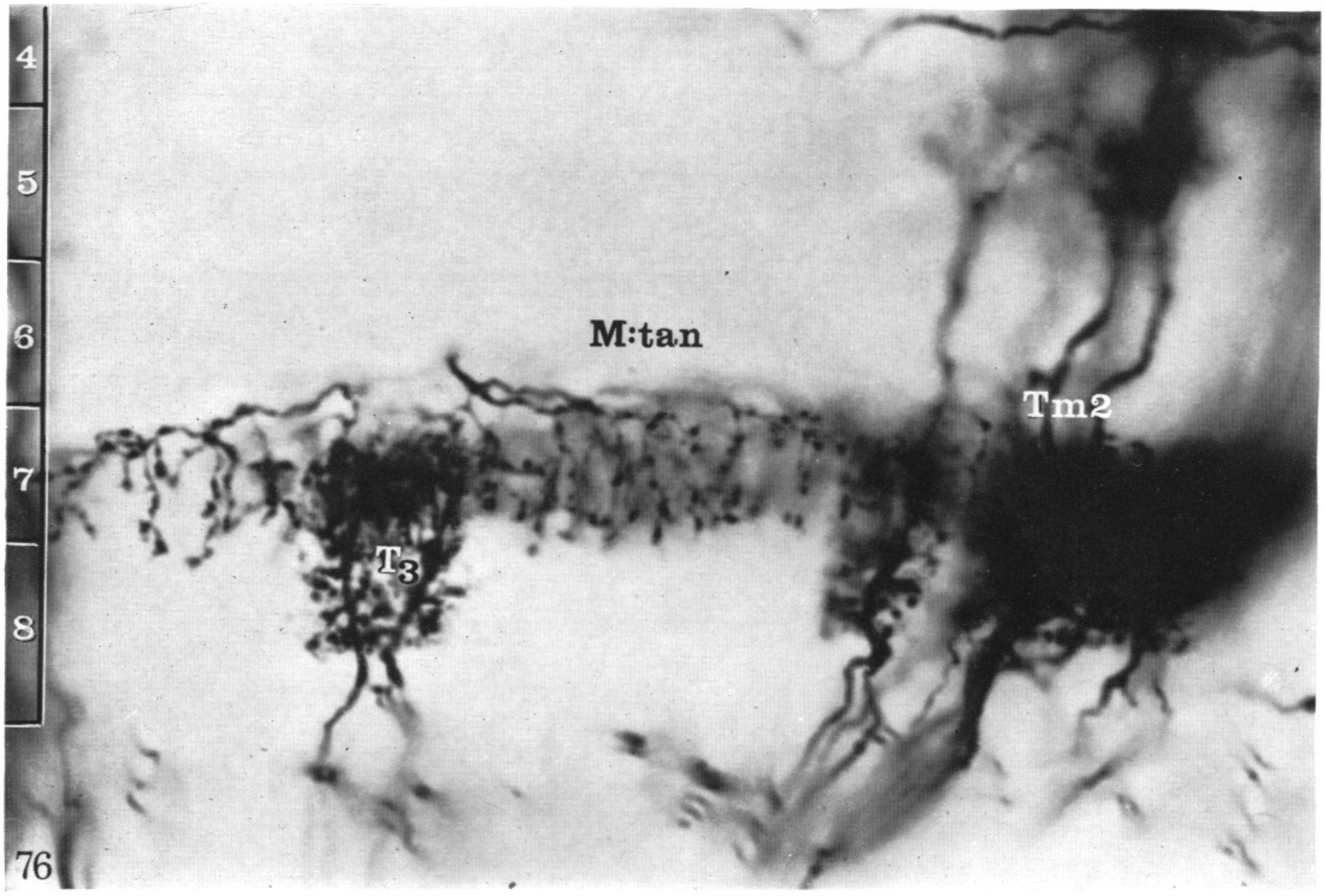

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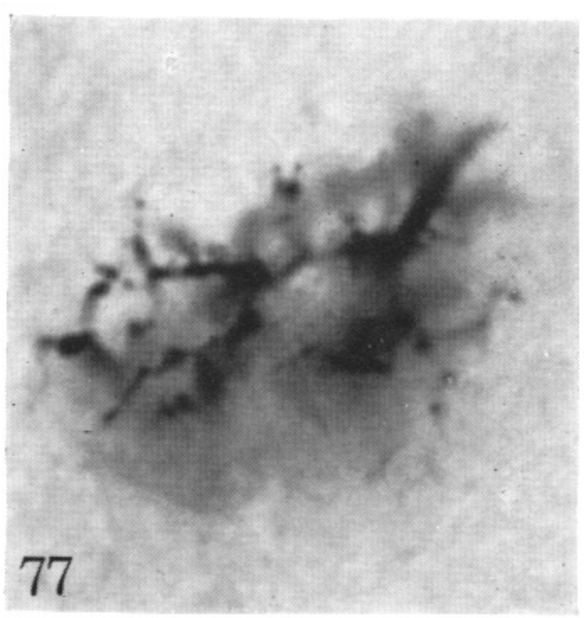

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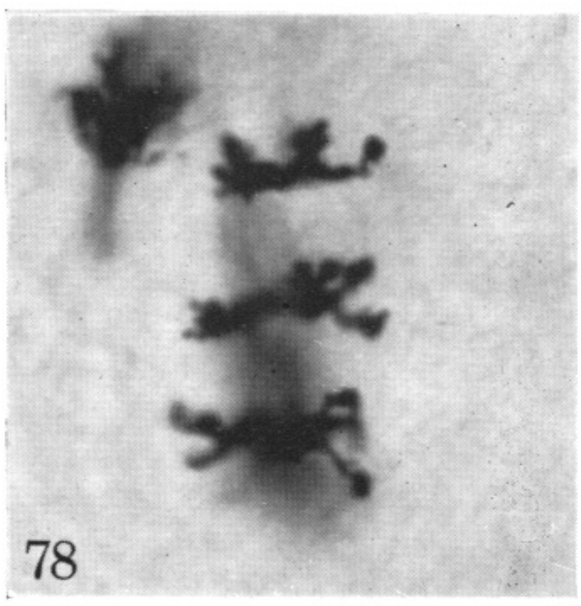

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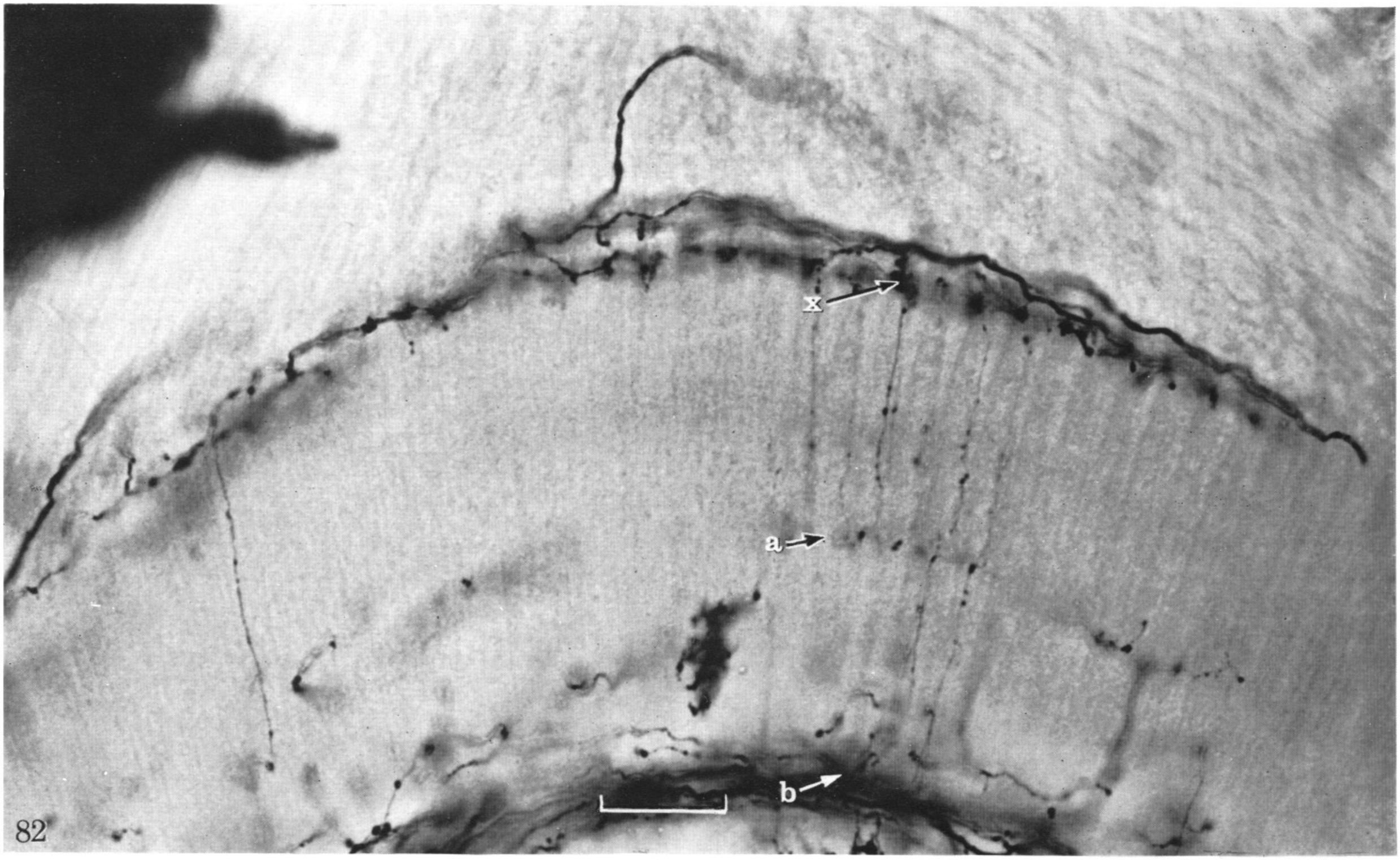

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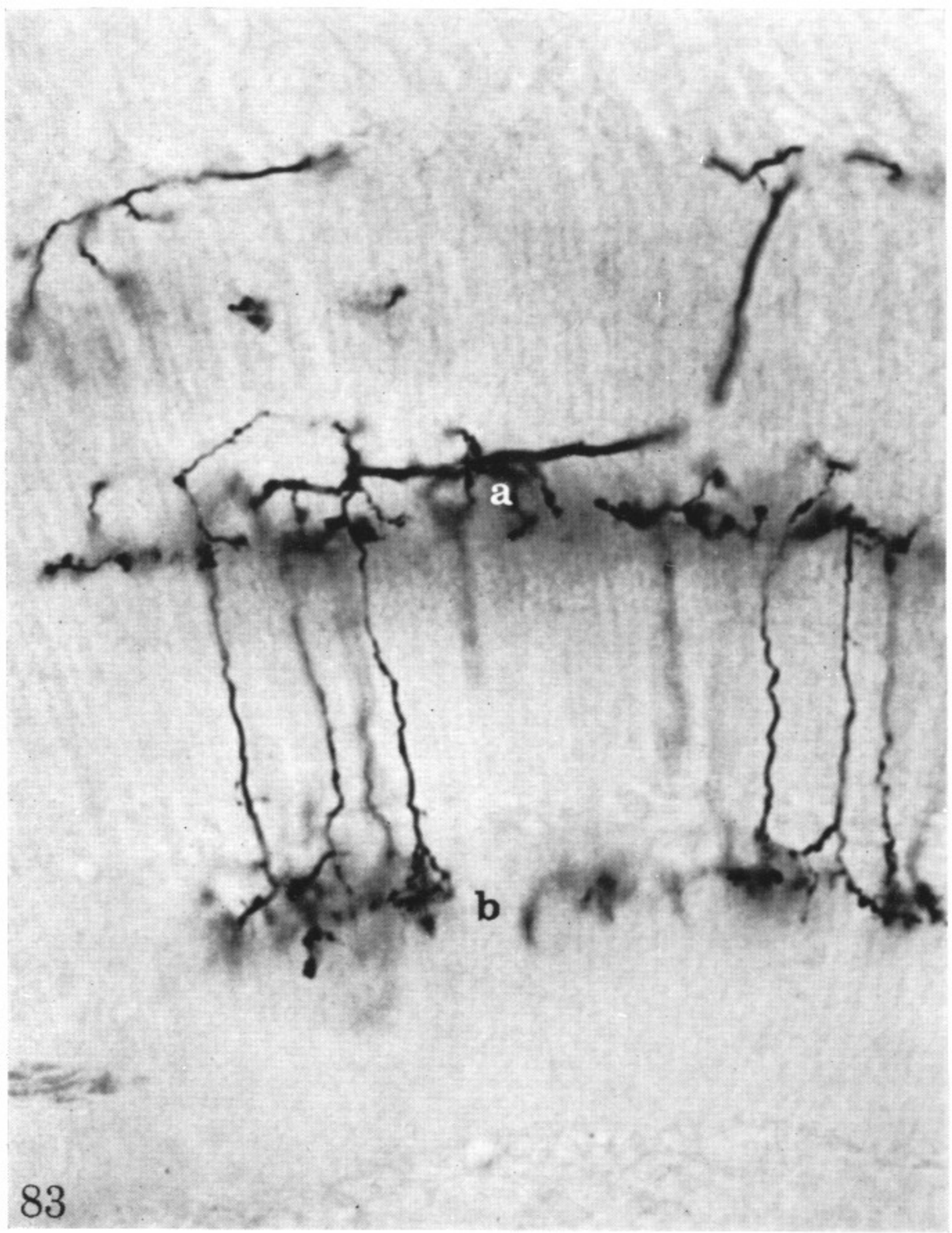

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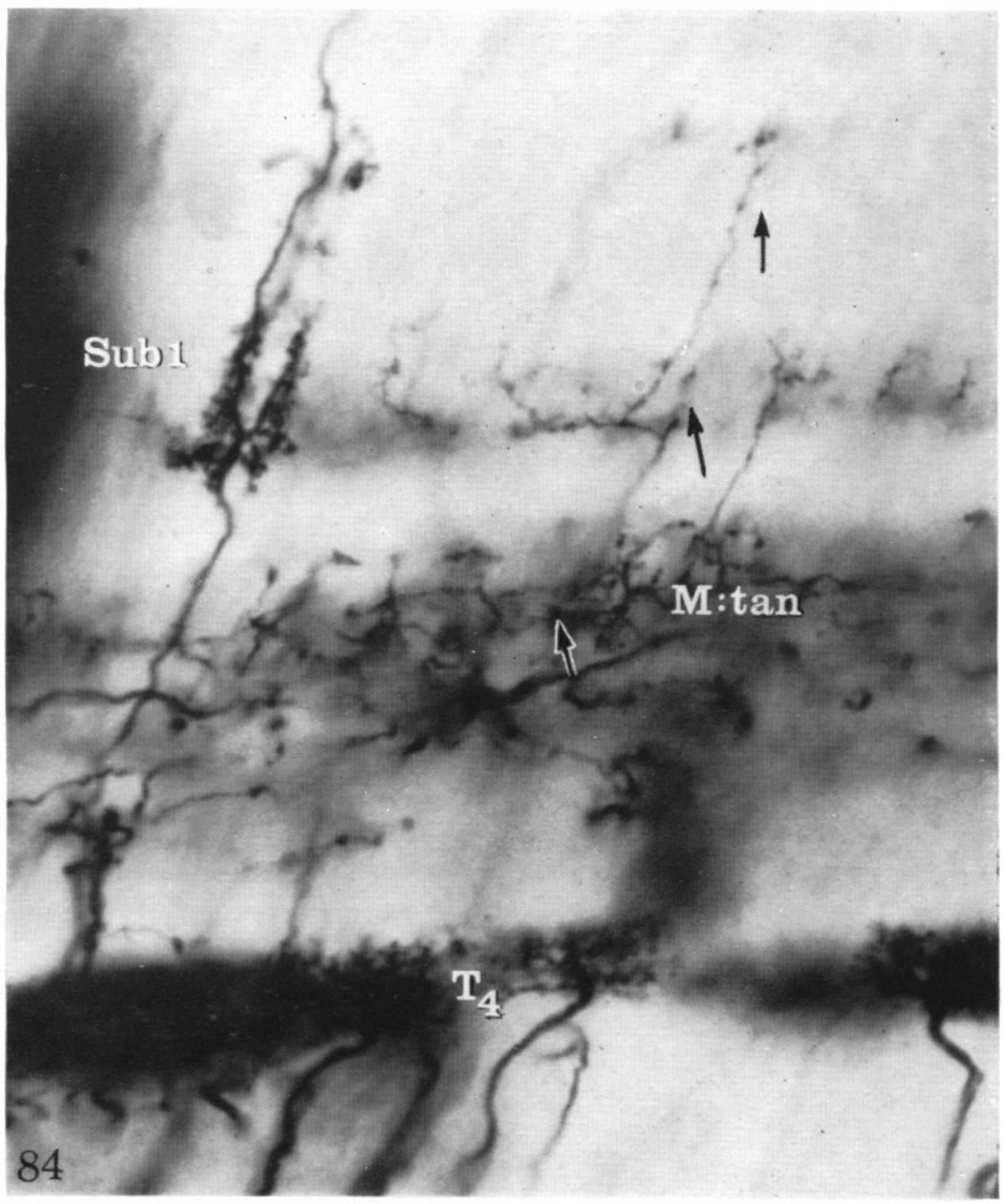

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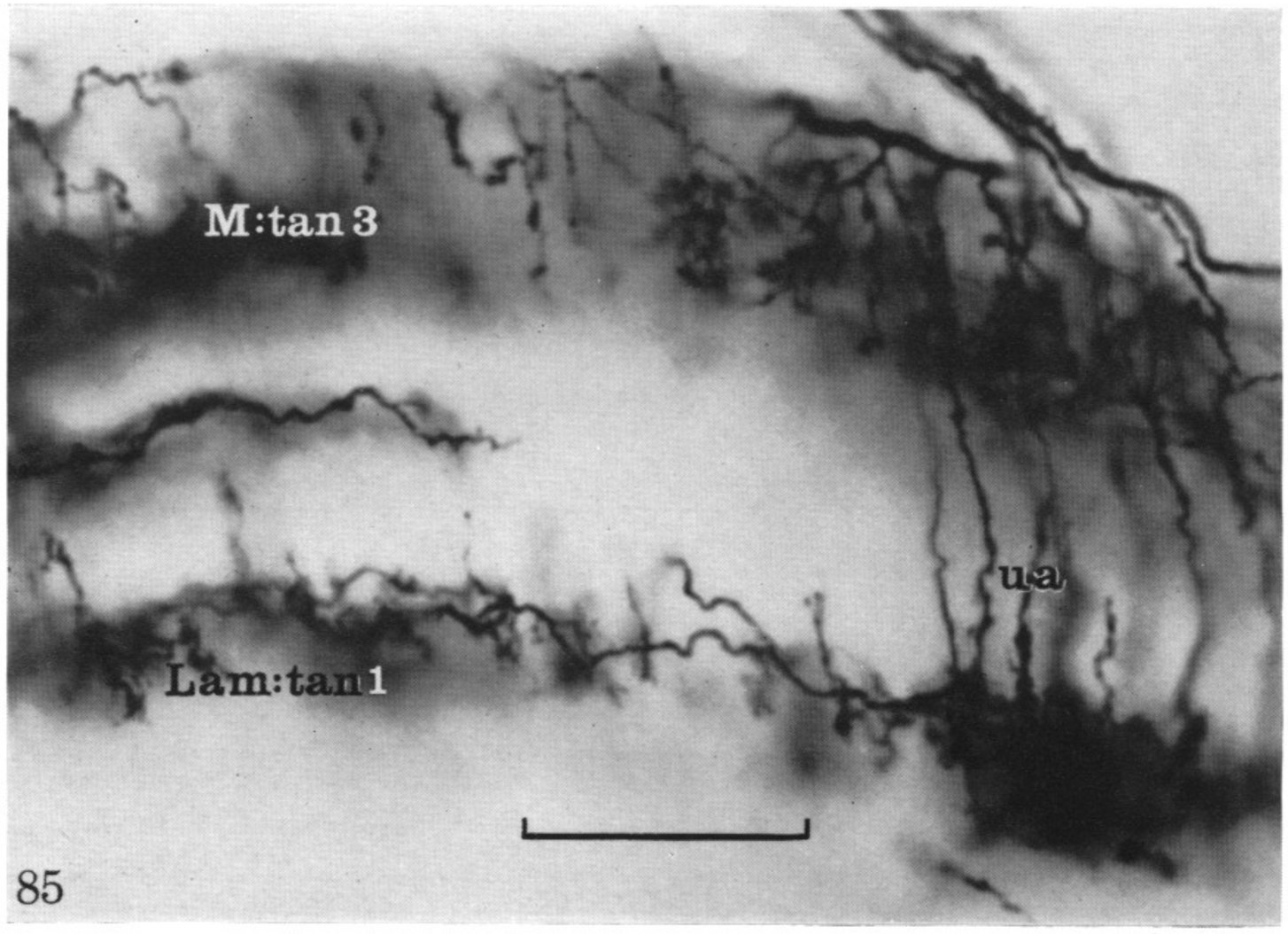

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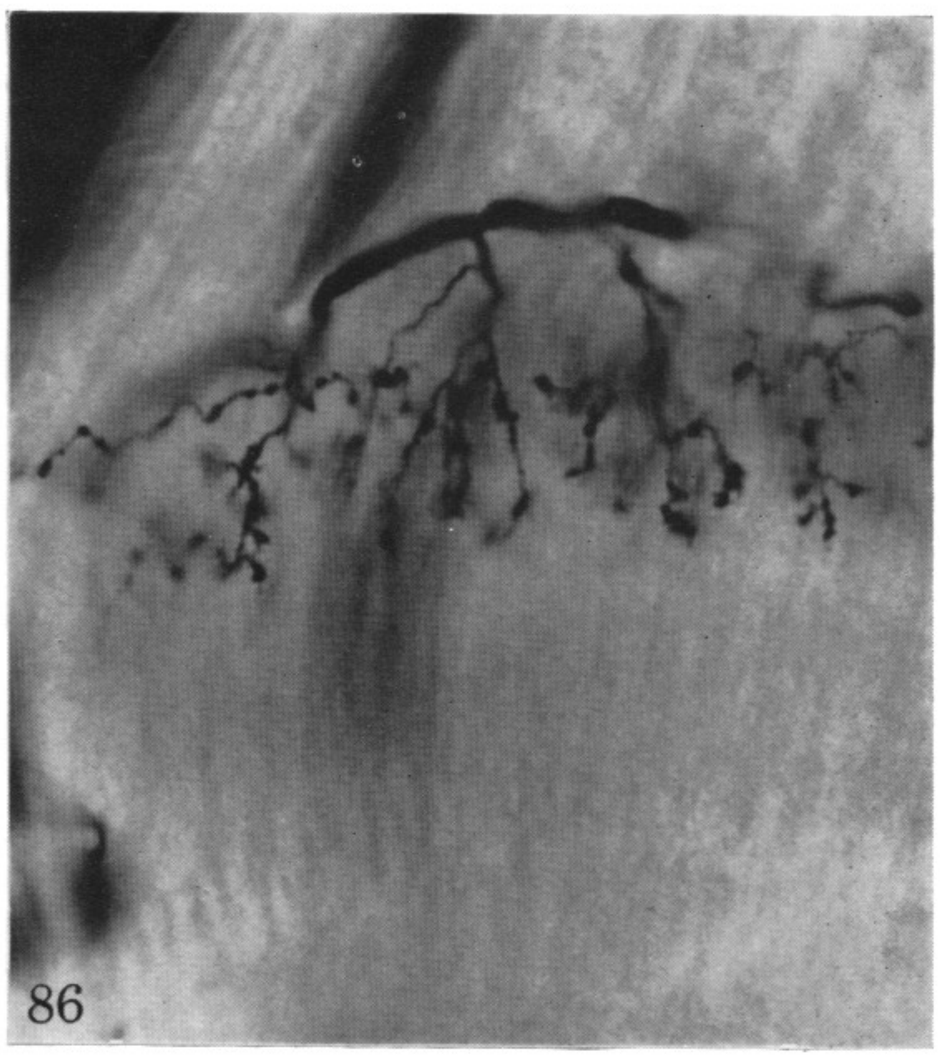

