THE ORGANIZATION OF A CEPHALOPOD GANGLION

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[Plates 29 to 39]

CONTENTS

The stellate ganglion of cephalopods is sharply divided into a ventral part containing only large cells and a dorsal part where there are also microneurons (amacrine cells). Axons proceed from the larger cells of the ganglion to the stellar nerves in distinct dorsal and ventral roots, which join as they leave the ganglion. The ventral roots contain only large motor fibres, one arising from each of the 30 000 ventral cells. The input to this part is from less than 2000 large fibres of the pallial nerve. These fibres branch abundantly in the ventral neuropil. After severing the pallial nerve massive degeneration occurs there, producing shrinkage of the whole ganglion. There is also degeneration in the dorsal neuropil, which therefore also has input from the pallial nerve.

The dorsal roots contain some large fibres, being the axons of the larger dorsal cells. In addition, they contain numerous small fibres. These include efferent chromatophore fibres, which degenerate after severing the pallial nerve and therefore pass through the ganglion presumably without synapse. There are also afferent fibres from the periphery in the dorsal roots and, after severing stellar nerves, degeneration appears in the outer layers of the dorsal neuropil and in the pallial nerve. No degeneration occurs in the central stumps of the ventral roots after this operation.

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The trunks of the small cells of the dorsal part form characteristic bundles of fine fibres in the outer dorsal neuropil and dorsal roots. These bundles carry varicosities and make plexuses in the bases of the dorsal roots, intertwined with collaterals of the outgoing large fibres and branches of the incoming afferents from the periphery. Probably these microneurons terminate within the ganglion and are concerned with reflex modulation of the output of the dorsal neuropil.

The arrangement of the dorsal and ventral divisions of the ganglion and roots of the stellar nerves is similar in *Sepia* and *Loligo* to that in *Octopus*. There are more numerous large terminal knobs in the neuropils of these decapods and these endings are also found within the cell layers, especially in the hind part of the dorsal region.

The course of degeneration within the ganglion was followed after section of the pallial and stellar nerves in all three species, more in detail in *Octopus*. Degeneration of terminations is already advanced 15 h after severing the pallial nerve (at about 24 °C); break-up within the nerve trunks comes later. Degeneration granules have mostly disappeared 3 days after the lesion. Severed stellar nerves of *Octopus* show very abundant sprouting from the central stump, the fibres turning back to invade the ganglion and form terminal knobs in the neuropil and throughout the cell layers.

Introduction

In spite of all the information available about single neurons, the network of nerve fibres in the neuropil is still little understood in molluscs, or indeed in any other animals. Electron microscopy shows much of the finer details but the pattern of connectivity is not easily revealed in thin sections. A thorough study of the structure and input and output pathways of one ganglion should help to show how its activities are organized, and provide a basis for work with electron microscope, microelectrode and pharmacology. In particular, I have been anxious to discover the significance of the presence of small as well as large cells. Cells with their processes confined to a limited region may be called amacrines (Cajal 1933; Strausfeld & Blest 1970). The term strictly means cells without axons (Greek a = without, makro = long, inos = fibre) but in octopuses as in other invertebrates with unipolar cells precise definition of axon and dendrites is difficult. The name amacrine is appropriate and accepted, but its meaning is perhaps not generally understood. There is a case for a term to cover all small neurons whose processes, whether axons or dendrites, all remain in the same neighbourhood. 'Microneurons' would be appropriate and this term has been used with essentially this meaning by Altman (1967). The significance of such cells is still uncertain and may be illuminated by study of situations such as the stellate ganglion where they are present in some parts but not others. Understanding of their function in a peripheral ganglion may throw light on the small cells that are so characteristic of the higher nerve centres of cephalopods and are known to be concerned with the memory system (Young 1965).

The stellate ganglion is a way station on the control pathway from the central nervous system to the muscles of the mantle of cephalopods. These muscles perform the functions both of respiration and locomotion. The ganglion is divided into two distinct parts, probably serving these two functions (Lund in Young 1971). The present paper describes the differing structure of the two parts of the ganglion, one with small cells and one without them.

The connexion with the palliovisceral lobe of the central nervous system is made by the pallial nerve (also known as the mantle connective). The connexion of the ganglion with the periphery is made by some 25 stellar nerves. These thus carry final motor fibres, originating in the cells of the ganglion, to the mantle muscles. The stellar nerves also carry the motor fibres to the chromatophores and skin, but the cell bodies of these fibres are in the central nervous system; they leave in the pallial nerve and pass through the stellate ganglion without synapse (Sereni & Young 1932). There are also afferent fibres in the stellar nerves both from the skin and from the substellar organs, which are probably proprioceptors, lying below the ganglion

(Gray 1960; Alexandrowicz 1960). It will be shown that some of the afferent fibres end in the stellate ganglion, while others run through to the pallial nerve and so on to the central nervous system.

Material and methods

The work was mainly done on *Octopus vulgaris* but the ganglia of *Sepia officinalis* and *Loligo vulgaris*, *L. forbesi* and *L. pealeii* were shown to have the same organization, in spite of the presence of giant nerve fibres.

The ganglia were all stained with Cajal's silver method, mostly after fixation in formaldehyde (Stephens 1971). Some of the observations have been made on material prepared for the study made forty years ago (Sereni & Young 1932). This included long series of animals in which the pallial or stellar nerves had been cut and time allowed for degeneration. The significance of the changes that can be observed in the ganglia could not have been appreciated at that time, although the staining is excellent. The operations were mostly done in June and July 1930 and 1931. The temperature of the sea water at Naples in the summer is around 23 °C, and degenerative changes are very rapid. Some experiments with *Sepia* were made in August and September at Plymouth, where the water temperature is around 17 °C. The experiments in which the stellar nerves of *Loligo* were cut were made at Woods Hole during the summer of 1961 (at about 19 °C).

Estimates of the number of nerve cells in the ganglion of *Octopus* were made by measuring and counting on photographs of one whole transverse section of a series, at a magnification of $\times 400$. It is possible to distinguish between the nuclei of small neurons and glia. The former have a regular outline and clear nucleoplasm. The latter are irregular and more granular. Correction was made for the inclusion of fragments in the section (Abercrombie 1946). The totals in the dorsal and ventral parts were estimated by counting the number of sections of the ganglion in the series, allowing for tapering at the ends.

The number of fibres in the pallial and stellar nerves were estimated by measurement and counting on transverse sections at $\times 1000$. Only the large fibres making the input to the ventral part were counted for the pallial nerve. For the stellar nerves a single trunk was chosen and as many as possible of the fibres in the dorsal and ventral roots counted. The ventral root estimate should be reasonably correct but it is impossible by light microscopy to estimate the small fibres in the dorsal root. The totals for all the nerves were obtained by assuming the trunk counted to be a typical sample of the total of 26 stellar nerves. This introduces further inaccuracies, since the nerves are of very unequal sizes. However, the trunk chosen was of about average size and the inaccuracy was probably not large.

A. The stellate ganglion of *Octopus*

1. *Division of the ganglion*

The ganglion is sharply divided into two parts approximately in the horizontal plane (figures 1, 2, plate 29; and 39, plate 33). The ventral part (more strictly ventro-medial) is composed only of relatively large cells (Lund 1971). The dorsal part contains many small, as well as large cell bodies. The ventral part is that facing the cavity of the mantle and is thus exposed when the mantle is opened. The pallial nerve enters through the ventral, large-celled region. The dorsal, small-celled part is close to the muscles and the stellar nerves seem to arise

from it. Actually each stellar nerve has two roots, one from each part of the ganglion (figures 2, 5, plate 29). The ventral roots contain only large fibres, the dorsal a mixture of large and small fibres. The two join close to the surface of the ganglion, but the separate bundles can be recognized within the nerves for a short distance more peripherally (figure 3). In *Octopus dofleini* a wall of cells partly separates the two sorts of neuropil.

2. *The ventral division and ventral roots*

The ventral part of the ganglion was estimated to contain 31 500 cells, distributed as in table 1. The diameters are of whole neurons measured transverse to the long axis. Note that there are no very small cells and that the distribution is perhaps bimodal, with fewer cells around 25 μm. The estimate for the number of fibres in the ventral roots of the stellar nerves gave 31 600 (table 2). The closeness of the agreement must be accidental, but it seems likely that each cell of the ventral part of the ganglion gives rise to one ventral root nerve fibre.

TABLE 1. CELLS OF THE STELLATE GANGLION

Stellate ganglion of *Octopus*. Numbers and diameters of cells

diam./μm	ventral side	dorsal side
< 5	0	16 600
10	0	36 000
15	8 100	16 400
20	5 000	8 900
25	3 500	5 900
30	5 400	1 600
35	4 800	1 050
40	3 000	450
45	1 200	450
50	300	150
55	100	150
60	100	150
	31 500	87 800

TABLE 2. ALL STELLAR NERVES OF ONE SIDE

diam./μm	ventral roots	dorsal roots
2	2 600	10 280 (really far more)
3	4 240	4 960
4	5 680	4 440
5	6 880	2 720
6	2 520	1 640
7	4 760	440
8	4 040	40
9	520	120
10	280	—
11	40	—
	31 560	24 640 (really far more)

3. *The ventral neuropil*

The ventral part of the ganglion receives from the pallial nerve bundles of fibres containing many of the large fibres of the nerve. These bundles can be seen to distribute in the ventral part of the neuropil, each dividing several times (figure 4). Some bundles of large fibres run to each region of the ventral neuropil and some individual fibres send branches to widely separate parts of the neuropil (figure 4). Counts were made of the composition of the bundles of large fibres

in the pallial nerve. The count is difficult because at the level close to the ganglion, where it can be approximately determined which of the large-fibre bundles run to the ventral neuropil, they are not cut strictly transversely. Moreover, the bundles going to ventral and dorsal neuropils are not easy to separate. The count therefore probably includes some fibres that did not really go to the ventral neuropil.

TABLE 3. PALLIAL NERVE: FIBRES RUNNING TOWARDS THE VENTRAL NEUROPIL

diam./μm	number
2	940
3	570
4	250
5	150
6	70
7	70
8	50
9	20
	2120

Evidently there are far fewer fibres entering the ventral neuropil from the pallial nerve than leaving it in the stellar nerves. This 2000 may indeed include many fibres that do not properly belong here, and therefore the whole ventral neuropil is probably activated by a few hundred relatively large fibres. These preganglionic fibres proceed radially throughout the ventral neuropil. Their finest branches have not been seen by light microscopy but the electron microscopy results of Barlow & Gray (1971) showed that they end in contact with collateral spines of dendrites of cells of the ganglion.

The neuropil of the two parts of the ganglion differs markedly with silver staining (figure 5). The ventral part shows a coarse uniform plexus of brown fibres, somewhat more darkly stained at the outer edge. These fibres are mostly branches of the preganglionic fibres entering from the pallial nerve. The lighter 'holes' in the neuropil contain the trunks of the large cells of this part of the ganglion, whose processes become the fibres of the ventral roots. They stain only lightly with silver and are hard to follow (figure 6). Each trunk gives many branches, one often arises shortly after entry to the neuropil, others more deeply. The complete tree of one cell has never been seen (Golgi methods have not been successful with this ganglion). The form of the cells has been approximately reconstructed from the study of this neuropil after degeneration of all the presynaptic fibres by severing the pallial nerve, and is shown diagrammatically in figure 7. The main trunk proceeds to the centre of the ganglion and there may swell into quite a large bulb, from which branches arise (figure 8, plate 29). Although the main trunks stain poorly they give off darkly stained 'dendritic' branches, which often run for great distances through the neuropil (figures 9, plate 29; 10, plate 30). These then divide further and the tree of each cell probably spreads through a large part of the ventral neuropil. These branches mostly appear smooth with the light microscope, but there are signs of collateral spines. Presumably the fine spines seen with the electron microscope are too small to show with the light microscope. In the ganglia with pallial nerve degeneration some presumed dendrites end in quite large masses (figure 11, plate 30). It is not clear whether these are normal or the result of transneuronal changes (see p. 419). More usually the dendrites taper away into exceedingly fine fibres (figure 9).

The main trunks of the cells join into bundles, often running tangentially for some distance.

Thus the cells for many of the fibres of the posterior stellar nerves lie near the front of the ganglion (figure 12, plate 30). These ventral root fibres do not usually give collaterals near the exit from the neuropil as the dorsal root fibres do (p. 416).

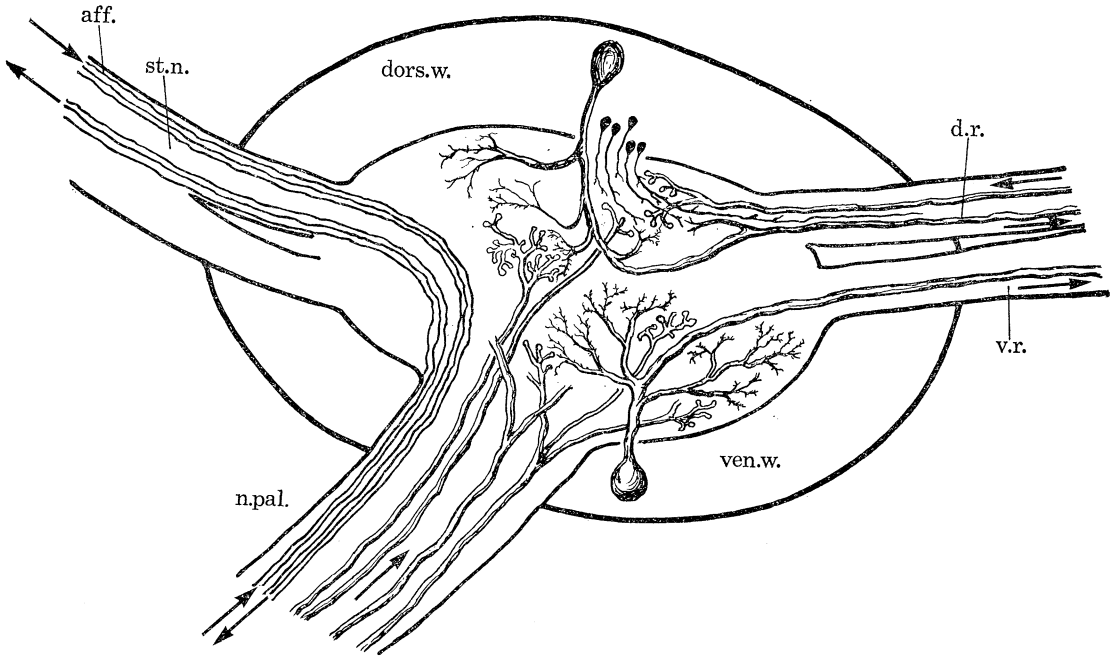

FIGURE 7. Diagram of the probable connexions in the stellate ganglion. It should be emphasized that the details of the finer branching are still speculative.

The outer neuropil of the ventral region is not sharply marked off from the inner, but it may contain rather more tangential fibres. Terminal boutons are seldom seen with the light microscope but some fine fibres of unknown nature accompany the main trunks of the cells (figure 6). Few or no incoming nerve fibres enter the cell layers.

There is of course abundant glia in the ganglion and a network of collagen-containing extracellular spaces known as gliovascular tissue (Stephens & Young 1969).

4. *The dorsal division and dorsal roots*

The estimates of the numbers and sizes of cells in the dorsal part of the ganglion are in table 1. The number of large cells is similar to that in the ventral part. The total number is much

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DESCRIPTION OF PLATE 29

All figures are of the stellate ganglion and all are stained with Cajal's method (except figure 21). Figures 1 to 49 are of *Octopus vulgaris*, 50 to 73 are *Sepia officinalis* and 74 to 89 *Loligo*.

FIGURES 1, 2. Sagittal sections showing the pallial and stellar nerves and the two parts of the ganglion.

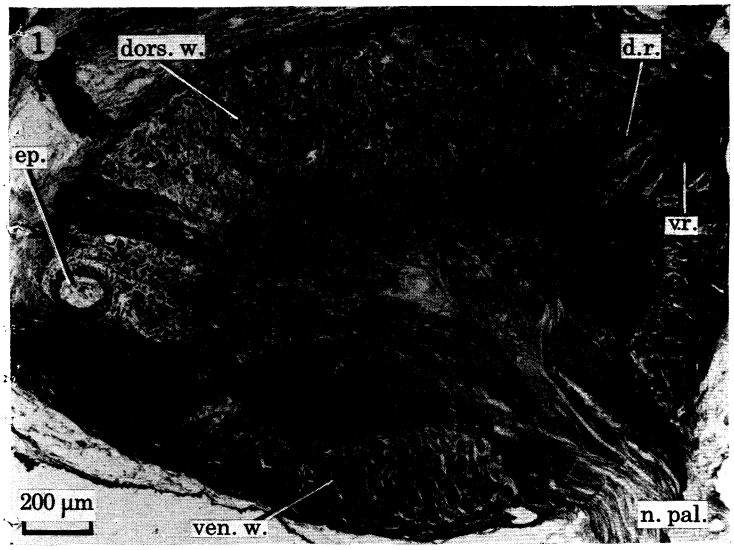
FIGURE 3. Cross-section of a small stellar nerve shortly after it leaves the ganglion.

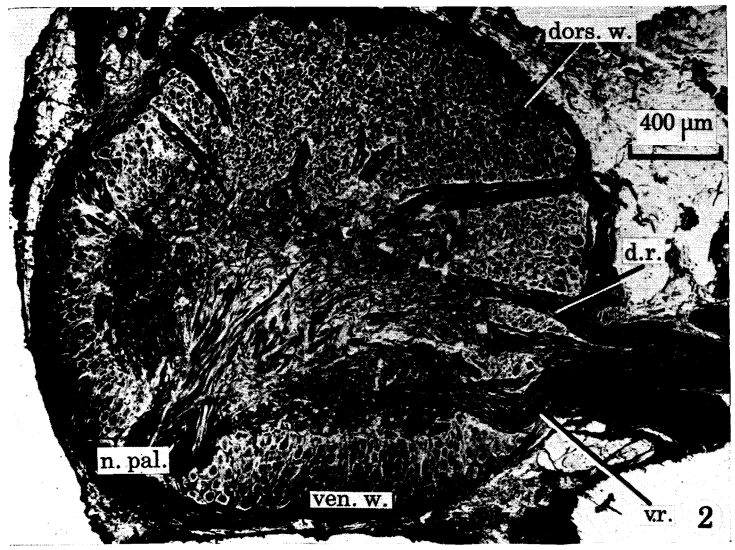
FIGURE 4. Sagittal section showing the entry of the pallial nerve and its large fibres dividing to reach different parts of the ventral neuropil.

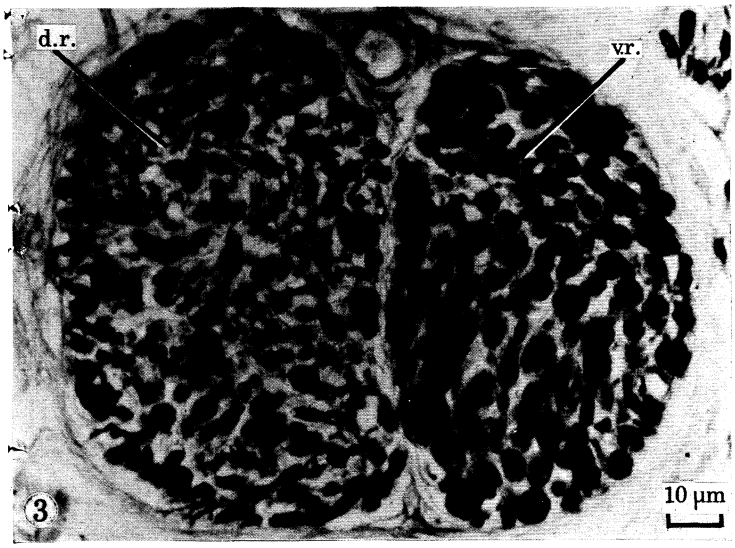
FIGURE 5. The two roots of a stellar nerve leaving the two distinct parts of the neuropil.

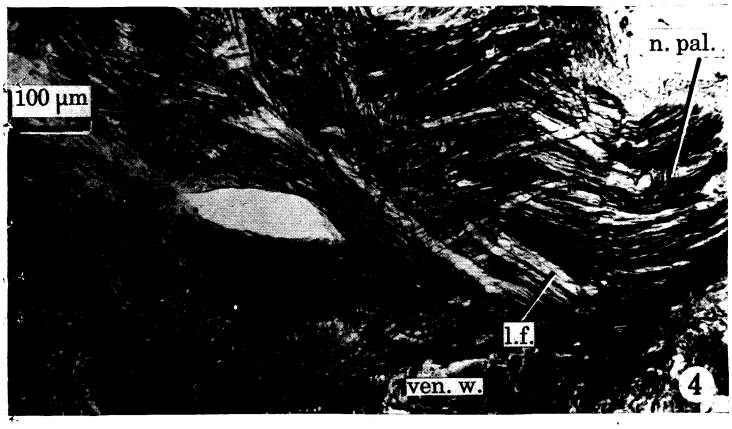
FIGURE 6. Ventral neuropil, showing trunks of the cells, accompanied by fine fibres of uncertain origin (compare figure 61).

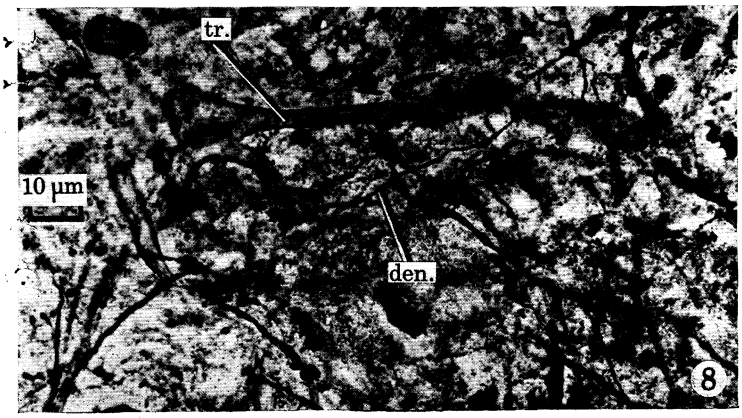
FIGURES 8, 9. Ventral neuropil 51 h after severance of the pallial nerve (Naples, July). The presynaptic fibres have mostly disappeared, leaving the trunks of the cells and their long dendritic branches sometimes ending in knobs.