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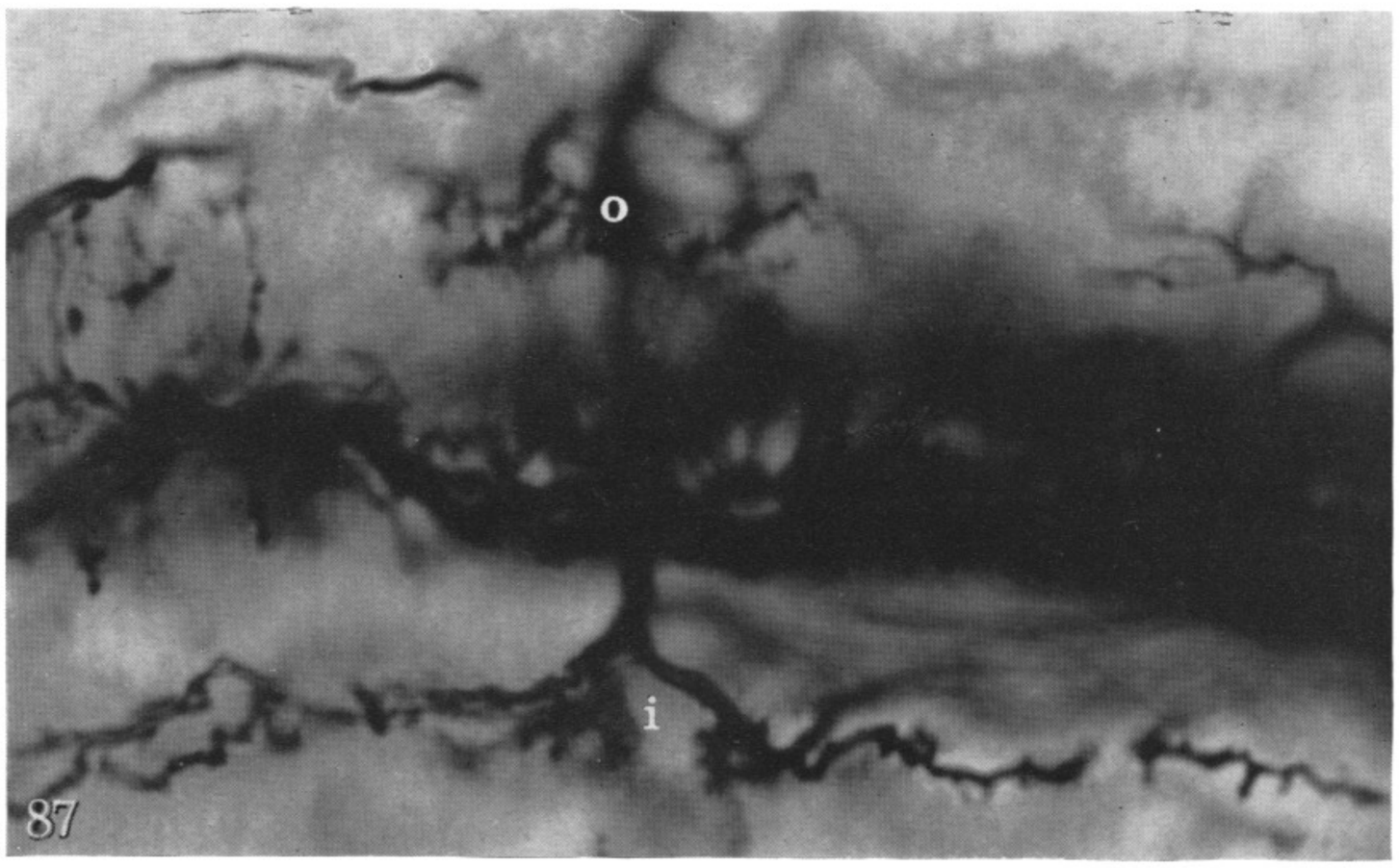

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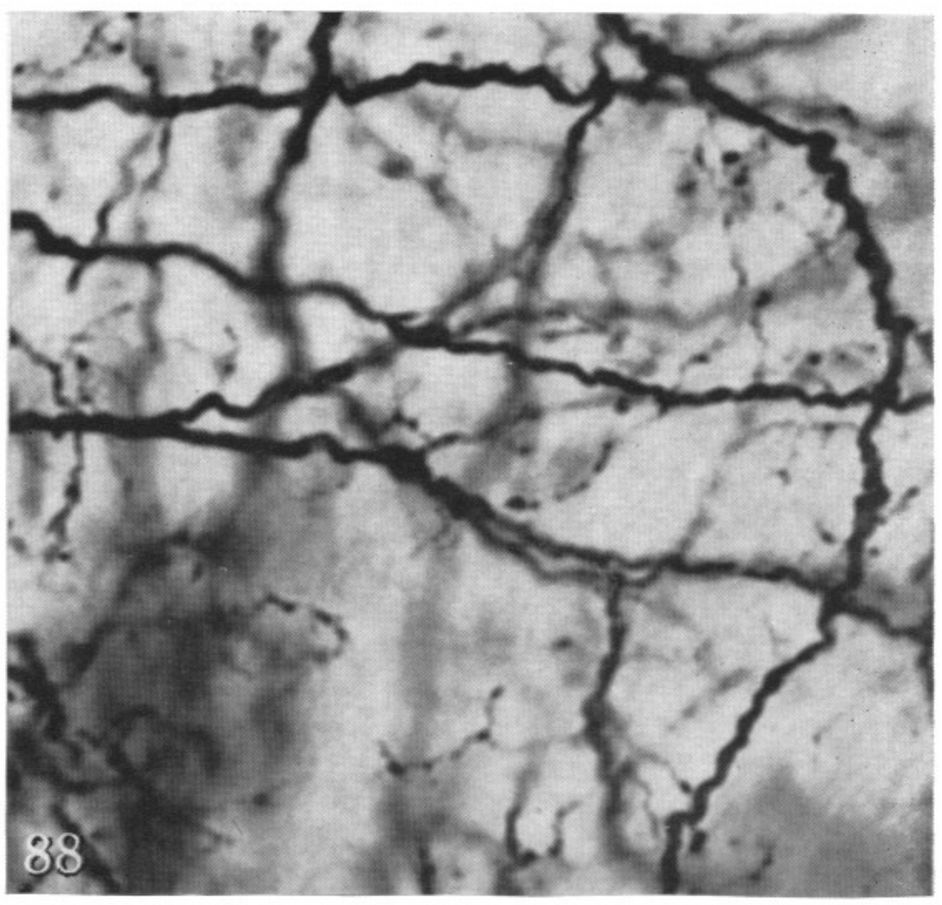

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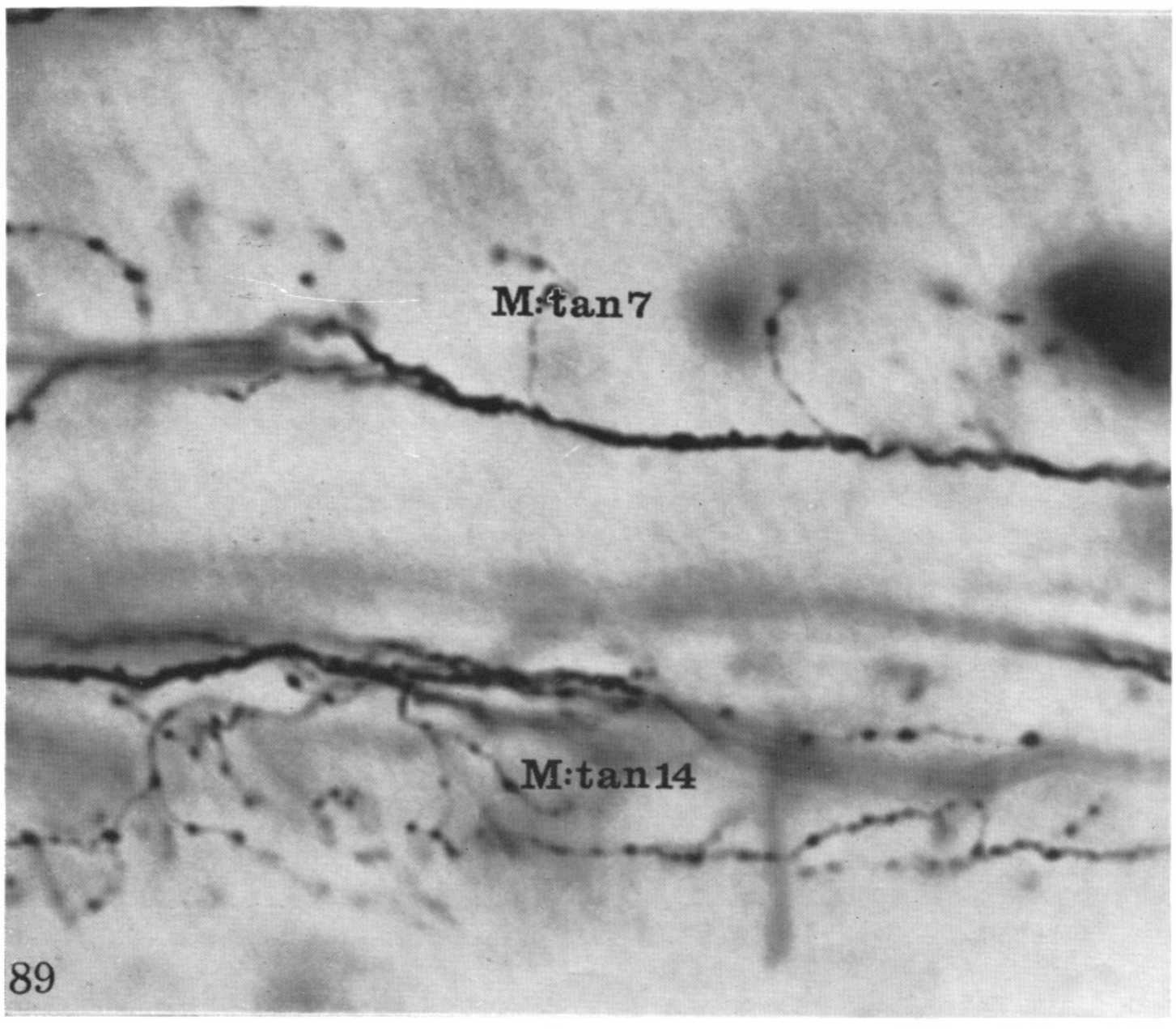

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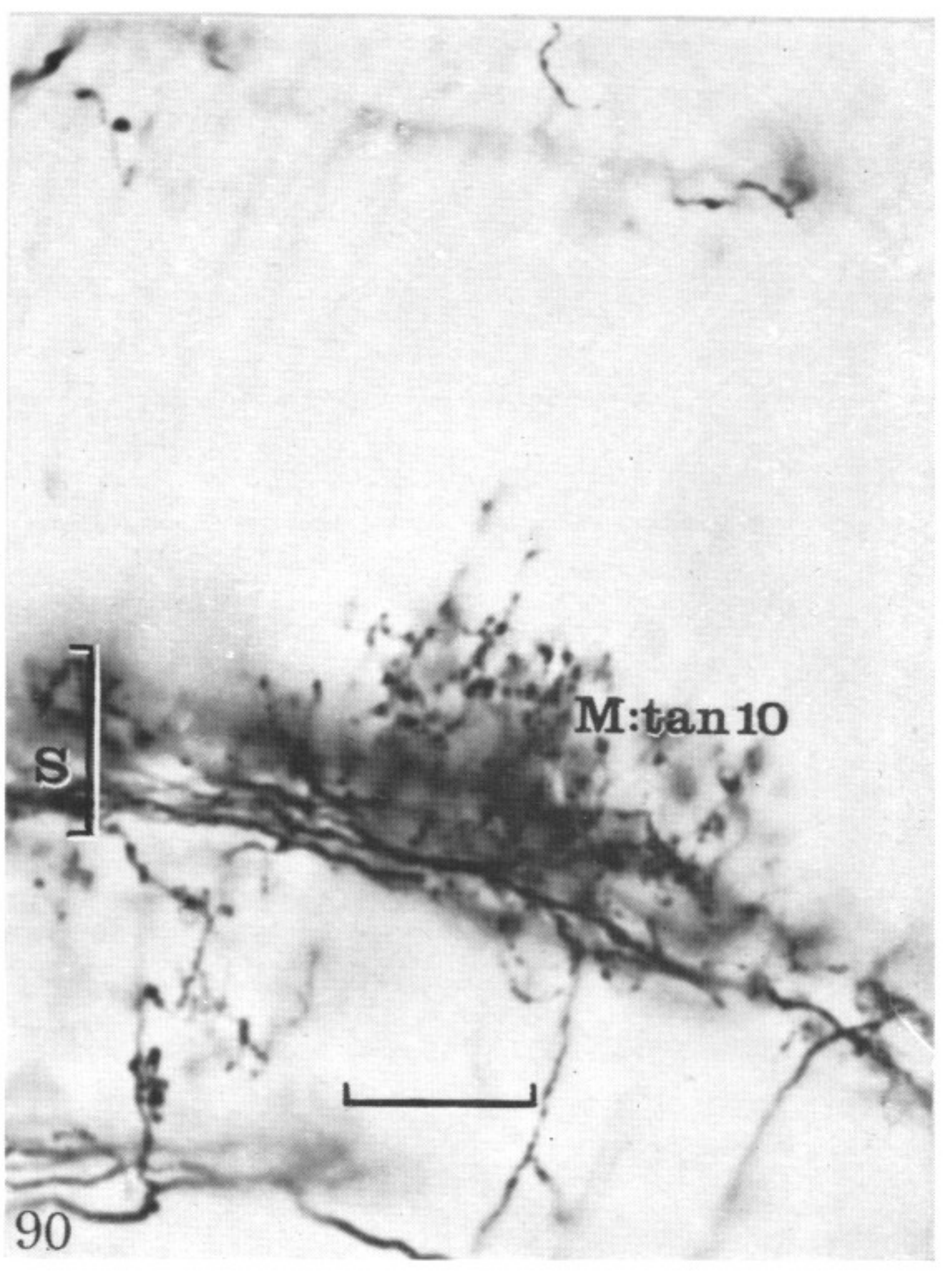

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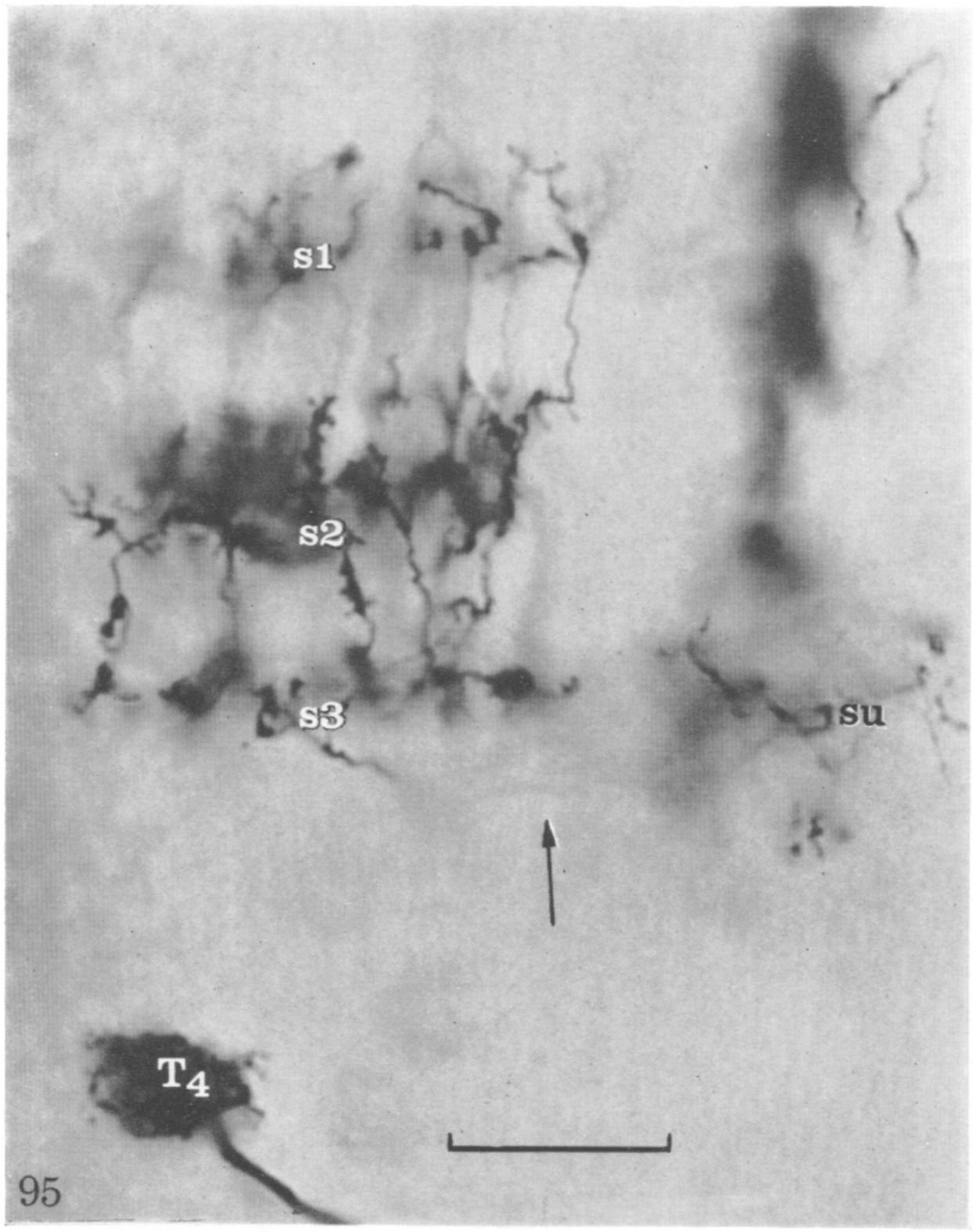

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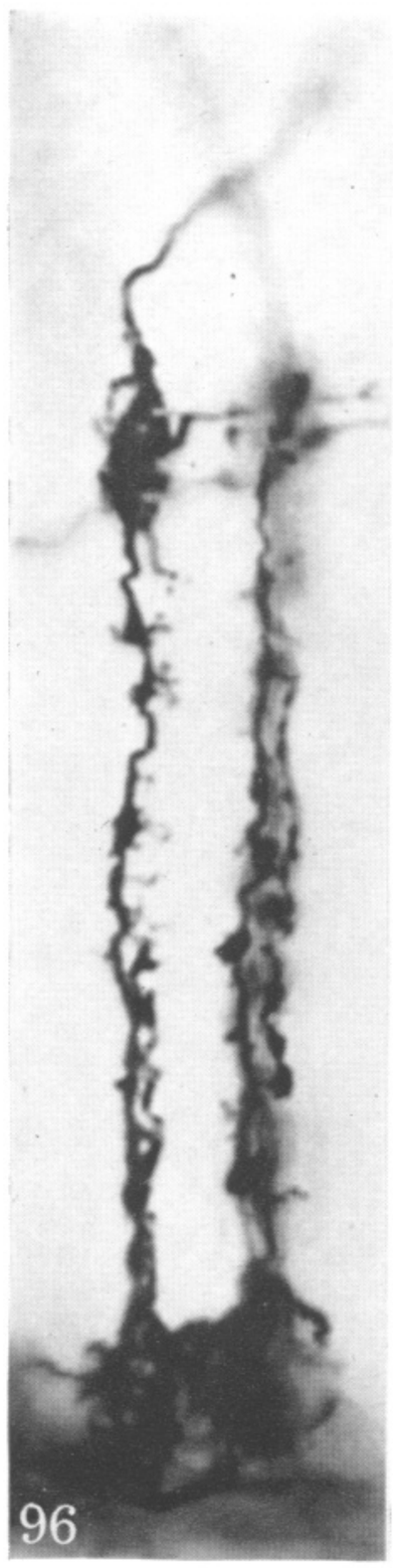

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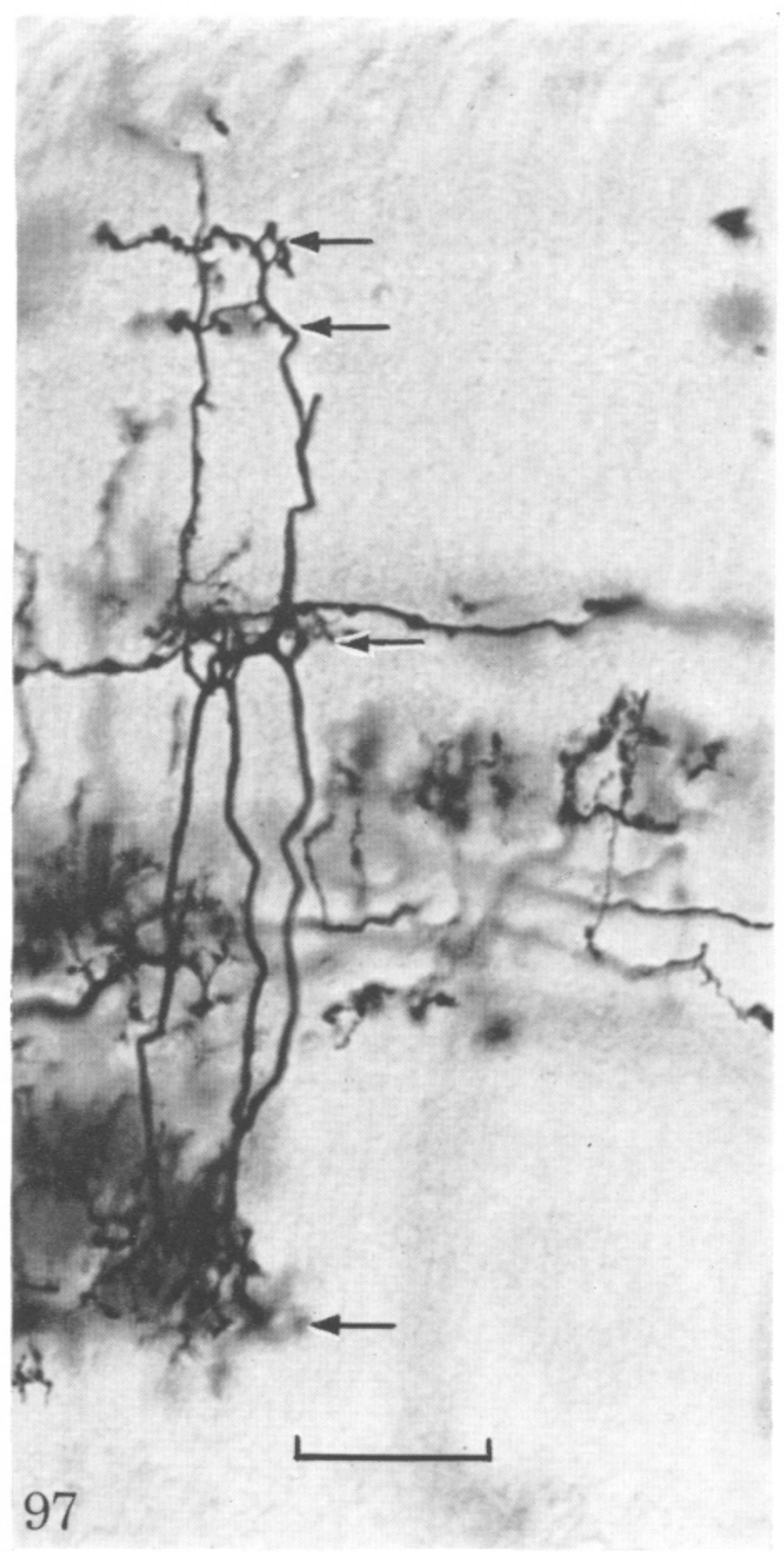

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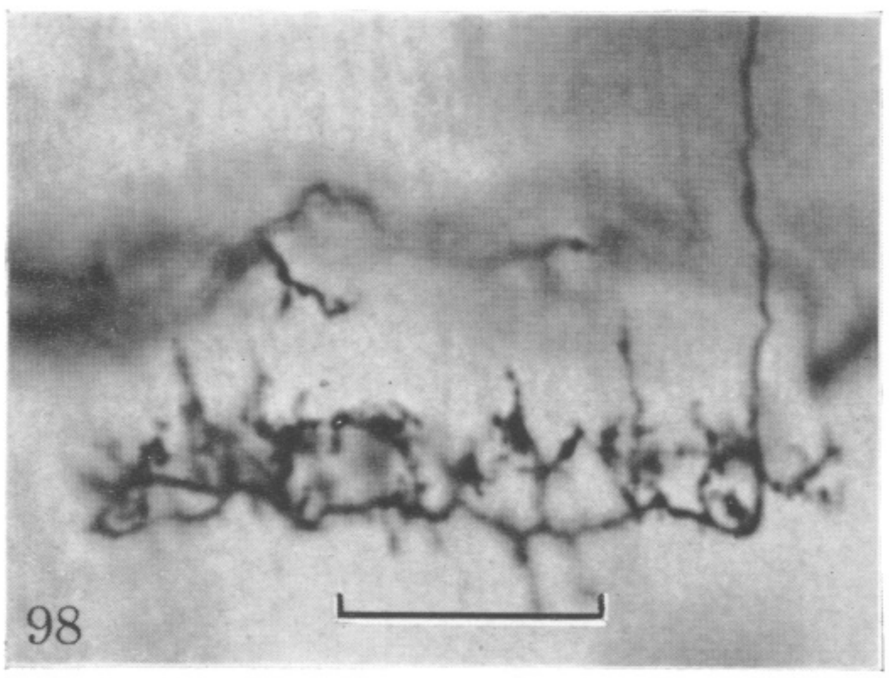