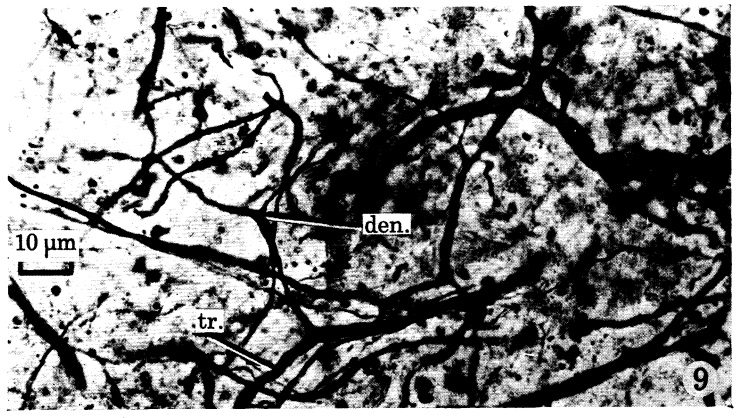












FIGURES 1 to 9. For legends see facing page

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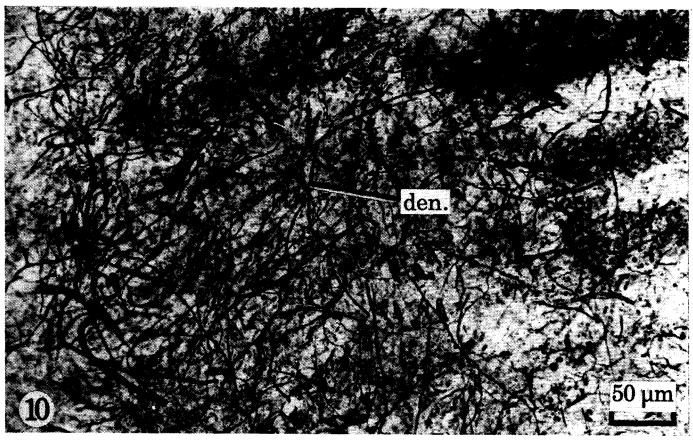

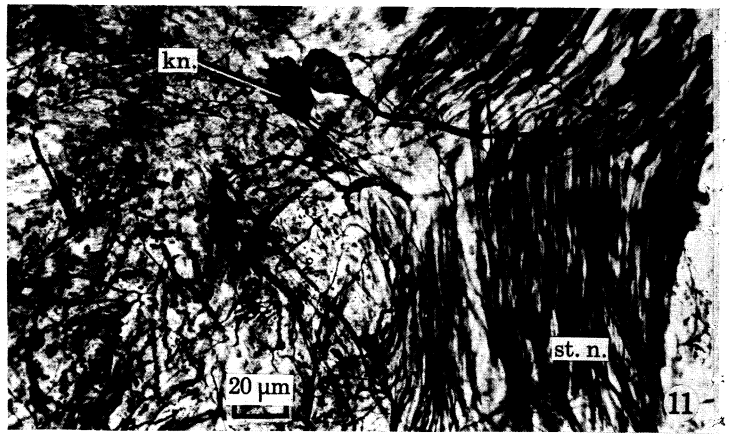

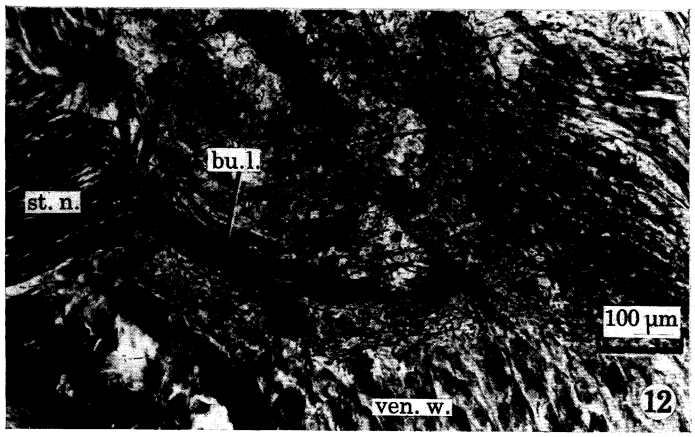

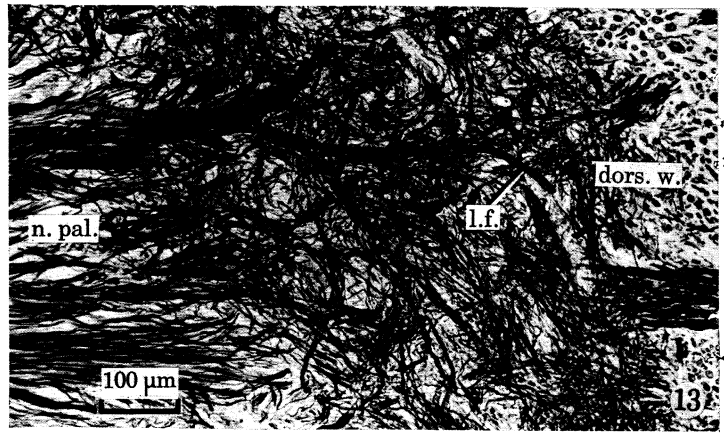

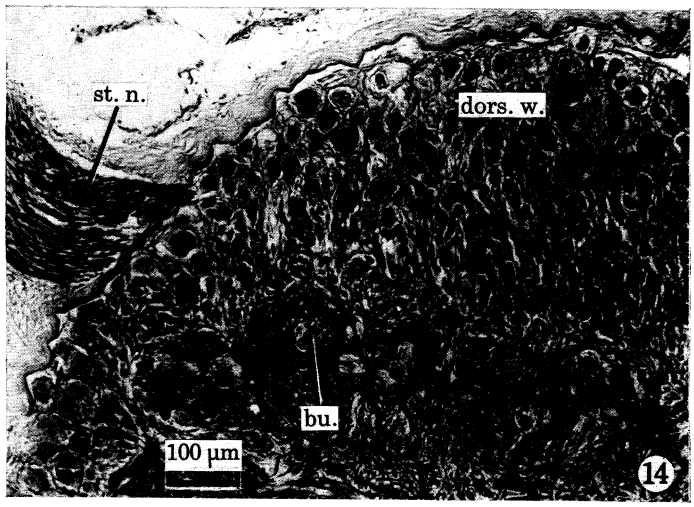

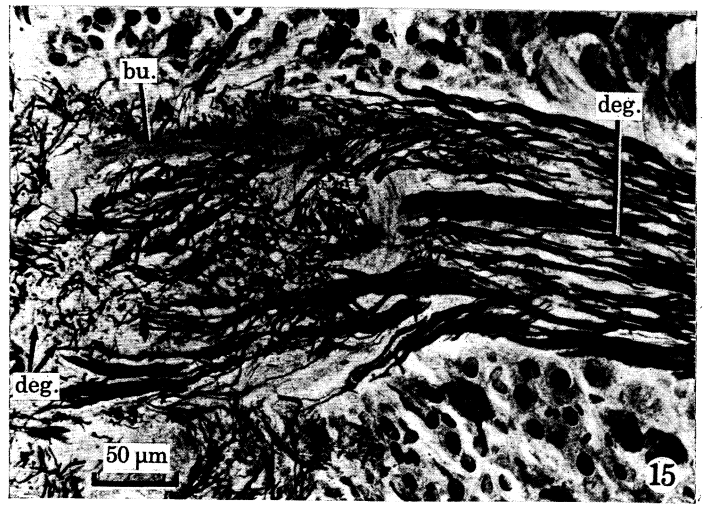

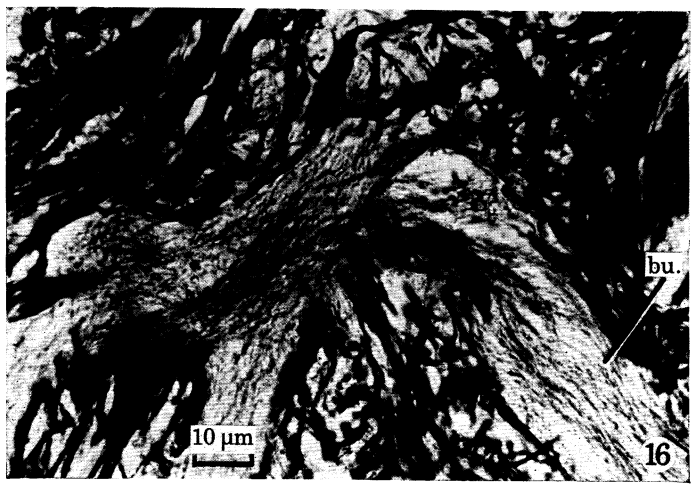

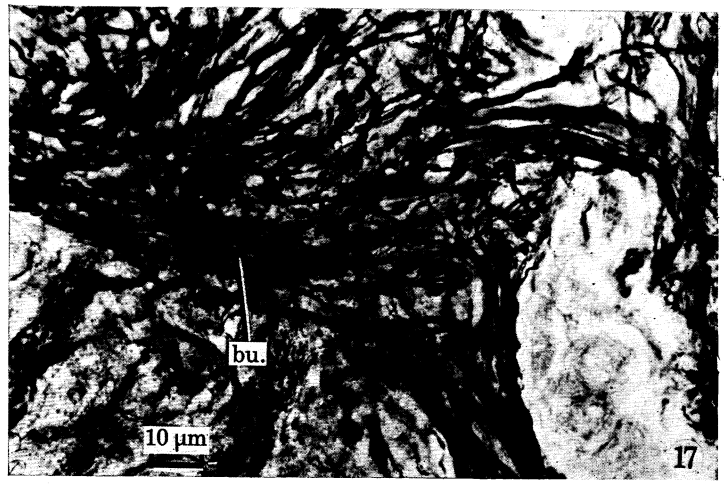

FIGURES 10 to 17. For legends see facing page

greater than was given in a previous estimate (Young 1965). The discrepancy is probably due to the fact that in the early estimate when nuclei were counted many smaller neuronal ones were omitted under the impression that they were glial. The present estimate is on material better stained to show the cell bodies, and gives a more reliable idea of the large number of small cells.

No close comparison of the numbers of cells in the dorsal part of the ganglion and of fibres in the dorsal roots is possible. The count of the cells is probably reasonably accurate, but if anything underestimates the number of small cells. The count of the nerves certainly greatly underestimates the number of small fibres, indeed no attempt was made to count them all. In a previous study far more were recorded (Young 1965). Electron microscopy shows groups of small fibres (< 1 μm) in the stellar nerves (Barlow & Gray 1972). Recently an estimate of the fibres of less than 1 μm has been made with the electron microscope by Dr D. Frösch (personal communication). There are at least 200000 in the stellar nerves of one side. Many of these small fibres are afferents and motor fibres to the chromatophores. It is not possible therefore to determine from the counts whether the smaller cells of the ganglion all send fibres out in the stellar nerves, but the figures suggest that very many do *not* do so.

The dorsal neuropil

The dorsal neuropil is more complex than the ventral and shows a less uniform appearance. In its inner part it more nearly resembles the ventral neuropil, whereas the outer part is complicated by the processes of the small cells and by afferent fibres entering from the stellar nerves (figure 5).

Conspicuous bundles run through from the pallial nerve to the stellar nerves and degeneration experiments show that these include both ascending afferents and descending fibres, presumably the latter are those to the chromatophores (see p. 418).

The dorsal neuropil receives large pre-ganglionic fibres from the pallial nerve (figure 13, plate 30). There is no estimate of their number, perhaps only a few hundred or even less. Single large fibres have been seen occasionally that might be pre-ganglionic to *both* parts of the neuropil, but probably the two parts are innervated by separate fibres. The preganglionic fibres branch in the inner part of the dorsal neuropil and spread widely throughout it, branching repeatedly. Their finest terminals have not been seen, but after severing the pallial nerve, degeneration appears in all parts of the neuropil (p. 417).

The inner and outer parts of the dorsal neuropil differ (figures 5, 14, plates 29 and 30). The inner shows a loose web of fibres rather like the ventral neuropil. It differs from the latter in having more numerous argentophil boutons of various sizes. The outer part of the dorsal neuropil shows a component not present in the ventral, namely bundles of very fine fibres, staining

DESCRIPTION OF PLATE 30

FIGURES 10, 11. As figures 8, 9 previous page.

FIGURE 12. As figures 8 to 11 showing bundle of axons running towards ventral root.

FIGURE 13. Large fibre running from the pallial nerve to the dorsal neuropil.

FIGURE 14. Transverse section of a normal ganglion to show the dorsal wall and neuropil with bundles of lightly staining fibres.

FIGURE 15. Dorsal neuropil and dorsal root 22 h after section of the pallial nerve (Naples, July). There are degeneration granules in the neuropil and in the root, but none within the bundles of fine axons.

FIGURE 16. Normal dorsal neuropil to show bundles of fine, lightly stained axons.

FIGURE 17. Normal dorsal neuropil to show bundles of fine fibres, with dilatations among them.

a characteristic light yellow with Cajal's stain (figure 14). These are believed to be the processes of the small cells characteristic of this part of the ganglion (figure 21, plate 31). Their course can only be determined in a general way by light microscopy. They are limited to the outer part of the neuropil and apparently do not penetrate to the centre. Indeed on entering the neuropil the bundles turn at right angles and run more or less tangential to the surface. They converge upon the dorsal roots of the stellar nerves (figure 15, plate 30). Here they make simple plexiform arrangements (figure 16, plate 30), from which individual bundles run outwards among the larger nerve fibres. It is uncertain how far these fine fibres run within the dorsal roots and stellar nerves. Probably they end at various levels, some within the ganglion, while others proceed at least as far as the outer sheath. Synapses have been seen within the roots (D. Frösch, personal communication). The collaterals of the efferent fibres are given off at various levels within the roots and presumably here make contact with the processes of the microneurons. It is not considered at present that any of these latter processes pass to the periphery, but evidence about this awaits further study with electron microscopy (D. Frösch, in preparation).

The Cajal stain does not allow resolution of the fibres within these bundles of fine fibres. However, it can be seen that they are multiple and there are dilatations among them, either of the fibres originating in the ganglion or of some other component, probably both (figure 17, plate 31). Many of the boutons spring from fine afferent axons entering with the stellar nerves, and degeneration is seen here after section of the stellar nerves (p. 420). These terminals do not degenerate after section of the pallial nerve (figure 18, plate 31). They are thus afferents from the periphery and they come into relation both with the trunks of the small cells and also with collaterals given off by the trunks of the large cells (see later). The details of the outer neuropil are hard to make out in normal material, where the collaterals of the large cells and the finer fibres are difficult to disentangle.

Analysis of the trunks of the large dorsal cells is complicated by the fact that even after degeneration of the presynaptic pallial nerve fibres two other sorts of fibre remain with them in the neuropil, namely the trunks of the small cells and the stellar nerve afferents with their boutons. The trunks of the large cells give a branch shortly after entering the neuropil, and then several others, often arising from a rather swollen region. The collaterals given off just within the neuropil may make connexion with the bundles of fine axons and the afferent endings among them. The trunks of the large cells eventually turn out into the stellar nerves and here

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Description of plate 31

Figure 18. Dorsal neuropil of ganglion 51 h after severance of the pallial nerve (Naples, July). The fine dilatations and terminals have not degenerated (compare figures 8 to 11 and 15).

Figure 19. Dorsal root, showing collateral dendritic branch of outgoing fibre.

Figure 20. Dorsal root of a ganglion whose stellar nerves had been cut 5 days previously. The fibres with collateral branches are still present, showing that they are dendrites, not afferents.

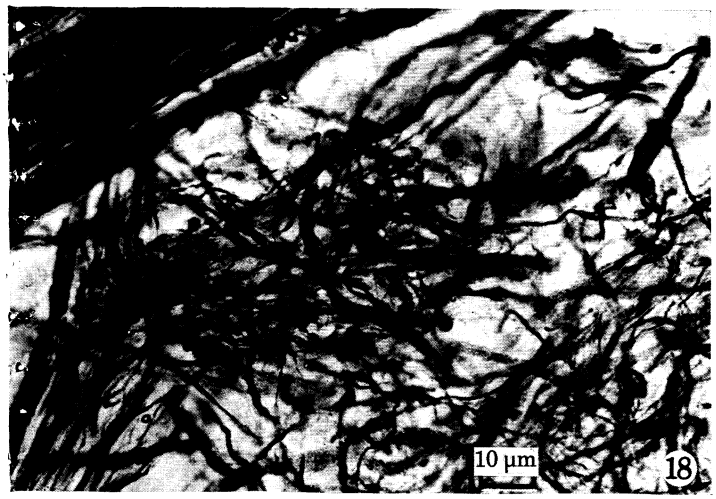
Figure 21. Portion of dorsal wall and neuropil. Fixed in osmium tetroxide, sectioned in Araldite and stained with azure blue.

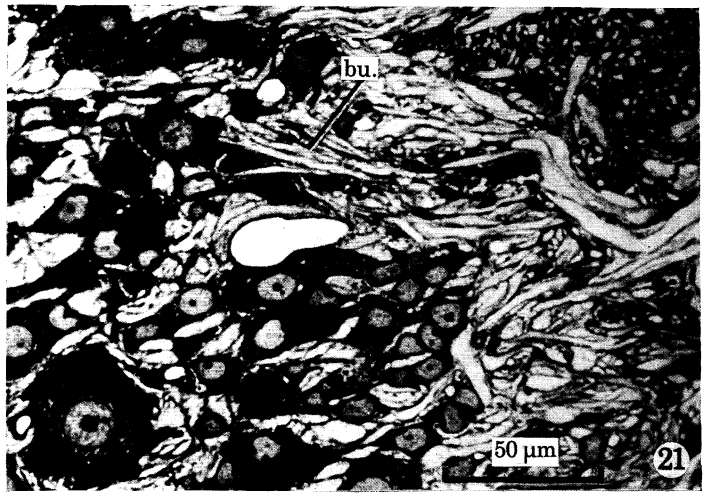
Figure 22. Dorsal root of normal ganglion to show simple plexus of incoming fibres.

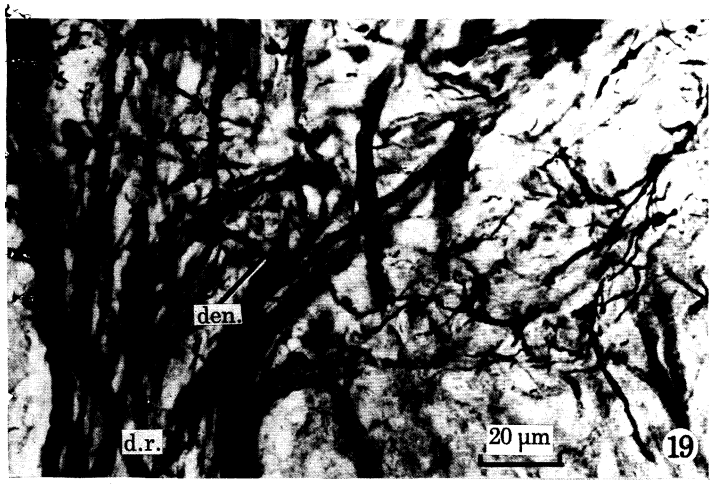
Figure 23. Neuropil of a ganglion whose pallial nerve had been cut 15 h previously (Naples, July). There are granules in both parts, more conspicuous in the ventral.

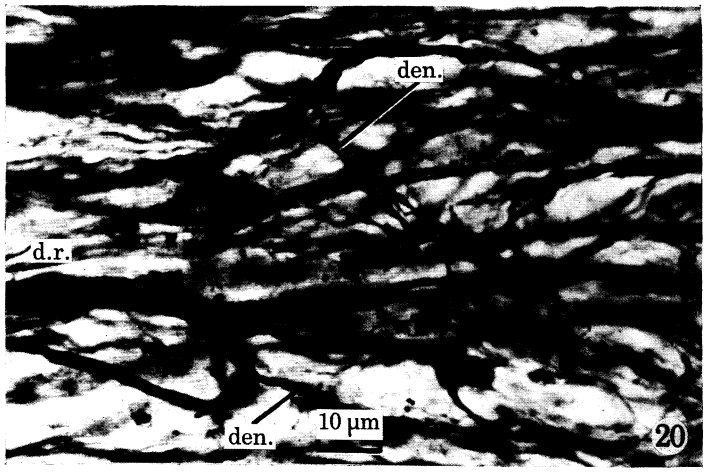
Figure 24. Twenty-two hours after section of pallial nerve (Naples, July).

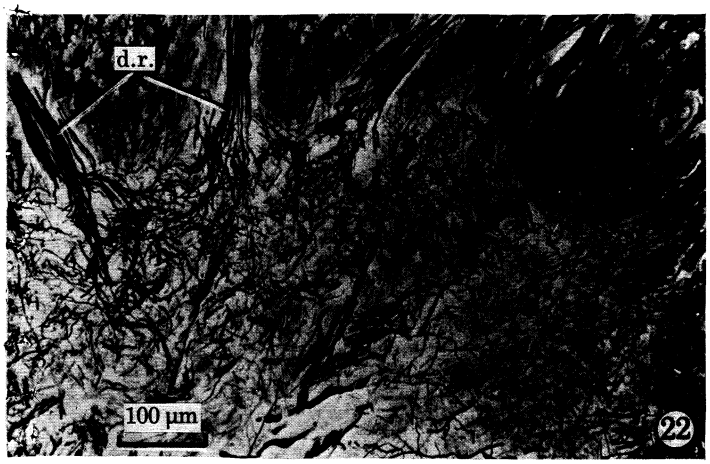
Figure 25. As figure 24, showing pallial nerve fibres still intact.

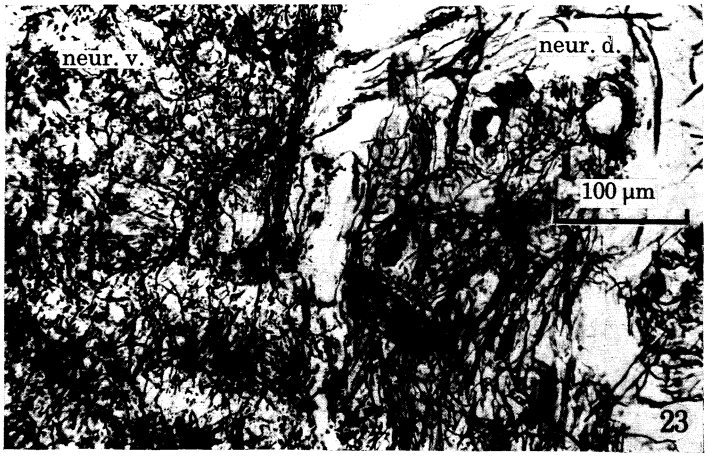


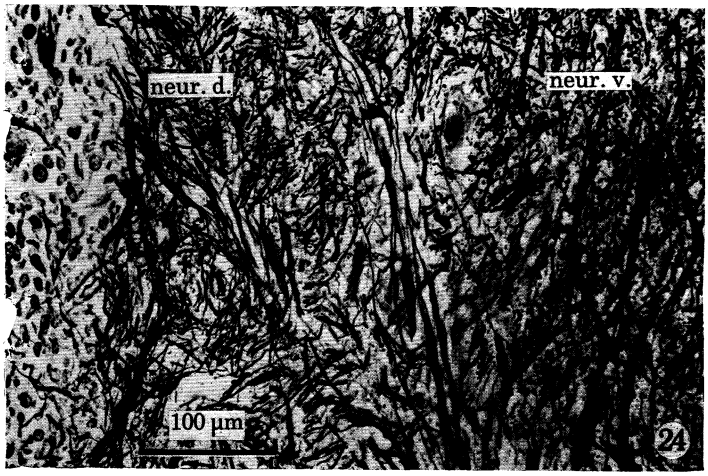


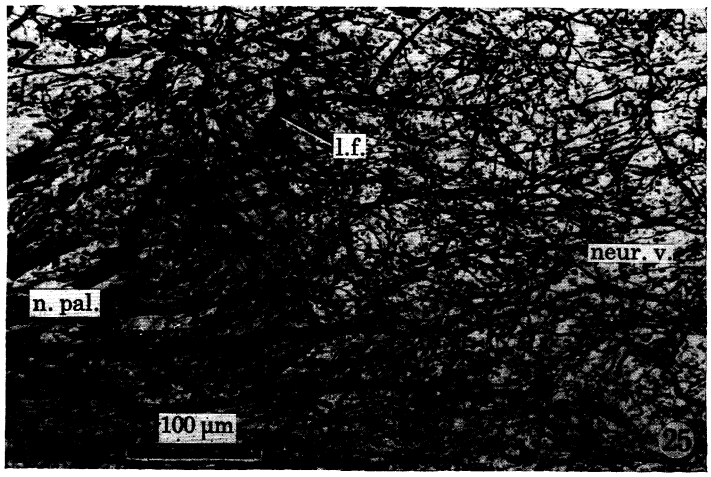












FIGURES 18 to 25. For legends see facing page

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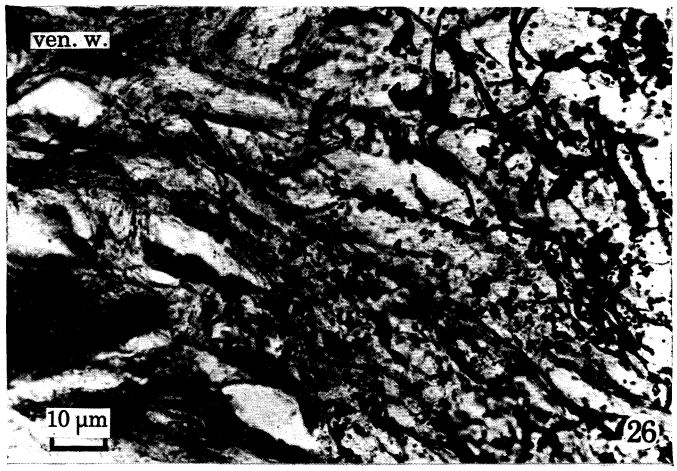

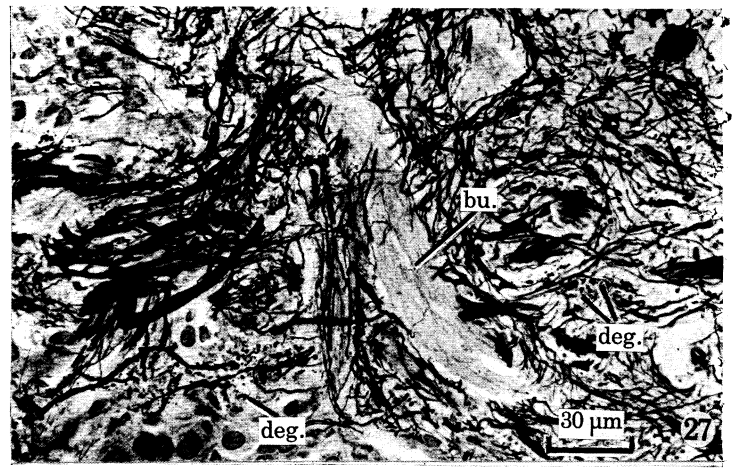

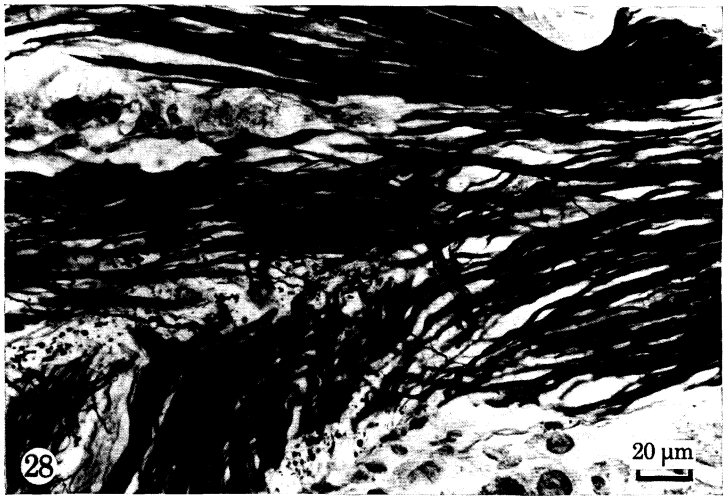

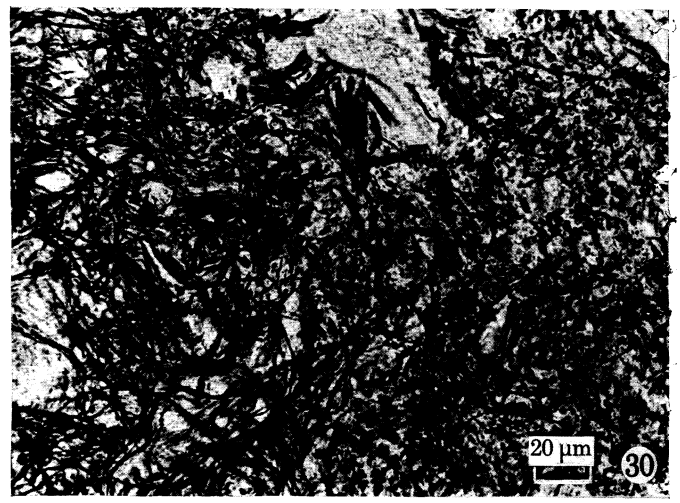

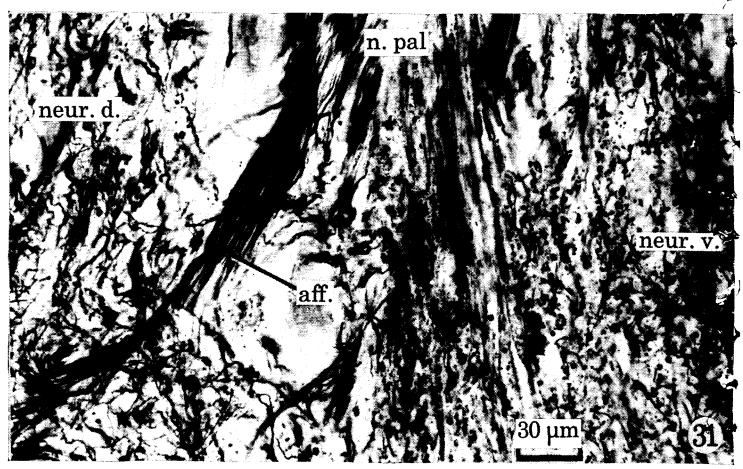

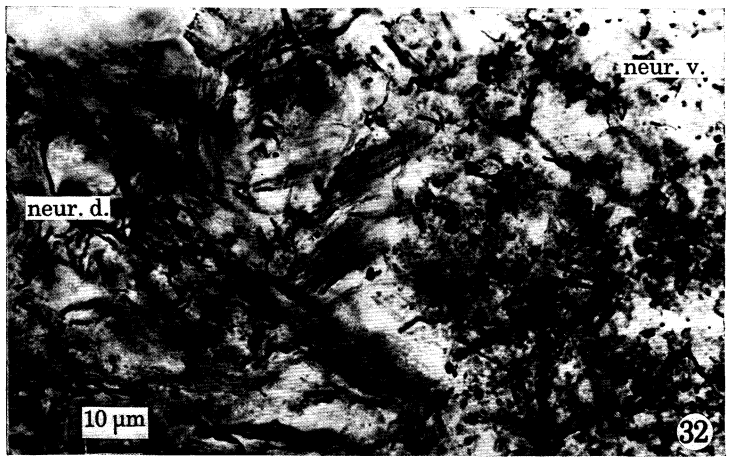

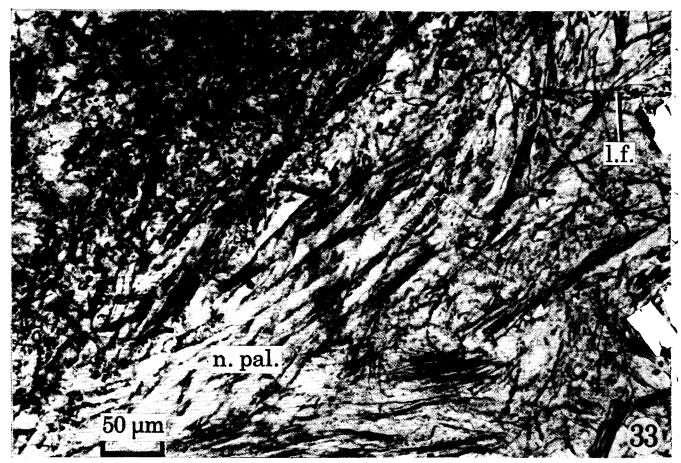

FIGURES 26 to 33. For legends see facing page

they stain brown with Cajal's method. As they leave the neuropil, each gives one or more further lateral branches, which run tangentially, just inside the cell layer (figure 19, plate 31). The branches are often given off as the nerve trunk passes through the cell layer, and therefore they proceed backwards towards the ganglion. This sometimes makes them look as if they were fibres entering the ganglion from the periphery. Their true nature is seen from the fact that they remain intact after cutting the stellar nerves, at a time when the incoming afferent fibres have already degenerated (figure 20, plate 31). These recurrent branches are, therefore, dendrites, and their branches in the outer neuropil are presumably in connexion with those of incoming afferent fibres and the trunks of the small cells.

The organization of this outer dorsal neuropil is further elucidated by degeneration studies. In the days immediately after cutting the pallial nerve numerous granules appear in the dorsal neuropil. Many of them are in the central part of it, but some also extend to the outer part, though they never appear among the bundles of fine fibres (figures 15, 27, 28, plates 30 and 32). After section of a stellar nerve, however, granules are limited to the outer neuropil and many of them lie among the fibres of the bundles believed to originate from the small cells (figure 44, plate 34). The afferent fibres entering from the periphery are therefore related both to the recurrent dendrites of the efferent fibres and to the processes of the small cells, though the detailed arrangement cannot be seen by light microscopy (figure 7).

The afferent fibres of the dorsal roots of the stellar nerves make a loose plexus where they enter the neuropil (figure 22, plate 31). This presumably allows some spread of the effects of local afferent stimulation, which has been observed physiologically (Gray 1960). However, if these afferents are involved in specific reciprocal reflex actions presumably their connexions must be rather limited.

Degeneration of the preganglionic fibres

After section of the pallial nerve there is massive degeneration in the ventral half of the ganglion, some in the dorsal part. No undoubted signs were seen in one animal killed 13 h after sectioning, but degeneration was already well advanced in another killed after 15 h (Naples, July). The ventral neuropil was filled with a mass of fine granules, and there were some, but fewer, in the dorsal neuropil (figure 23, plate 31). At this time the fibres in the peripheral stump of the pallial nerve itself showed no signs of degeneration (i.e. the endings break up before the main length of the fibre). The granules occurred equally in all parts of the ventral neuropil. In the dorsal neuropil they were in scattered patches, some at the inner, others in the outer part.

DESCRIPTION OF PLATE 32

FIGURE 26. As figure 24, showing large degeneration granules in ventral neuropil, but not extending into cell layers (ven.w.).

FIGURE 27. As figure 24, dorsal neuropil to show scattered degeneration of pallial nerve fibres, not extending among the bundles of fine axons.

FIGURE 28. As figure 24. Degeneration granules extending among the fibres of the dorsal root.

FIGURE 29. As figure 24. Degeneration in dorsal neuropil does not extend among bundles of fine axons.

FIGURE 30. Pallial nerve cut 26 h (Naples, July).

FIGURE 31. As figure 30, showing intact fibres running between stellar and pallial nerves, presumably afferents.

FIGURE 32. Pallial nerve cut 38 h (Naples, July).

FIGURE 33. Pallial nerve cut 51 h (Naples, July), showing ventral neuropil with large presynaptic fibres now degenerating.

In an animal killed after 22 h the granules were larger in both parts (figures 24 to 28, plates 31 and 32). The fibres in the main preganglionic nerve trunks had still not degenerated, and the larger branches can be seen among the granules in the neuropil (figure 25). The granules are very abundant right to the extreme outer edge of the ventral neuropil, but do not extend into the cell layers (figure 26).

In the dorsal neuropil the granules are relatively much less abundant than in the ventral, leaving a greater proportion of fibres intact (figure 27). The granules occur especially at the centre (in the inner neuropil), but are also found at the extreme edge and in the dorsal roots of the stellar nerves. They are not associated with the bundles of trunks of the small cells (figures 27, 29, plate 32).

After 26 h the granules were even coarser (figures 30, 31, plate 32) and the preganglionic fibres had broken into granules in the pallial nerve trunk as well as throughout the neuropil. However, not all the fibres in the pallial trunk were degenerating and those that were still intact run through from the stellar to the pallial nerve. These are presumably afferents from the periphery (figure 31). They do not always run in compact bundles but may divide up and re-join as they pass through the neuropil. Degenerating fibres also pass through the ganglion to the dorsal roots of the stellar nerves. These are presumably the chromatophore fibres. No degeneration was seen in the ventral roots, whose large fibres appear very clearly among the granules of the degenerating preganglionic fibres.

The next stage available is 38 h and the granules are still very conspicuous, but now fewer and mainly smaller than before (figure 32, plate 32). By 51 h the granules were fewer still in both parts of the neuropil (figure 33, plate 32). The ventral part still shows the remains of the larger presynaptic fibres, now filled with granules. Otherwise, this neuropil contains only a few granules and the trunks of the cells of the ganglion and thin dark fibres, which are probably all dendritic branches of these trunks (figures 8 to 11). Some of these dendrites are at least 300 μm long (figure 34, plate 33). The dendrite of figure 34 is of special interest since it seems to come from the trunk of a cell of the dorsal neuropil, but proceeds into the ventral. This was not a common appearance and probably the dendrite really belongs to a displaced ventral neuron.

The dorsal neuropil retains far more fibres than the ventral, the excess being presumably the branches of the incoming afferents from the stellar nerves and the processes of the small cells. Indeed, the fine branches and the knobs seen among the bundles of small cell trunks show especially clearly in this neuropil, since the pallial nerve fibres are lacking.

There are still remains of degenerating fibres in the dorsal roots of the stellar nerves, presumably chromatophore fibres. In spite of the full degeneration of the efferent fibres there

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Description of plate 33

Figure 34. As figure 33, showing a very long dendrite.

Figure 35. As figure 33, showing intact fibres running from stellar to pallial nerves.

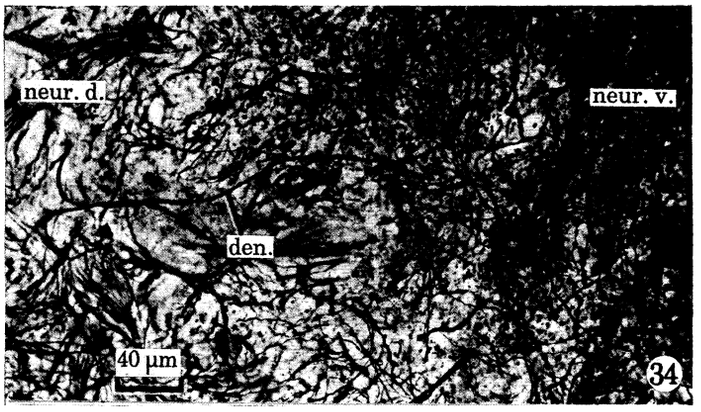
Figure 36. Pallial nerve cut 4 days (Naples, July). Degenerated fibres in pallial nerve.

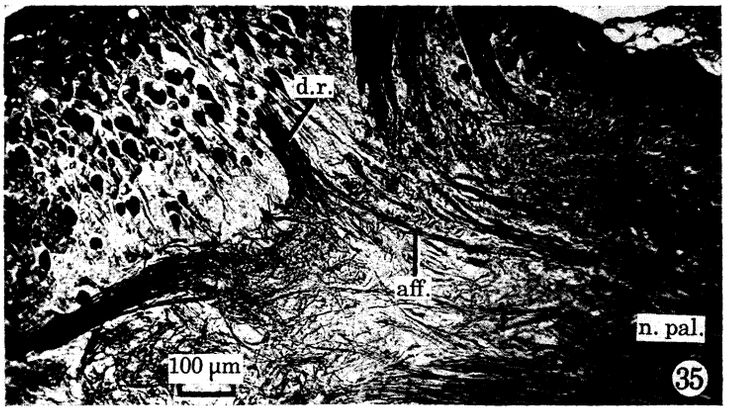
Figure 37. As figure 36. The granules have nearly all gone from the neuropil.

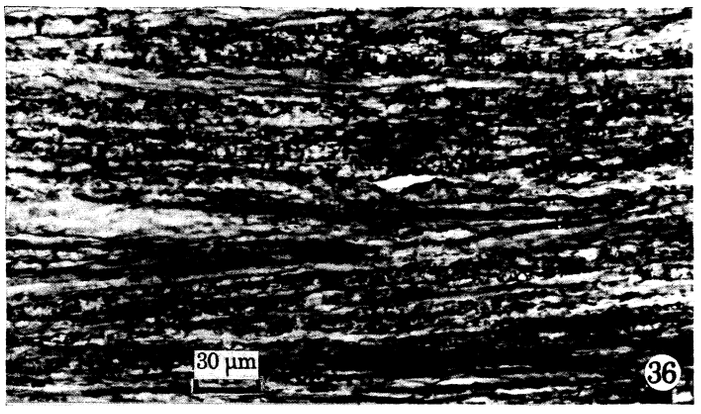
Figure 38. Pallial nerve cut 7 days (Naples, August). The whole ganglion is greatly shrunken, especially the neuropil.

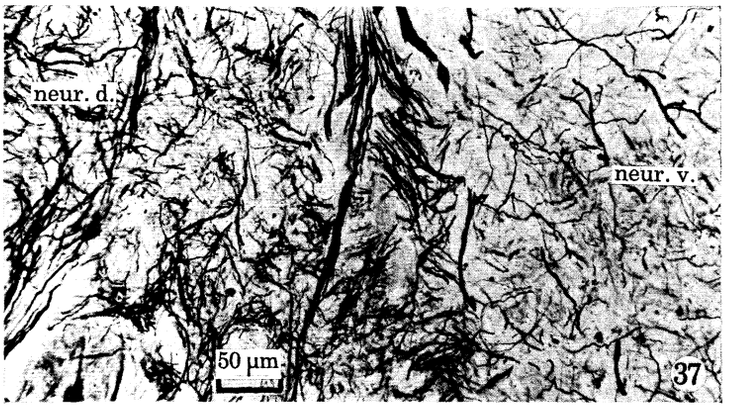
Figure 39. The control ganglion from the opposite side to figure 38.

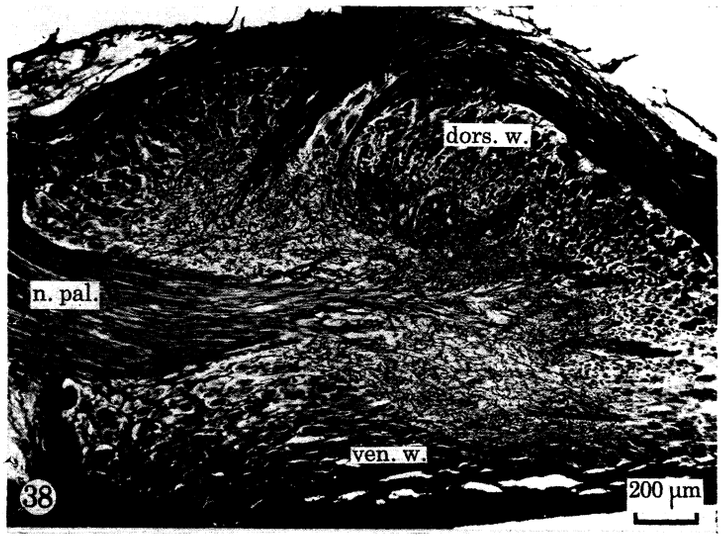
Figures 40, 41. Ventral and dorsal neuropils 18 days after severance of the pallial nerve; the granules have all gone. The large trunks appear very clearly in the ventral neuropil. Compare figure 68, plate 37.

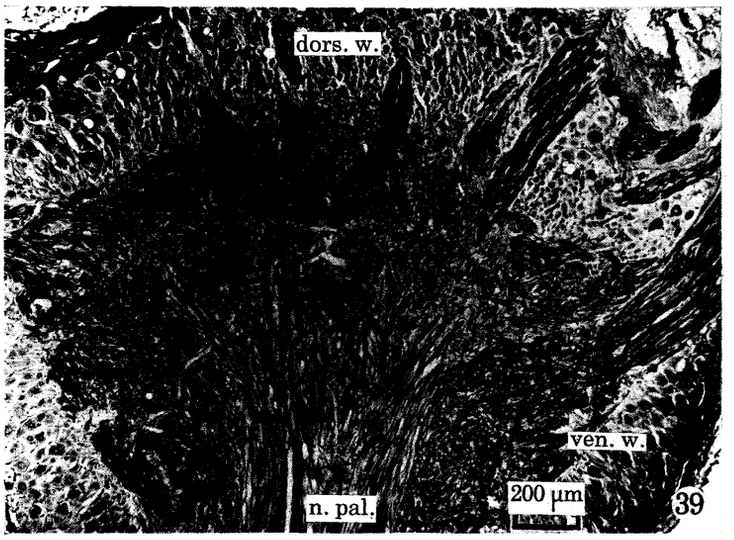


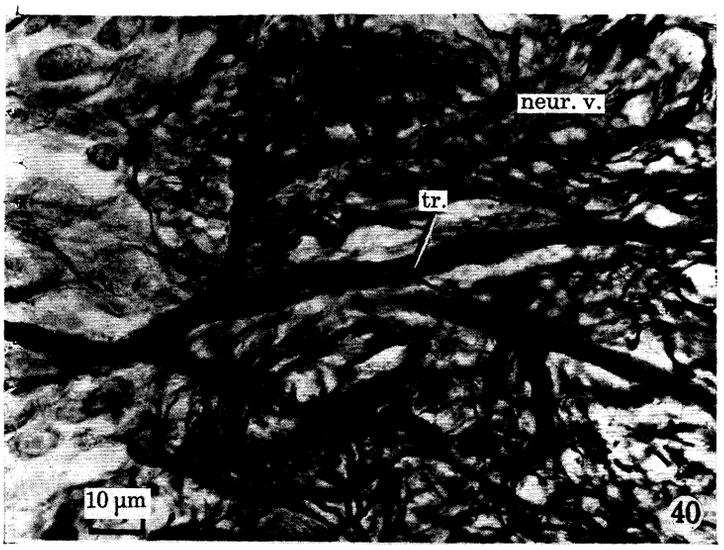


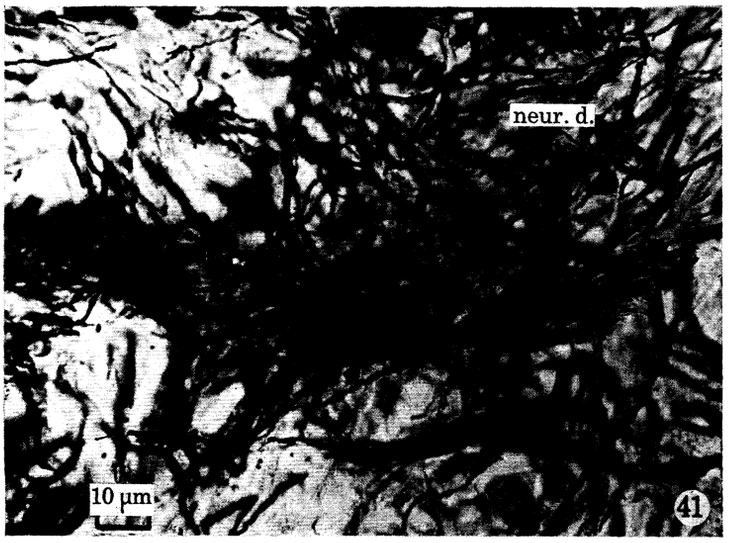












FIGURES 34 to 41. For legends see facing page

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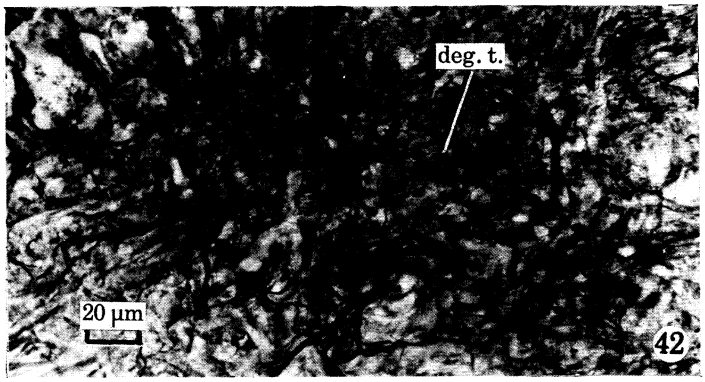

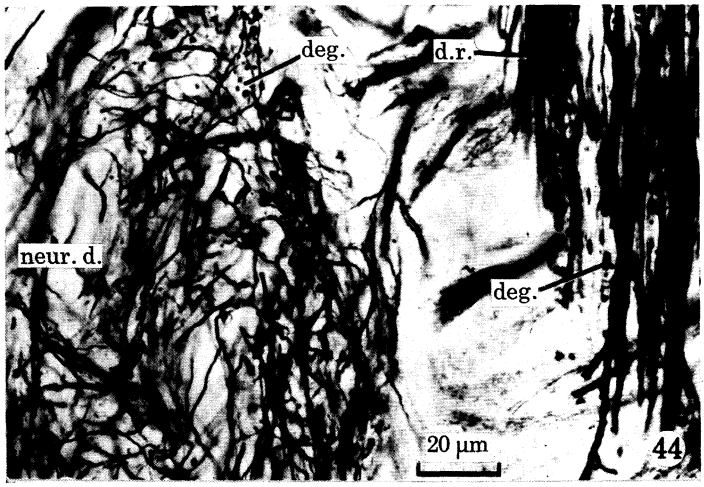

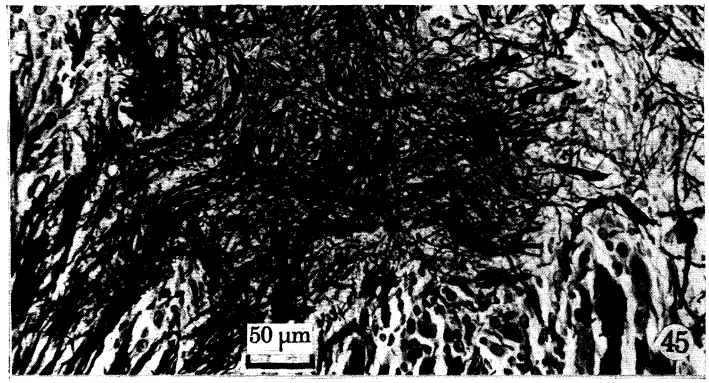

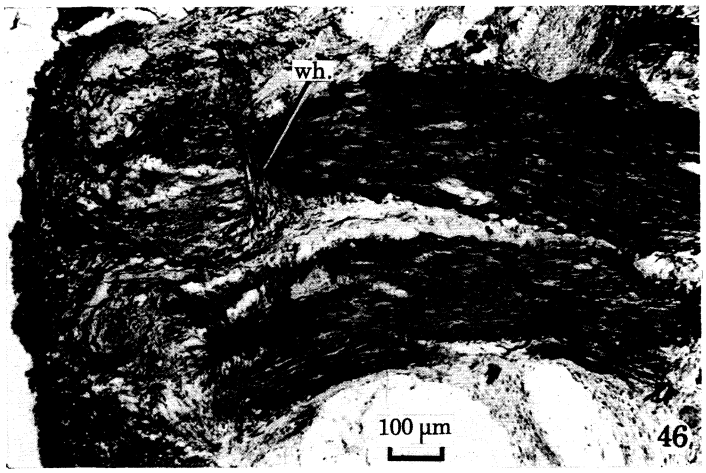

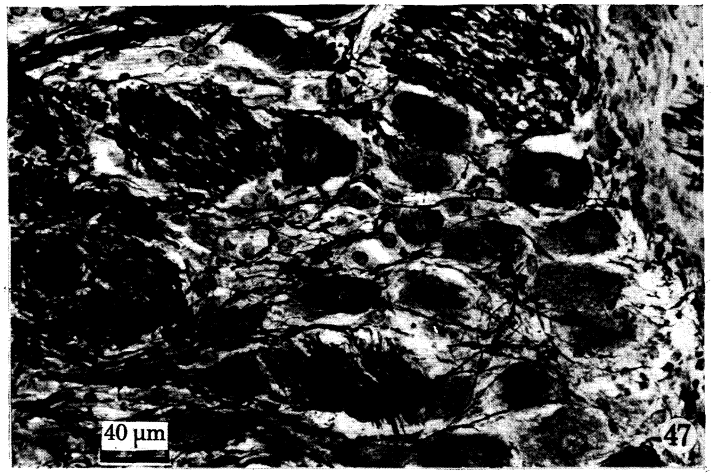

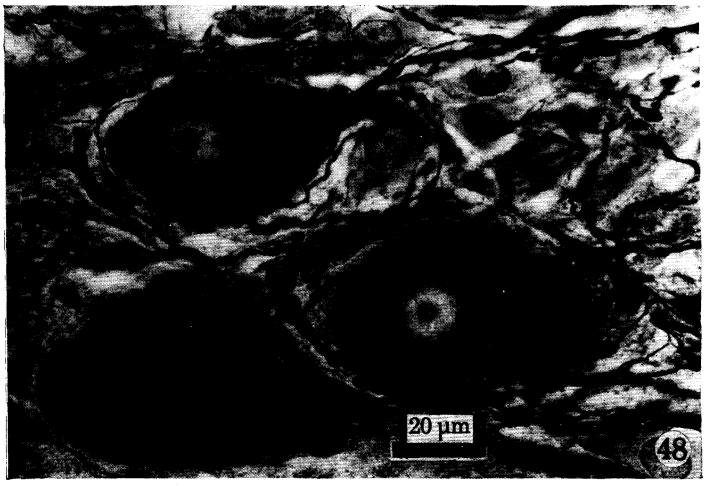

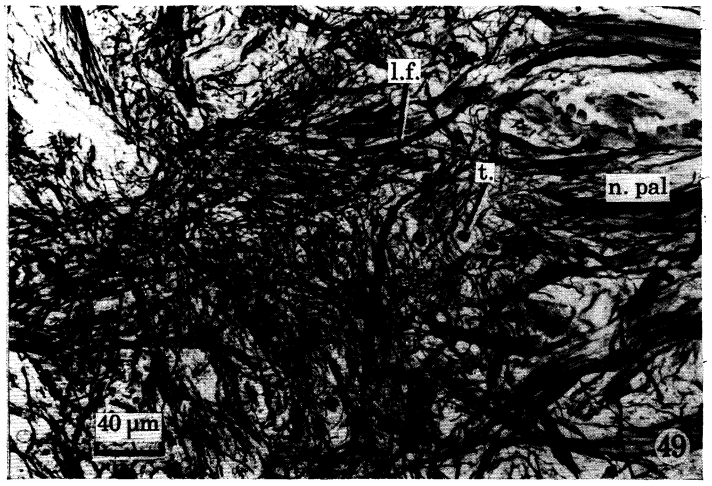

FIGURES 42 to 49. For legends see facing page

are still many bundles of intact fibres in the pallial nerve. These must have their cell bodies more distally. They probably do not arise from cells of the ganglion but pass through the neuropil from the stellar to the pallial nerve (figure 35, plate 33).