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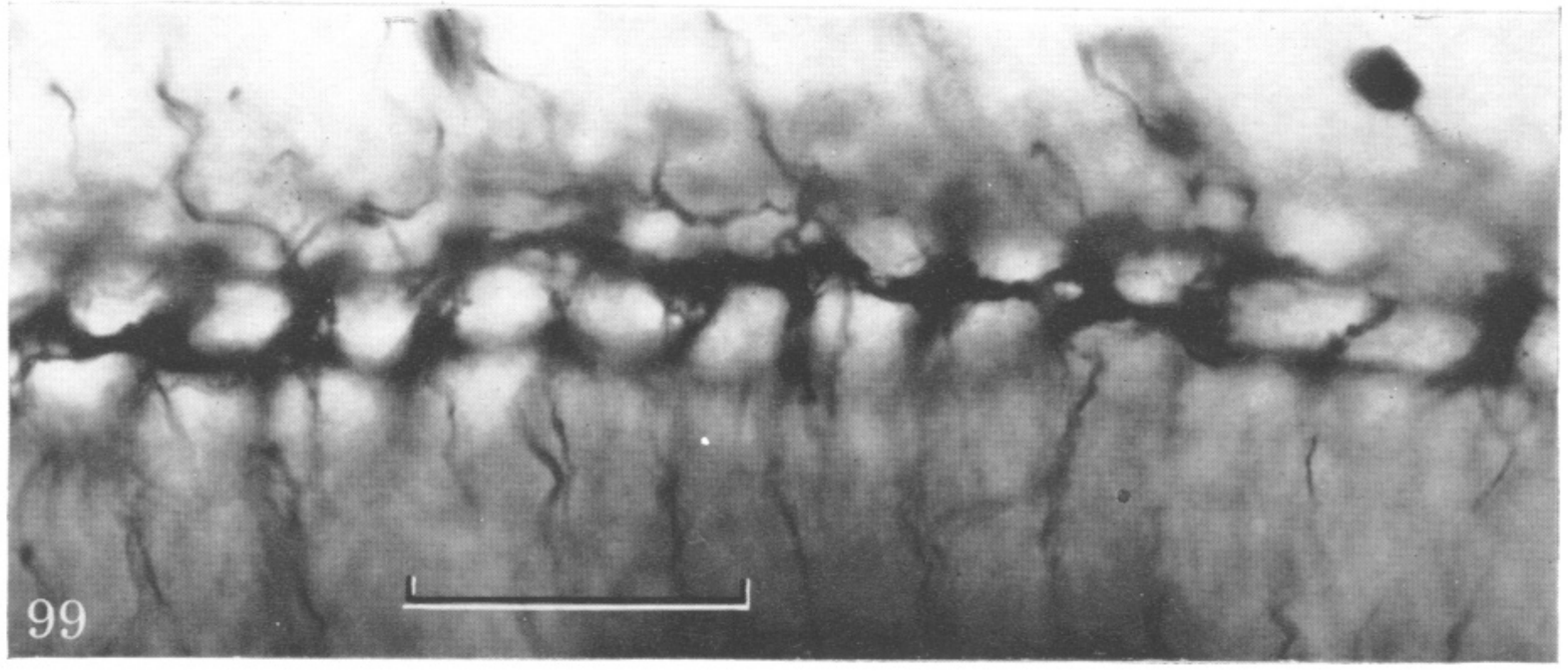

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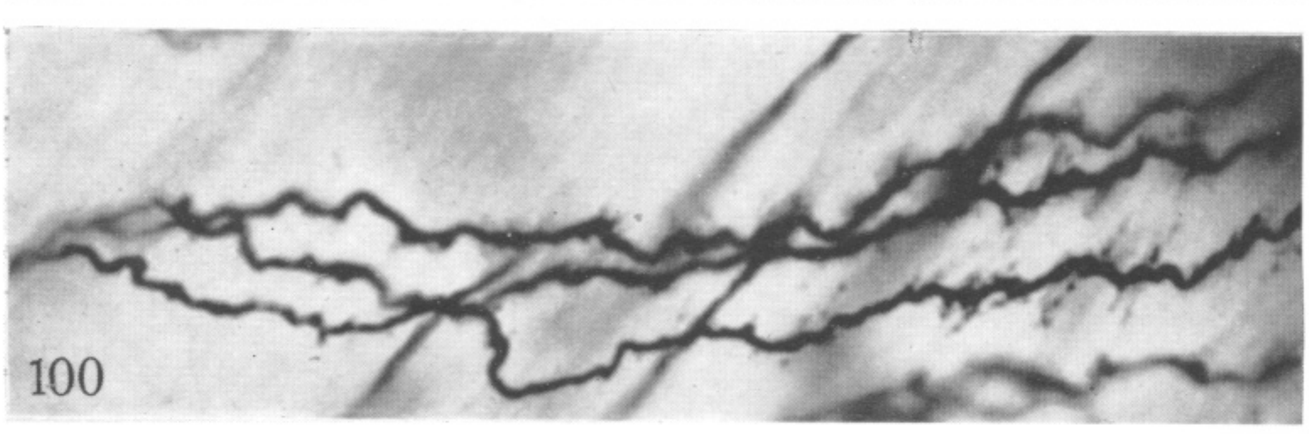

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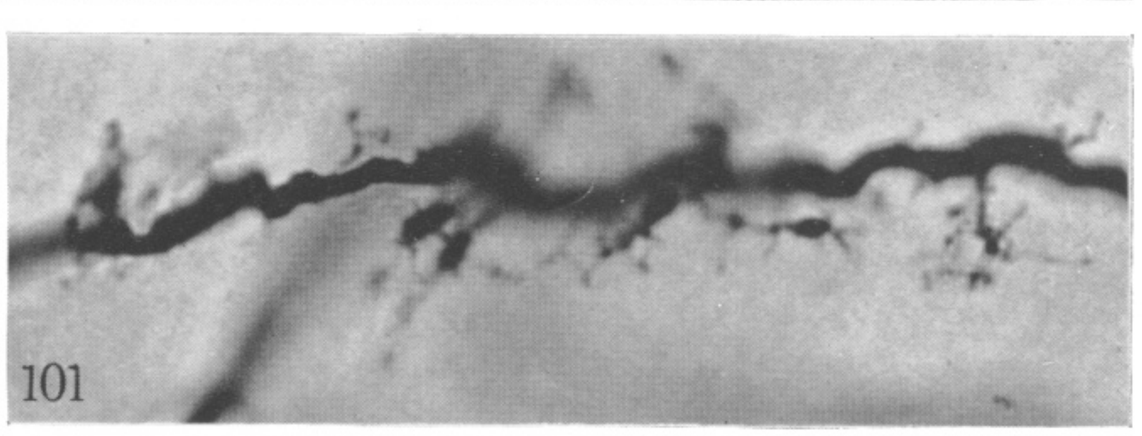

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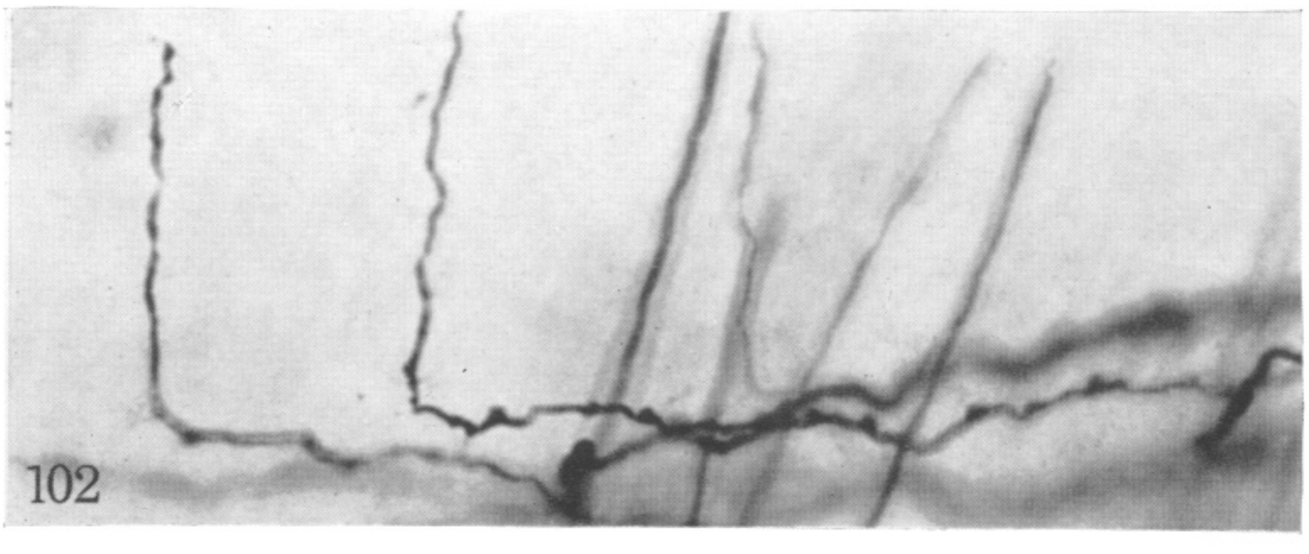

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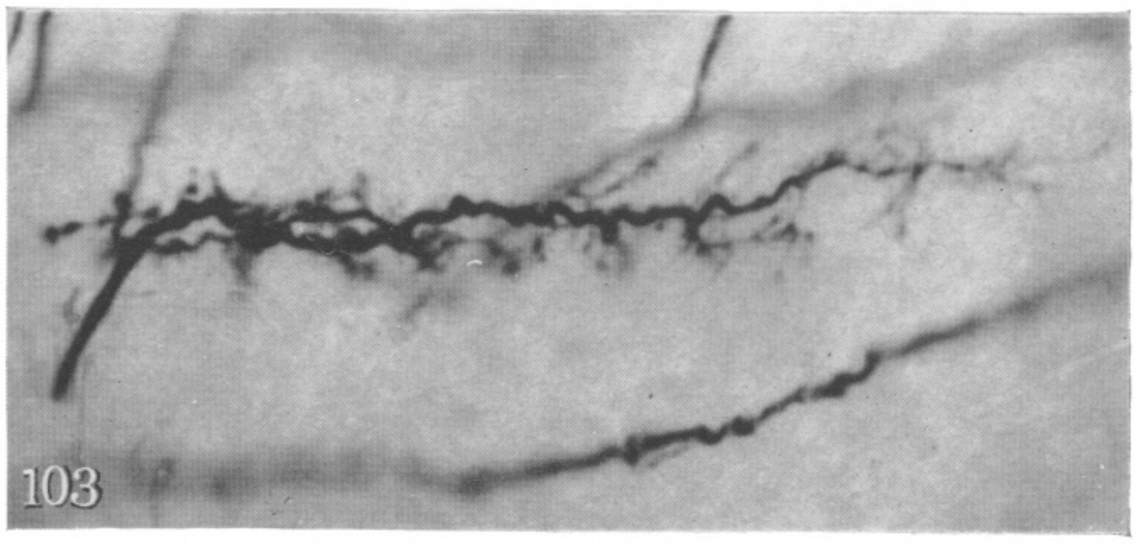

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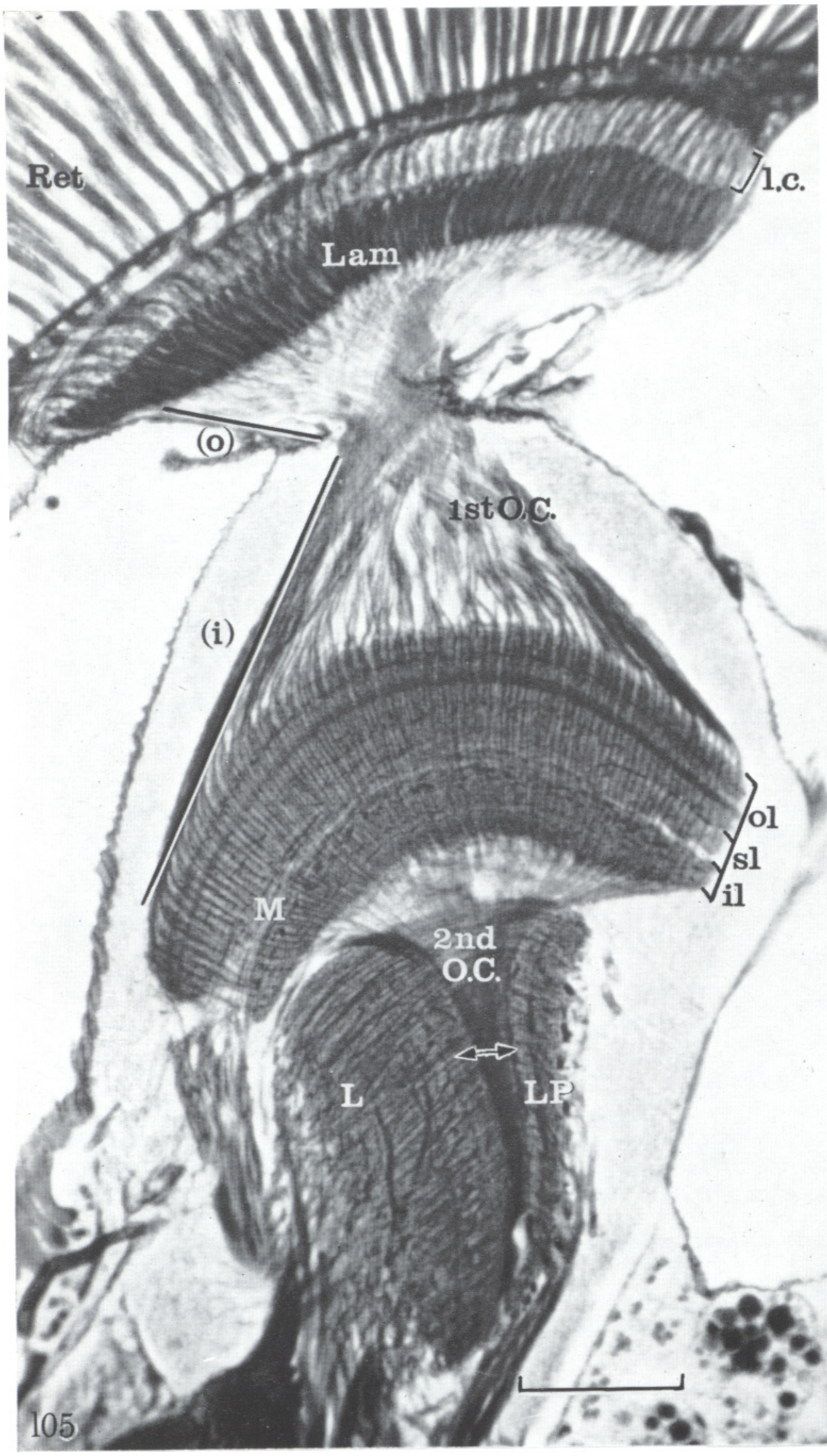

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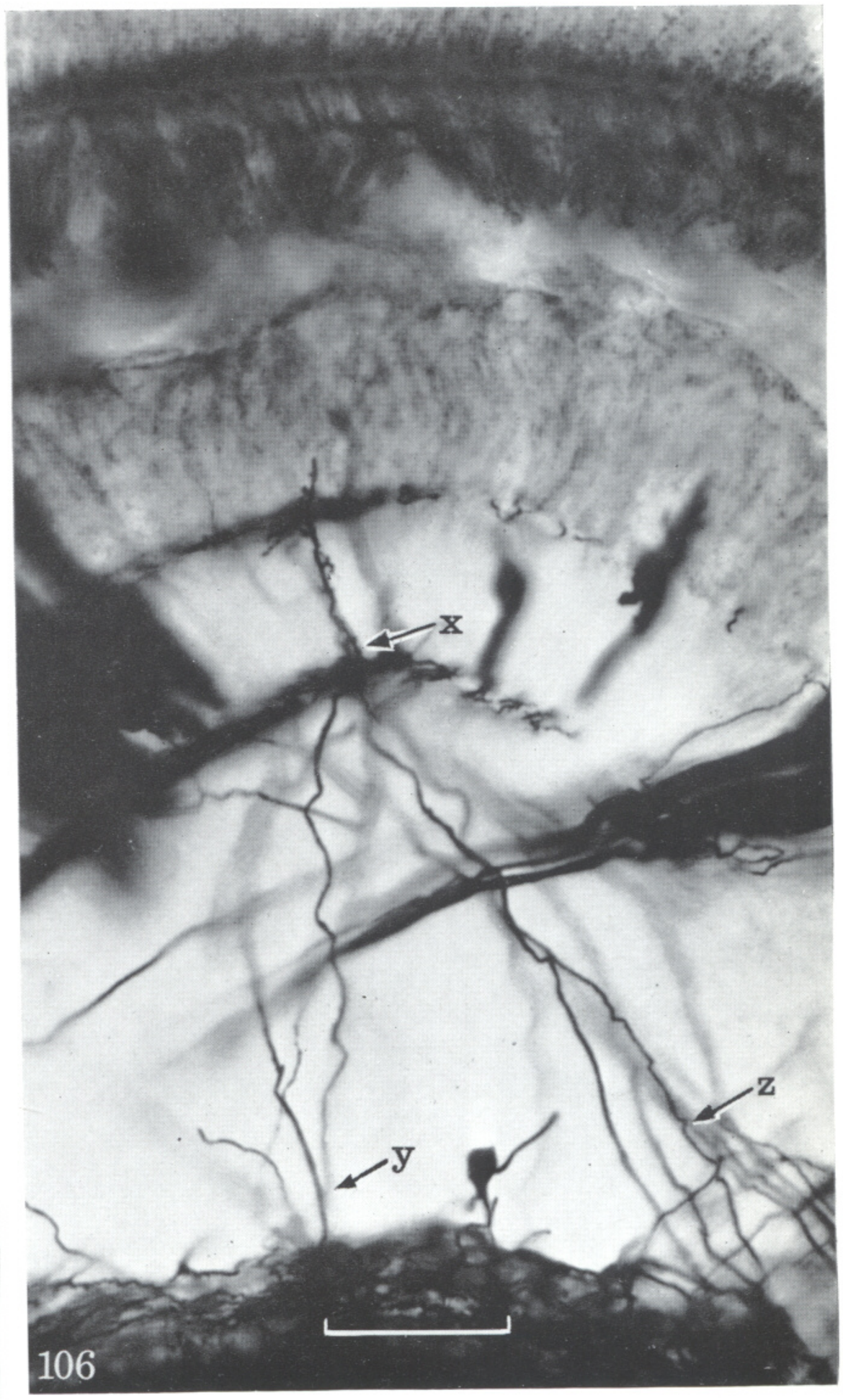

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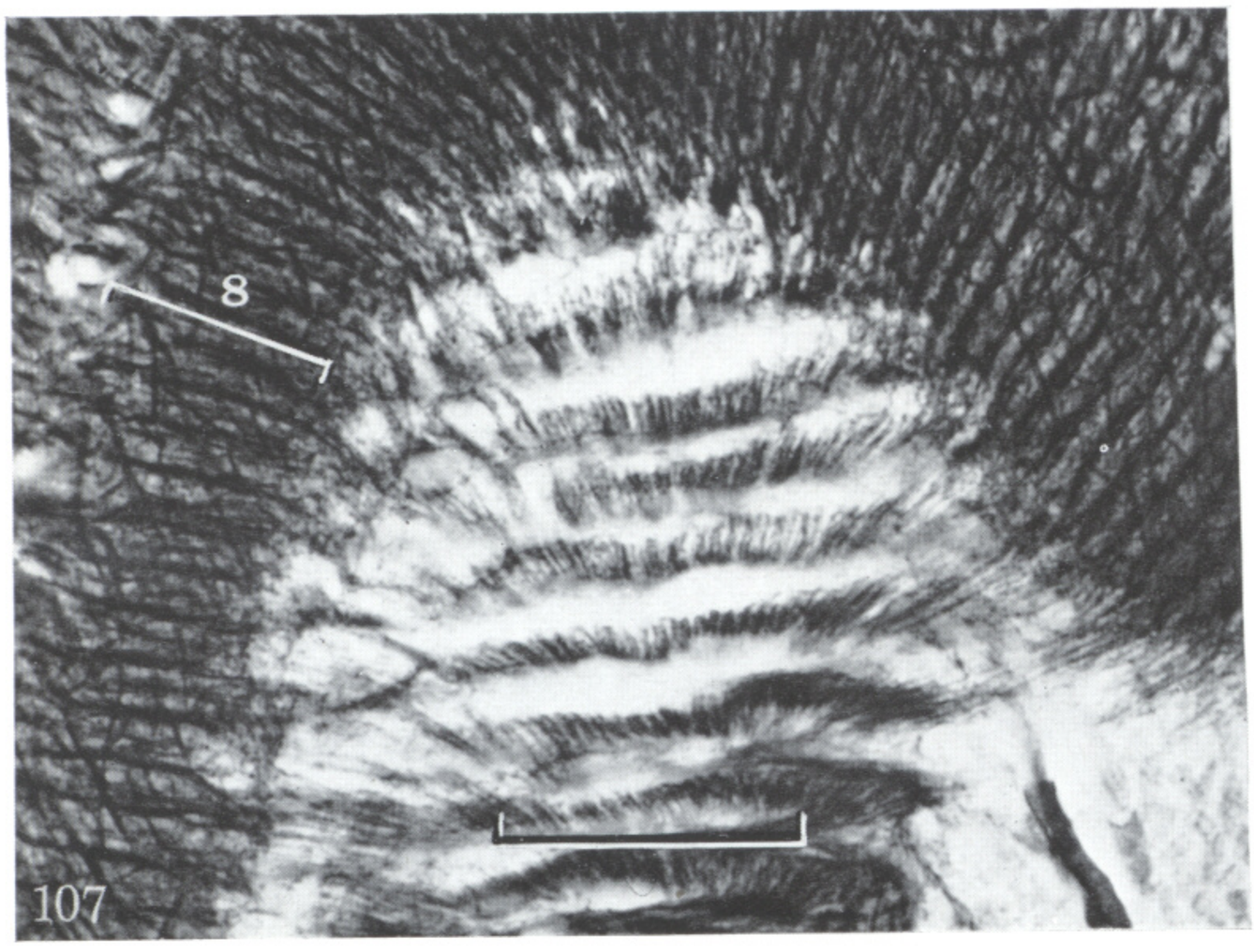

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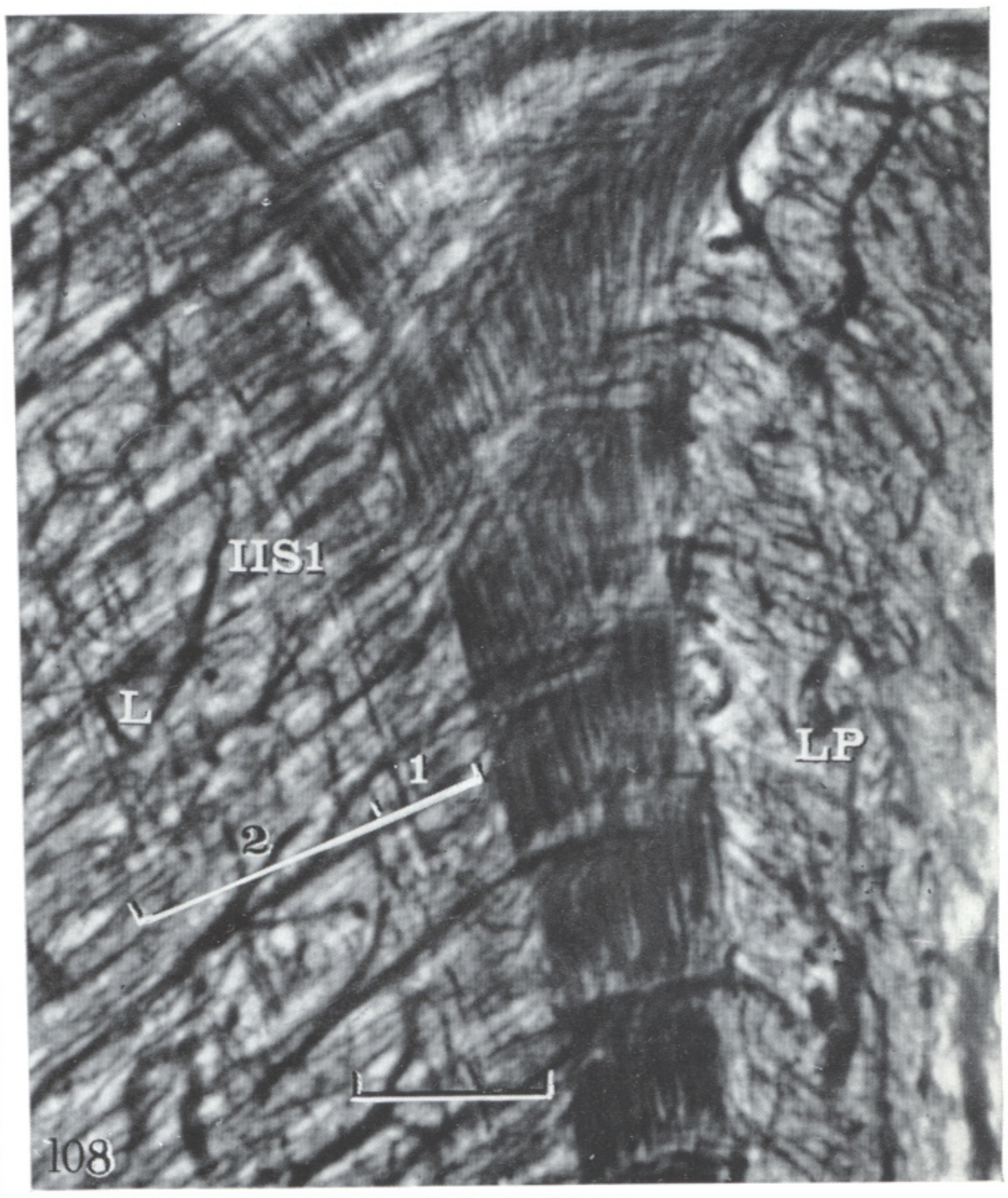

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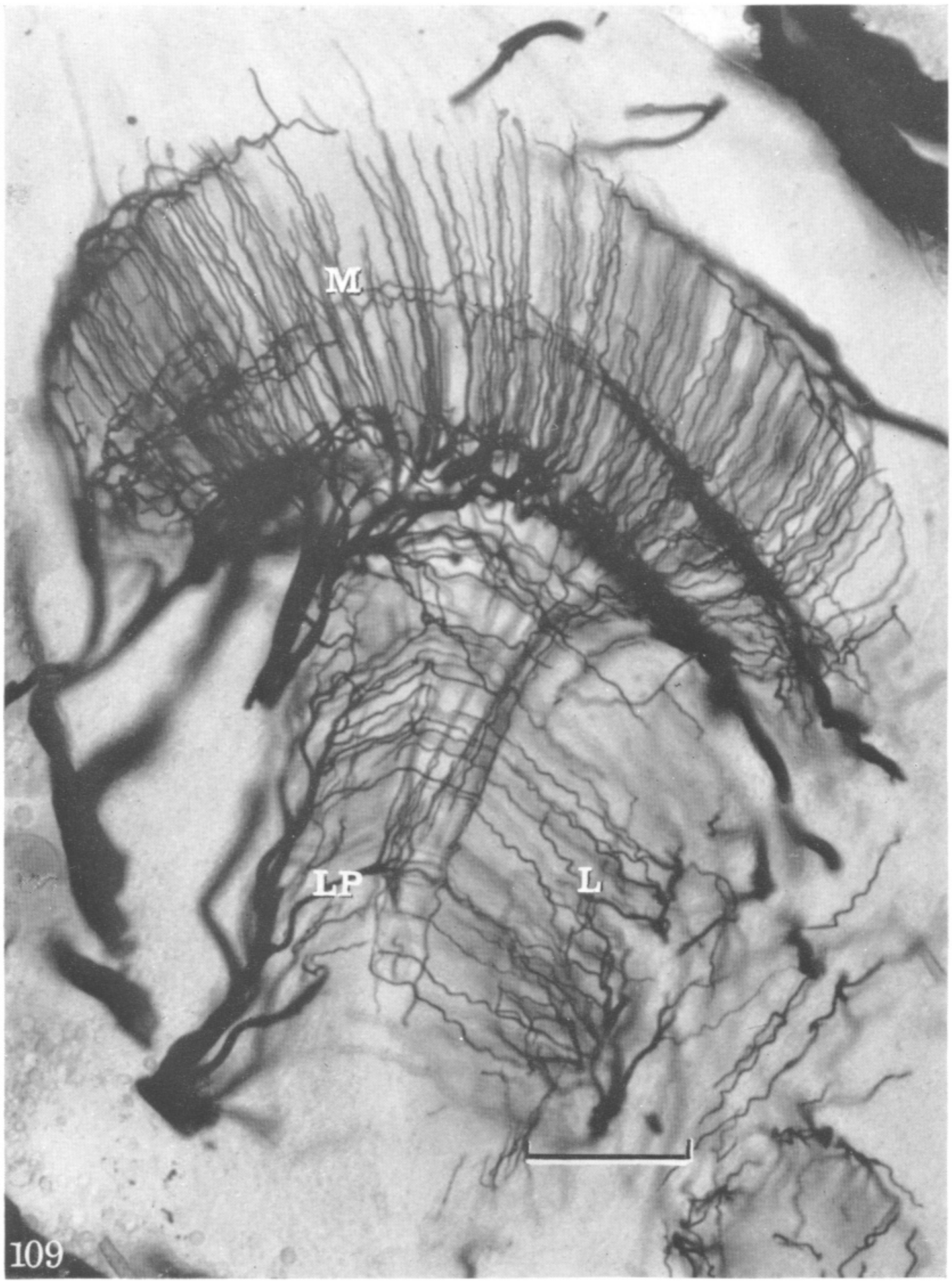

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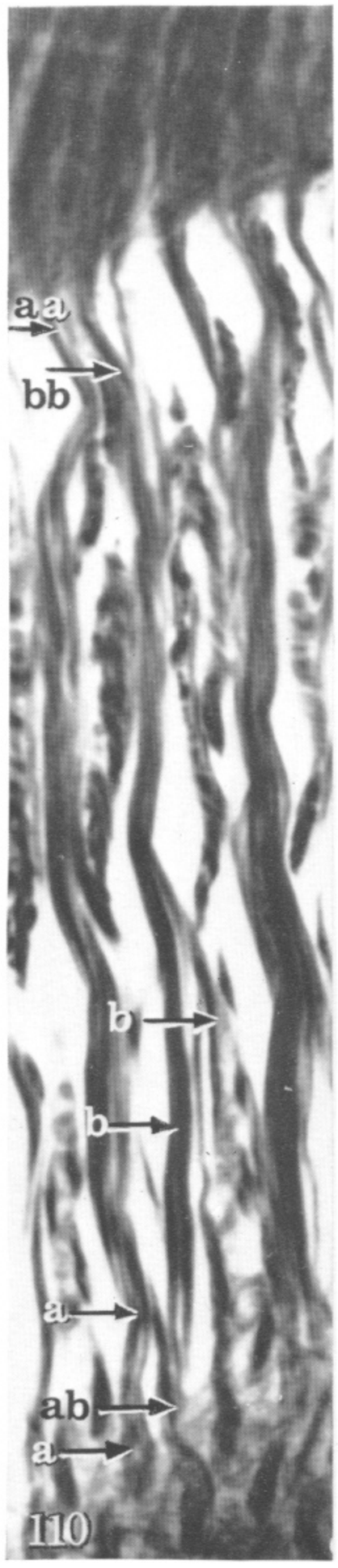

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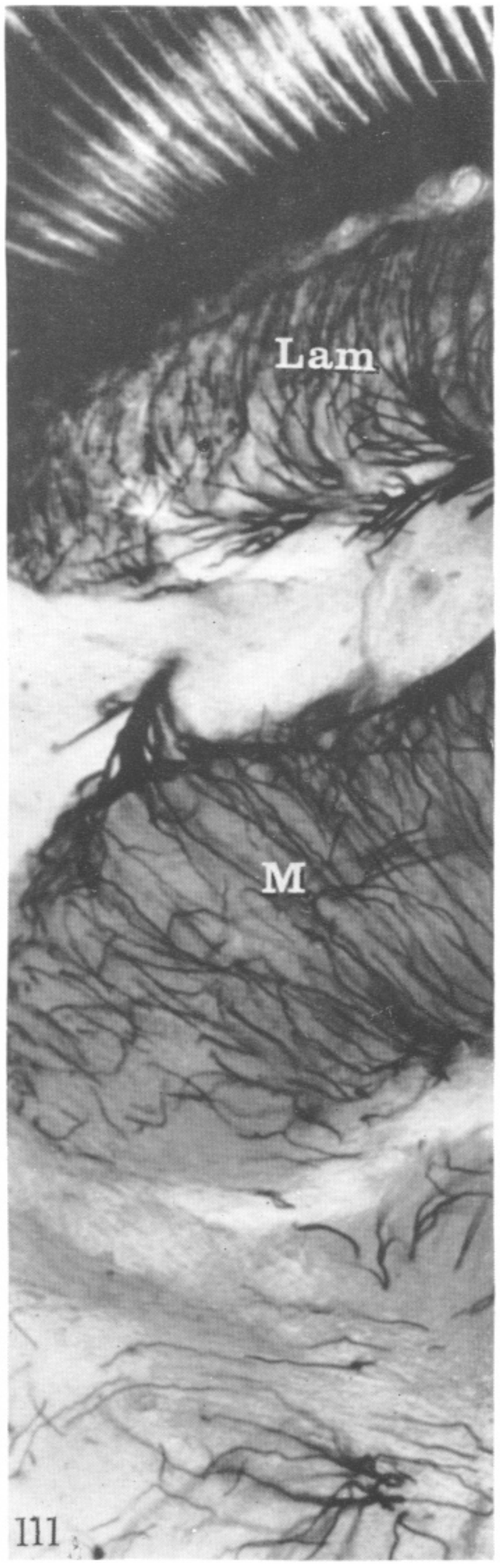

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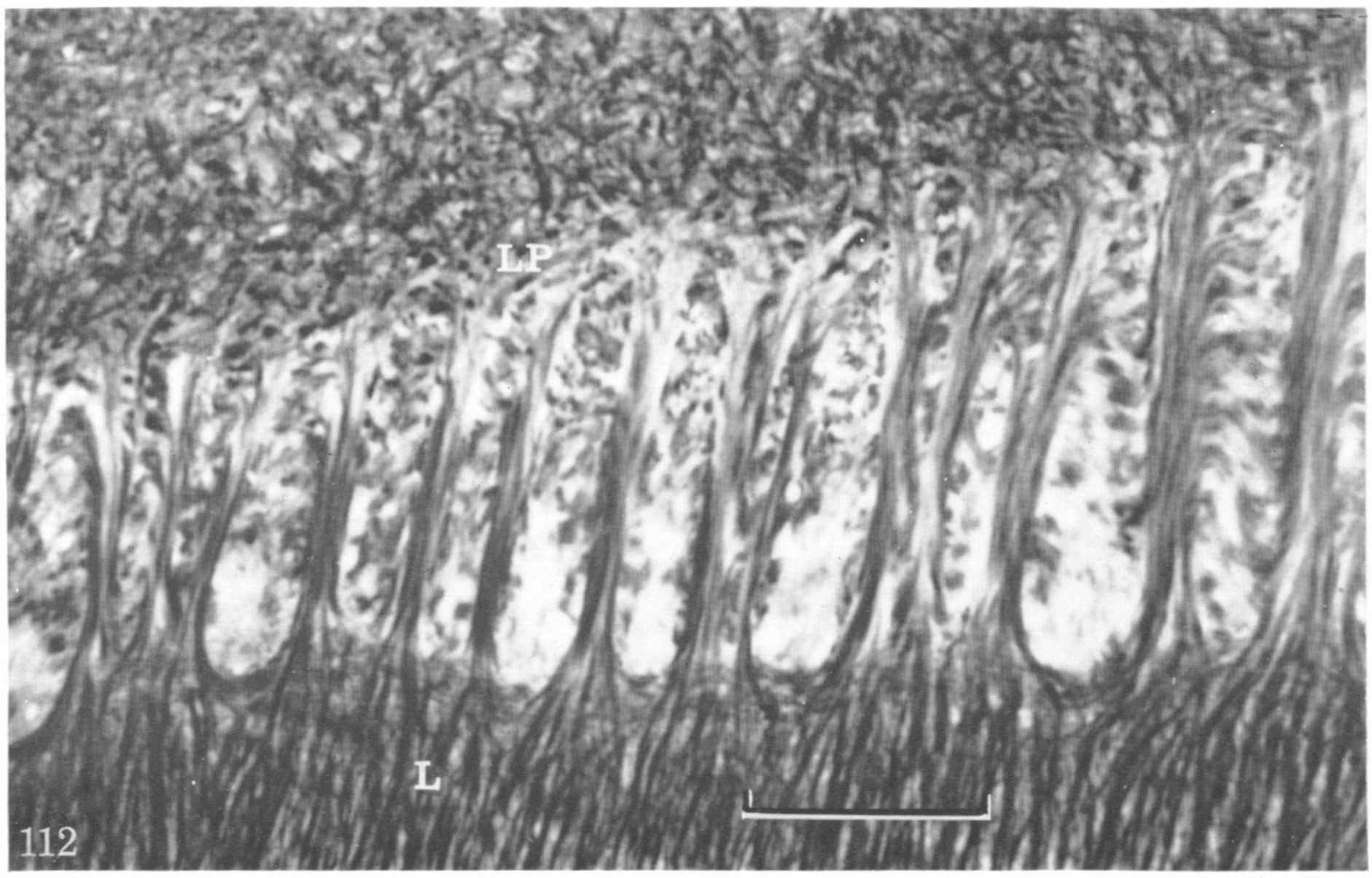

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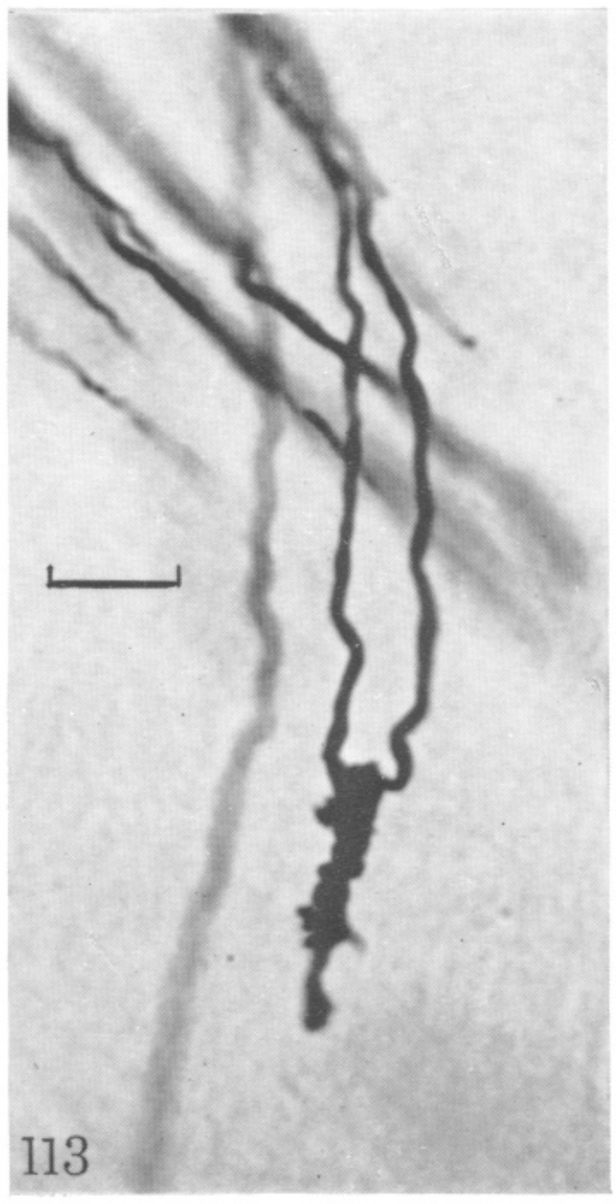

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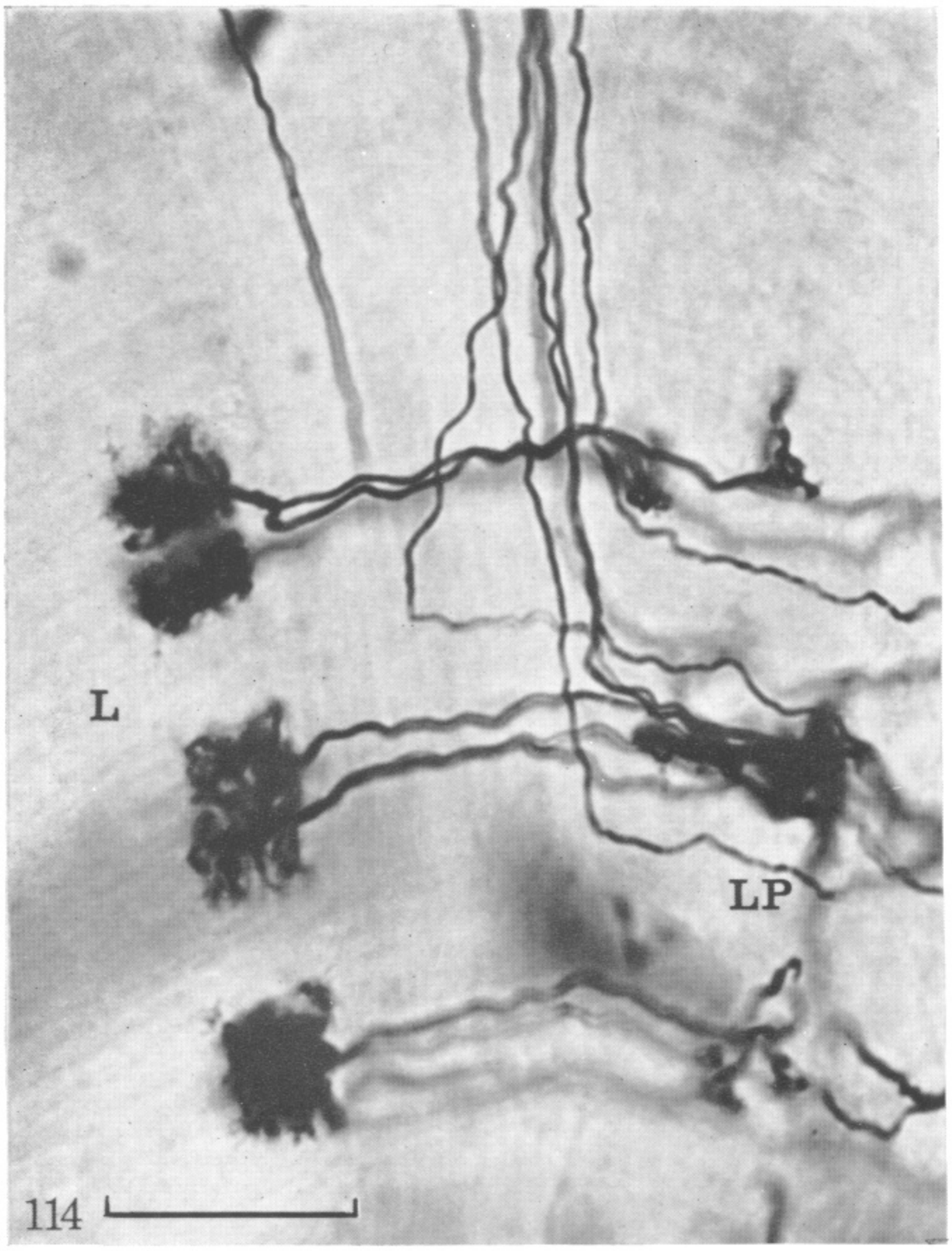

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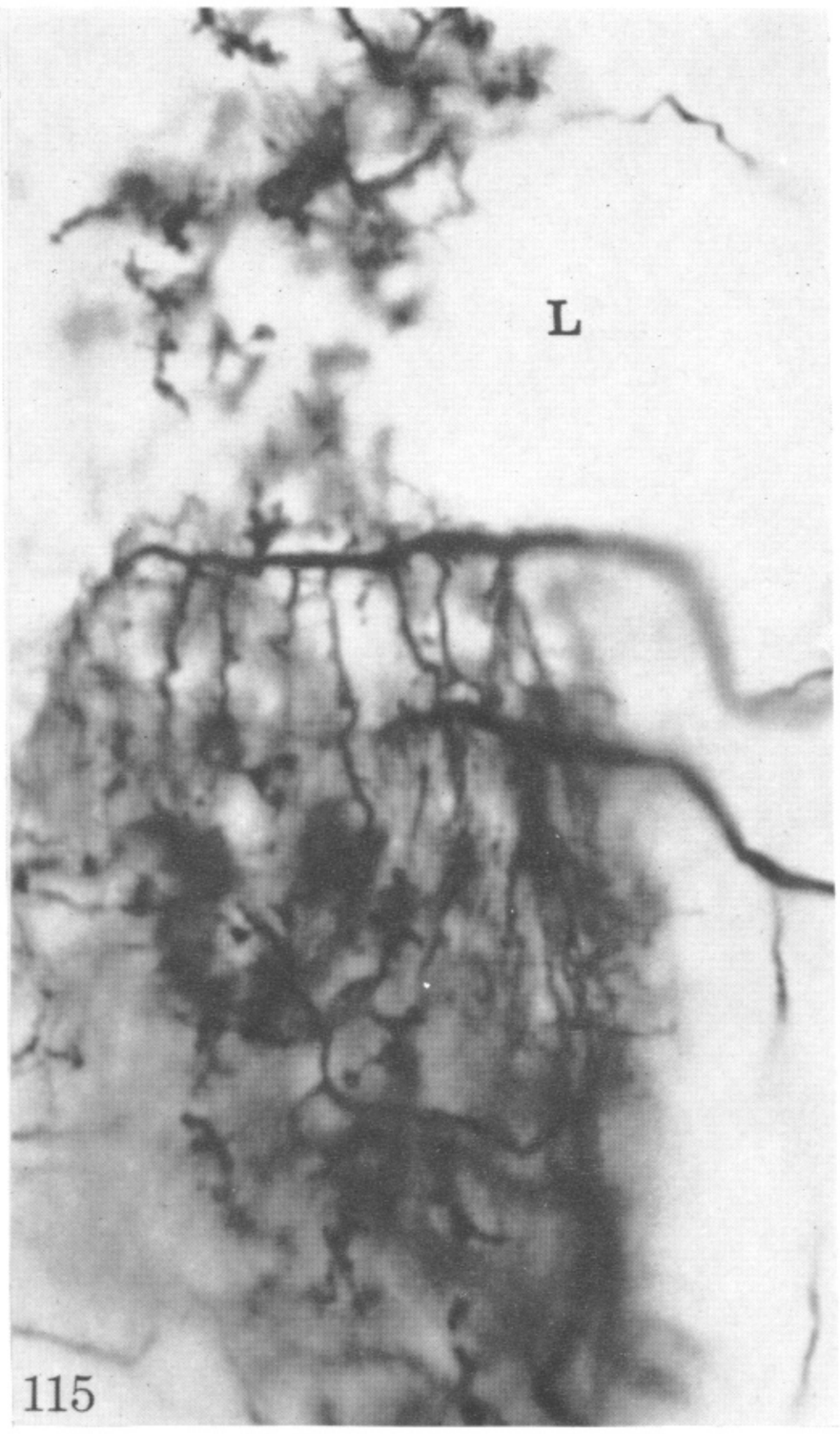

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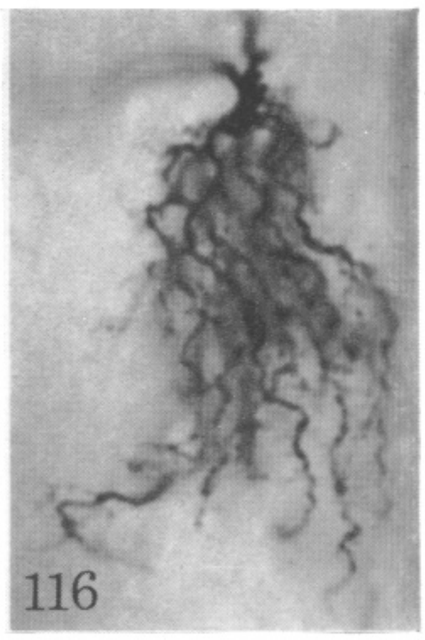
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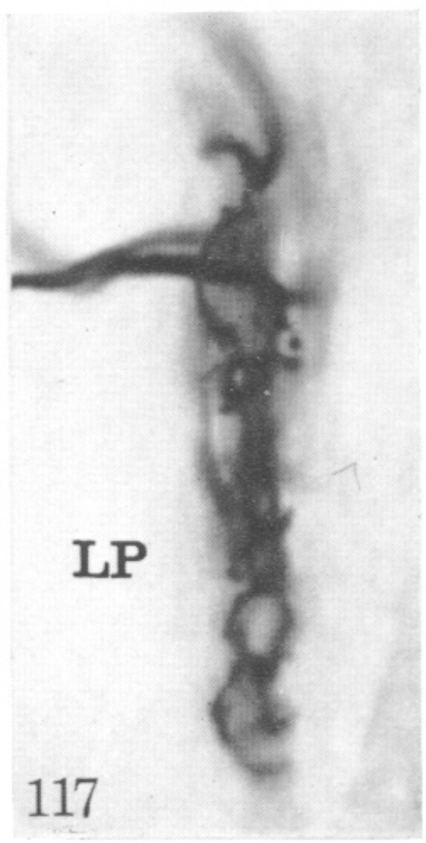