At 3 days after severing the pallial nerve the granules have gone or can be seen only as a very fine powder in the ventral neuropil. The efferent fibres of the ventral roots, of course, appear clearly. The dorsal neuropil still contains granules and a far greater complexity of fibres remains there than in the ventral region.

At 4 and 5 days the fibres in the peripheral stump of the pallial nerve itself show full degeneration (figure 36, plate 33) (except, of course, the intact afferents). In the ganglion the granules have nearly all gone, leaving in the shrunken ventral neuropil only the darkly staining fibres, most or all of which are dendrites of the large cells (figure 37, plate 33). Their appearance is certainly unusual for dendrites, but in places these fibres can be shown to join up with the main trunks of the cells (see, for example, figure 9). The dorsal neuropil is more complex but also shrunken. There are still degeneration granules in the dorsal roots of the stellar nerves.

At 7 days the neuropils were both much shrunken, especially the ventral, and the whole ganglion was much smaller than that on the other side (compare figures 38, 39, plate 33). The great reduction of the neuropils shows what a large proportion of their volume is normally occupied by endings of the preganglionic fibres, but of course the post-synaptic elements may have shrunk.

At 11, 16 and 18 days there was a vigorous regeneration from the peripheral stump of the pallial nerve, presumably of the afferent fibres from the periphery (Sereni & Young 1932). The ventral neuropil contains little but the lightly stained trunks of the cells and their dendritic branches. The course of the trunks of the cells of the ganglion can now be followed especially clearly through the neuropil (figure 40, plate 33). Some of the collaterals end in claw-like branches and terminal lumps. It cannot of course be concluded that they have this form in the normal ganglion. Probably these represent the changed form of collaterals that previously made contact with the presynaptic terminals. The trunks stain more readily than in normal ganglia and their course to the roots appears clearly. The dorsal neuropil remains more complex than the ventral (figure 41, plate 33).

At 41 days in an animal with no regeneration of presynaptic fibres the ganglion was shrunken. The ventral neuropil is very empty except for the trunks and branches of the cells, some of which seem to be degenerating transneuronally (figure 42, plate 34). The collateral branches in the dorsal roots are still well seen, as are the finer incoming afferents. No evidence has been seen of sprouting of these afferents to fill the space left by degeneration, but it is hard to prove that it does not occur.

Description of plate 34

Figure 42. Pallial nerve cut 41 days and not regenerated (Naples, September). Signs of transneuronal degeneration (deg.t.).

Figures 43, 44. Stellar nerve cut 15 h (Naples, July). There is degeneration in the dorsal roots and outer dorsal neuropil.

Figure 45. Stellar nerve cut 22 h (Naples, July). Large masses in dorsal neuropil.

Figure 46. Central stumps of stellar nerves cut 5 days (Naples, August).

Figures 47, 48. Stellar nerves cut 4 days (Naples, August). New fibres have invaded the ganglion.

Figure 49. Stellar nerves cut 4 days. The presynaptic fibres appear clearly in the dorsal neuropil, also some large terminal swellings of unknown origin (t).

In animals allowed to survive for 3 months or more functional regeneration of the actions of the ganglion and chromatophores was seen (Sereni & Young 1932; Sanders & Young 1972). The neuropil has not yet been closely studied in such animals.

Degeneration after cutting stellar nerves

The material available after cutting stellar nerves is less abundant, but very useful. In most of the experiments only a few stellar nerves were cut. This leaves an intact blood supply to the ganglion, but means that conclusions about absence of degeneration in any part must be cautious. In two experiments the pallial nerve was cut on one side and a few stellar nerves on the other, allowing precise comparisons.

Thirteen hours after cutting stellar nerves no changes were seen in the neuropil. After 15 h there was clear degeneration of fibres in the dorsal roots and many granules appeared in the dorsal neuropil (figures 43, 44, plate 34). The degeneration was much less widespread than that seen in the ventral neuropil of the same animal after severing the pallial nerve (figure 23). The degeneration in the dorsal neuropil after stellar nerve section is in the form partly of isolated granules, but also of swollen terminals, mainly in the outer neuropil, close to the cell layer. Many of these granules are associated with the bundles of small axons in the outer neuropil and dorsal roots, though not all the larger bundles carry granules. There is no degeneration in the ventral neuropil.

After 22 h the picture was essentially the same. There are many fine granules in the central stellar stumps and outer part of the dorsal neuropil. They become fewer passing inwards. There are large masses of axoplasm in the dorsal neuropil probably due to central changes in cut efferent fibres (figure 45, plate 34). There are no definite signs of degeneration in the ventral neuropil. There are degenerating fibres in the pallial nerve.

After 38 h the central stumps of the stellar nerves were putting out very numerous fine branches capped with terminal bulbs. These fibres run in many directions, often around the central stump, and back up into the ganglion, where they complicate the picture of degeneration. The peripheral stumps of the stellar nerves show much less activity. There are numerous bundles of intact fibres running from pallial to stellar nerves, but of course it is early to say that these are centrifugal, they might be still undegenerated.

At 43 h the degeneration in the dorsal neuropil was still evident as granules of various sizes (mostly very small). Some apparently intact boutons remained, and may be branches or ends of dendrites of the small cell trunks. Indeed these fibres are more prominent than they are in the neuropil in the control normal ganglion. There was no clear sign of degeneration in the ventral

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Description of plate 35

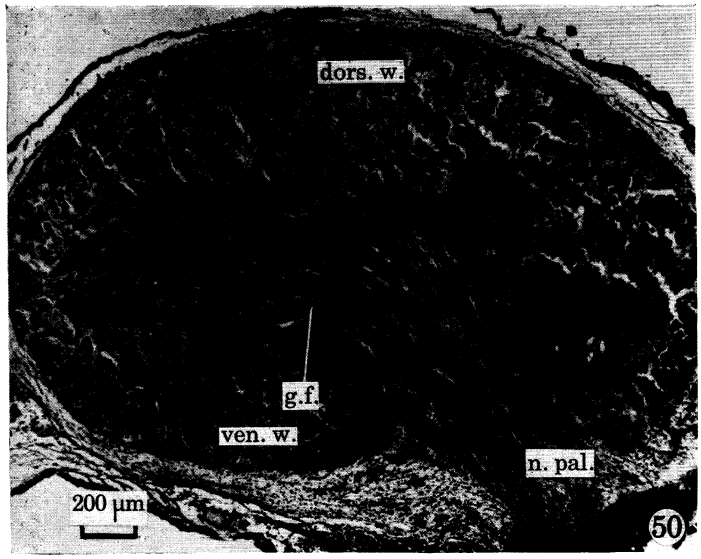
Figures 50, 51. *Sepia.* Sagittal sections to show origin of giant fibres by union of the trunks of many cells in the dorsal wall of the ganglion. The pallial nerve had been cut 33 days previously and the ganglion has shrunk (Naples, April).

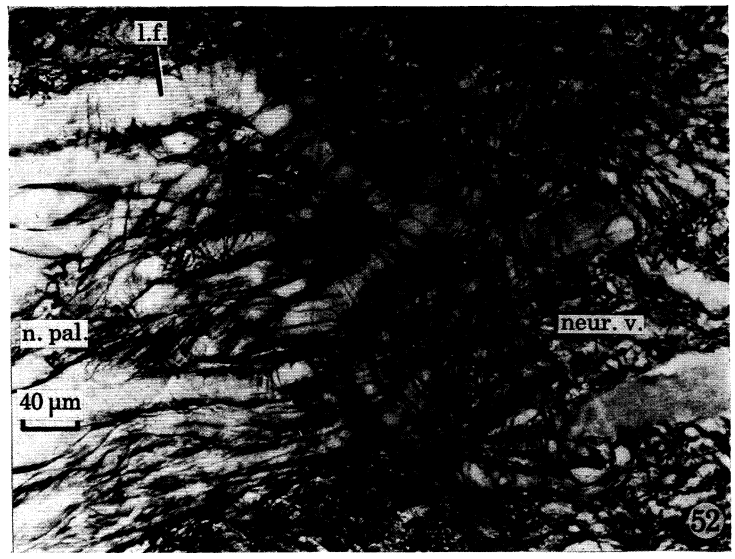
Figure 52. *Sepia.* Entrance of pallial nerve to the ganglion, showing branching of the presynaptic fibres.

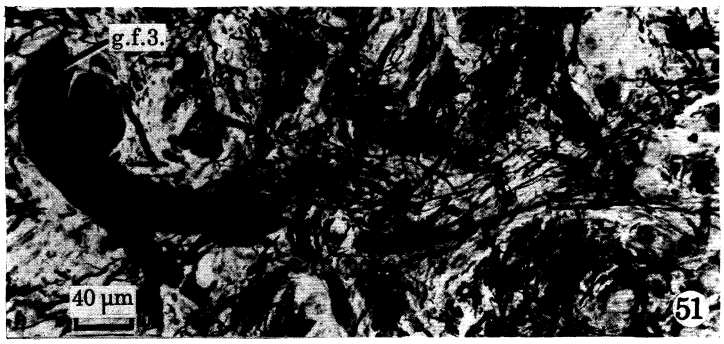
Figures 53, 54. *Sepia.* Synapses on the third-order giant fibres.

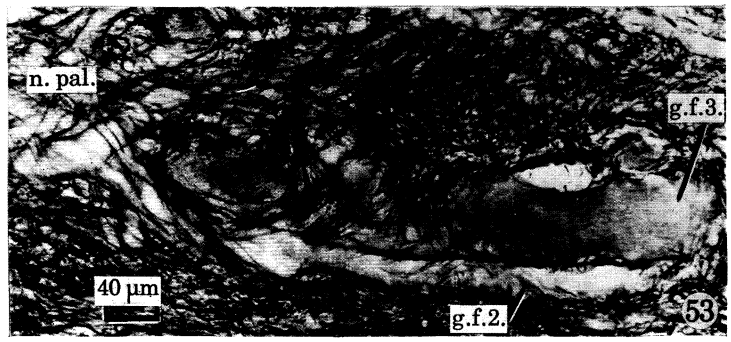
Figure 55. *Sepia.* Terminal knobs perhaps making synapse with giant fibres. The pallial nerve had been cut 33 days previously, so these fibres do not arise in the central nervous system (Naples, April).

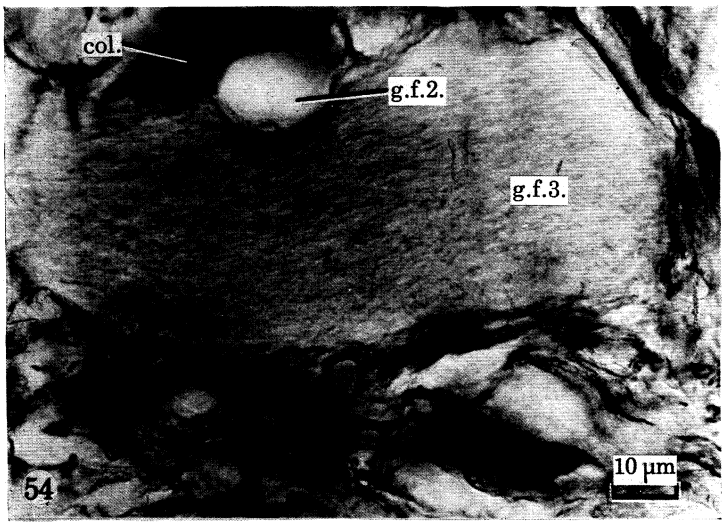
Figures 56, 57. *Sepia.* Transverse sections of successively more posterior levels to show the cell walls, neuropils and roots of the stellar nerves.

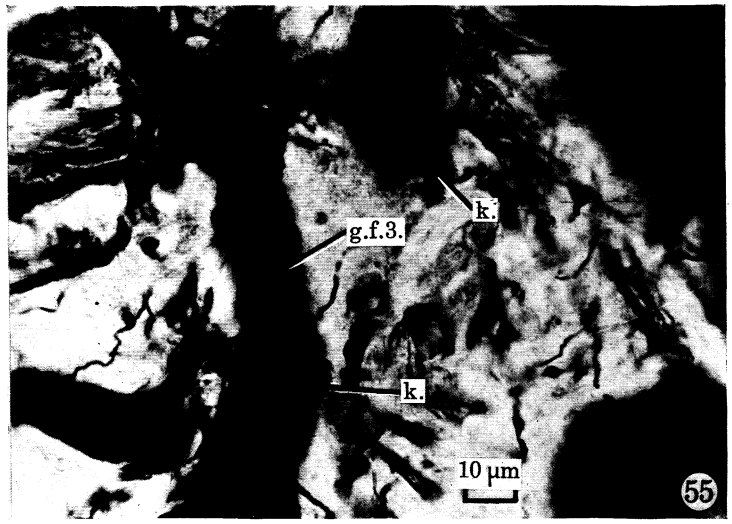


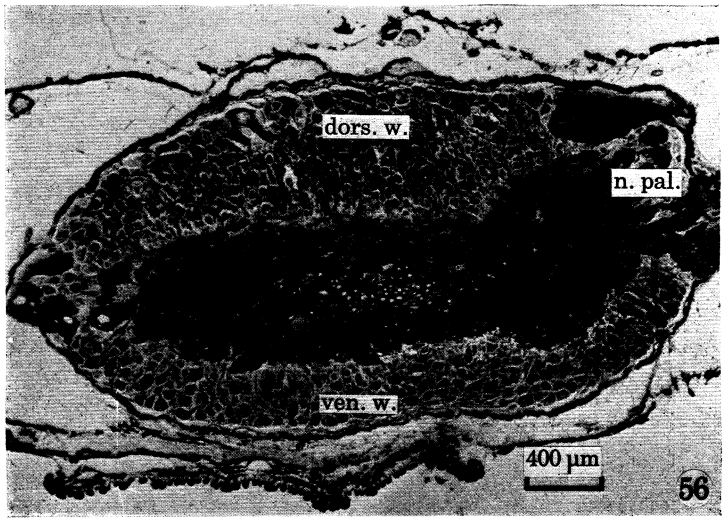


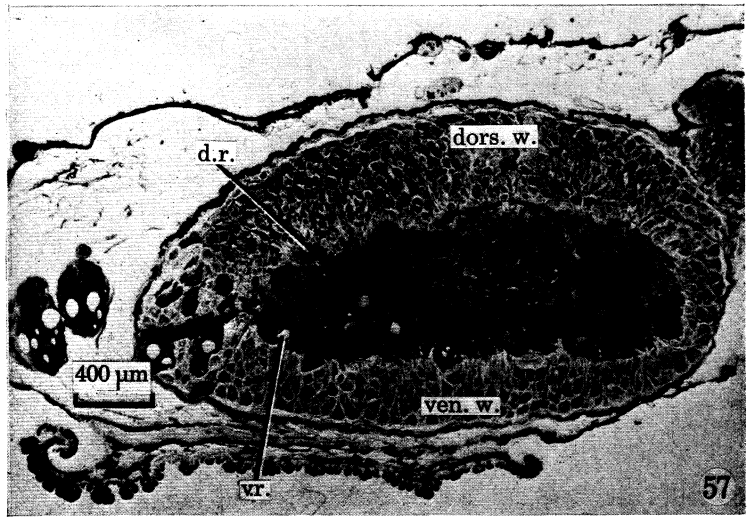












FIGURES 50 to 57. For legends see facing page

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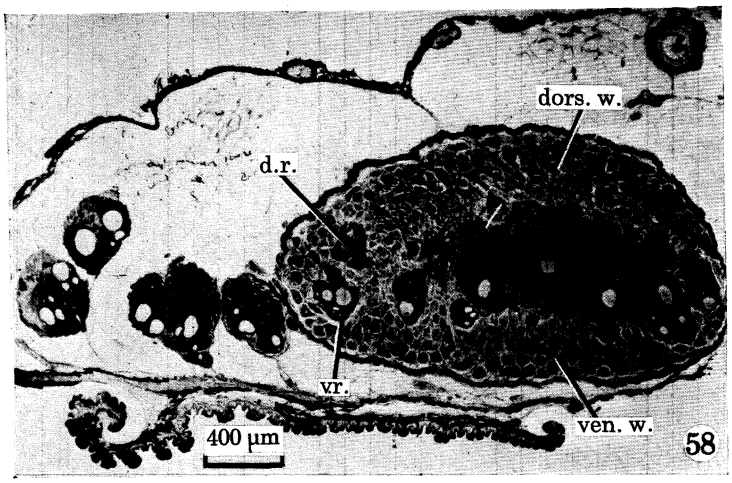
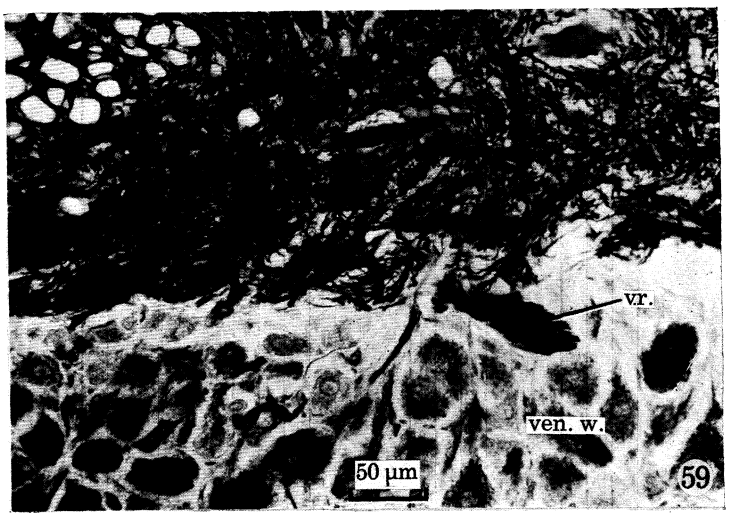
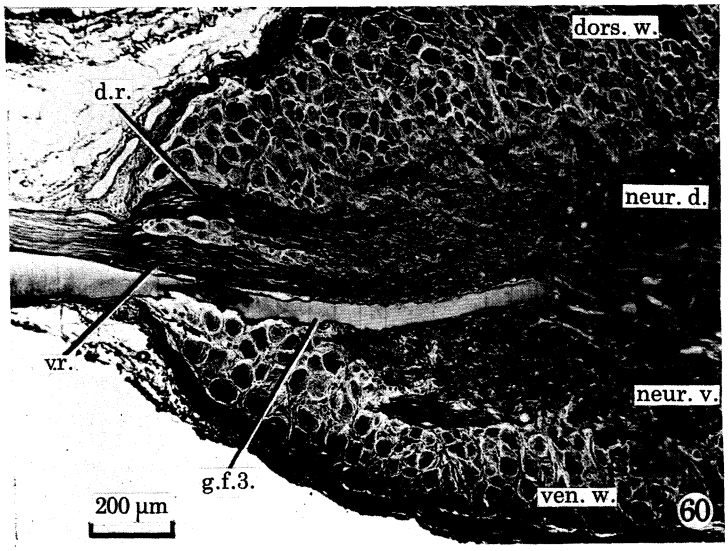
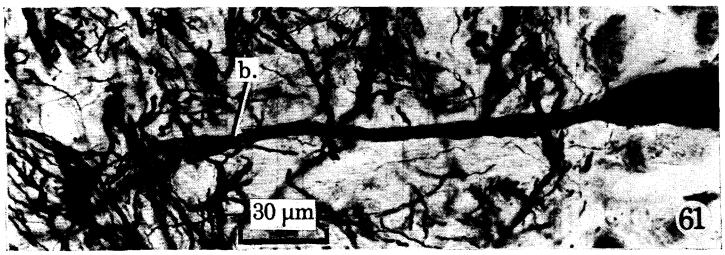
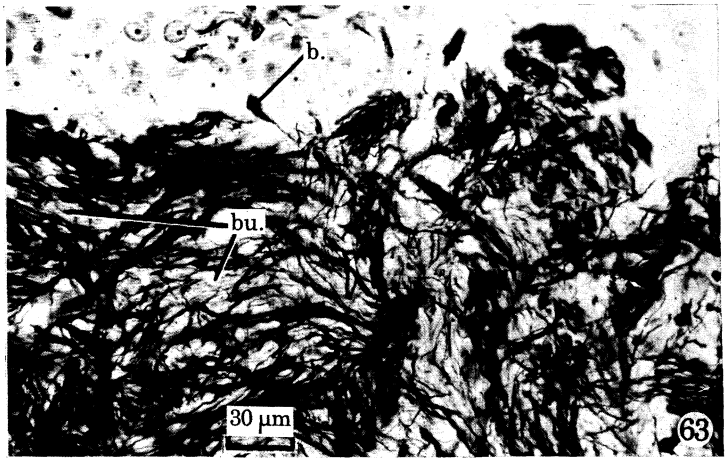
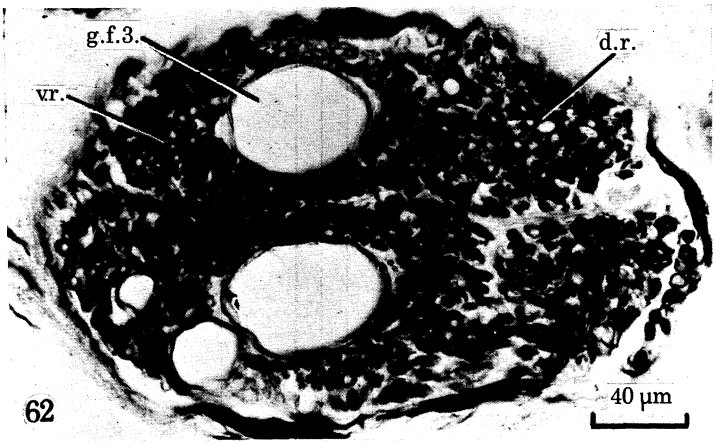


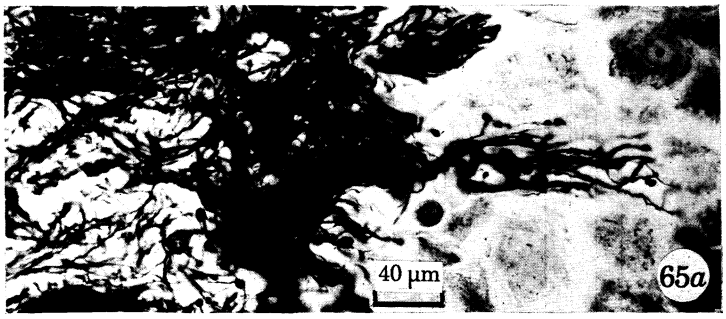


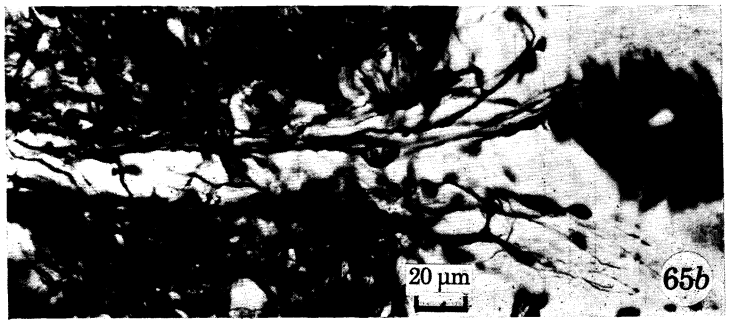












FIGURES 58 to 65. For legends see facing page

roots or ventral neuropil, but the situation is complicated by the presence of the regenerating terminal knobs, which are beginning to invade the neuropil.

This invasion was accentuated in animals killed at 4 days or later after cutting the stellar nerves close to the ganglion. The central stumps became surmounted with whorls of fine fibres (figure 46, plate 34). These penetrate the ganglion and are found not only in the neuropil but among the cell layers, close to the neuronal somata (figures 47, 48, plate 34). They are evidently able to proceed in pathways between the glial and neuronal surfaces. They are especially conspicuous in the dorsal part, but are present also in the ventral. Such fibres invading the cell layers are never seen in a normal *Octopus*, though they are common in *Sepia* and *Loligo* (p. 423). These very numerous endings are a spectacular and unexpected result of severing the stellar nerves. They closely resemble the knobs seen in the whorls of fibres around the cut ends of the stumps. It is, therefore, presumed that they are the ends of fibres that have grown back into the ganglion, but it cannot be excluded that they are the products of some reaction of the branches of the cells within the ganglion. If they come from the cut stumps it would be interesting to know from which class of fibres. They are only present in the dorsal cell layers, which they enter from the neuropil. It is possible that they are processes of the microneurons. This would agree with the fact that they are only seen when cuts are made close to the ganglion (assuming that the microneurons do not proceed far in the nerves, see p. 416).

The dorsal neuropil at this time has a rather loose, open appearance. It has clearly lost many fibres and yet many small dark ones remain, besides the main trunks of the large neurons and the bundles of fine trunks of the small cells. The preganglionic fibres of the pallial nerve can be seen very clearly in the dorsal neuropil (figure 49, plate 34). Some abnormal swollen terminals at the centre of the dorsal neuropil have not been identified, probably they are the ends of trunks of cells that have undergone retrograde degeneration.

In an animal killed 5 days after cutting the stellar nerves the dorsal neuropil showed disorganization but few degeneration granules. Many of the thin dark fibres were still intact and therefore they are not all stellar nerve afferents. Some of them are collaterals of the outgoing dorsal root fibres (figure 20, plate 31). This problem is also complicated by the presence of the fibres invading from the cut stumps.

No further new features were seen at still longer periods after cutting stellar nerves. The collaterals of the outgoing fibres appear clearly even after considerable degeneration times. This is important as showing that they are attached to efferent fibres and are not branches of incoming fibres.

Description of plate 36

Figure 58. *Sepia*. Section posterior to figure 57.

Figure 59. *Sepia*. Ventral cell wall and neuropil, showing bundles of fibres collecting as the ventral roots.

Figure 60. *Sepia*. Origins of dorsal and ventral roots from the respective neuropils.

Figure 61. *Sepia*. Pallial nerve cut 33 days (Naples, April). Fine fibres still accompany the trunks of the ventral wall cells (compare figure 6).