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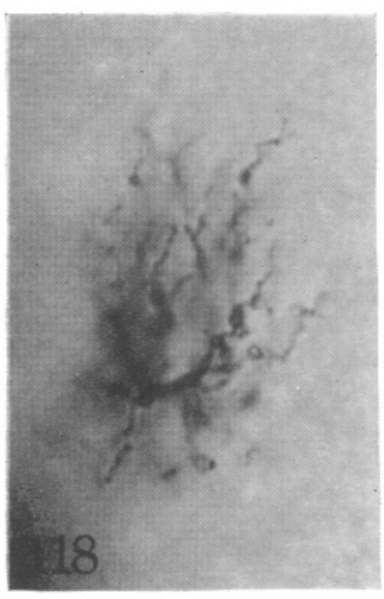
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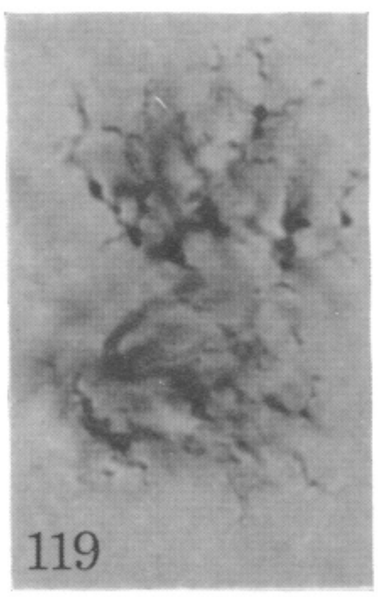
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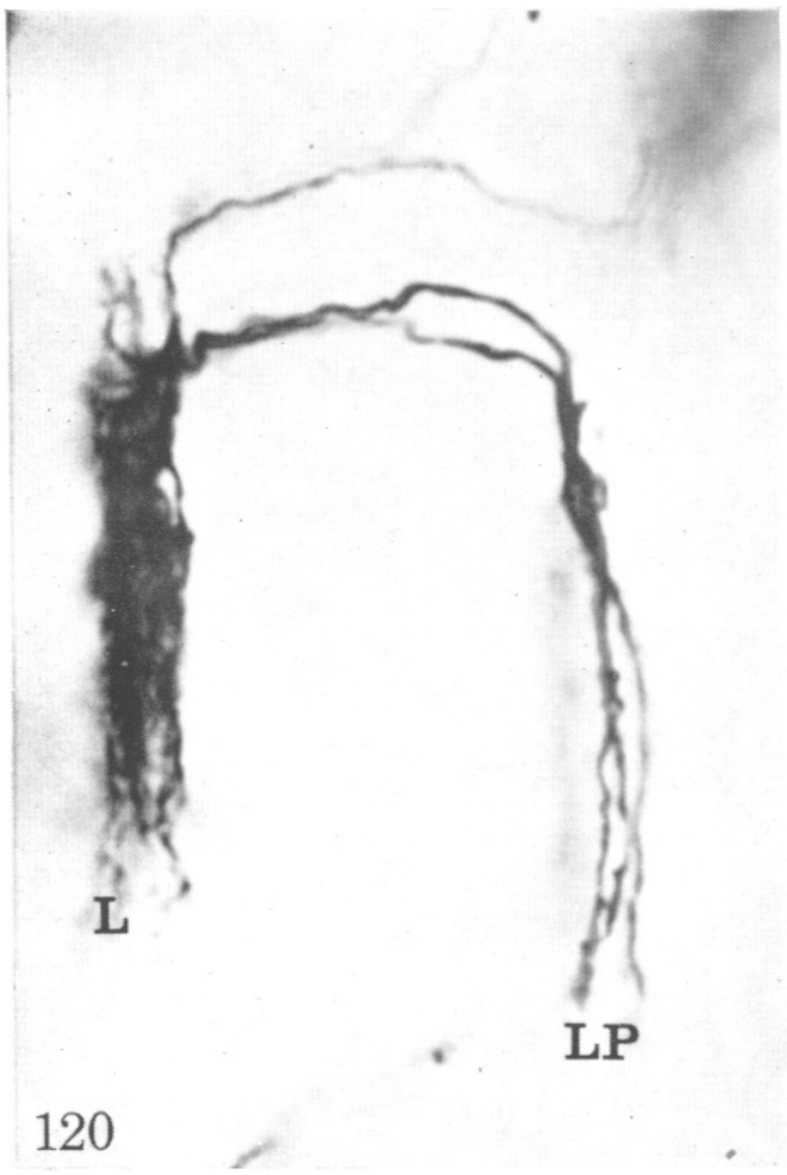

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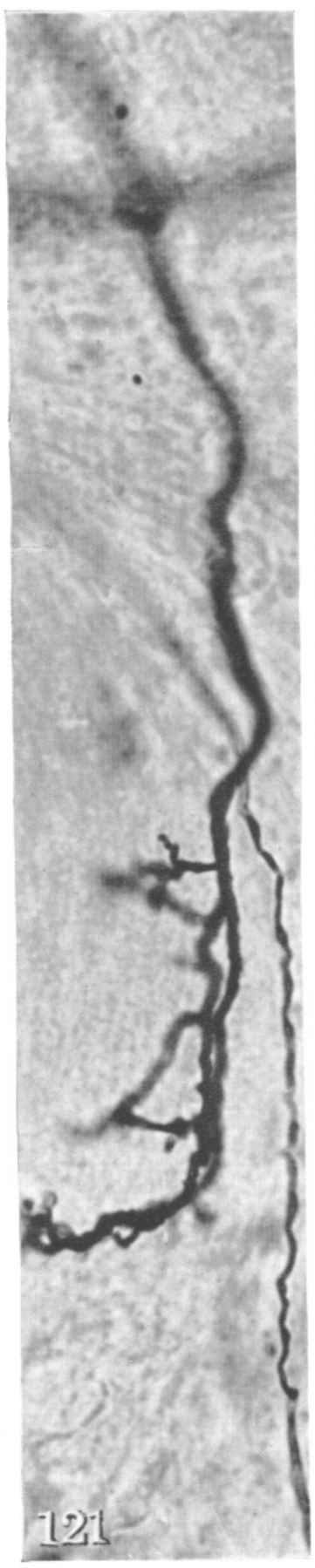
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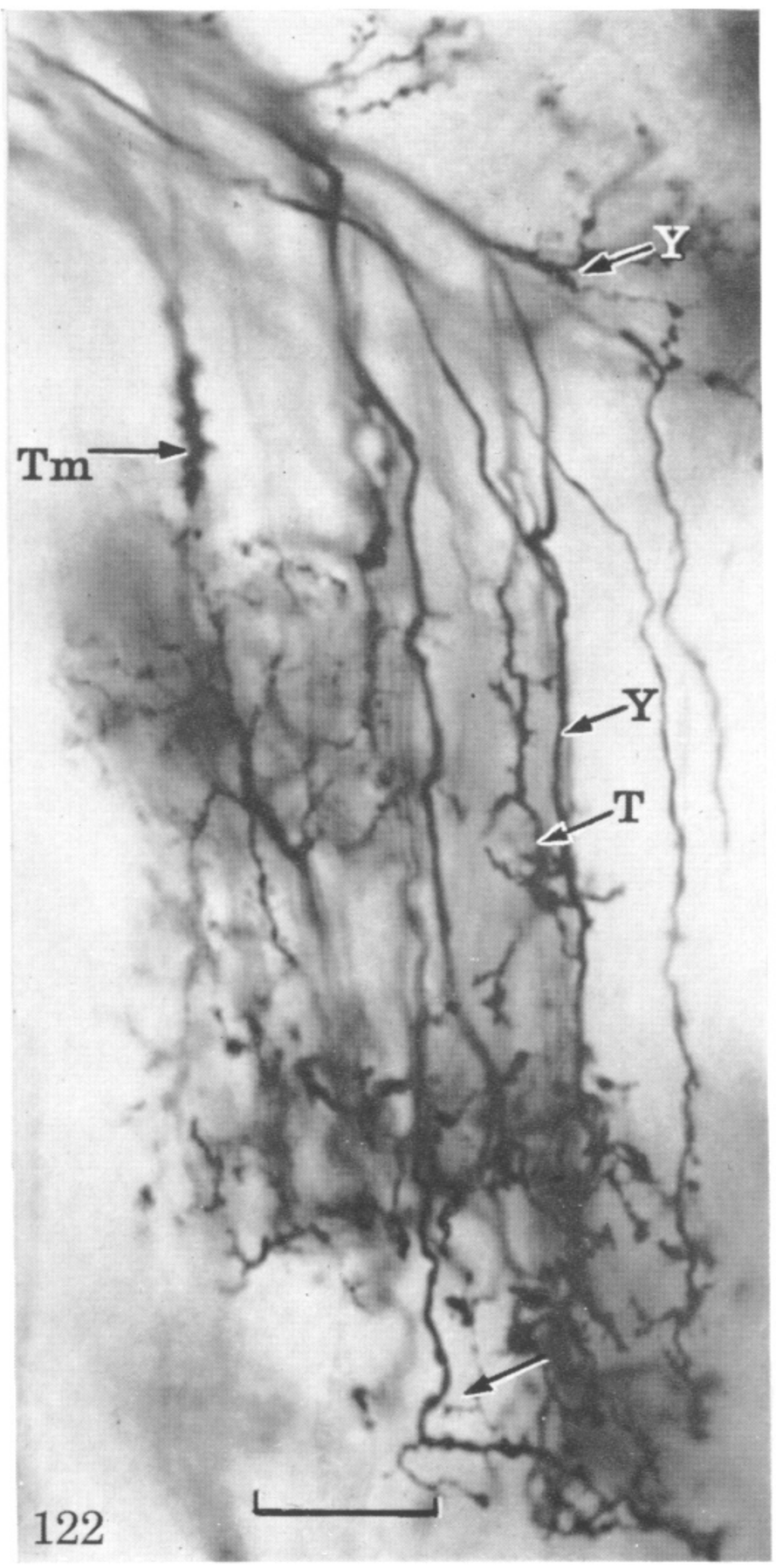

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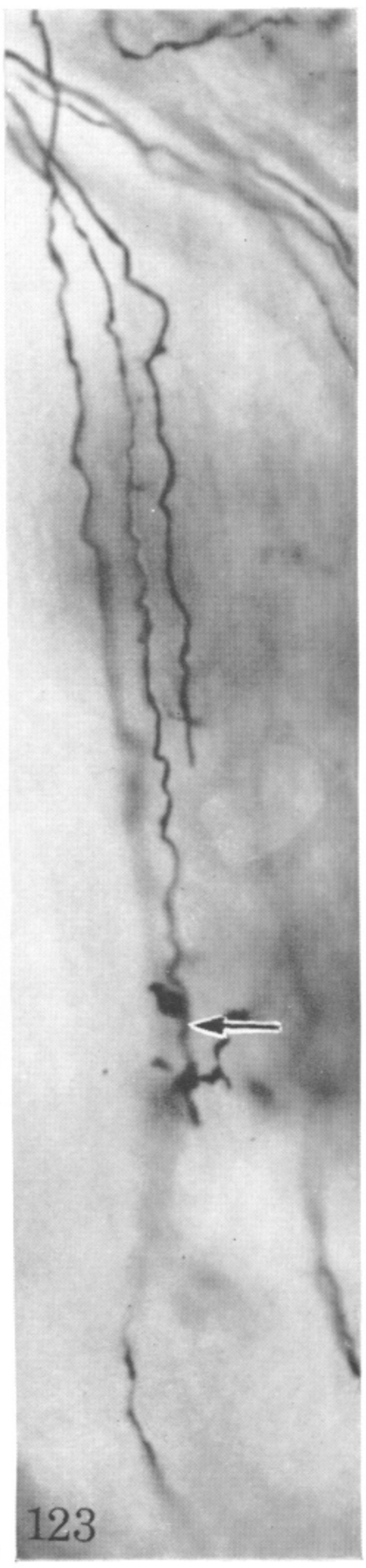
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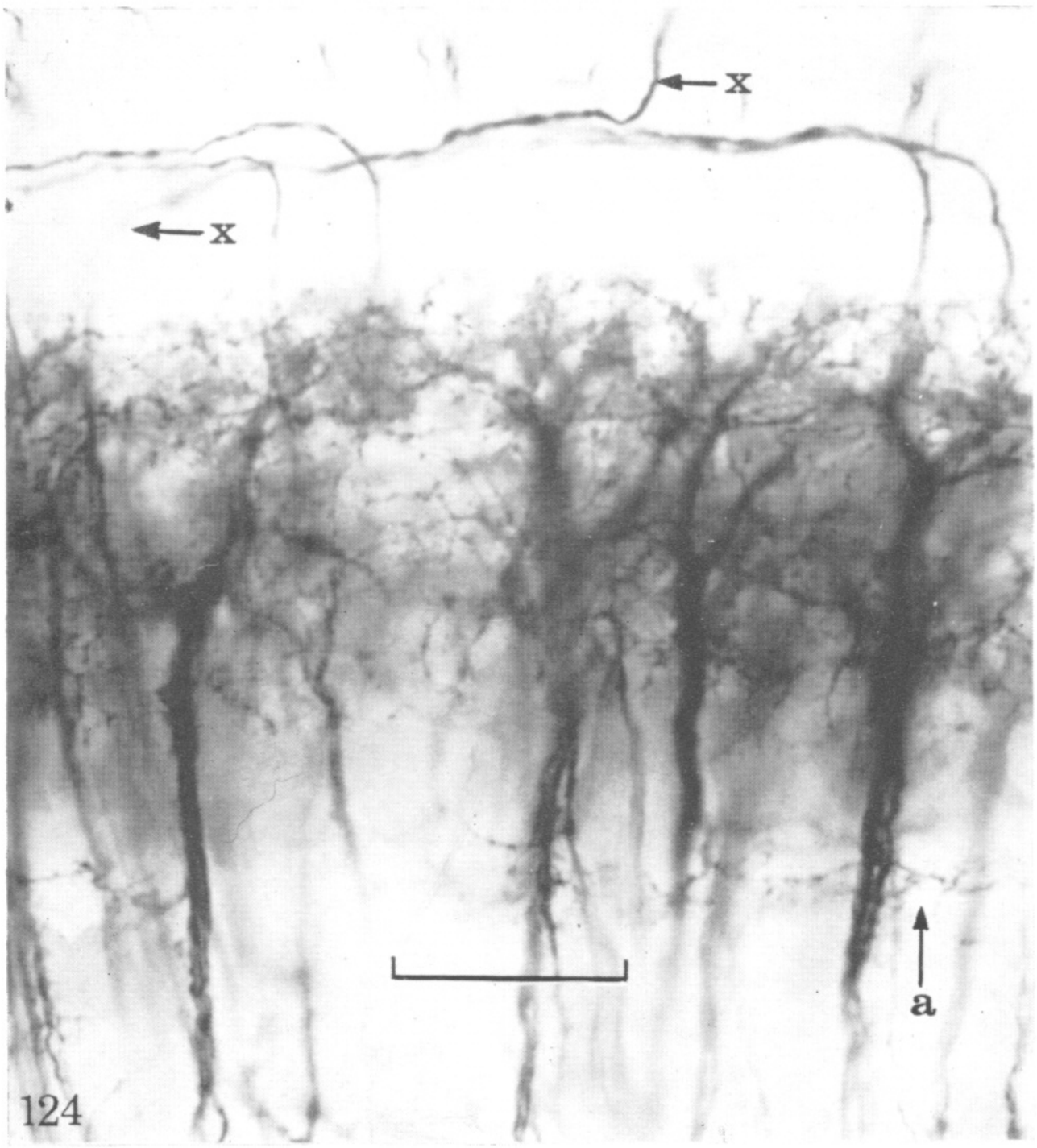

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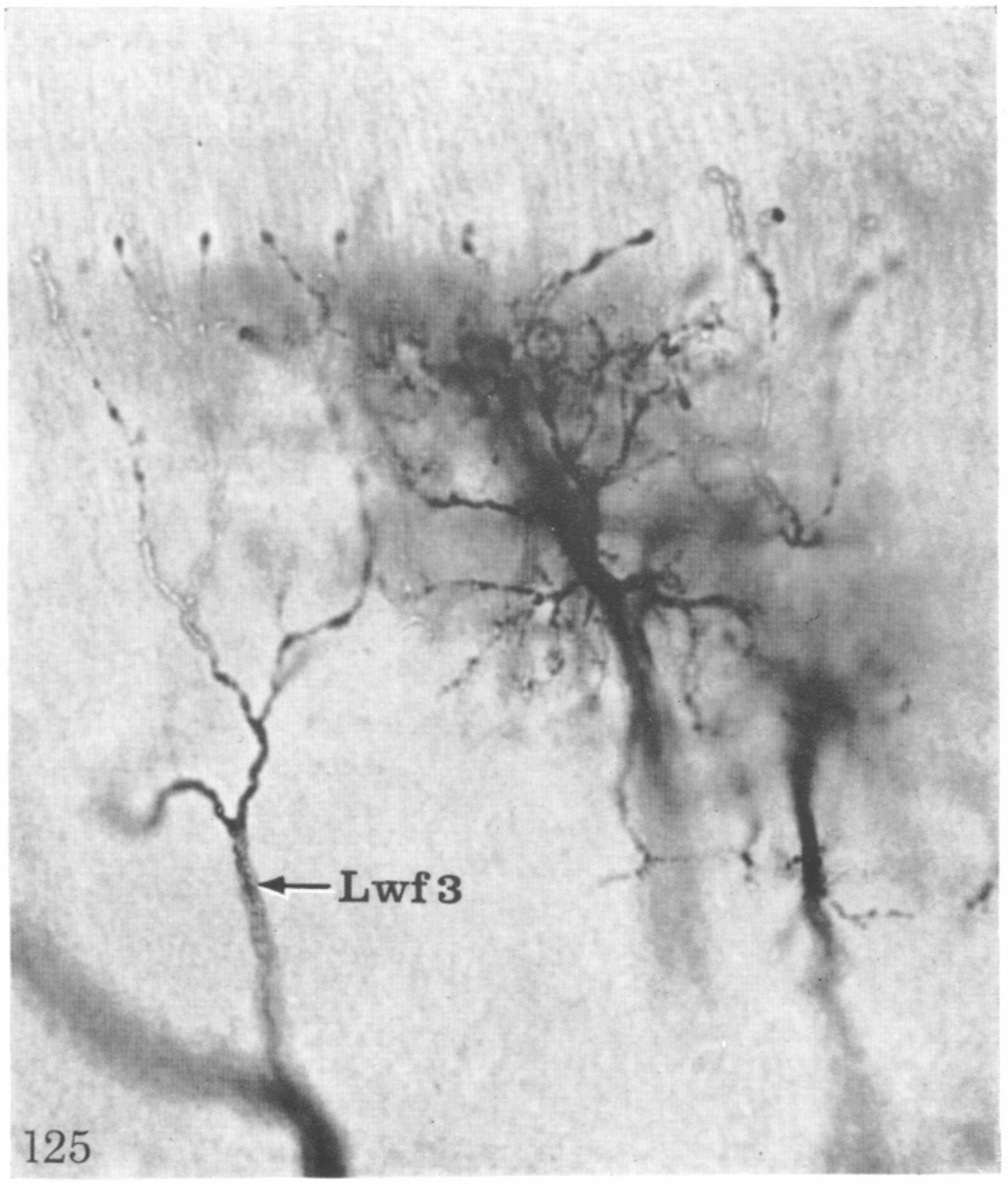

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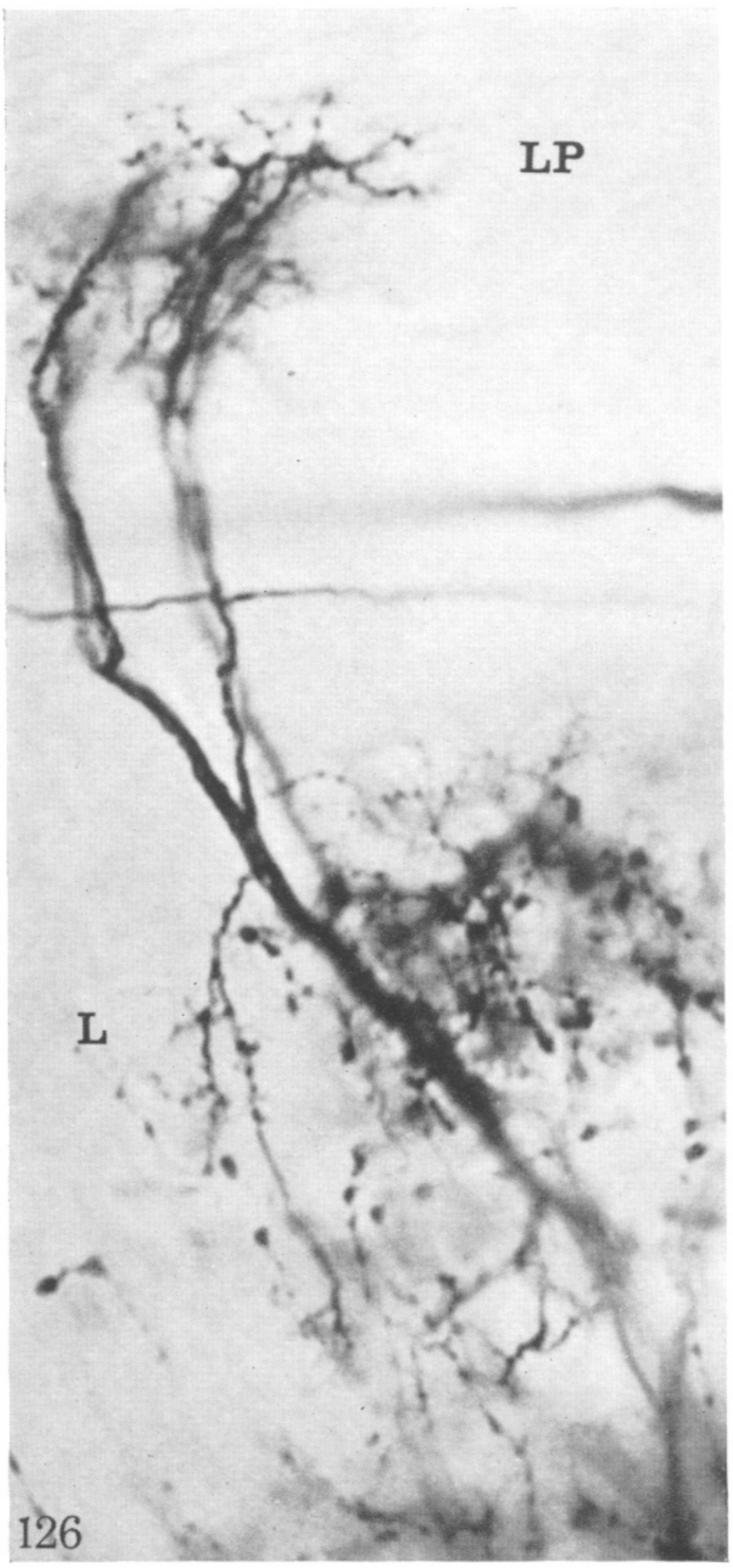

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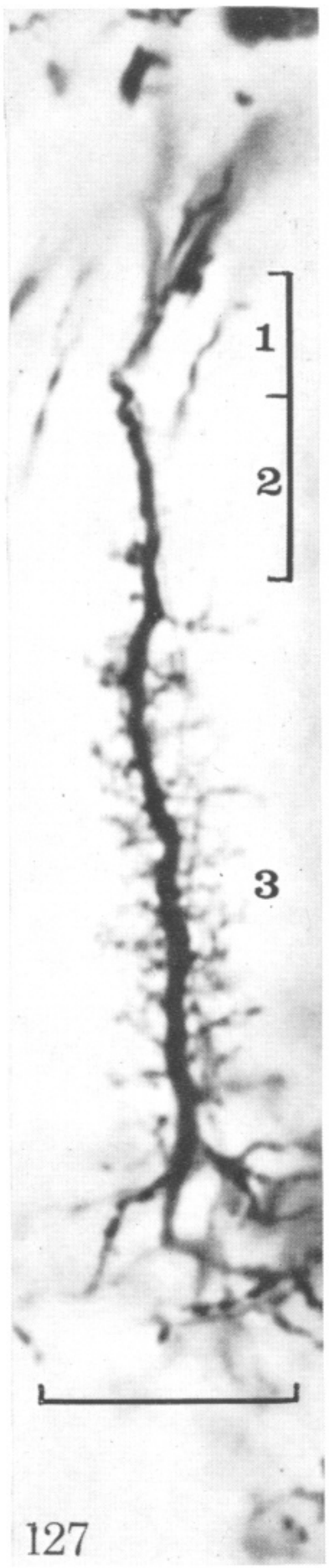

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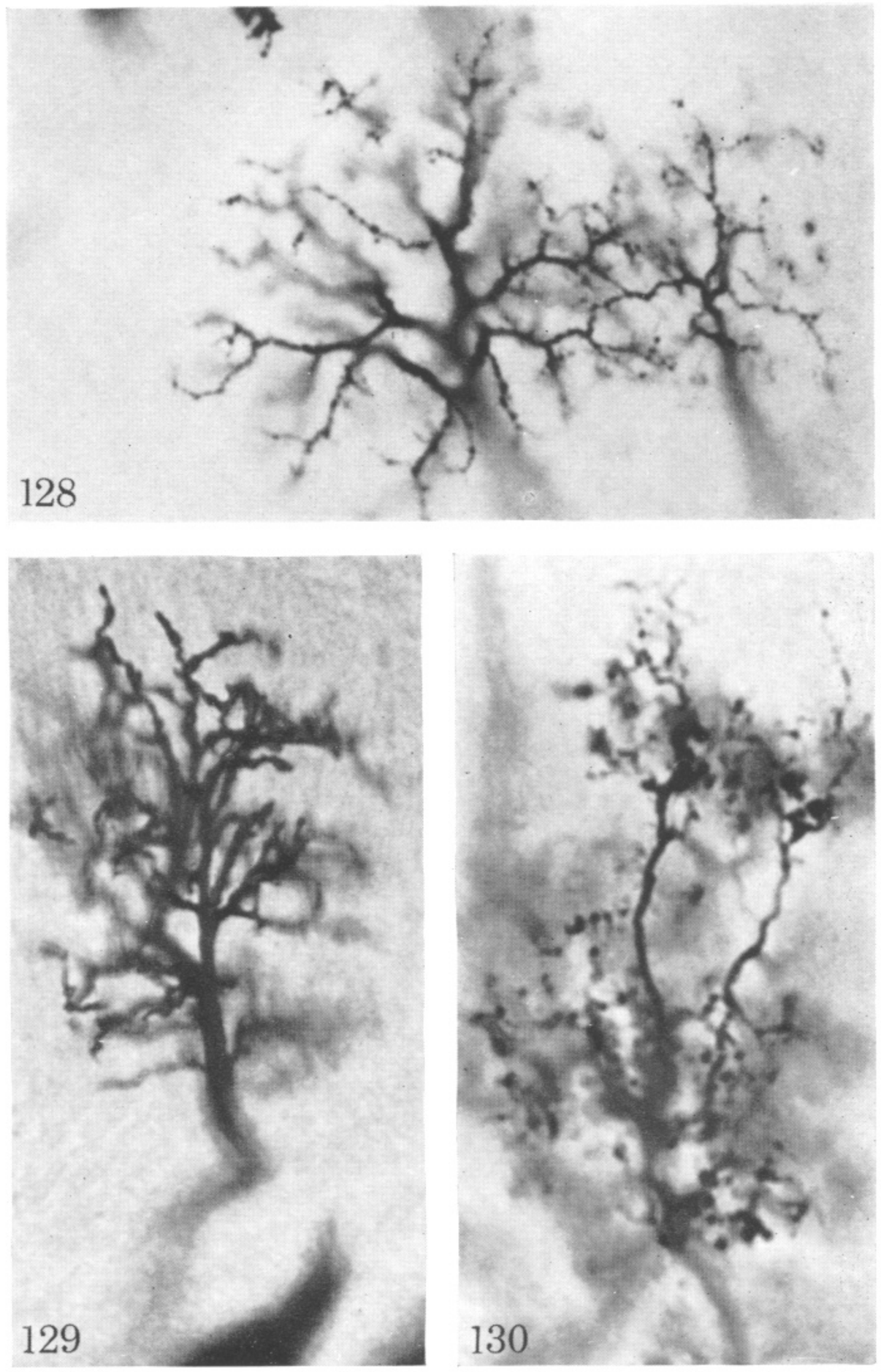

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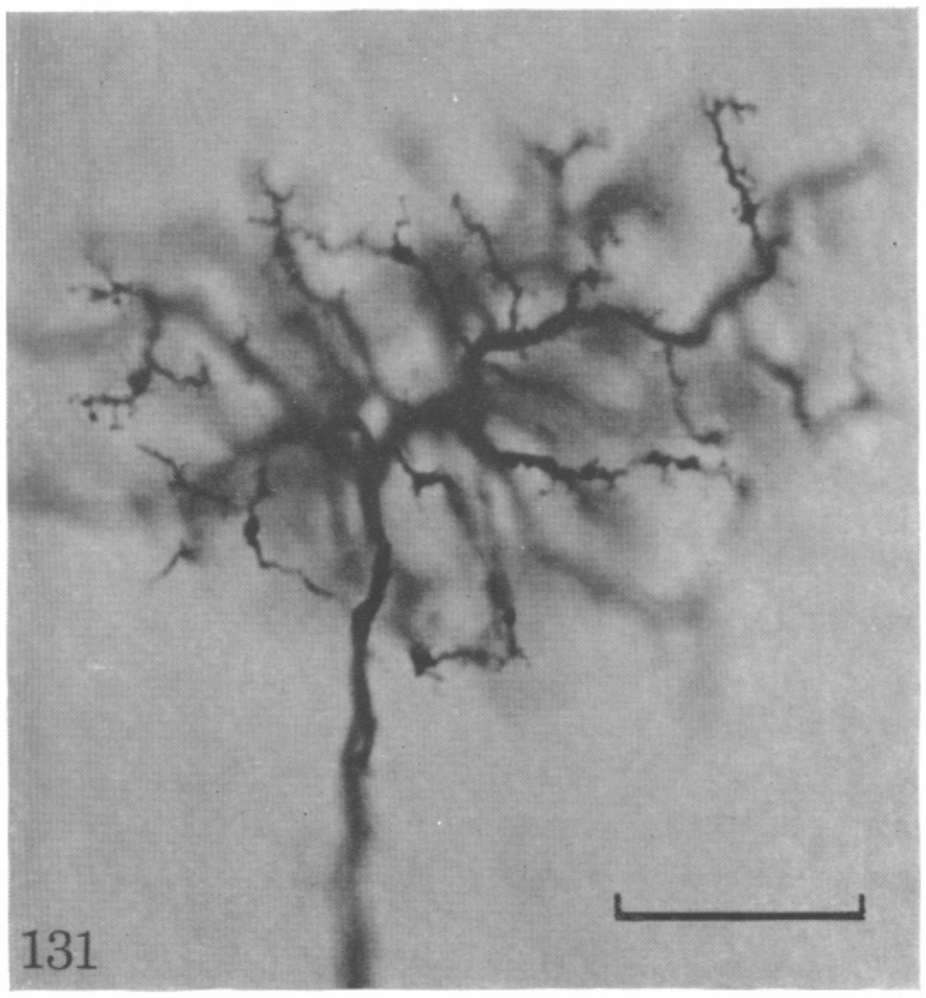

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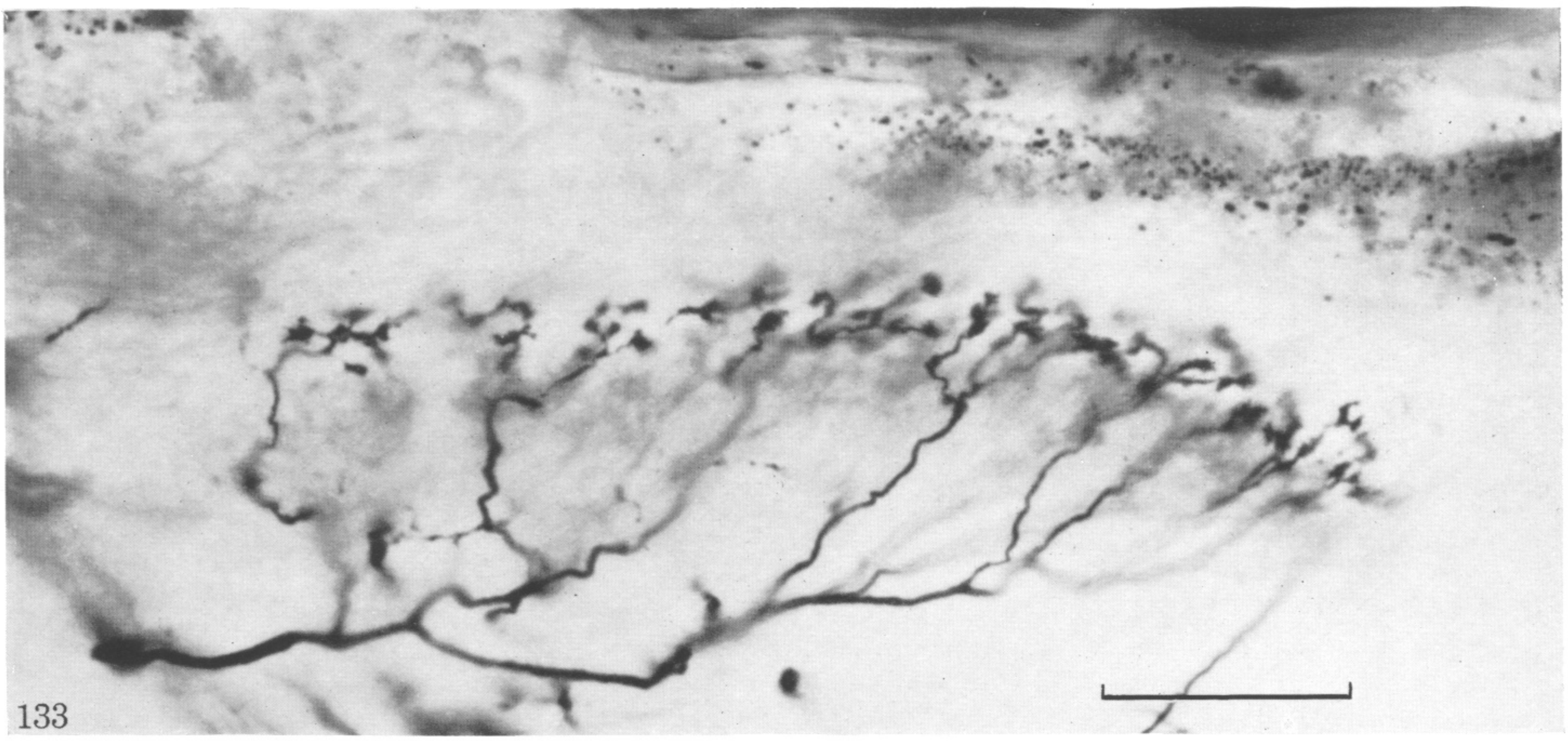

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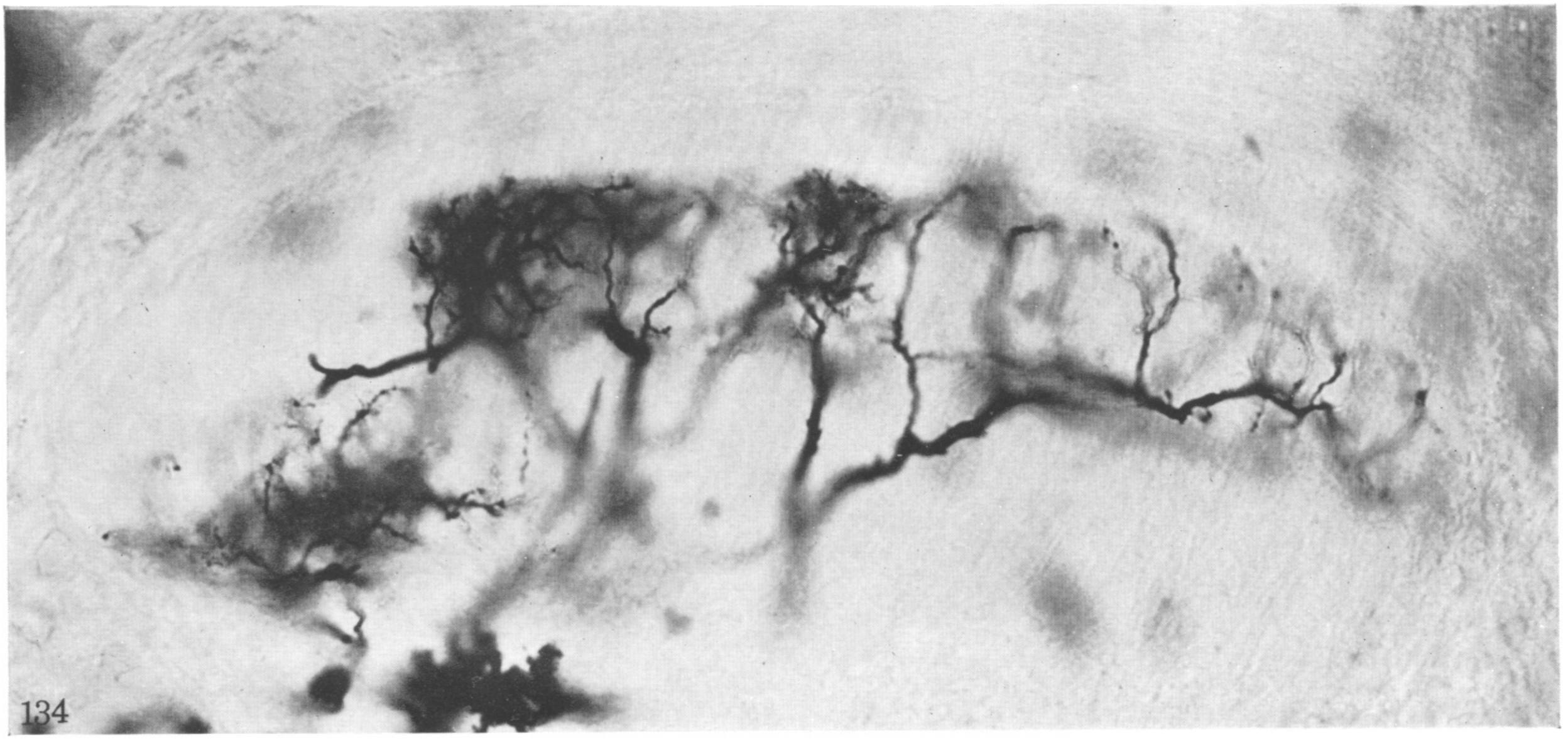

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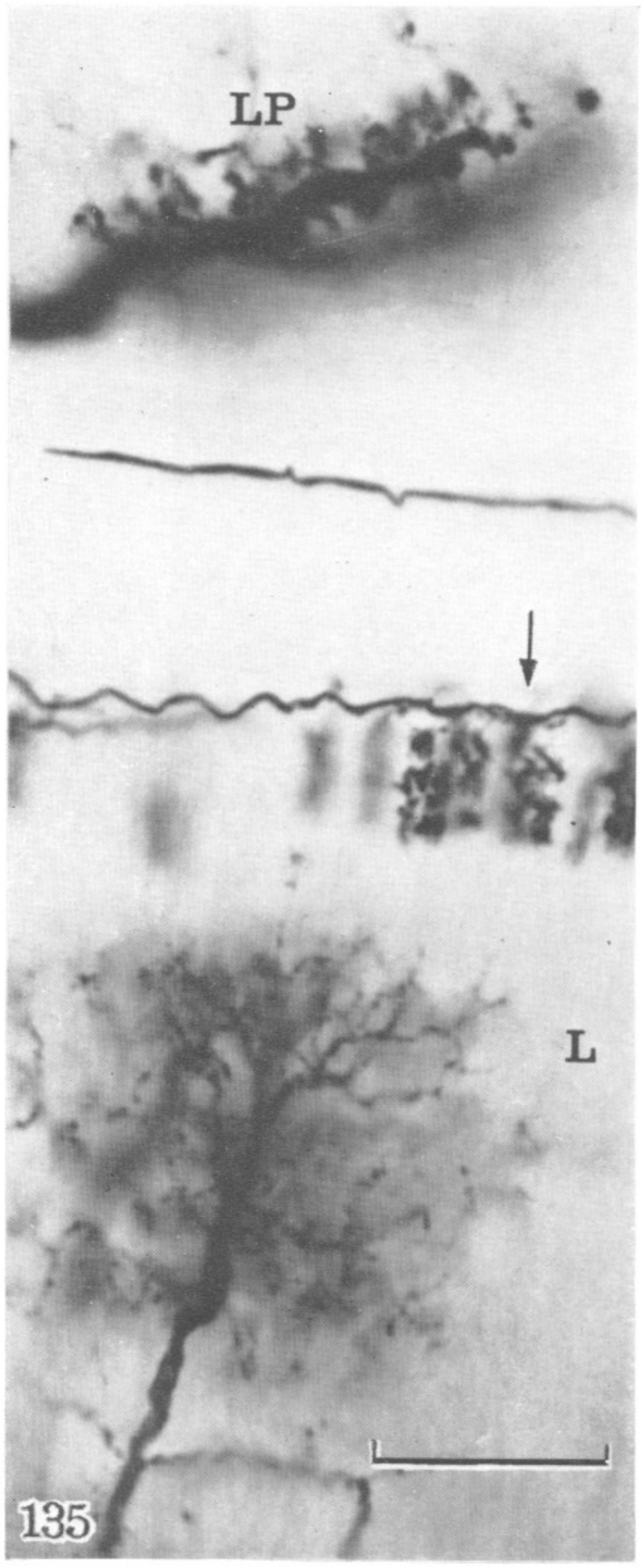

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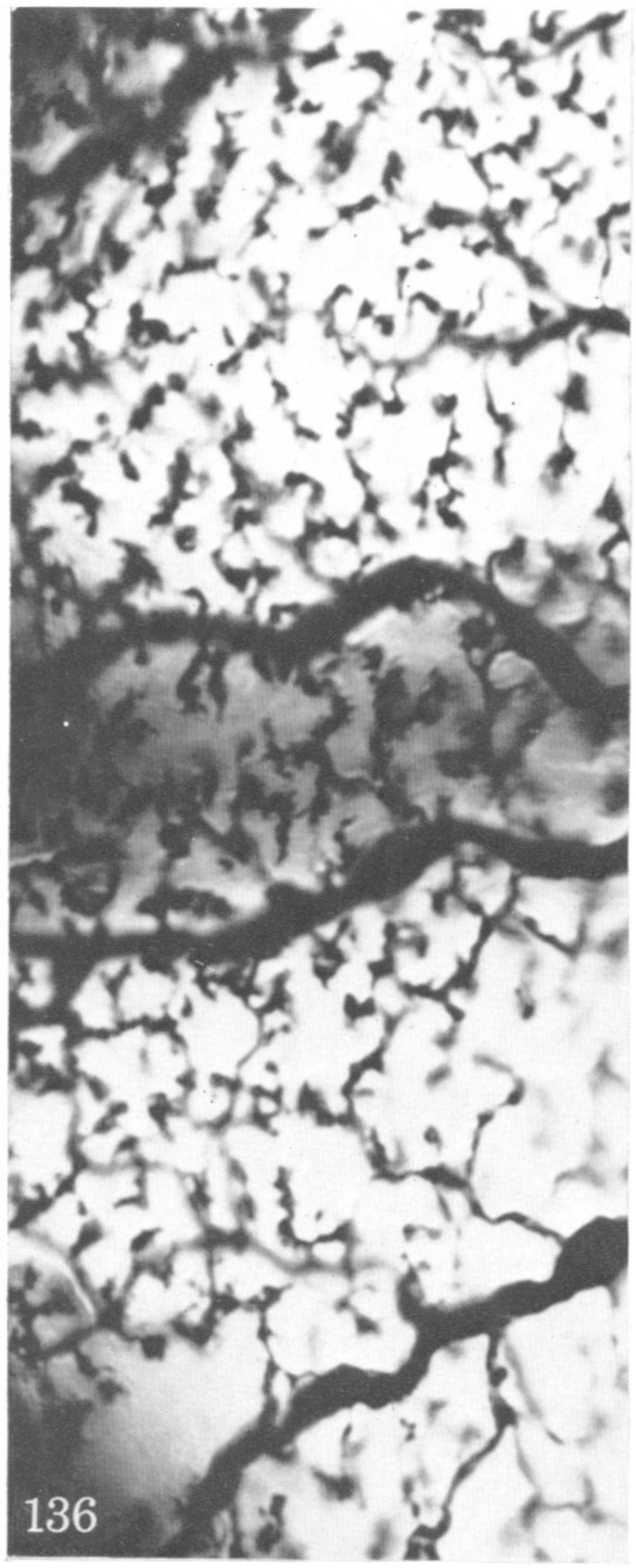

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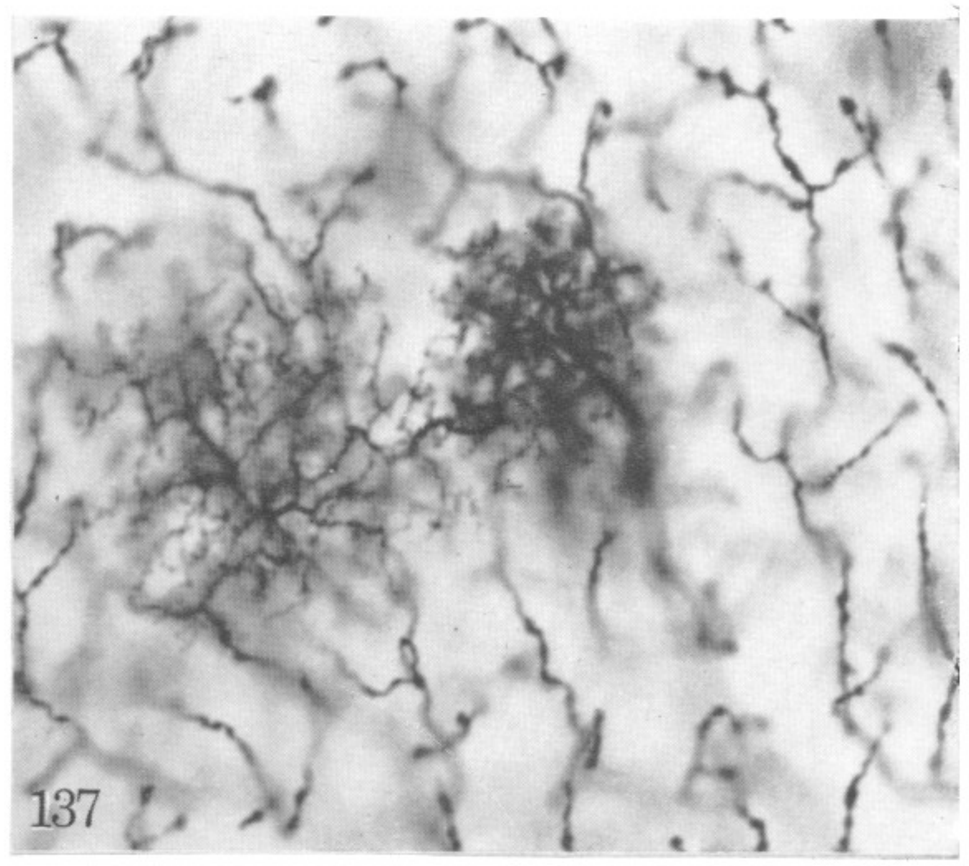

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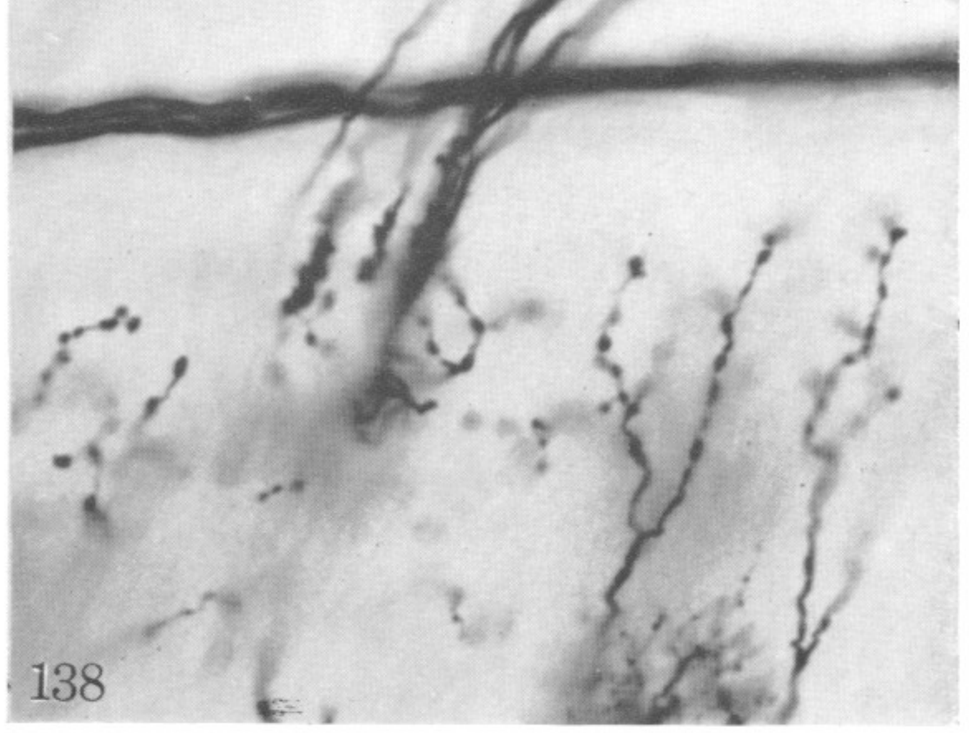

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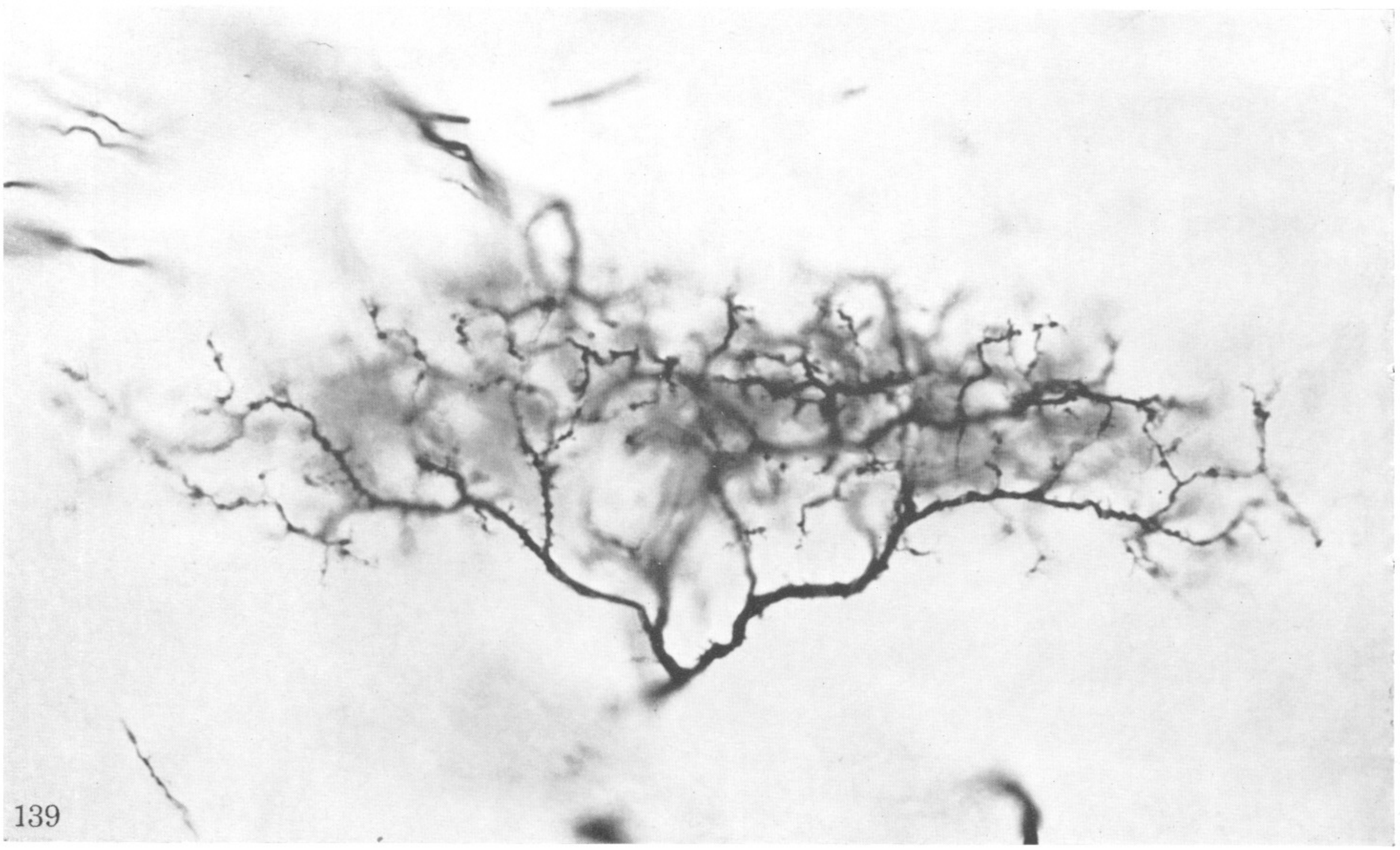