Figure 62. *Sepia*. Cross-section of the roots of two stellar nerves just outside the ganglion.

Figure 63. *Sepia*. Dorsal neuropil, showing bundles of fine fibres.

Figure 64. *Sepia*. Stellar nerves cut 31 h (Plymouth, August). Dorsal root showing degenerating afferent fibres.

Figures 65*a*, *b*. *Sepia*. Dorsal neuropil with tangles of fibres, bearing boutons, some of which proceed into the cell layers.

B. The stellate ganglion of *Sepia*

1. *The giant fibres*

The ganglion is divided into dorsal and ventral parts as in *Octopus*, the ventral having only large cells, the dorsal small as well as large (figures 50, 56 to 58, plates 35, 36). There are giant fibres arising not from a giant fibre lobe as in *Loligo* but from the dorsal wall of the ganglion (Young 1939). They can be followed from the ventral roots of the stellar nerves to the centre of the ganglion, where they turn dorsally and divide into numerous trunks, thus each arises from many cells (figures 50, 51, plate 35). Although the main trunks can be readily seen to be formed by the union of small ones, it has not yet been possible to follow the finer trunks to individual nerve cell bodies. We cannot therefore say how large or numerous these cells are. But the fibres are certainly syncytial and the cells lie in the dorsal wall of the ganglion, although the fibres leave in the ventral roots.

The giant fibres receive presynaptic fibres from the pallial nerve. These form a group of about 10 large fibres (up to 100 μm), usually lying at one side of the pallial nerve (Young 1939). They divide several times on entering the neuropil and the branches spread out along the outgoing trunks of the third order giant fibres (figures 52, 53, plate 35). The latter give collateral spines, arching around the incoming presynaptic fibre (figure 54, plate 35).

It may be that there is a further input to the giant fibres from the stellar nerves. Boutons are seen near the main trunks (peripheral to the fusion) even 33 days after section of the pallial nerve, but it is not certain that these are true synaptic contacts (figure 55, plate 35).

2. *The ventral division of the ganglion*

The two neuropils are distinct, though less sharply separated than in *Octopus* (figures 56, 57 and 60, plates 35, 36). The ventral cell wall consists only of large cells. The neuropil here is a loosely textured and irregular network, among which run the branches of the presynaptic fibres of the pallial nerve (figure 59, plate 36). The finer branches of these have not been clearly seen. Boutons of various sizes occur occasionally in the outer ventral neuropil and on the main trunks of the cells as they enter the neuropil, but they are not common and are rarely found further into the cell layer. There are some tangentially running fibres in the outer neuropil, but no bundles of fine ones such as are seen near the dorsal cell layer. The ventral bundles are of rather coarse fibres and they are probably mostly or all axons of the ventral cells running to make the ventral roots of the stellar nerves (figures 56 to 58). There may, however, be an input to these ventral pathways from the stellar nerves, since long after section of the pallial nerve (33 days) bundles of fine fibres were seen accompanying the main trunks of the ventral cells nearly to the cell body (figure 61, plate 36, compare figure 6, plate 29). Most of the dark fibres persisting after this operation are probably dendritic branches of the large neurons (p. 418).

3. *The dorsal and ventral roots*

The nerve fibres arising from the ventral cells turn backwards and collect into bundles in the outer neuropil and these form the ventral roots, after they have been joined by the giant nerve fibres (figures 56 to 58). These roots are entirely composed of large fibres. The dorsal roots also form up gradually from the front of the ganglion and run back as bundles just within the neuropil. The two roots of each nerve run separately through the neuropil (figures 57 and 58) and then through the cell layers (figure 60, plate 36). They join at the outer border of the cell layer

and leave in a common sheath (figure 62, plate 36). The two bundles remain distinct within the sheath for a few millimetres and it should be possible to stimulate or record impulses separately from each bundle.

4. *The dorsal neuropil*

The dorsal neuropil is more tightly woven than the ventral with many more small fibres (figure 63, plate 30). These come from the small cells as bundles, running mainly tangentially. The fine fibres are very numerous, but the bundles do not stand out as conspicuously as they do in *Octopus* (at least in these preparations). The bundles run towards the dorsal roots and break up into complicated tangled knobs and plexuses of neuropil (figures 65*a*, *b*, 66 and 72, plates 36 and 37). Boutons of various sizes occur in these plexuses. Some are probably swellings along the course of the fine fibres (figure 66), others are the ends of dendrites and some of these are quite large (diameter > 20 μm) (figure 72). The large knobs are more evident at the posterior end of the ganglion. Fibres often proceed from the tangles in the neuropil into the cell layer and end as knobs against the cell body or first part of the axon (figures 65*a*, *b*). The knobs are not endings of pallial nerve fibres since they remain after section of that nerve (p. 423). The reason for their entering the cell layers is not clear. A few fibres entering the cell layers end as networks around the cells (figure 67, plate 36). In a few animals the stellar nerves had been cut and degeneration was seen in the central stumps and outer dorsal neuropil (figure 64). There are thus afferents in the dorsal roots similar to those of *Octopus*. The trunks of the larger cells of the dorsal wall divide into several branches where they enter the neuropil. As in *Octopus* this appears especially clearly after degeneration of the fibres of the pallial nerve (compare figures 40, plate 33 and 68, plate 37). The trunks then pass to the centre of the neuropil and on to the dorsal roots, where they give collateral branches, very similar to those in *Octopus* (figure 69, plate 37) and there come into relation with the tangles of fine fibres in the dorsal neuropil.

In this region therefore there are at least four components: (1) the large trunks of the main cells and their collaterals, (2) the fine trunks of the small cells, (3) numerous darkly staining fibres, some of which are presumably stellar nerve afferents, finally, (4) degeneration shows that pallial nerve fibres also end here.

5. *Section of the pallial nerve in* Sepia

Material is available at periods of 4, 7, 8, 18 and 33 days after operation. Some of these experiments were at Naples in April, others at Plymouth in August, that is at water temperatures around 17 °C in both places. At 4 days the ventral neuropil had already lost its characteristic texture, and there were numerous granules. These were most abundant at the centre of the ganglion, but reach also the extreme outer edges of both neuropils (figure 70, plate 37). In the dorsal neuropil the granules are not especially related to the bundles of small axons and indeed, as in *Octopus*, may perhaps not be related to these fine fibres at all (figure 71, plate 37). Other large and small terminal boutons in the outer dorsal neuropil remain intact, and some of these extend into the cell layers.

After the longer periods of degeneration, the ventral neuropil became more empty. After 8 days it already contained few granules, leaving the branching trunks of cells. The dorsal neuropil remains of course the more complicated, with the fine fibres and many terminal masses, which are therefore certainly not the ends of fibres of the pallial nerves (figure 72, plate 37). The only further change by 33 days was contraction of both neuropils, with crowding of the remaining fibres (figure 50, plate 35). The dorsal neuropil remains much more complex

than the ventral. When the fibres of the pallial nerve itself have all degenerated there are left bundles running through from the stellar nerves. These branches sometimes do not run direct from each stellar nerve to the pallial nerve but pass through a plexus within the neuropil. This plexus presumably therefore consists of afferent fibres and may serve to allow some spread within the ganglion of influences entering from the stellar nerves (? pain and/or proprioception). The plexus is seen in a normal *Sepia* in figure 73, plate 37 and is similar to that shown in *Octopus* in figure 22, plate 37.

C. The stellate ganglion of *Loligo*

The arrangement is essentially as in *Octopus* and *Sepia*, but altered by the separation of the cell-bodies of the giant fibres into a distinct lobe at the hind end of the ganglion. This lobe is clearly a derivative of the dorsal wall, with which it is continuous (figure 74, plate 38). Its cells have their own characteristics, distinct from those of the small cells of the rest of the dorsal wall (figure 75, plate 38). They are a uniform population with diameters between 40 and 25 μm (figure 76, plate 38). Their nuclei are between 25 and 12 μm, that is to say rather larger (relatively) than those of the small cells elsewhere in the ganglion. The trunks of these cells of the giant fibre lobe of course unite to make the syncytial third order giant fibres (Young 1939).

The two sides of the ganglion, dorsal and ventral, with and without small cells, are distinct, but are somewhat differently arranged from those in *Sepia* and *Octopus*. The large-celled portion is displaced postero-laterally, so that the stellar nerves emerge through it (figures 77 to 79, plate 38). The cells of the ventral wall are few, but all very large, up to 100 μm diameter (probably more in a large squid), with nuclei up to 30 μm. Their axons make large trunks running through the loose web of the ventral neuropil. They pass to the stellar nerves in bundles distinct from those coming from the dorsal neuropil. The dorsal and ventral roots are thus separate and join as they leave the ganglion (figures 80 and 81, plate 38). The ventral neuropil shows the clear spaces in which the trunks pass. The branches of the incoming pallial nerve fibres run irregularly among these trunks (figure 82, plate 39). There are a few small argentophil fibres running tangentially in the outer part of the neuropil, but no compact bundles of fine fibres. The axons of the ventral cells collect into bundles of rather large fibres, running just within the neuropil to the roots (figure 82). Argentophil boutons of various sizes are common in the ventral neuropil and presumably include endings of the pallial nerve pre-synaptic fibres (figure 83, plate 39). They are very common in the outer neuropil and may also occur in the cell layers (figure 84, plate 39).

Description of plate 37

Figure 66. *Sepia*. Dorsal neuropil. Fibres of various sizes, some varicose, others with terminal swellings.

Figure 67. *Sepia*. Dorsal neuropil sending fibres to end around cell body.

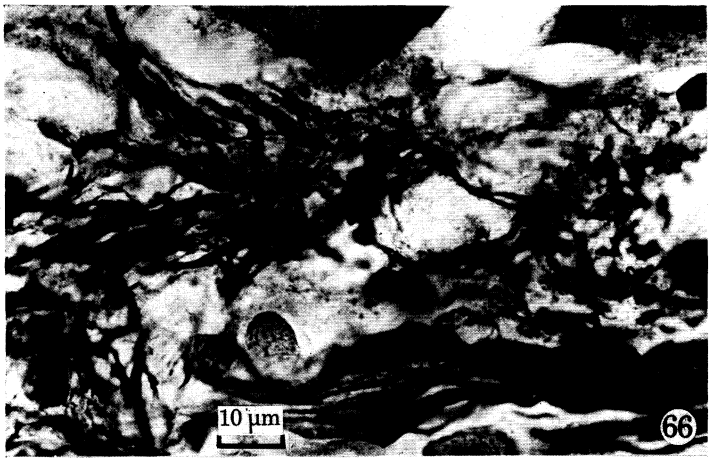
Figure 68. *Sepia*. Trunk of cell of the dorsal wall dividing where it enters the neuropil. Pallial nerve cut 33 days previously (Naples, April), compare figure 40, plate 33.

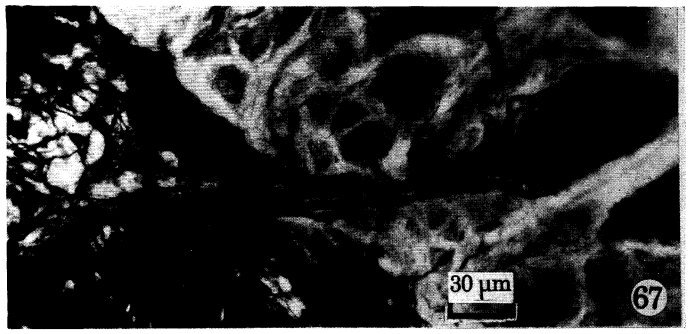
Figure 69. *Sepia*. Dorsal root. The large fibres leaving the neuropil give collateral dendritic branches (den.).

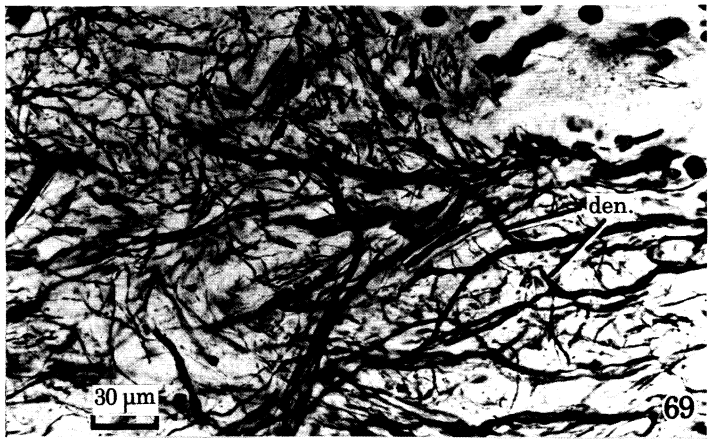
Figures 70, 71. *Sepia*. Pallial nerve cut 4 days (Plymouth, August). Dorsal neuropil showing granules not especially related to the fine fibres.

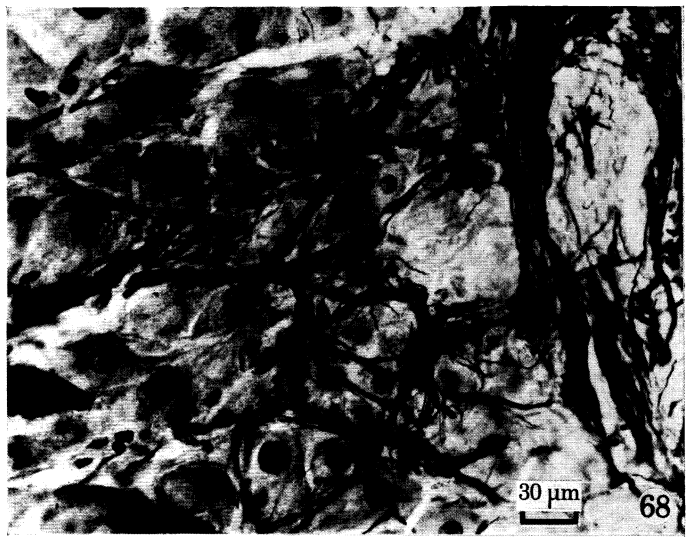
Figure 72. *Sepia*. Pallial nerve cut 8 days (Plymouth, August). Dorsal neuropil and cells with terminal spheres still intact.

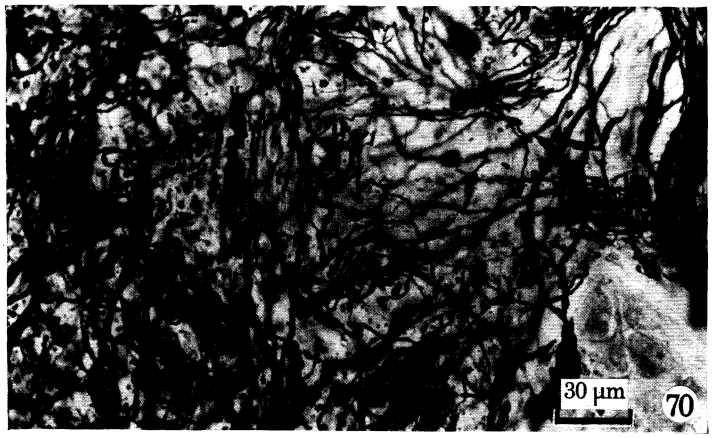
Figure 73. *Sepia*. Plexus of fibres at entry of dorsal roots of stellar nerves.

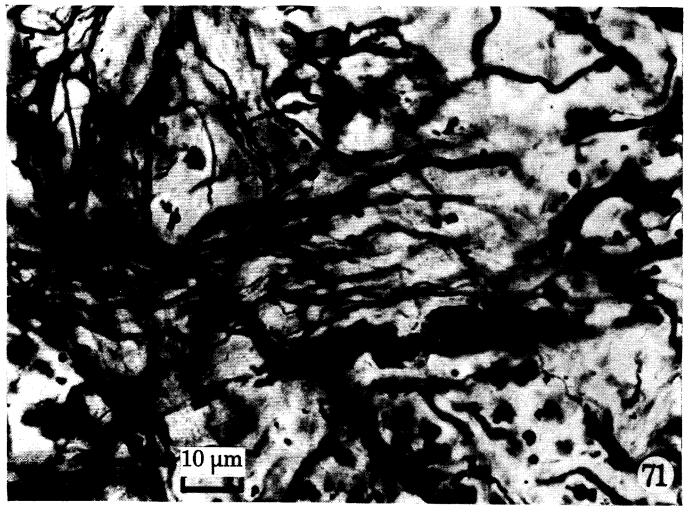


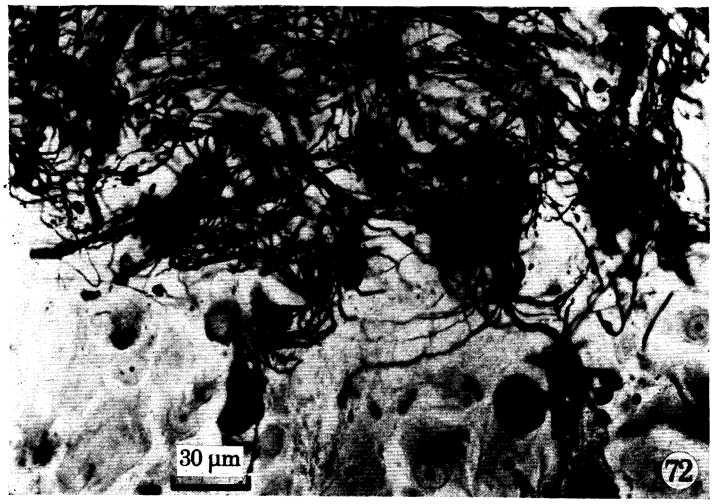


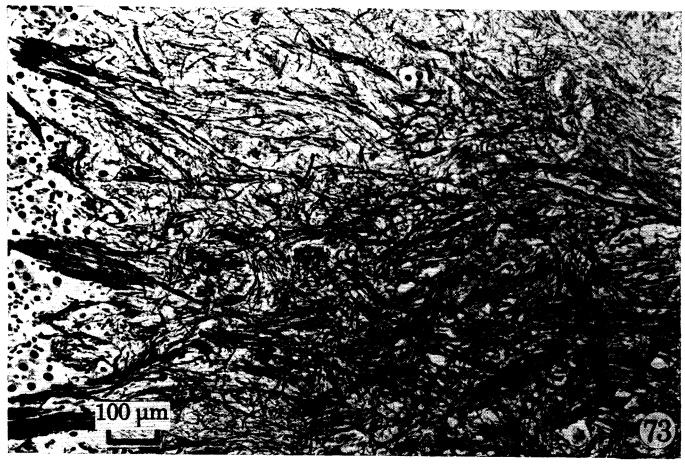












FIGURES 66 to 73. For legends see facing page

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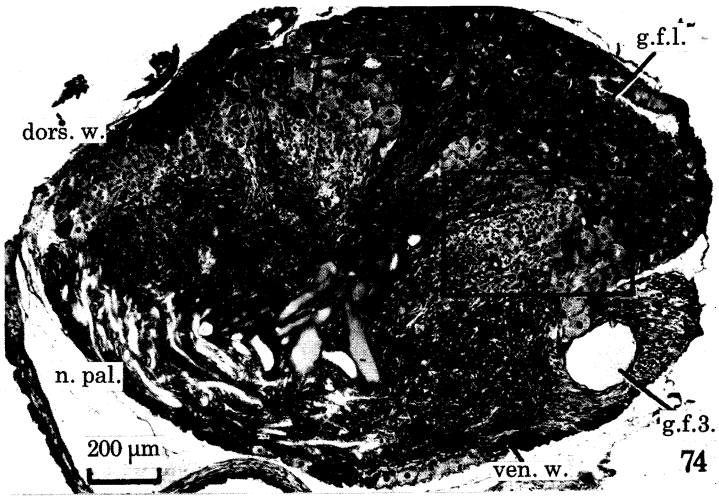

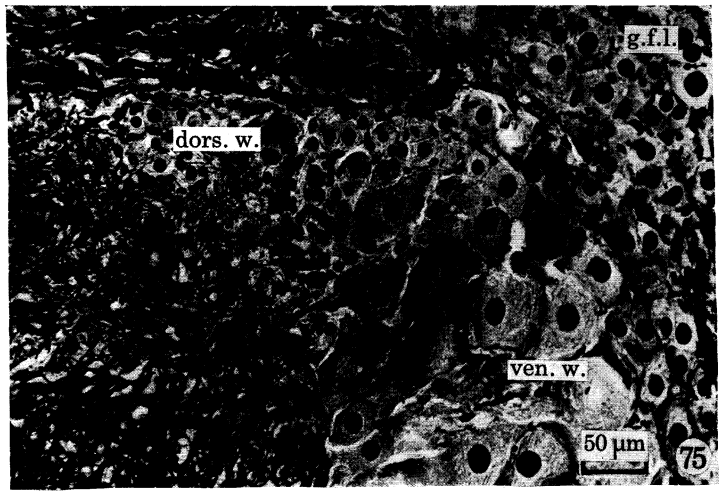

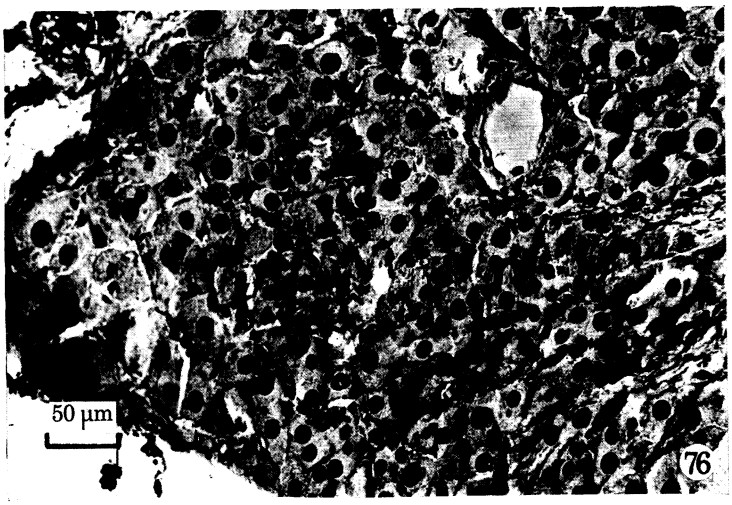

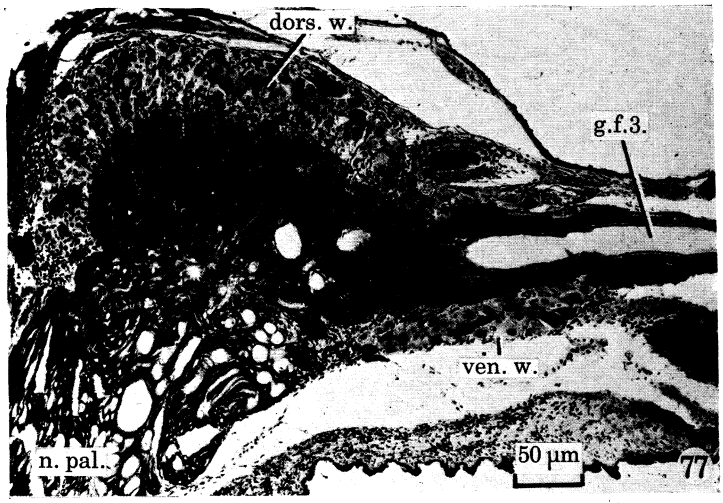

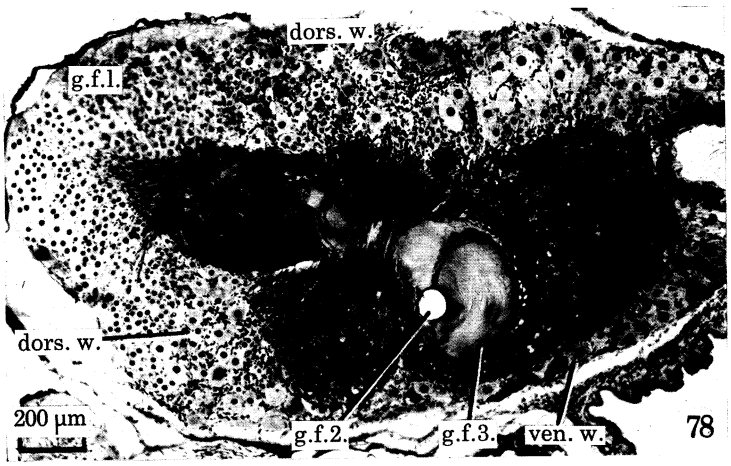

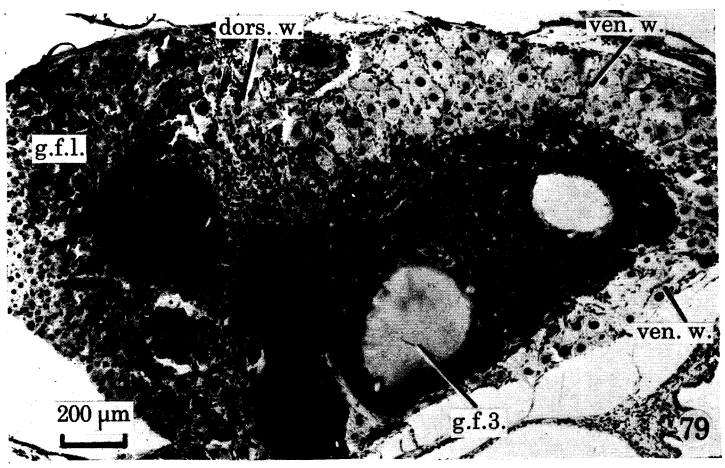

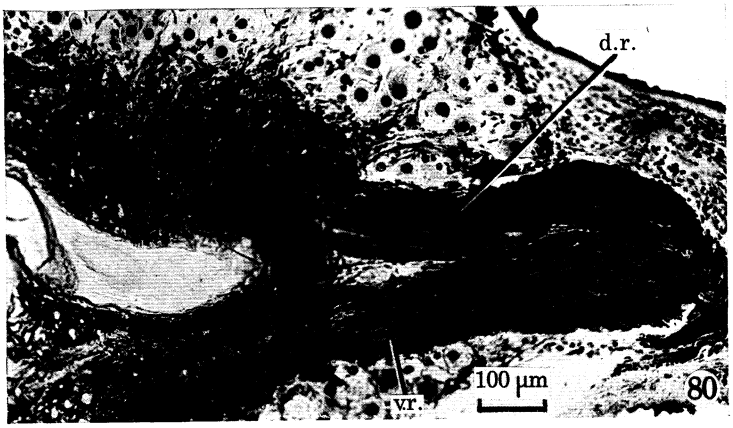

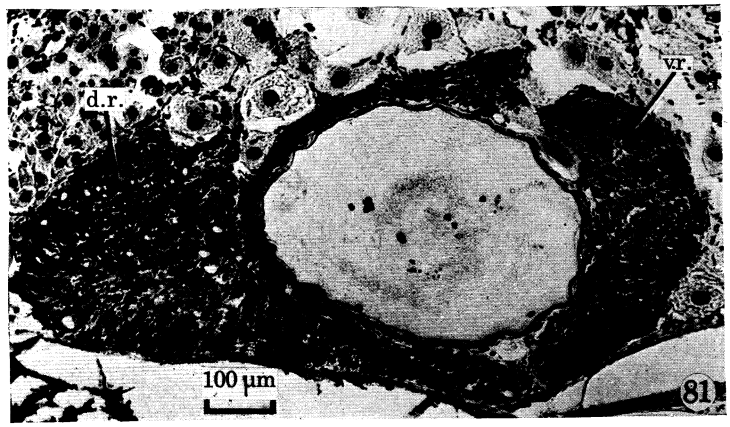

FIGURES 74 to 81. For legends see facing page

The dorsal (small-cell) region

The region with small cells occupies the whole of the dorsal wall at the front end of the ganglion, where the ventral wall is almost without cells (figure 77, plate 38). The dorsal wall has the typical arrangement of large cells on the outside, decreasing passing inwards to relatively small ones next to the neuropil. The largest are up to 50 μm in diameter (probably larger in a large squid), but with rather small nuclei, 10 μm diameter. The smallest cells have diameter 10 μm or even rather less, with nucleus 6 μm.

The neuropil differs markedly from that of the ventral region. It is differentiated into a central region with mainly large fibres and an outer neuropil with many very fine ones. There are bundles of fine trunks, which run tangentially just within the neuropil (figure 85, plate 39). These bundles are similar to those in *Octopus* and *Sepia*, though less compact than in *Octopus*. Among them are numerous swellings (figures 85, 86 and 89, plate 39). Some of these are varicosities along the course of the trunks of small neurons (figures 85 and 89). Others are probably terminal swellings on the ends of dendritic branches of the cells of the ganglion.

Some fibres penetrate within the cell layer and end in contact with the trunks or cell bodies of the larger cells (figure 87), but probably not the smaller cells. These knobs within the outer neuropil have some resemblance to the smaller of the numerous terminal knobs of the smaller second order giant fibres ending in the giant cell lobe (figure 88), which may also send branches up into the cell layers to end around the cells.

Where the larger fibres of the dorsal roots of the stellar nerves join the neuropil they show the same lateral branches as in *Octopus* (figure 86). In this region there are also numerous fine fibres and endings, presumably stellar nerve afferents. The branches pass into the outer neuropil close to the layer of small cells, meeting there the bundles of numerous small axons. In this region there is thus a very complex tangle of fibres of various sizes. Many of them end in large or small swellings or show boutons *en passage* (figure 89).

The stellar nerves were cut in a number of *Loligo pealii* at Woods Hole and the animals survived for 1 to 5 days. Degeneration granules were seen in the stellar nerves, showing that afferents are present, but their detailed distribution in the ganglion could not be made out.

Thus in summary, in the front of the ganglion the walls are all composed of the 'dorsal' type, including many small cells. Only laterally are there some ventral type cells (figure 77, plate 38). In the middle of the ganglion both types of cell wall are present (figure 78). At the

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DESCRIPTION OF PLATE 38

FIGURE 74. *Loligo vulgaris.* Sagittal section.

FIGURE 75. *L. vulgaris.* Sagittal section of area outlined in figure 74, showing cell-types of dorsal and ventral walls and giant fibre lobe.

FIGURE 76. *L. vulgaris.* Sagittal section of giant fibre lobe.

FIGURE 77. *L. forbesi.* Transverse section near the front of the ganglion to show the pallial nerve and dorsal and ventral walls.

FIGURE 78. Transverse section somewhat behind figure 77. The walls of 'ventral' type lie mainly laterally and of 'dorsal' type medially.

FIGURE 79. Transverse section posterior to figure 78. The wall is now almost all of 'ventral' type, even at the dorso-lateral edge.

FIGURE 80. *Loligo forbesi.* Sagittal section of small stellar nerve, showing the two roots.

FIGURE 81. *L. forbesi.* Transverse section of hinder stellar nerve where it leaves the ganglion, showing the two roots.

hind end the walls are almost wholly composed of the ventral (large) cells, except of course for the giant fibre lobe (figure 79). The neuropils do not show quite the same sharp separation since the fibres passing between the stellar nerves and the small cell region pass through the large-cell (ventral) neuropil.

Discussion

1. *The two divisions of the ganglion*

The stellate ganglia of these three widely different cephalopods are thus all built on the same plan, which must be a very ancient inheritance. We may note, however, that *Nautilus* has no stellate ganglion. The division into two parts presumably reflects the two functions of the mantle, respiratory and locomotor. Unfortunately there are no critical experiments to determine which part is related to each. The fact that the ventral has no peripheral afferents suggests that this may be the respiratory part, operating only under the command of the central nervous system, without modulation from the periphery. However Gray (1960), who found motor units active either in inspiration or expiration, suspected that there might also be convergence on these of afferents from the periphery, although no afferent discharges occurred in the peripheral stumps of stellar nerves during normal respiratory activity. The question of the relation of the afferents to the respiratory neurons therefore requires further investigation. Gray also found evidence of afferent neurons not associated with those responsible for the respiratory rhythm.

The dorsal part of the ganglion certainly receives afferents from the periphery and has small cells, which would be likely to be involved in more complicated locomotor and other behavioural actions. Gray showed that some of the afferents are proprioceptive, but others may be nociceptive. He was unable to decide on their functions and it is therefore not possible to speculate on the detailed operation of the system. It may be that it involves reciprocal reflex inhibition, but Gray saw no sign of this. The mantle may be held tightly contracted for many seconds if the water is foul, presumably involving inhibition of the dilator muscles. Again, the whole mantle is sometimes stretched out into a long cone when an octopus is approaching a potentially dangerous object, thus demanding adjustment of the two antagonistic sets of muscles. It may also be held inflated, as in the dymantic response in *Octopus*, or in a *Sepia* that has been picked up.

There has been debate as to the significance of the synapse in the stellate ganglion on the pathway to the mantle muscles (Fröhlich 1910; ten Cate 1929; Sereni & Young 1932; Gray 1960; Wilson 1960). Stimulation of the central end of one stellar nerve of an octopus produces

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Description of plate 39

Figure 82. *L. forbesi.* Ventral cell wall and neuropil, showing bundles of large fibres running to ventral roots.

Figure 83. *L. forbesi.* Ventral neuropil showing terminal boutons.

Figure 84. *L. forbesi.* Ventral cell wall, showing fibres and boutons among the cells.

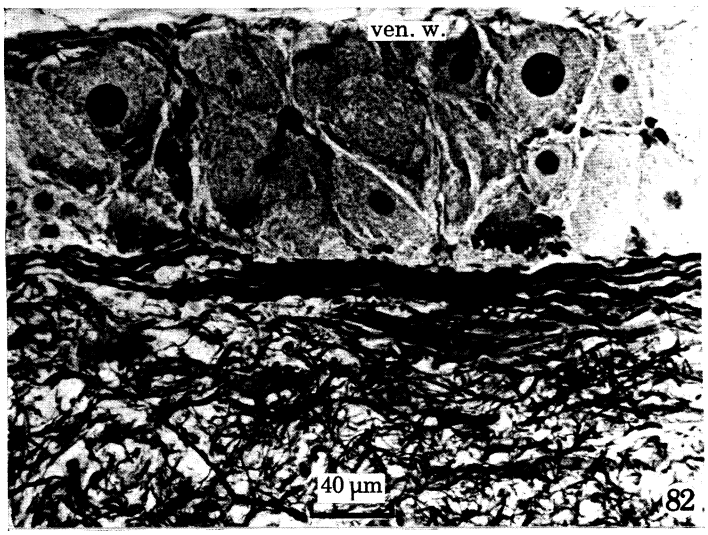
Figure 85. *L. forbesi.* Dorsal neuropil, showing fine fibres, some with varicosities.

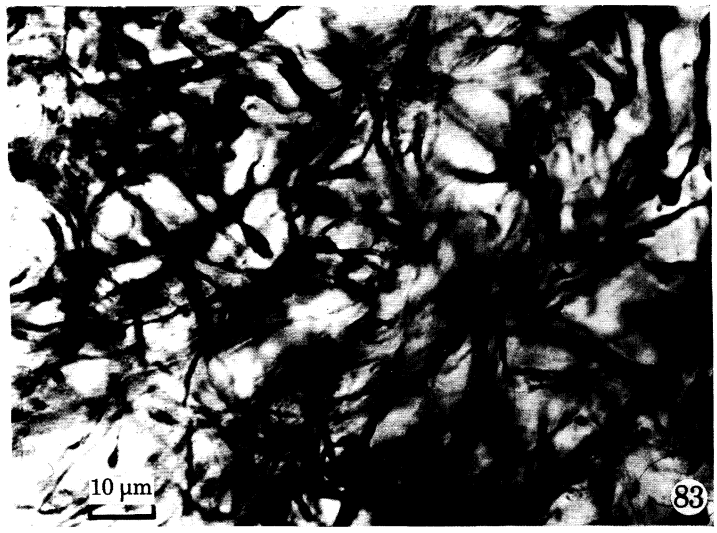
Figure 86. *L. forbesi.* Dorsal neuropil at hind end of ganglion showing numerous knobs.

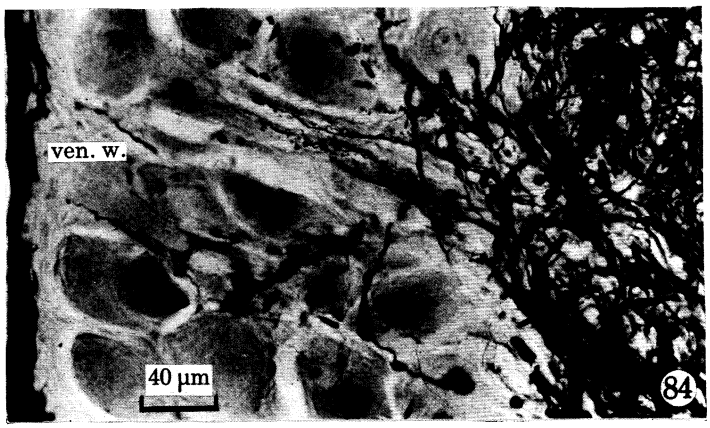
Figure 87. *L. forbesi.* Hind end of ganglion, showing fibres and terminals among the cells of the dorsal wall.

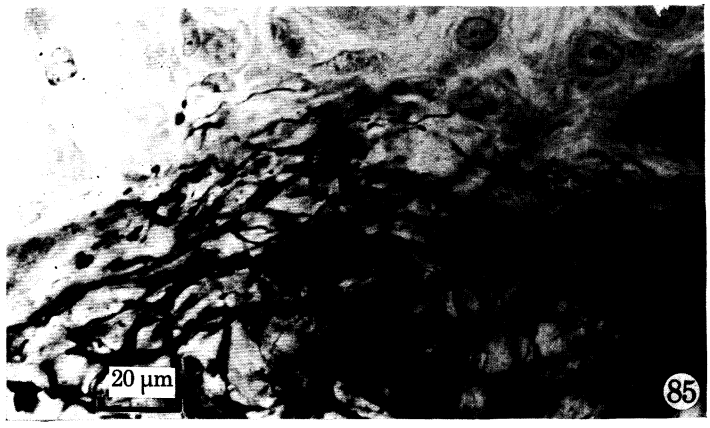
Figure 88. *L. forbesi.* Giant fibre lobe, to show endings of the accessory second-order giant fibre among the third-order trunks.

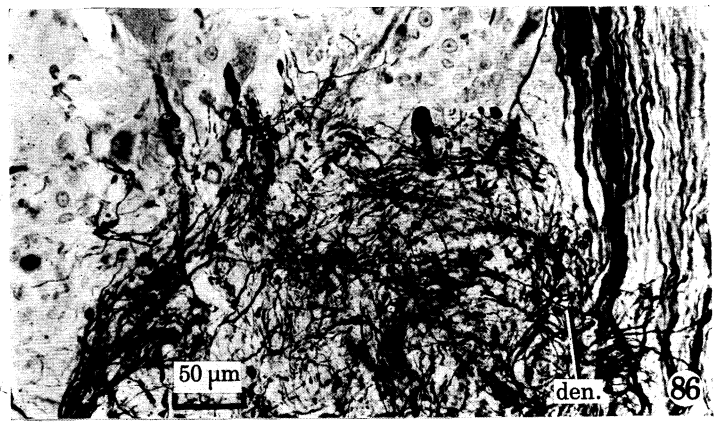
Figure 89. *L. forbesi.* Dorsal neuropil to show terminal swellings (dendrites?) and fine varicose fibres.

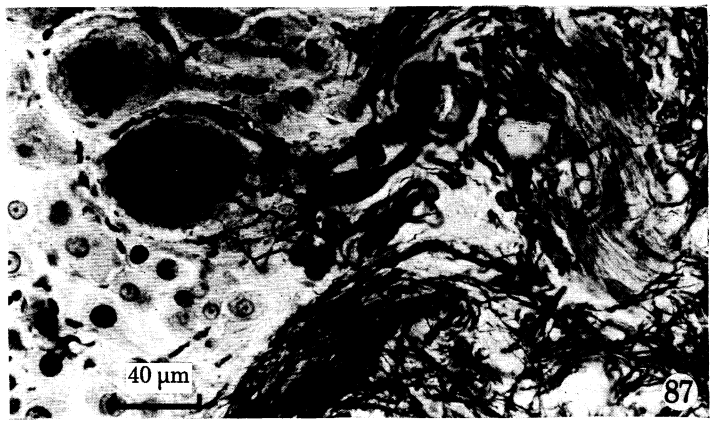


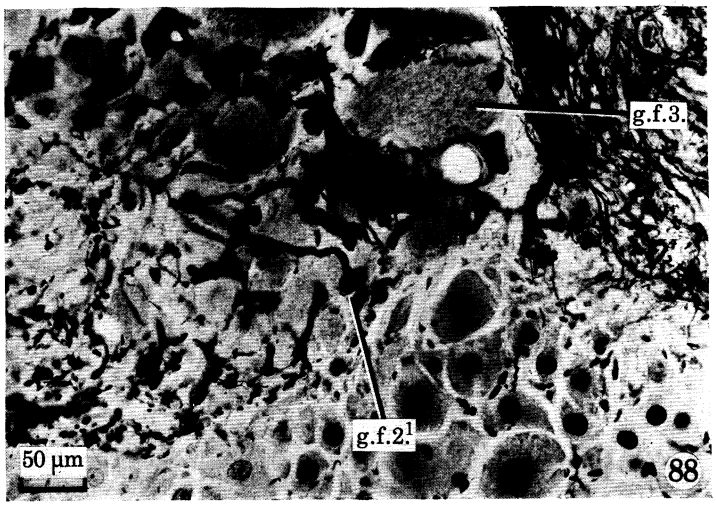


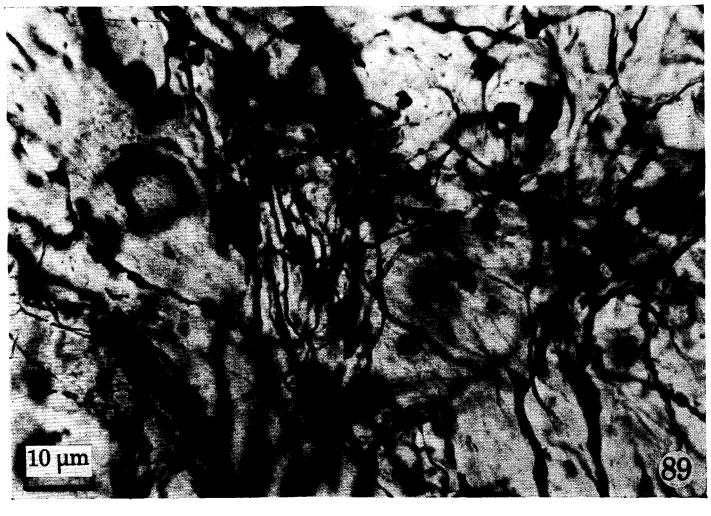












FIGURES 82 to 89. For legends see facing page

(*Facing p.* 426)

contraction elsewhere in the mantle. There are, therefore, possibilities of reflex interactions, but their relation to influences coming from the central nervous system is not clear. Some recent further experiments (unpublished) have shown that stimulating the central end of one stellar nerve produces contractions only in the nearby parts of the mantle. These responses are abolished by cutting the next one or two stellar nerves, raising the suspicion that they may be axon reflexes.

2. *Significance of the small cells*

The function of the small neurons remains obscure. It seems likely that their processes are confined to the ganglion, though even this is not certain (p. 416). A possible suggestion is that they play a part in reciprocal reflex action, perhaps acting in inhibition of the unwanted contractions of antagonistic muscles. Miledi has recorded inhibitory as well as excitatory synaptic potentials in cells of the stellate ganglion of *Octopus* and squids after stimulation of either pallial or stellar nerves (personal communication). An inhibitory function has been suggested for cells similar to amacrines in various situations. Some of their synapses seem to transmit as well as to receive signals, for instance in the retina (Kidd 1962; Boycott & Dowling 1969), medial geniculate nucleus (Morest 1971), granule cells of olfactory bulb (Price & Powell 1970*a*, *b*), small cells of the superior cervical ganglion (Matthew & Raisman 1969; Williams & Palay 1969), optic tectum of the frog (Sétáló & Székeley 1967), and lateral geniculate nucleus (Lieberman & Webster 1972). This seems to be the condition of these microneurons of the stellate ganglion (Barlow, Gray & Young 1971; Barlow & Gray 1972). Presumably they have some modulating action, perhaps inhibitory, which is absent from the ventral part of the ganglion. It is an attractive hypothesis that such small cells have provided the basis for the development in higher nervous centres of longer lasting inhibition as the basis of memory (Young 1965). The microneurons of the vertical and subfrontal lobes are also amacrines, without axon, and with serial synapses (Gray & Young 1964; Gray 1970). It is interesting that microneurons are absent from centres in the octopus brain that may reasonably be supposed to lack reciprocal reflex inhibition, notably the chromatophore lobes (Young 1971). The control of colour patterns is primarily through the eyes, presumably without feedback from any form of mechanoreceptors, which would be irrelevant. In many of the motor centres of the suboesophageal and buccal lobes there are small neurons as well as large, and presumably these are somehow involved in the mechanism of reciprocal reflex action.

3. *Degeneration in the ganglion*

Degeneration can proceed very fast in cephalopods at summer temperatures. It is well under way at the ends of fibres after 15 h, rather later in the main nerve trunks. The granules seen stained by Cajal's method are presumably pieces of axoplasm, and they may occur in rows. The granules have mostly been removed after 3 days. Similarly, rapid degeneration has been found after cutting the superior frontal to vertical lobe tract (Young 1971). On the other hand, preliminary experiments with the nerve to the posterior salivary gland showed the survival of fibres for two weeks, perhaps longer. It is not certain whether this indicates a real difference in the fibre types; it is not excluded that some as yet unidentified nerve cell bodies are involved along the pathway to the posterior salivary gland. Wilson (1960) reports evidence of response through the peripheral stumps of stellar nerves up to 34 days after removal of the stellate ganglion at 15 °C. If these responses were truly due to intact fibres this indicates a surprising difference in rate of degeneration between 15 and 25 °C. In our experiments at about

15 °C both with *Octopus* and *Sepia* degeneration was well under way after 4 days. At summer temperatures in Naples it is even faster and the granules would have mostly been removed by this time. The course of the break-up can be readily followed by simple Cajal silver staining. With Nauta-Gygax and Glees methods degeneration can still be followed for up to 6 days at 23 °C (Lund 1965).

The material for this work has been collected over a period of years at the Laboratories at Plymouth, Woods Hole and Naples, and I am grateful to the Directors and staff of all of these laboratories for their help. I am also greatly indebted to Miss P. R. Stephens for preparation of some of the material and of the plates and to the late Mr J. Armstrong and Miss T. Hogan for photography. Professors E. G. Gray and R. Miledi, F.R.S. and Dr M. Nixon kindly assisted by criticizing the manuscript.