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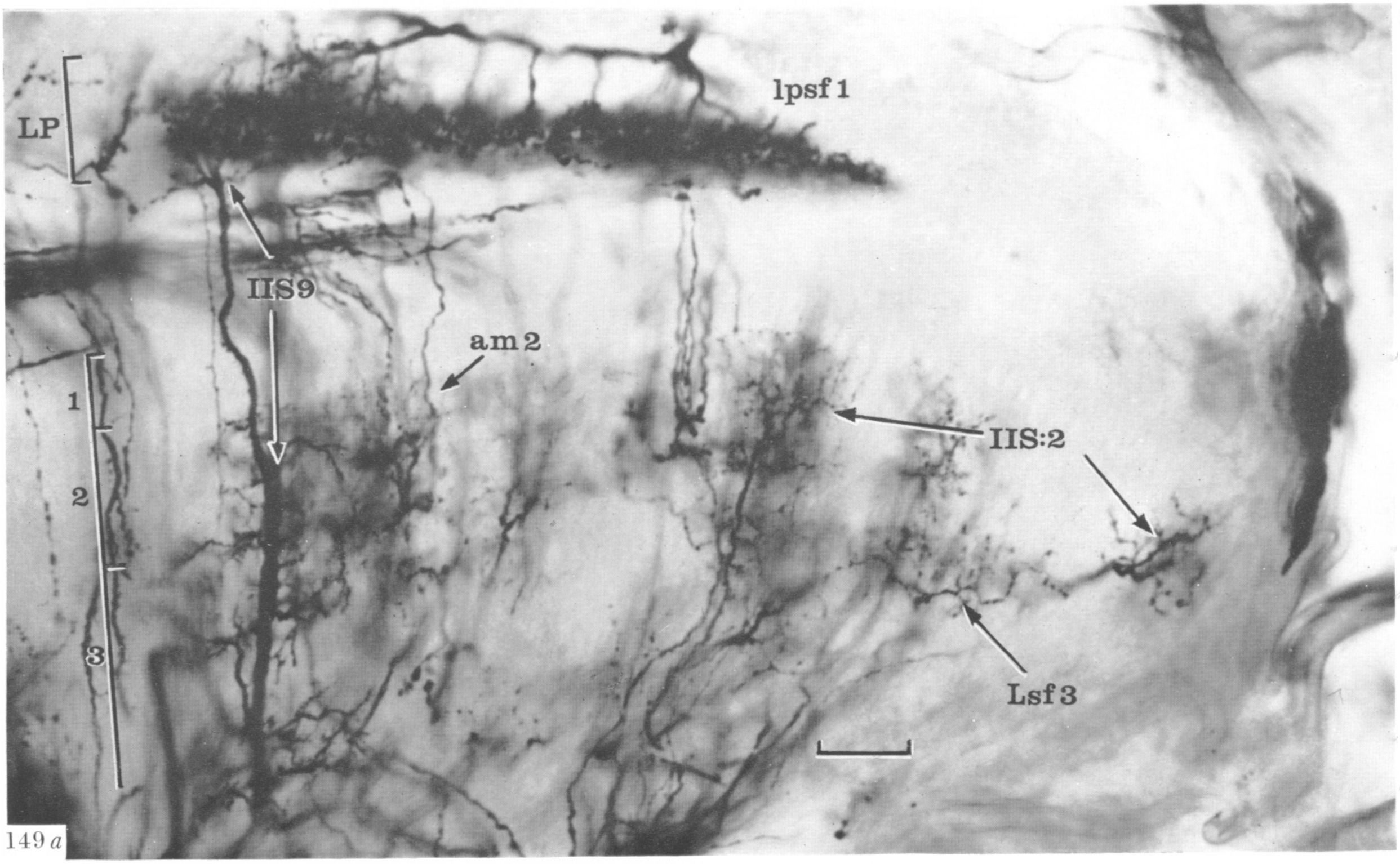

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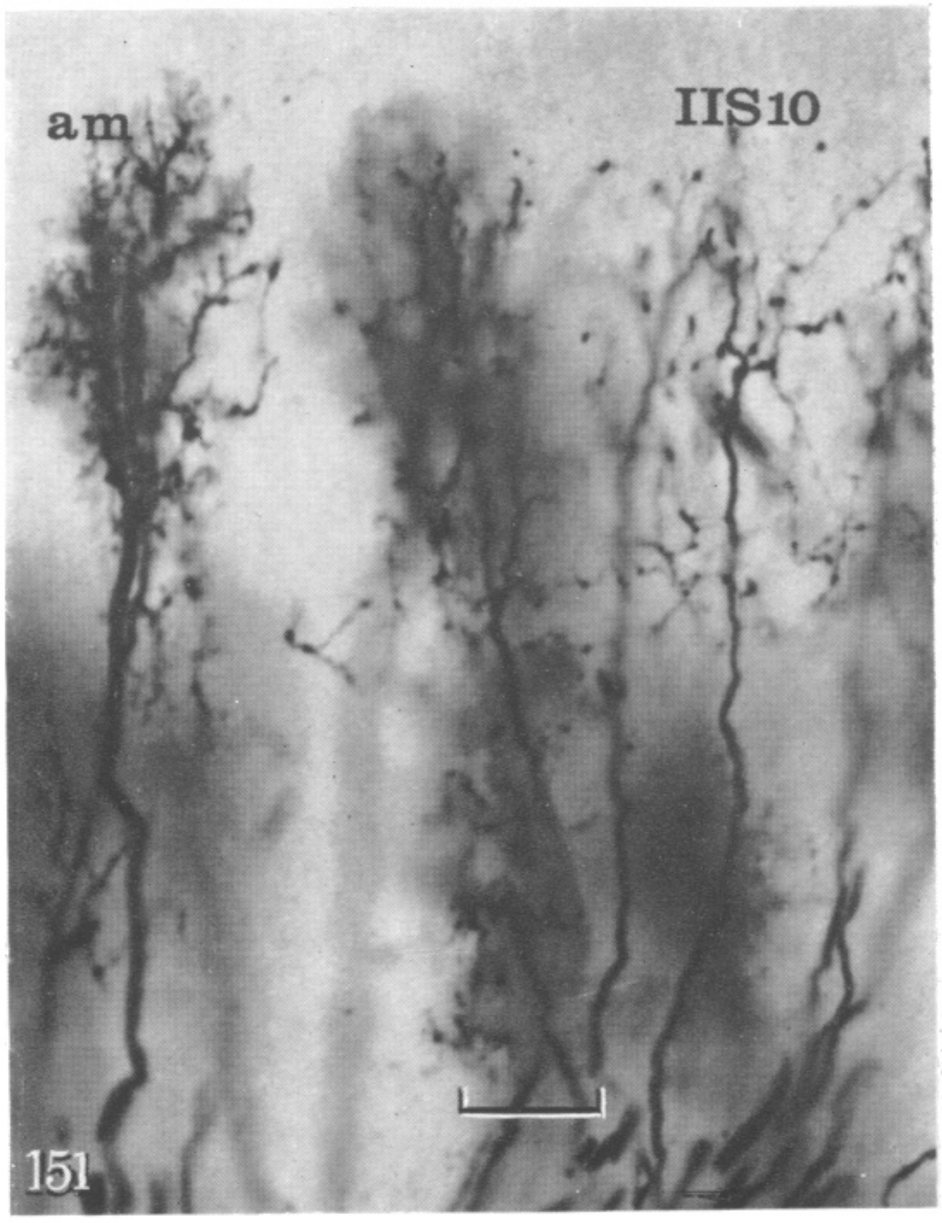
149 *b*



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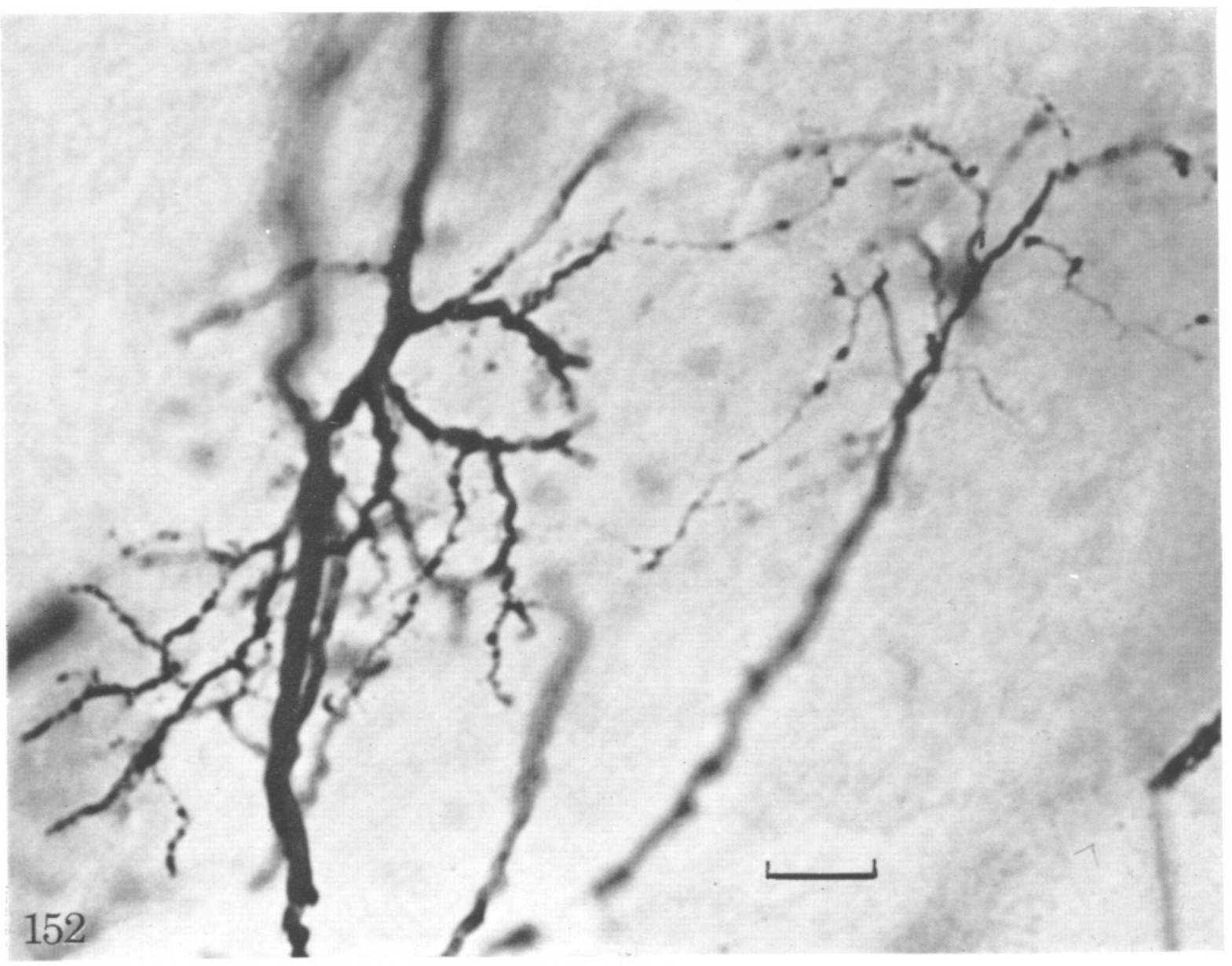

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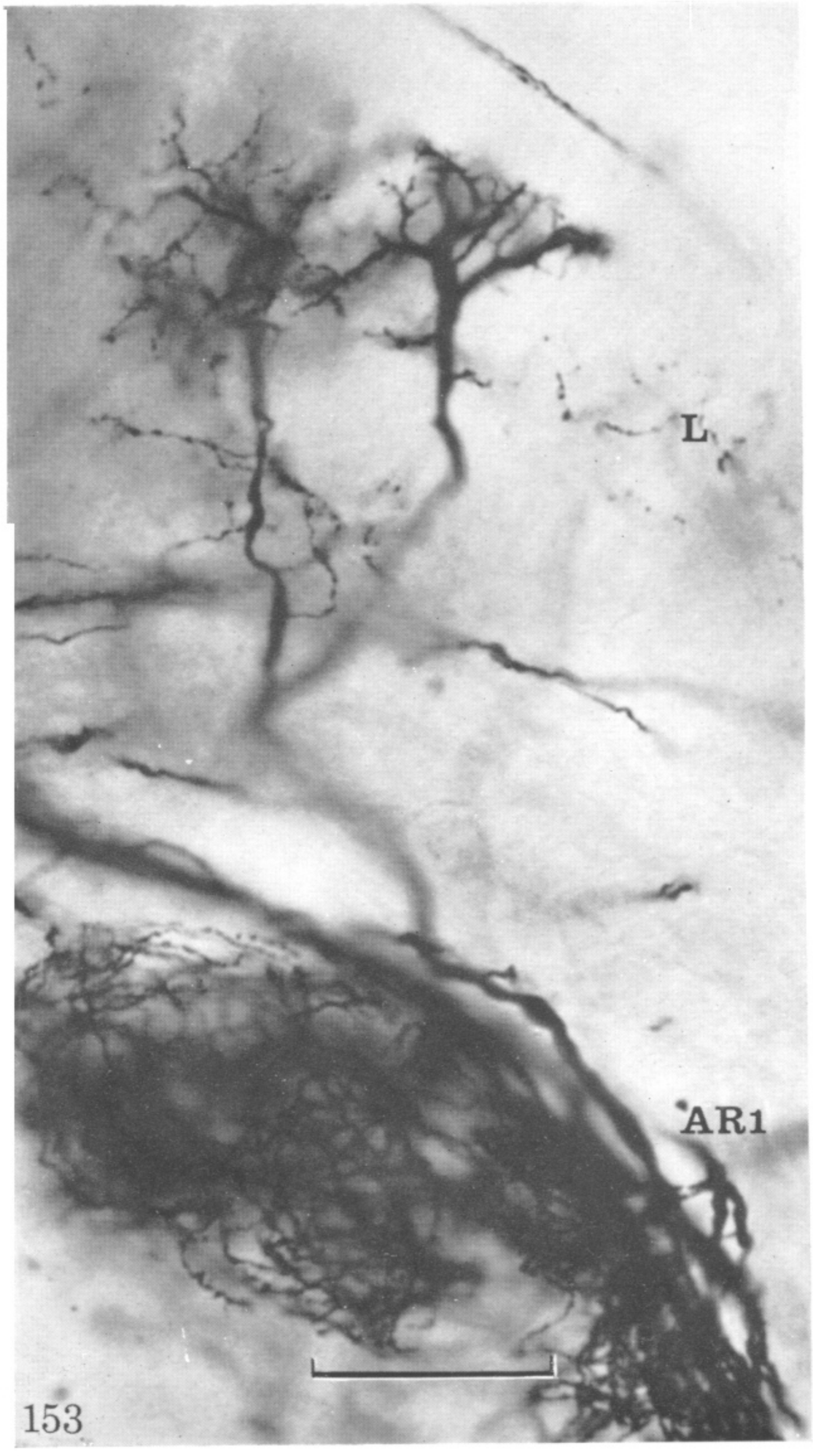

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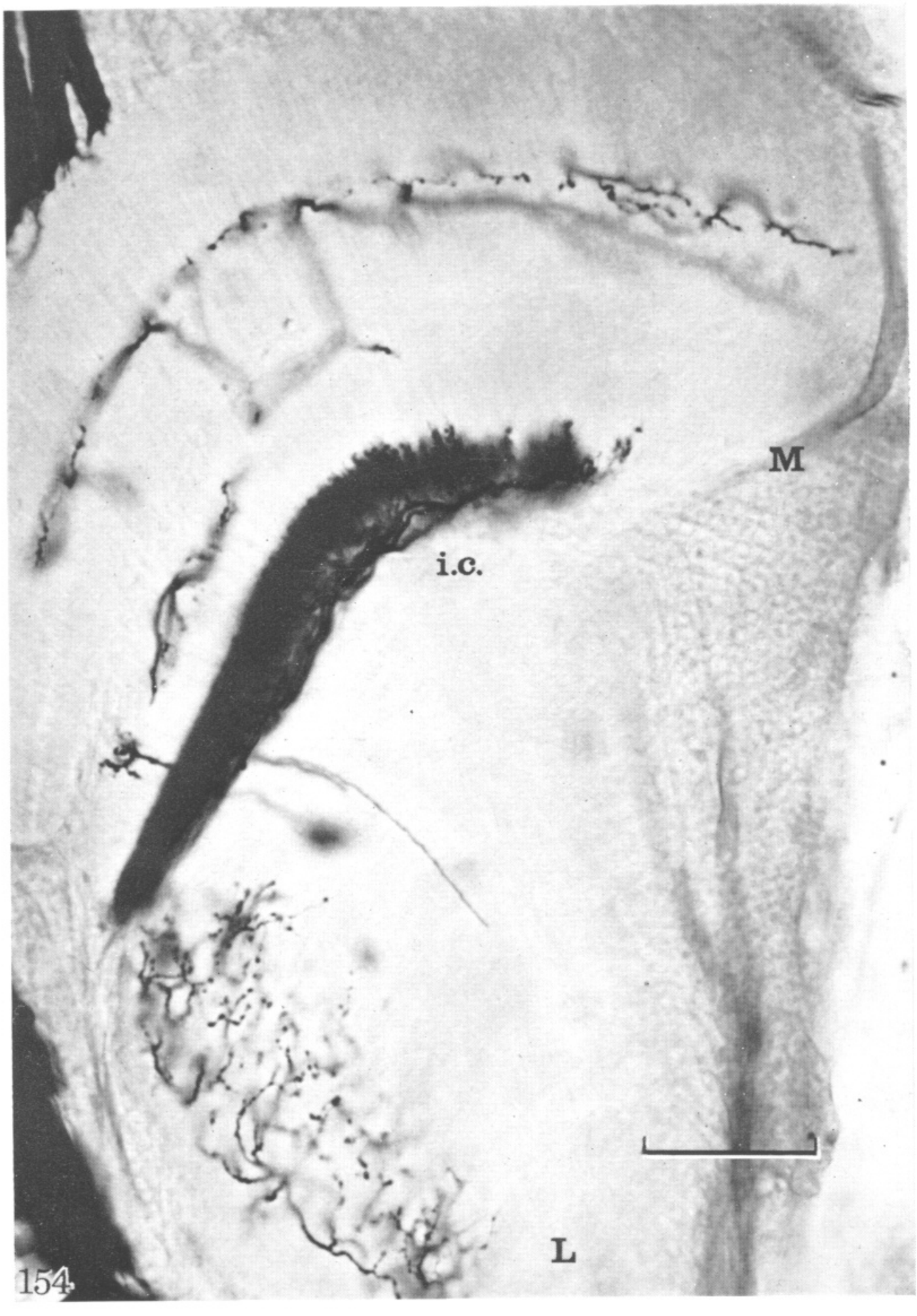

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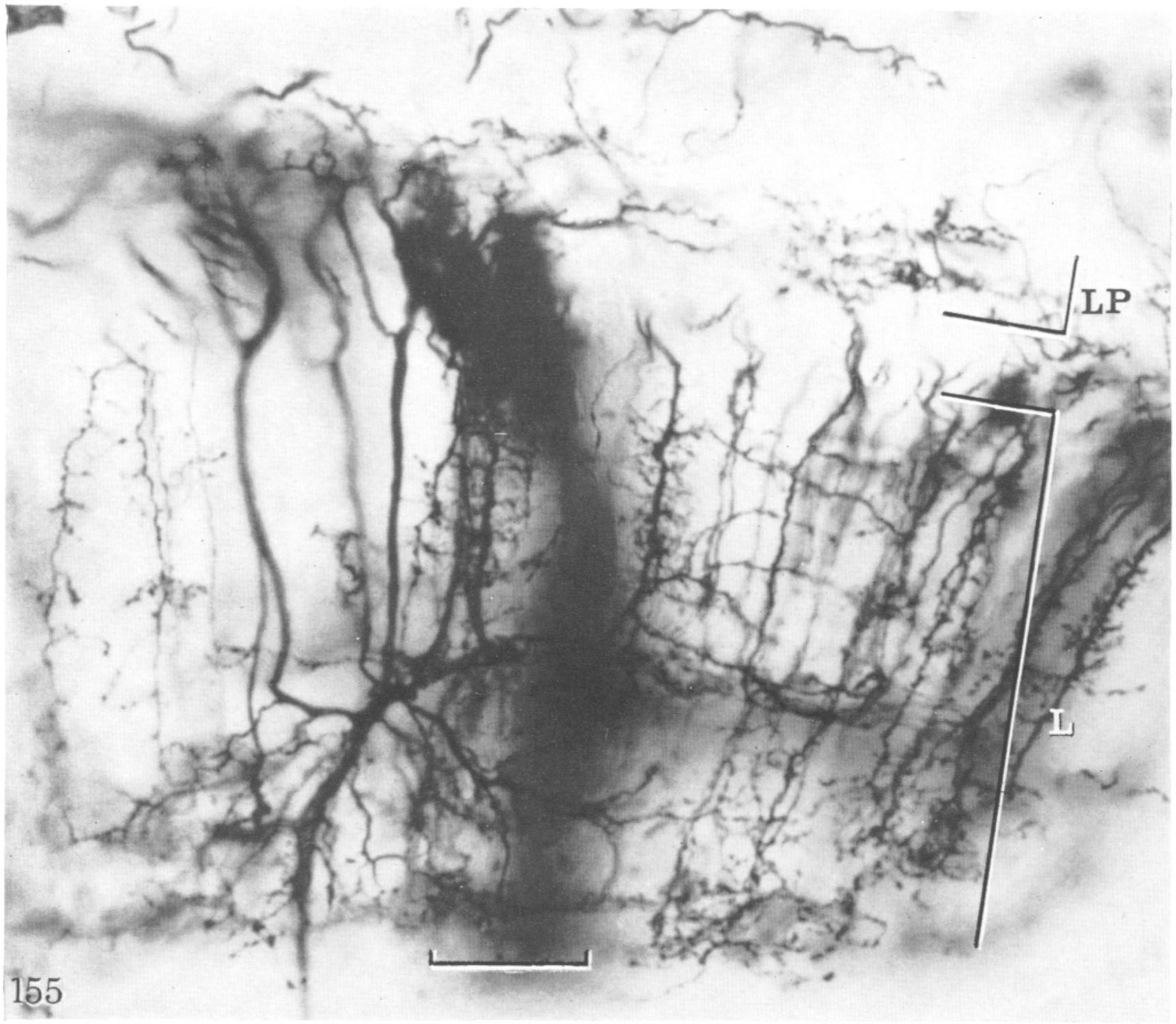

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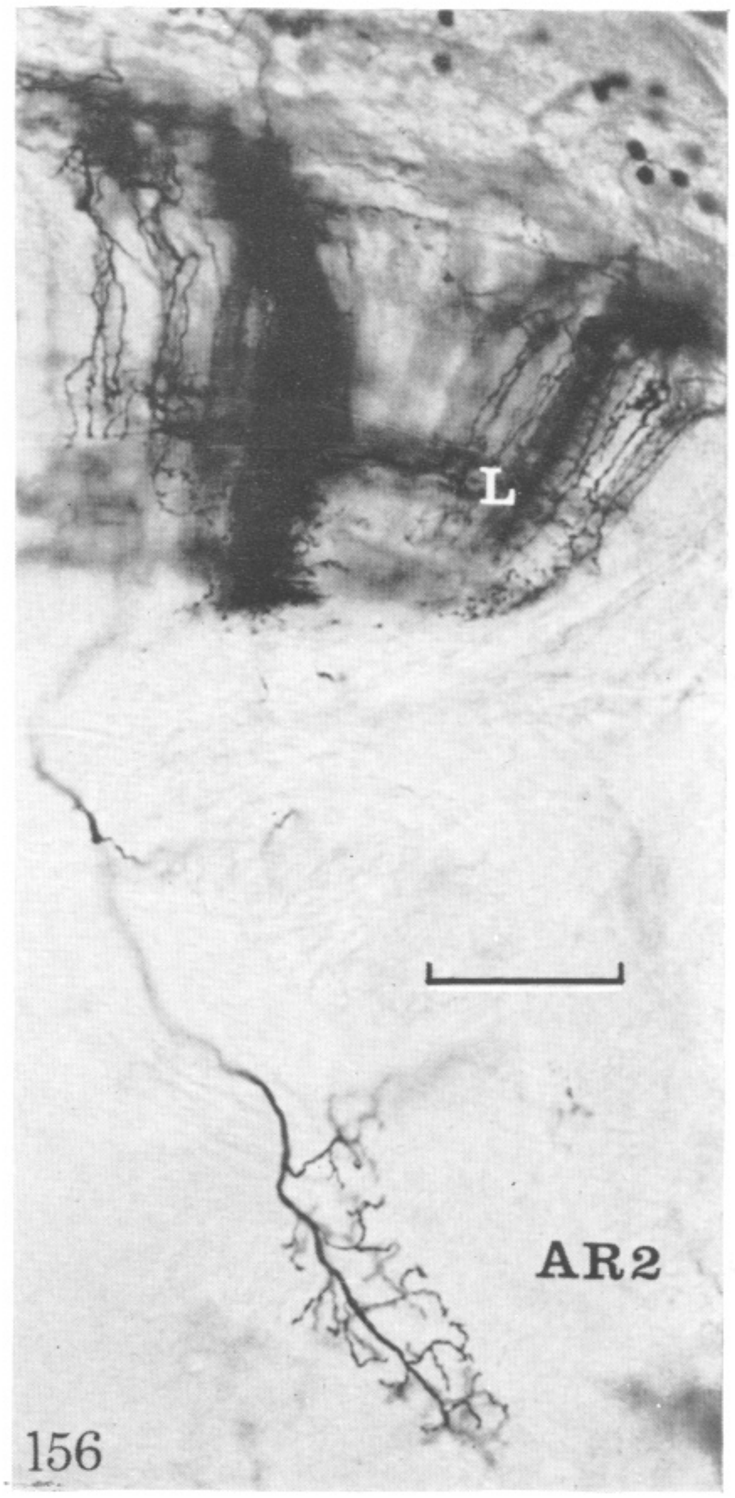

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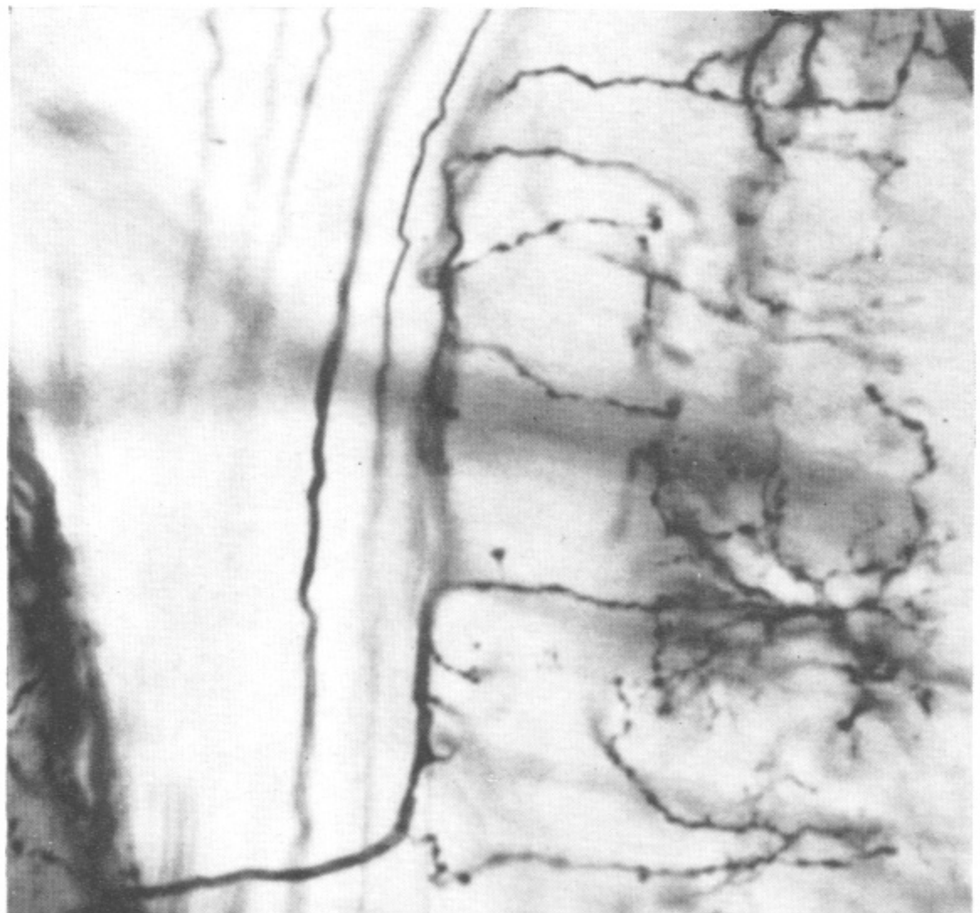

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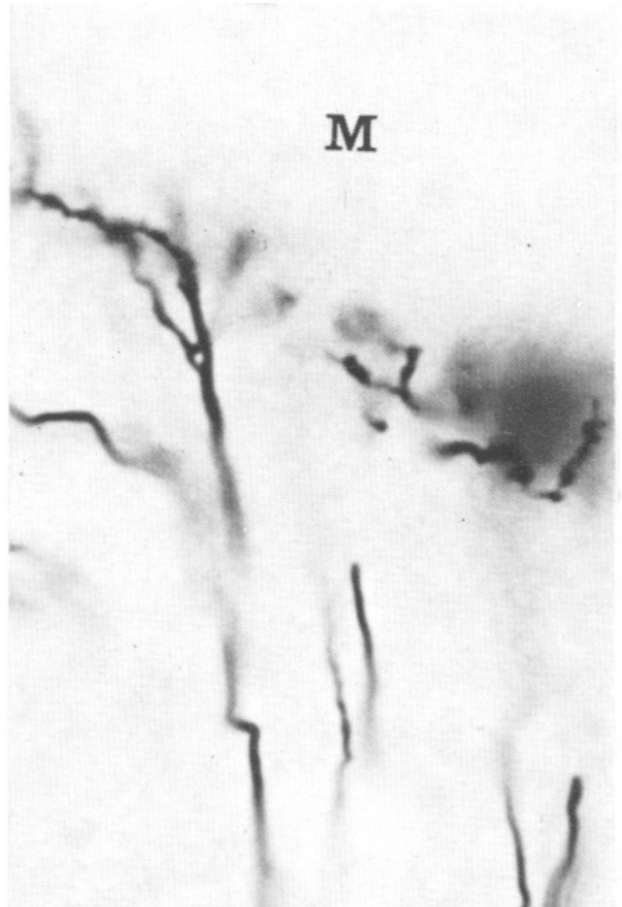

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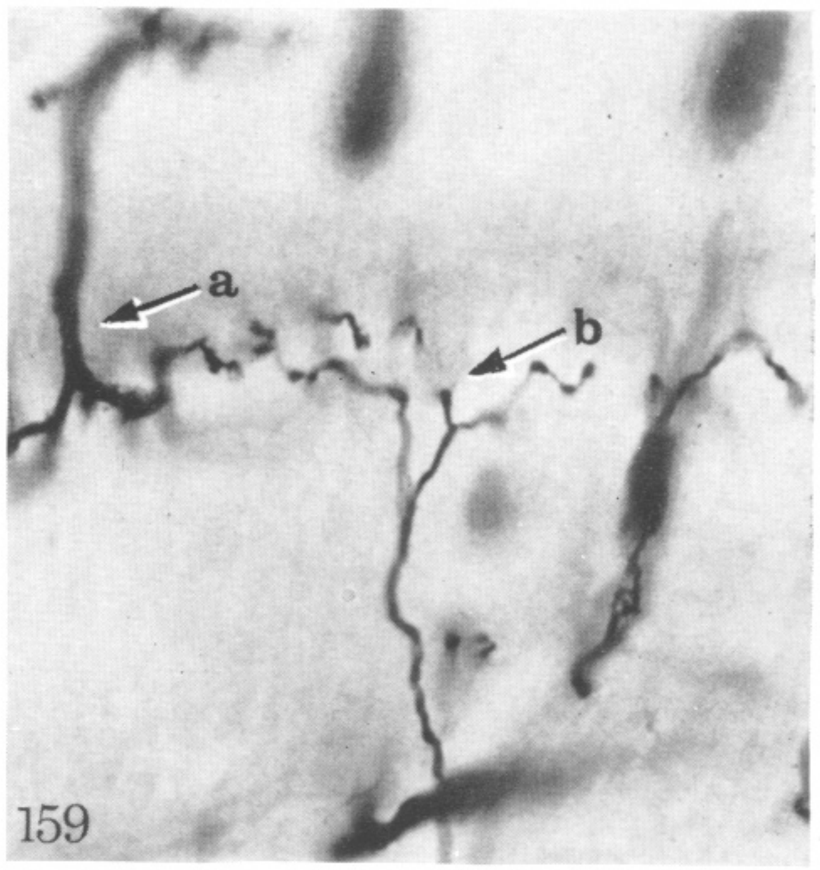

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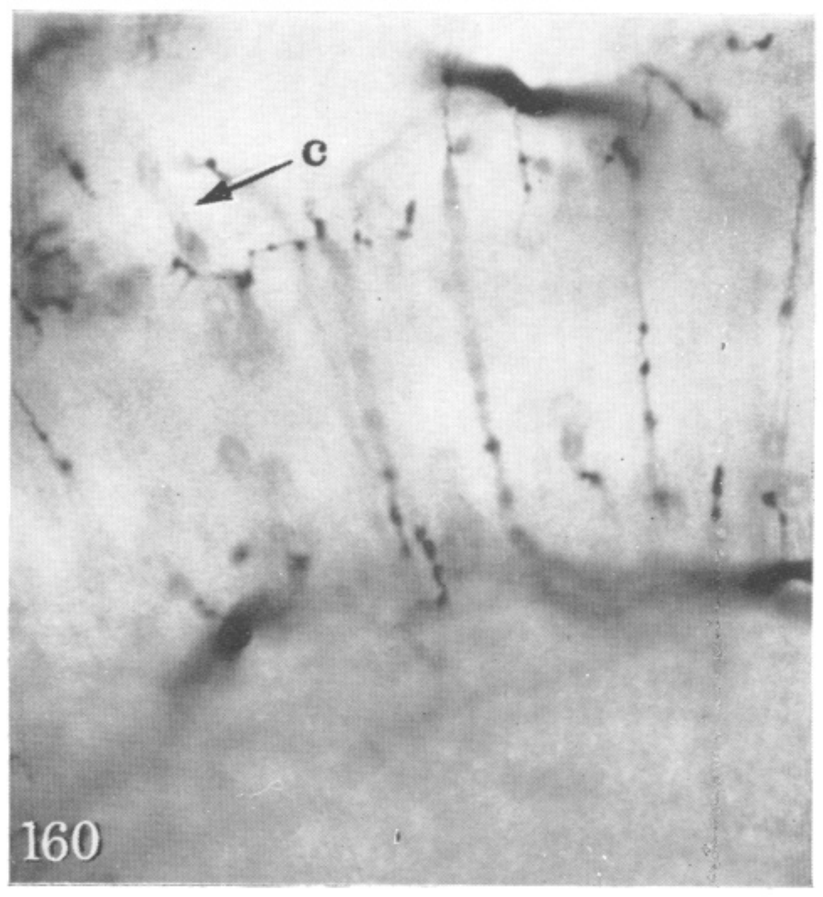

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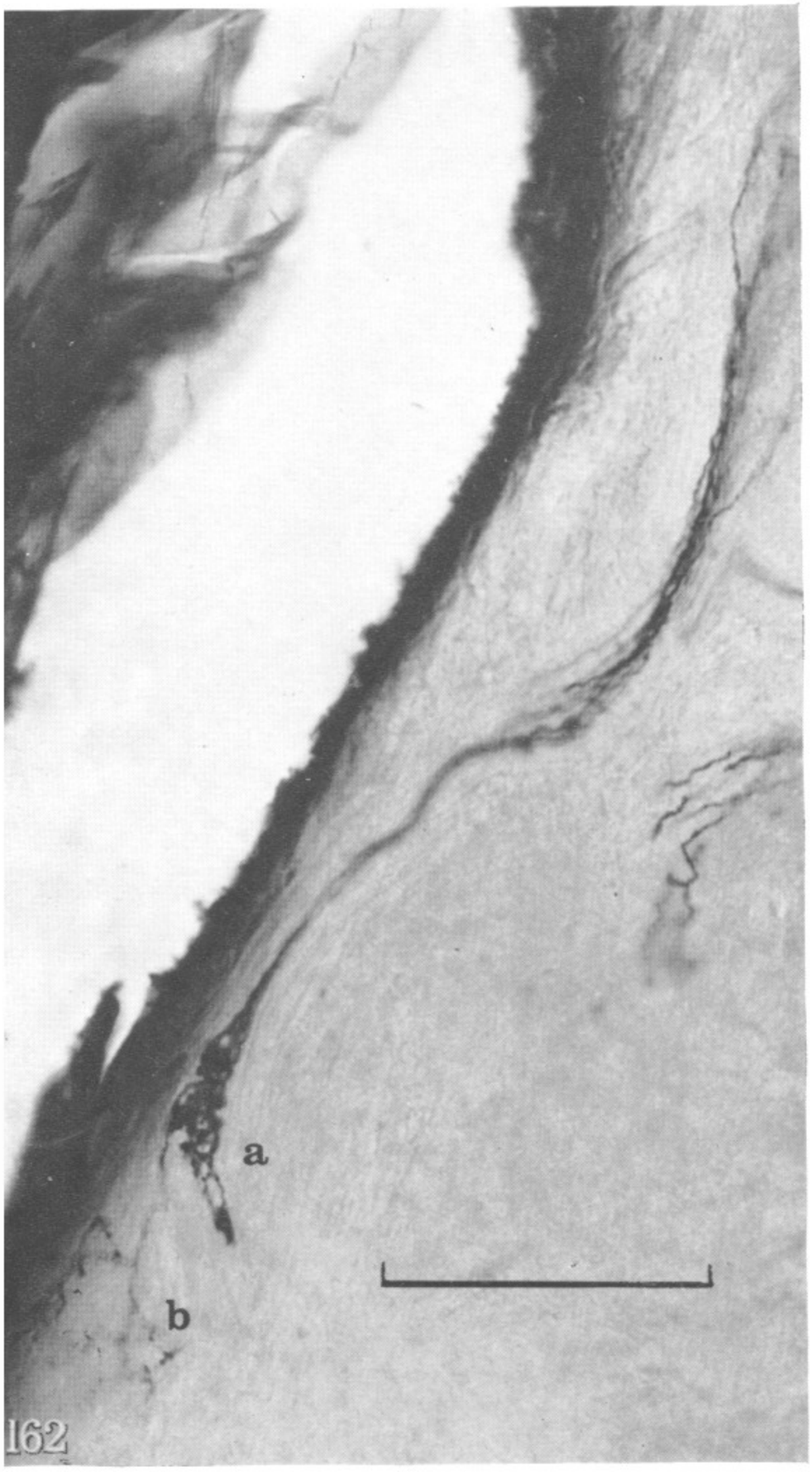

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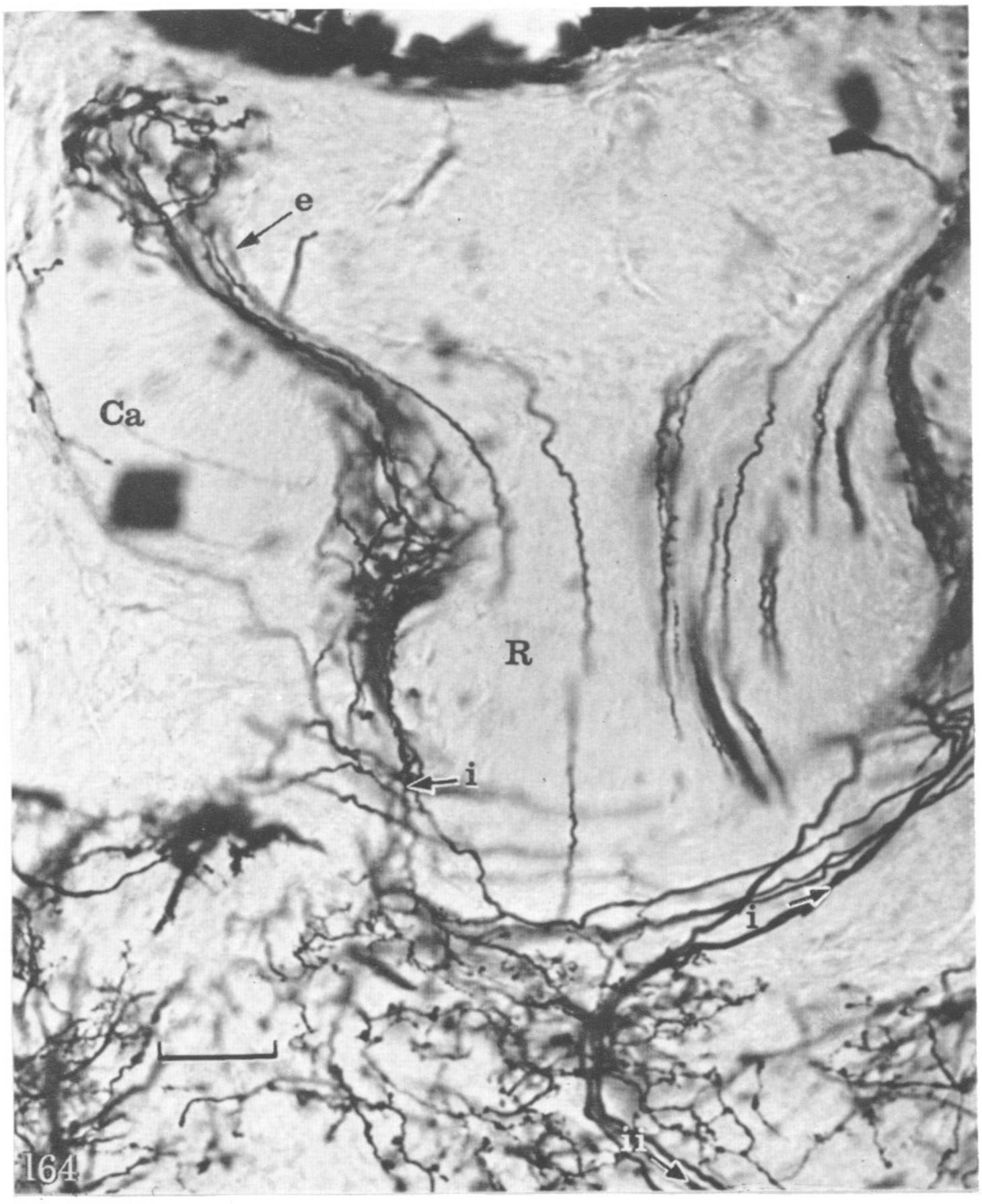

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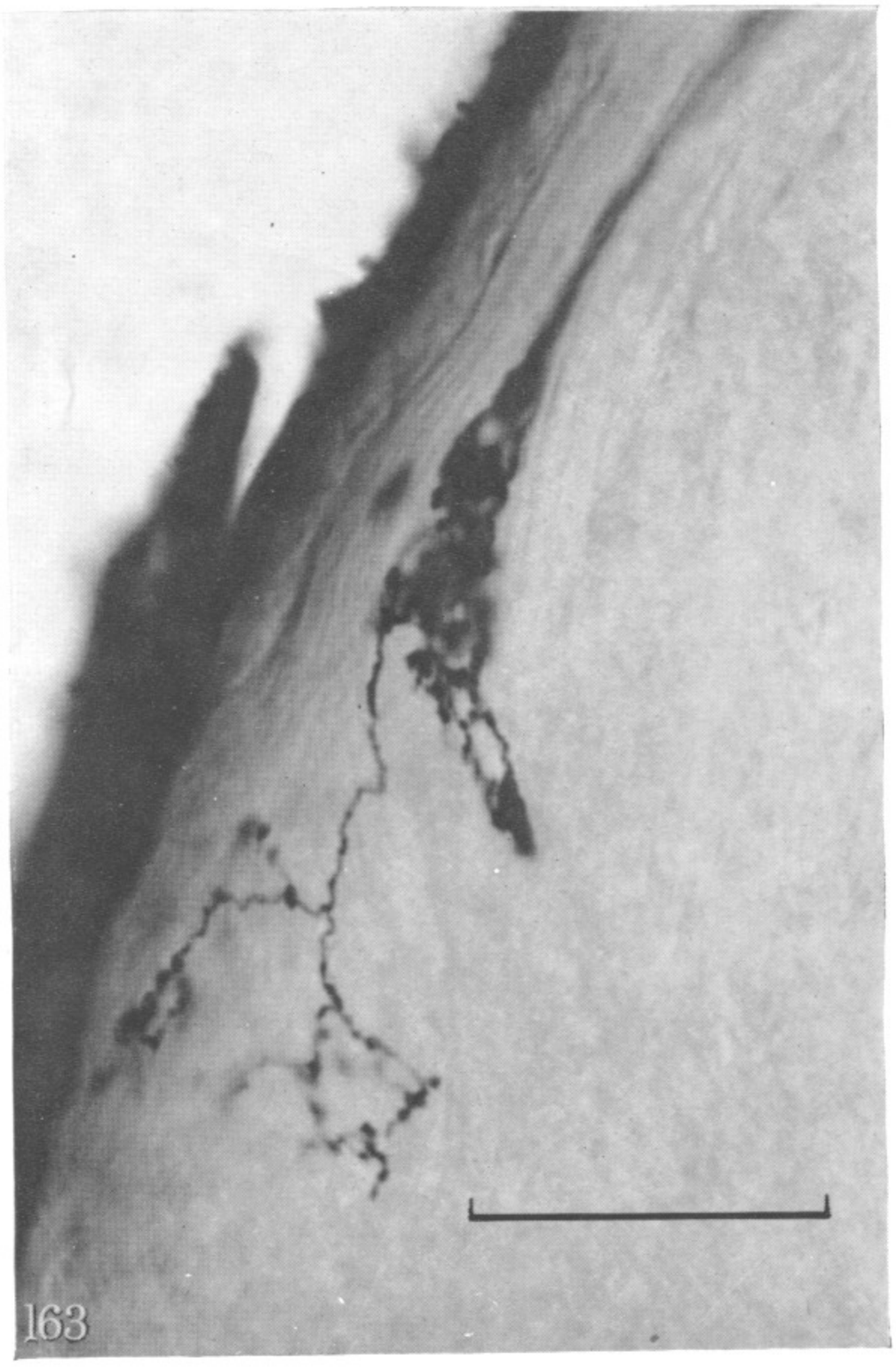

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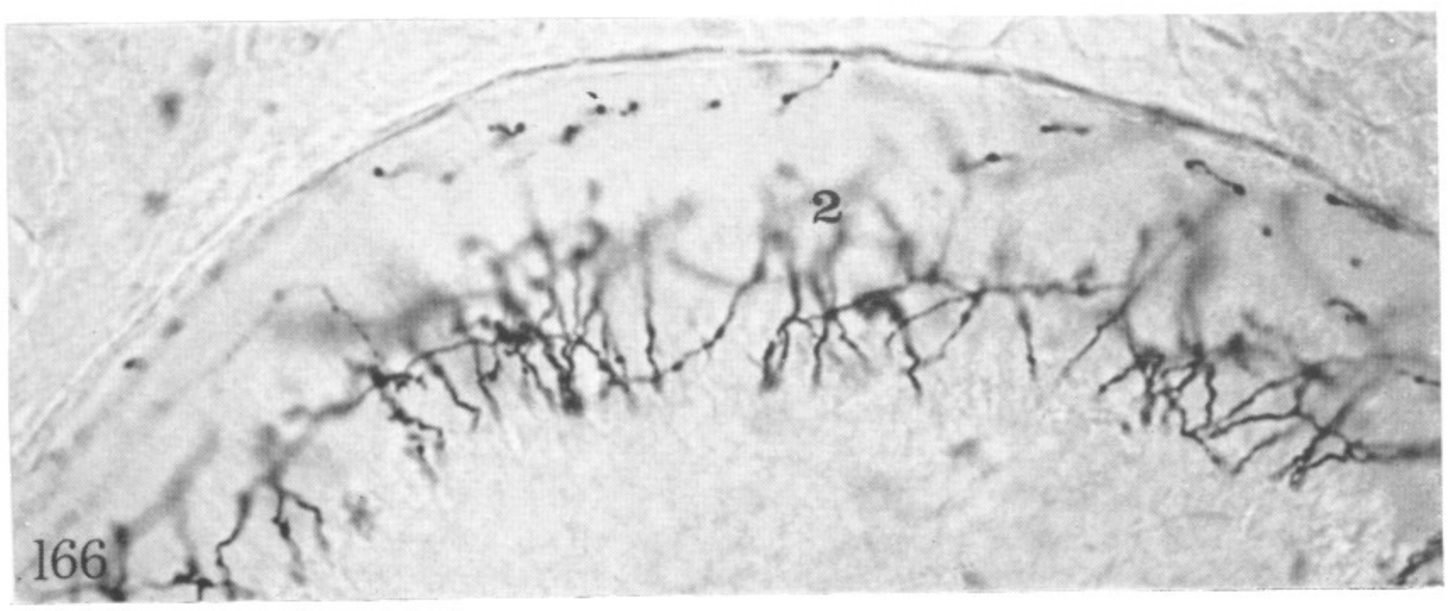

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