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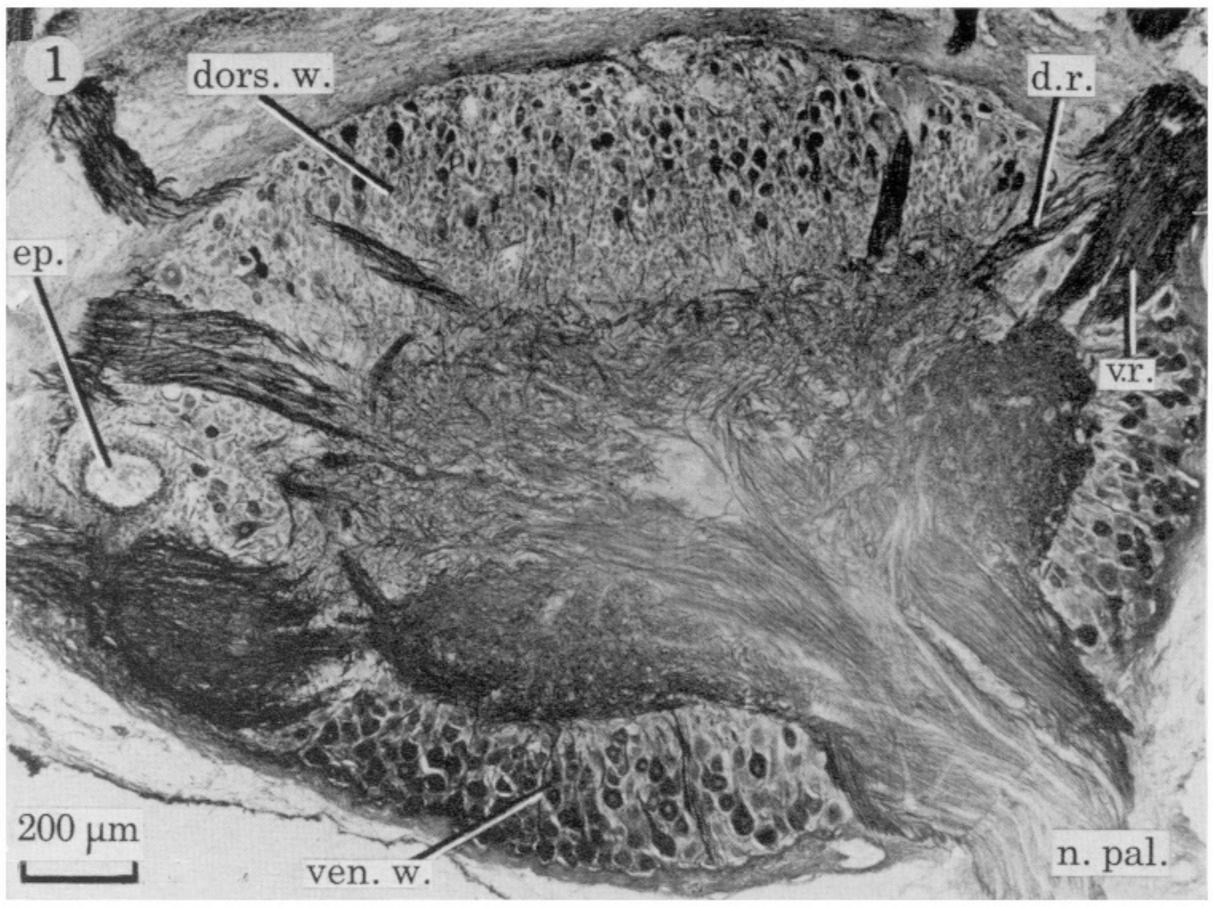
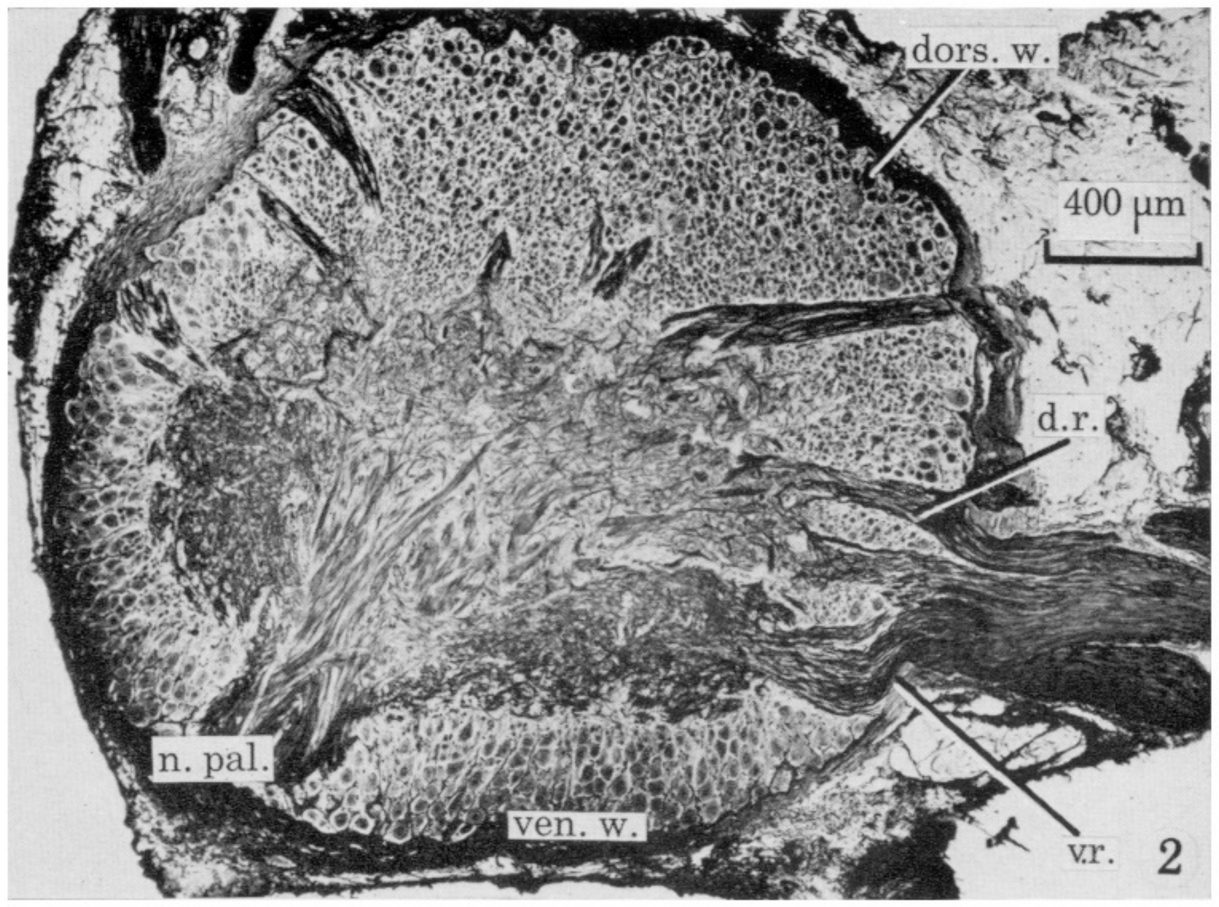
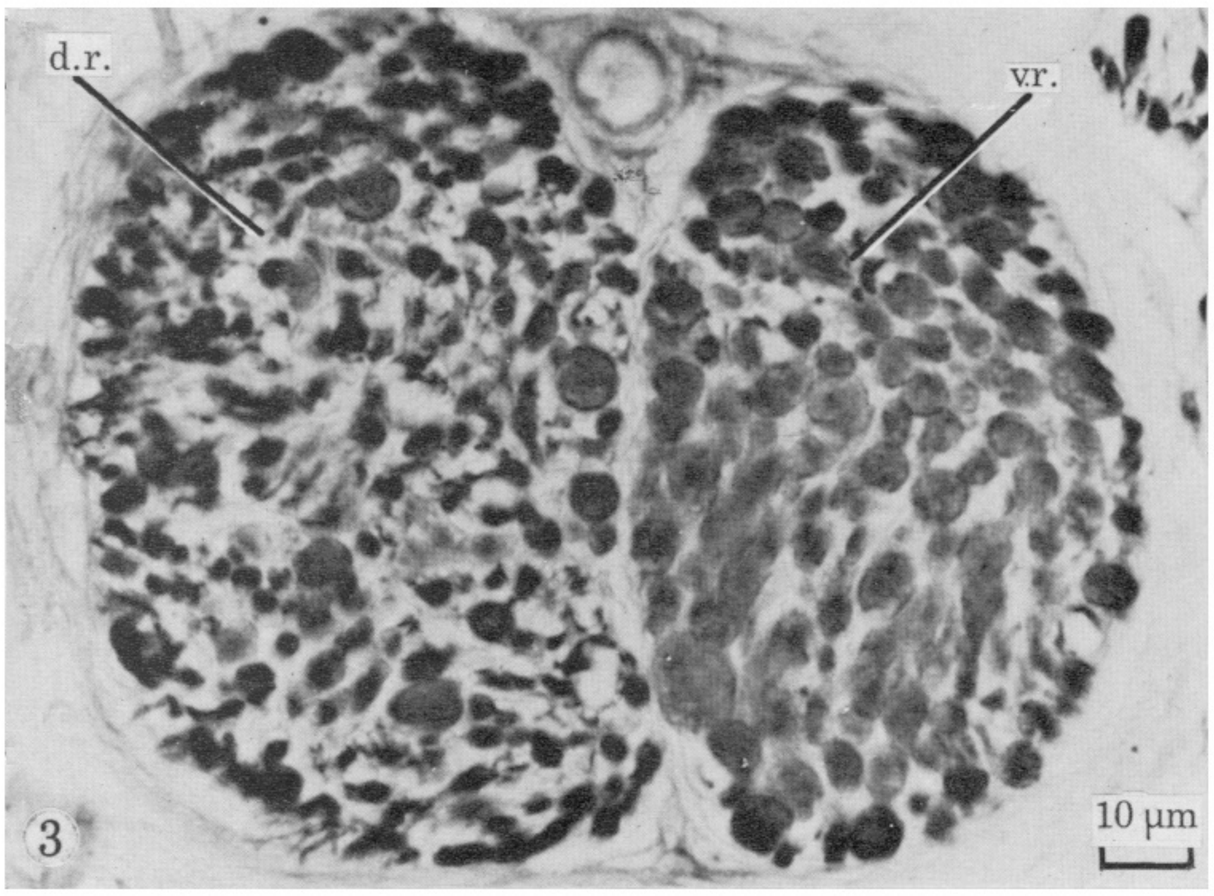
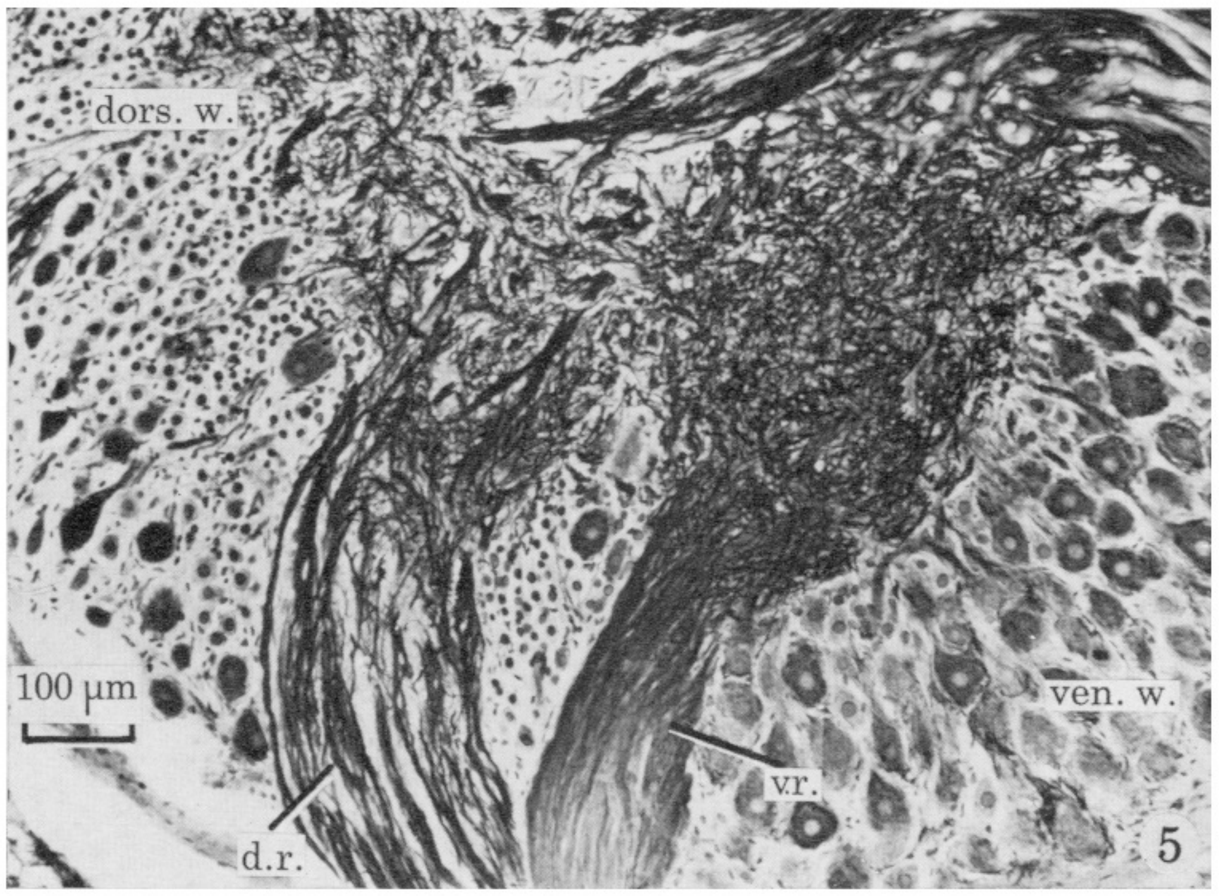
Abbreviations used on figures

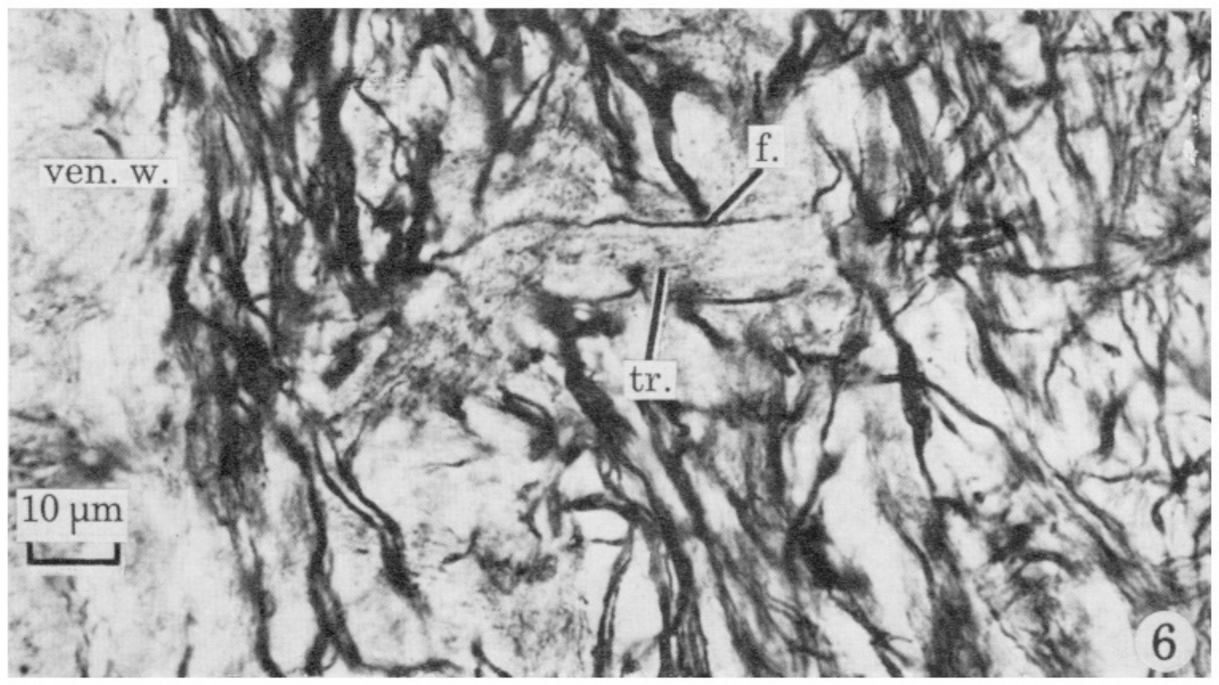
aff.	bundle of intact fibres, presumably afferents
b.	bouton
bu.	bundle of fine fibres
bu.l.	bundle of large axons
col.	collateral of second-order giant fibre
deg.	degeneration granules
deg.t.	transneuronal degeneration
den.	dendritic branch of trunk of cell
dors.w.	dorsal cell wall of ganglion
d.r.	dorsal root of stellar nerve
ep.	epistellar body
f.	fine nerve fibre
g.f.l.	giant fibre lobe
g.f. 2	second-order giant nerve fibre
g.f. 2^1	endings of accessory second-order giant fibres
g.f. 3	third-order giant nerve fibre
k.	terminal knob
kn.	knobs on the ends of dendrites
l.f.	large fibre of pallial nerve
neur.d.	dorsal neuropil
neur.v.	ventral neuropil
n.pal.	pallial nerve
st.n.	stellar nerve
t.	terminal swellings in neuropil after severance of stellar nerves
tr.	trunk of ganglion cell
v.r.	ventral root of stellar nerve
ven.w.	ventral cell wall of ganglion
wh.	whorls of regenerating fibres

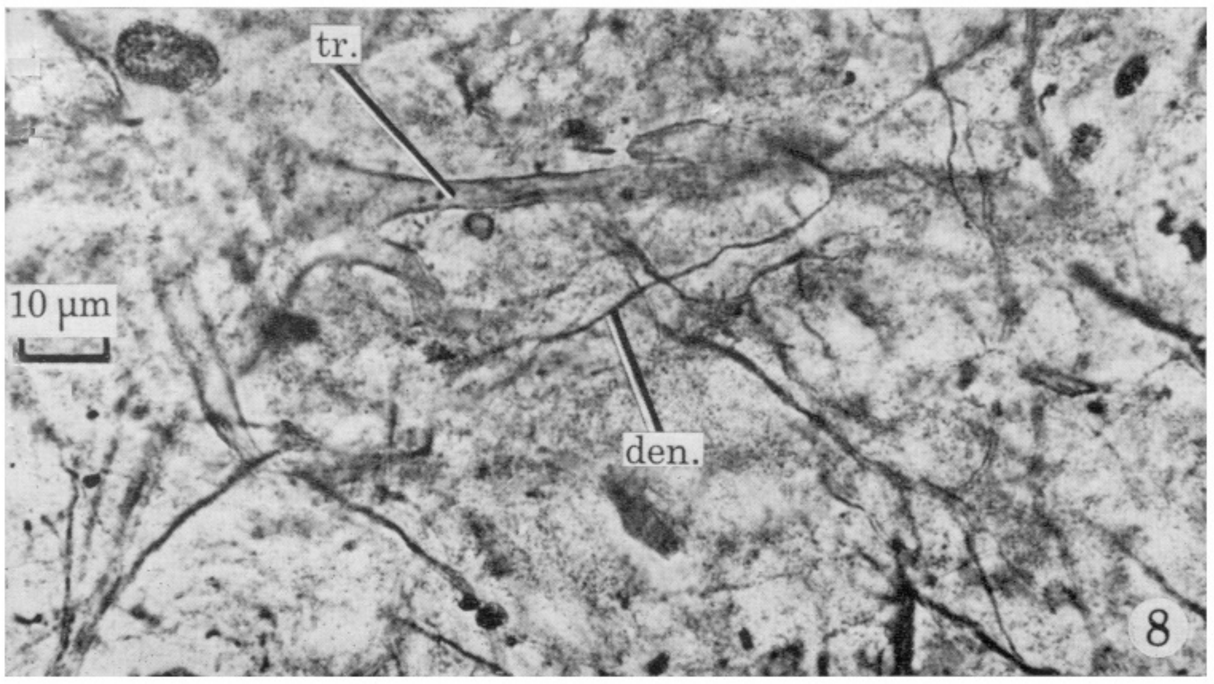


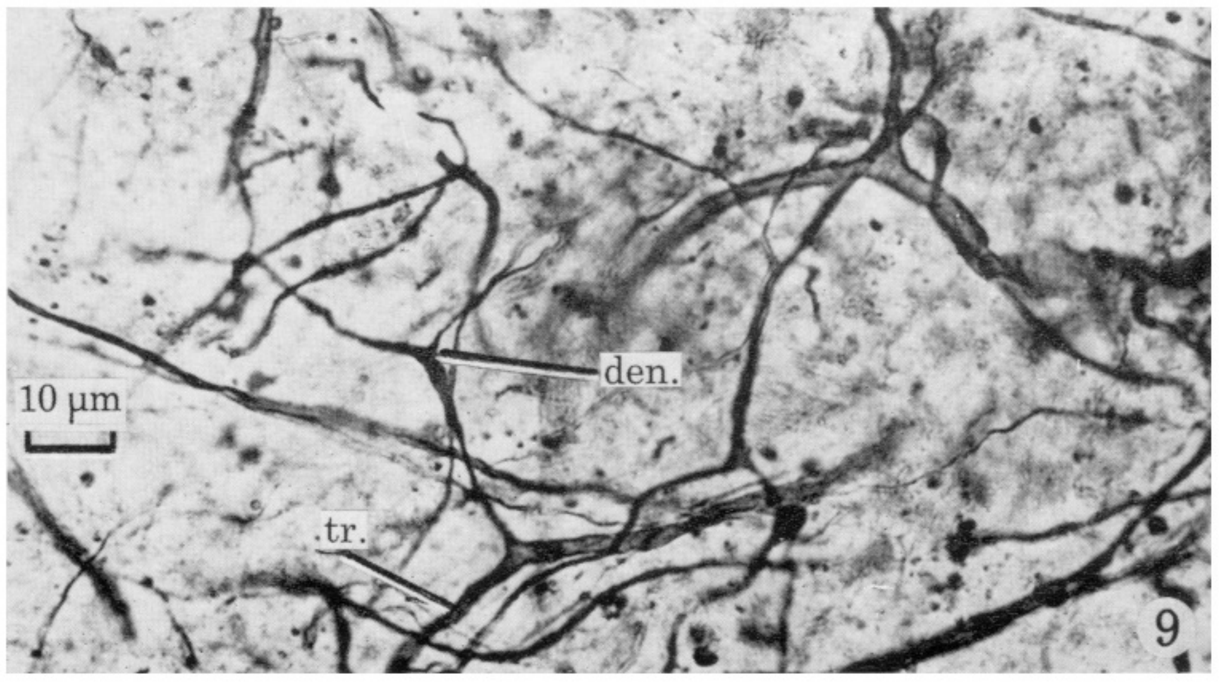












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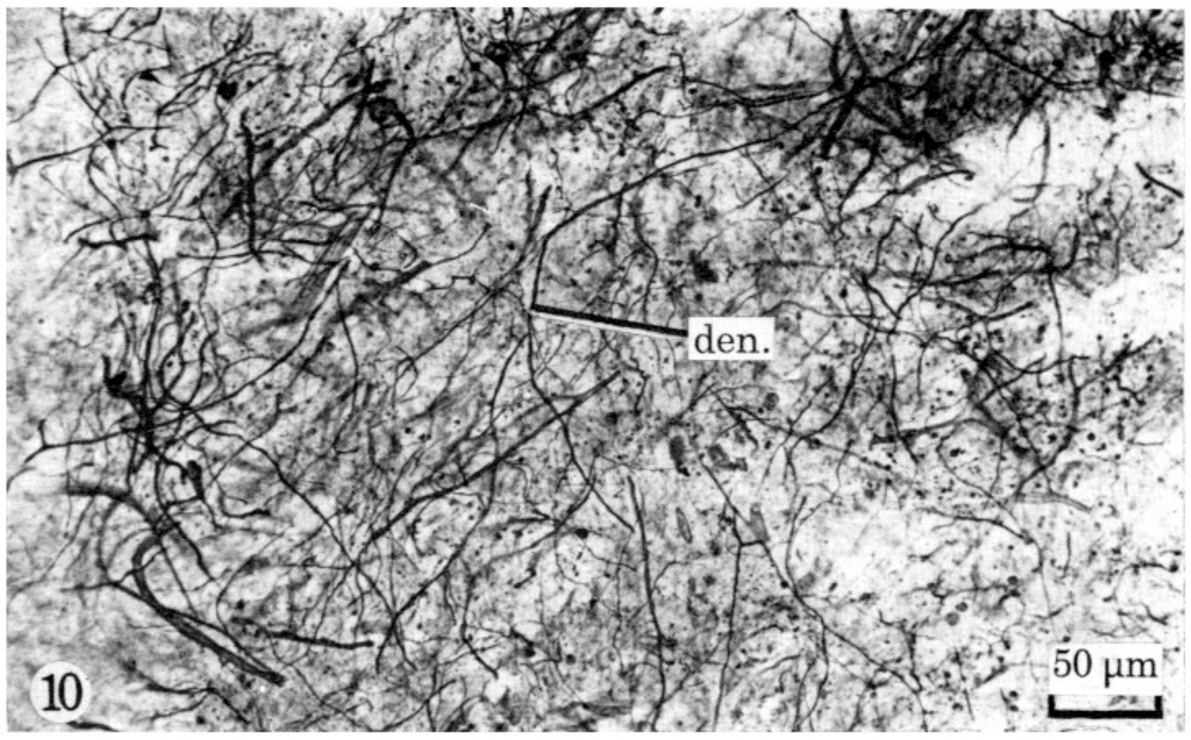

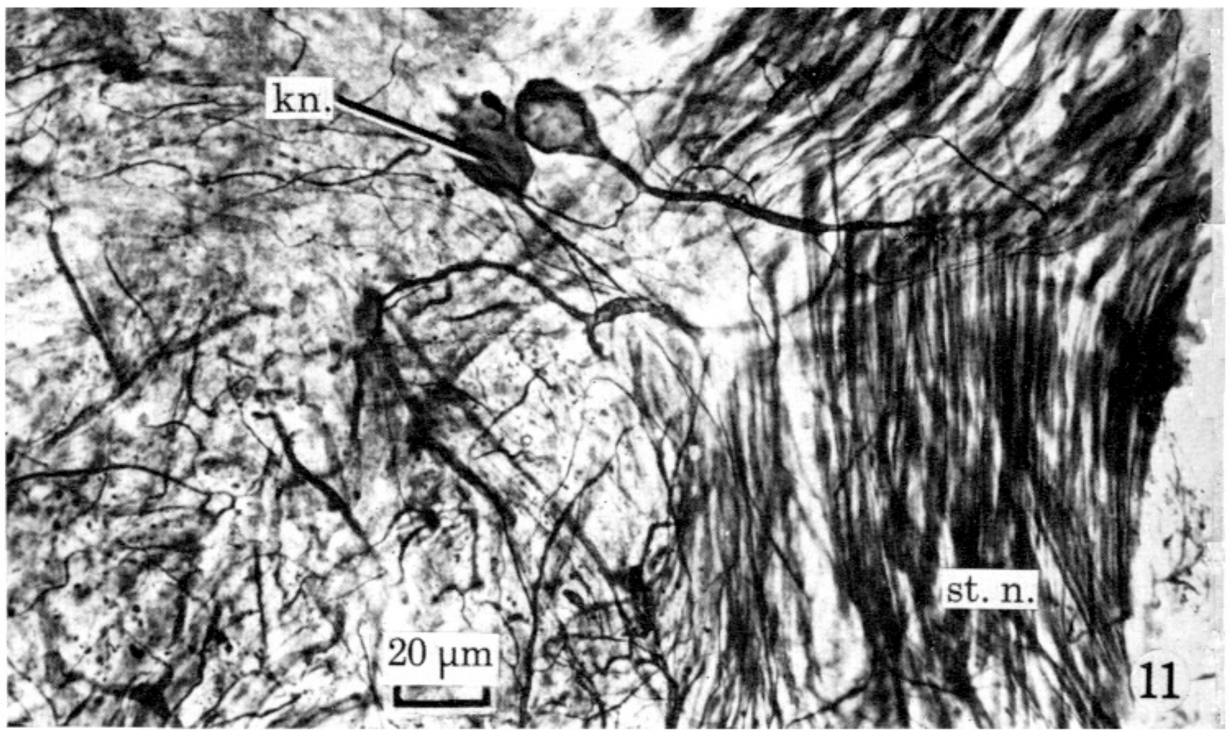

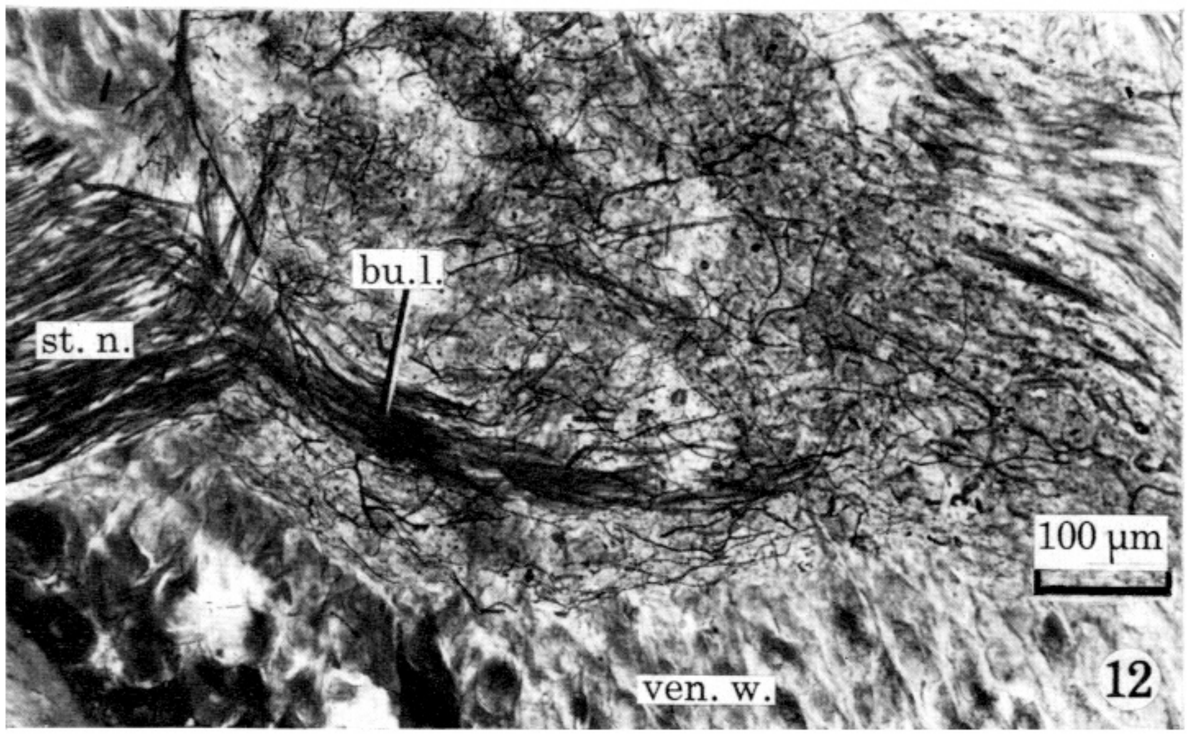

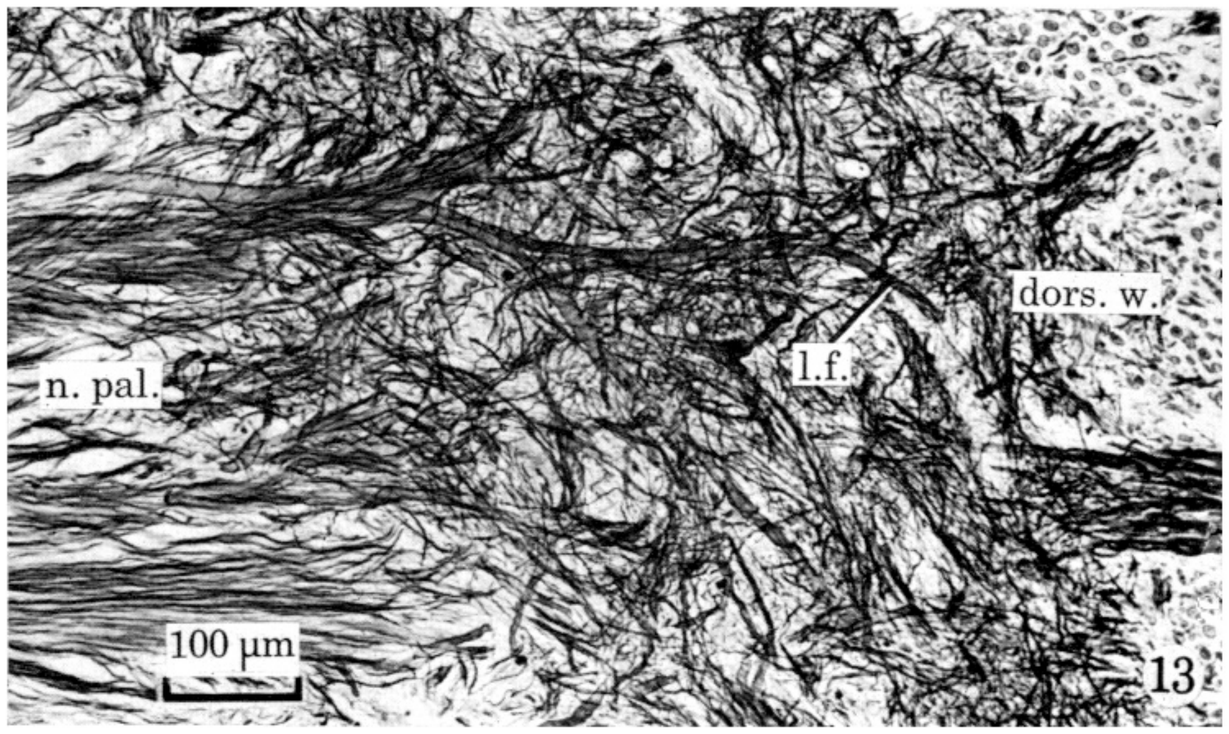

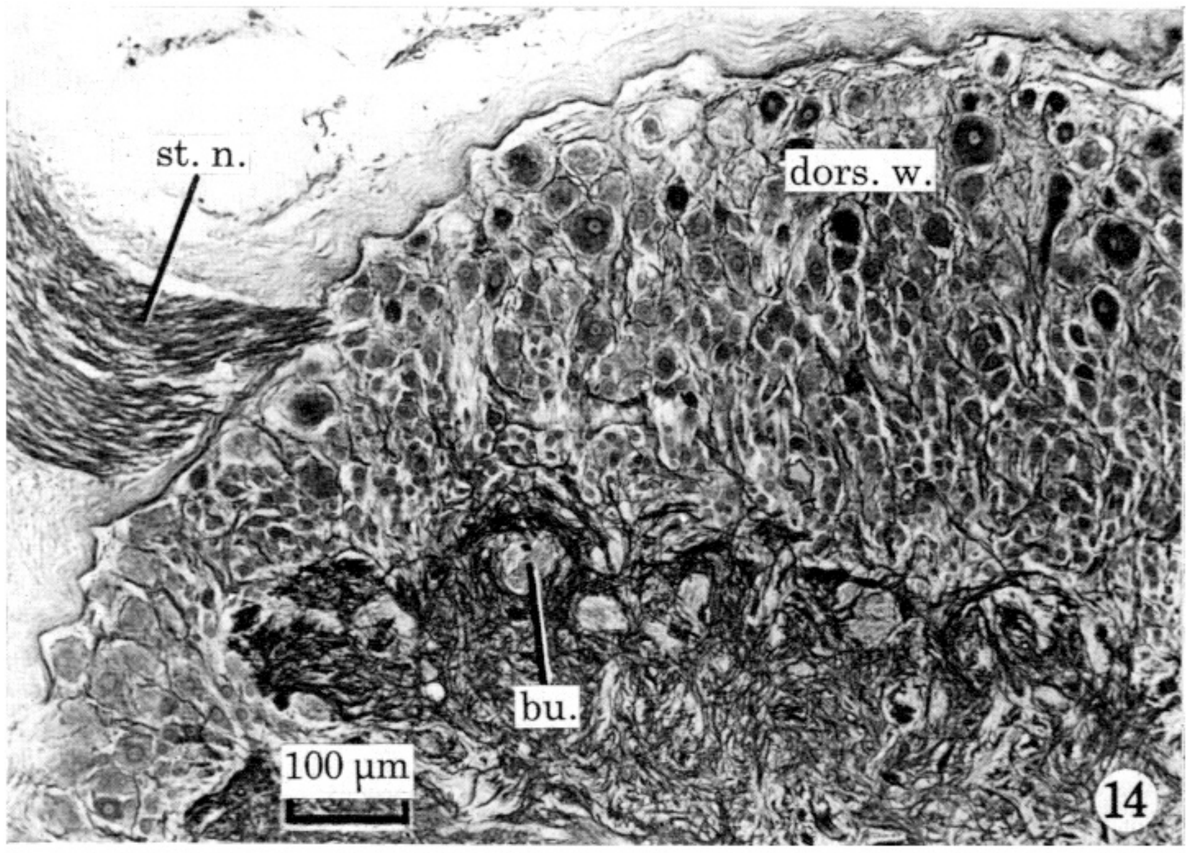

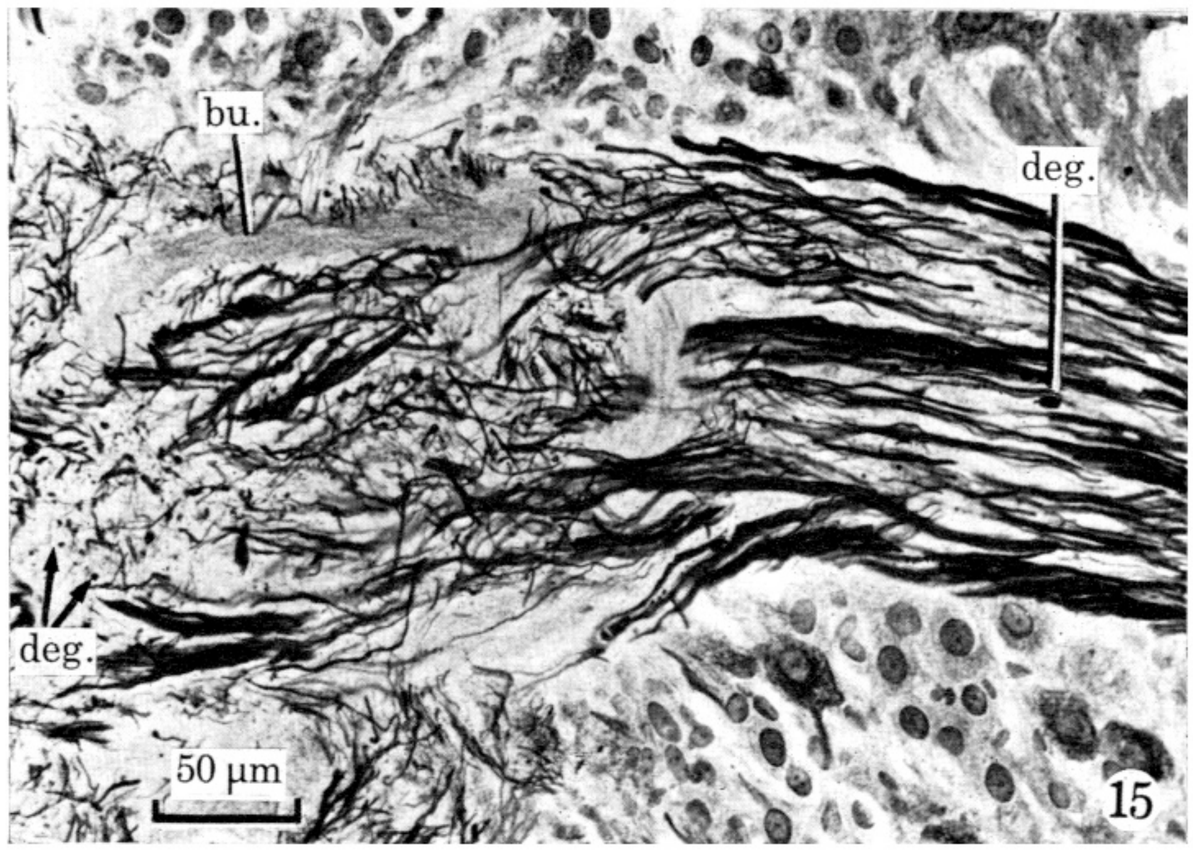

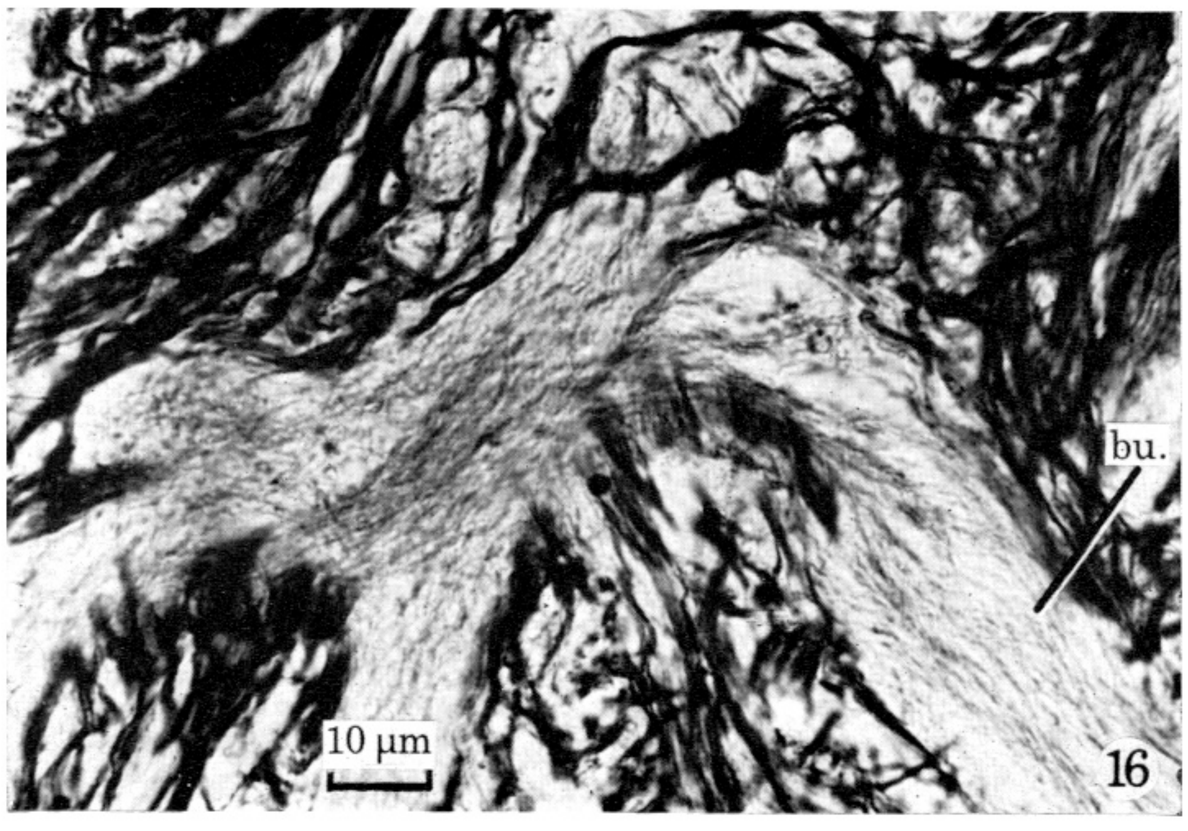

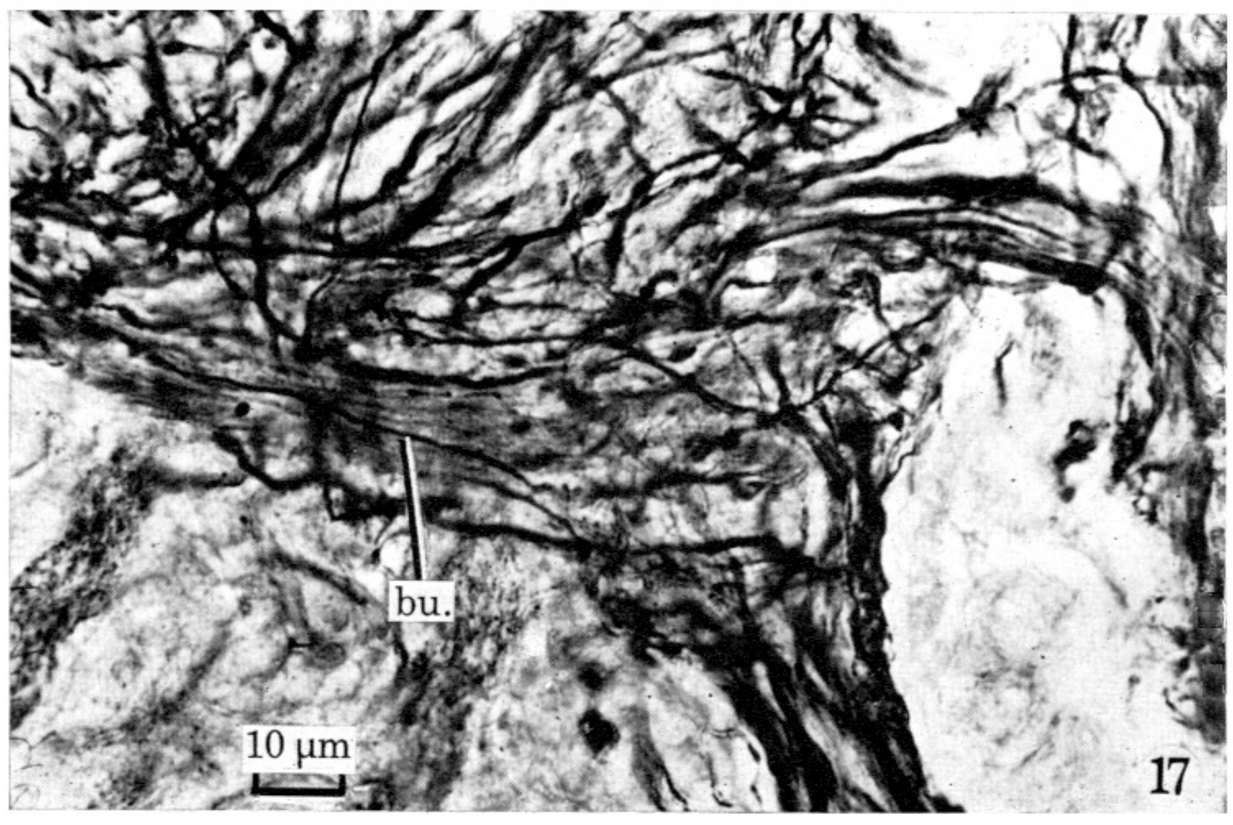

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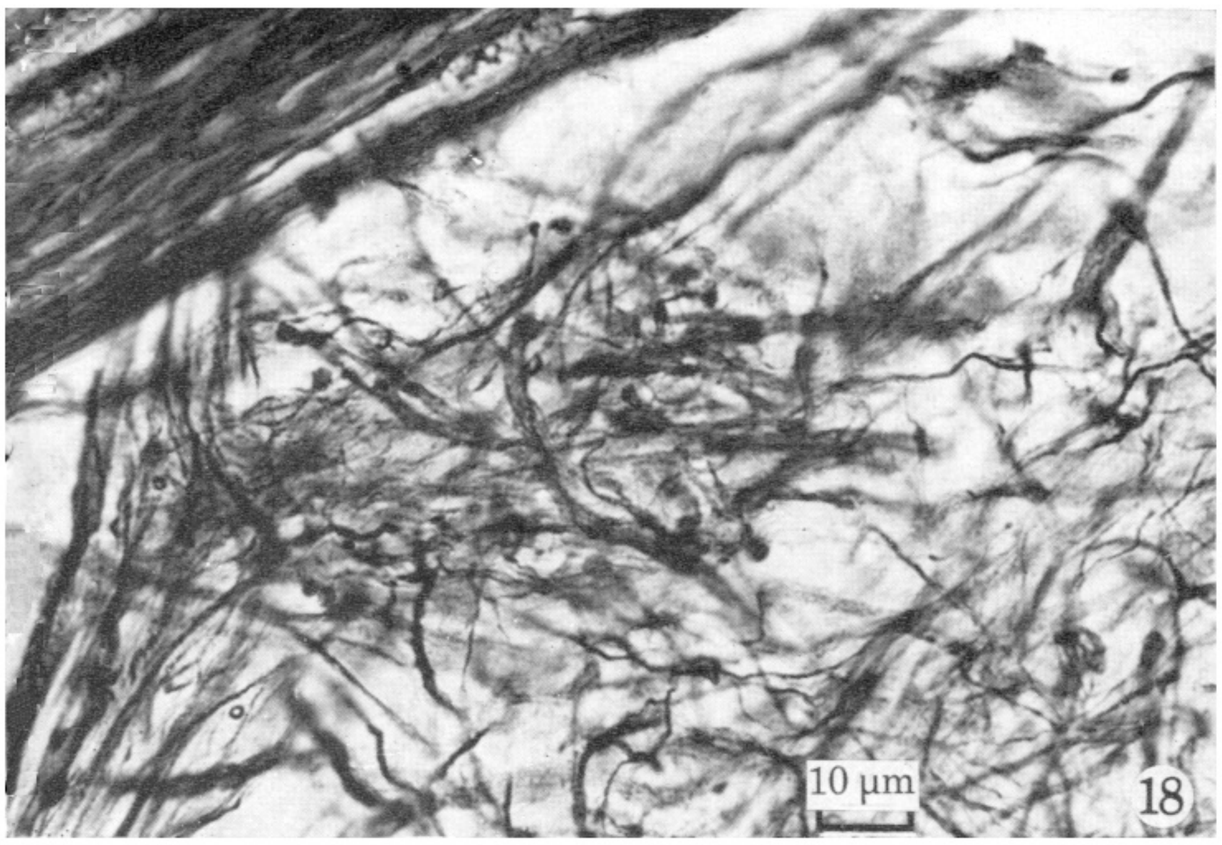

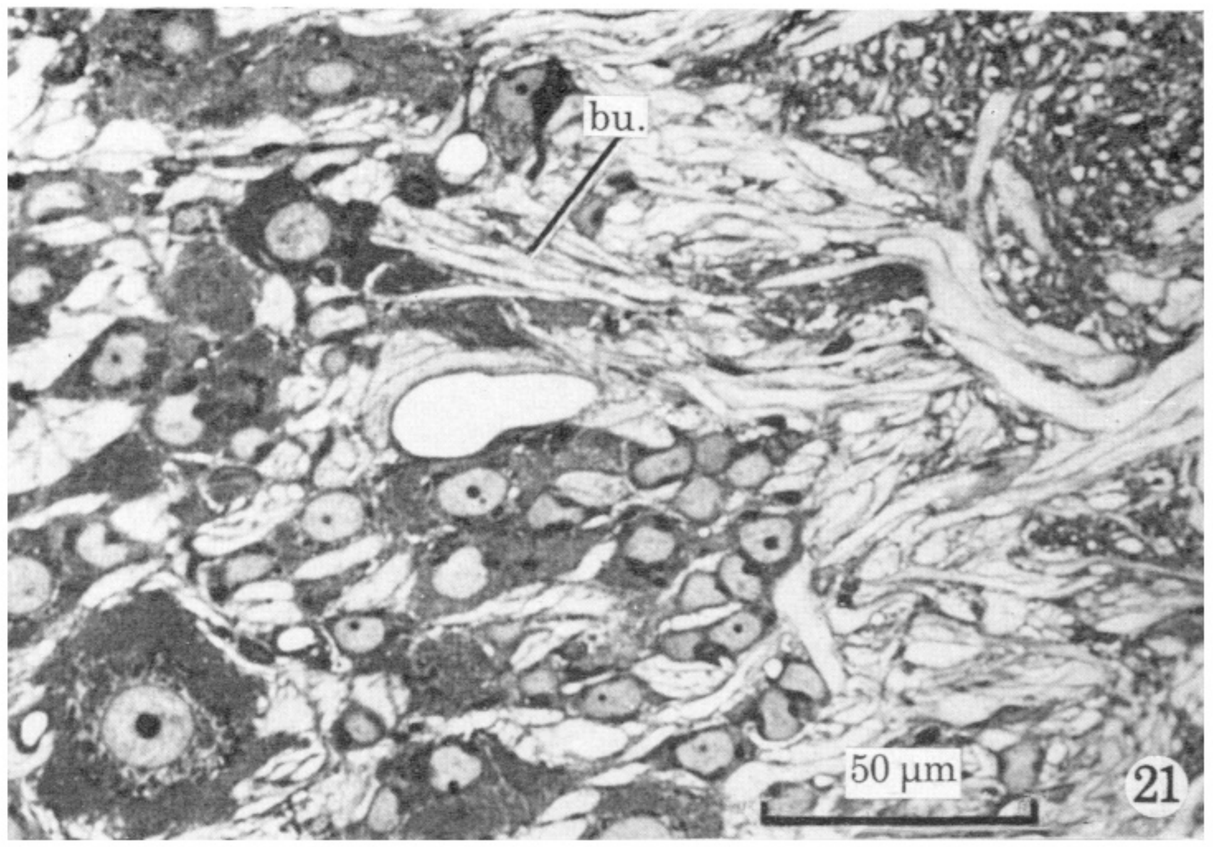

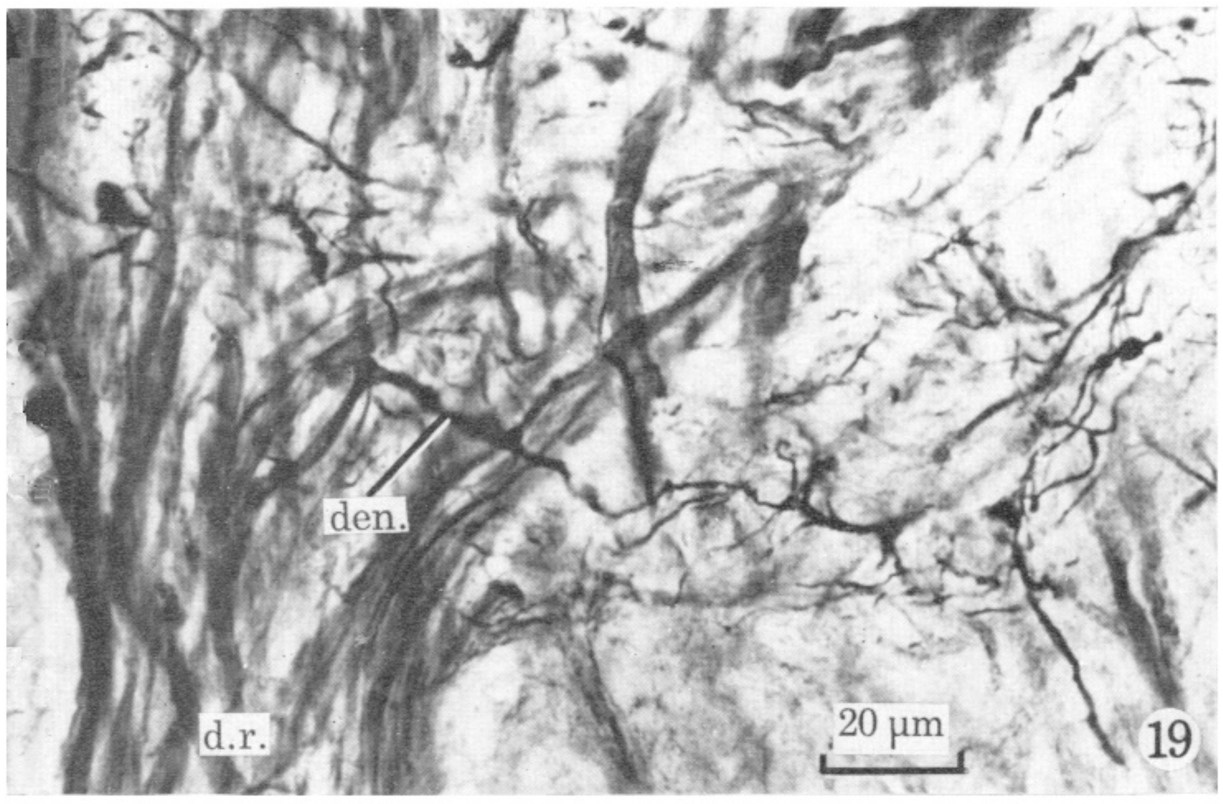

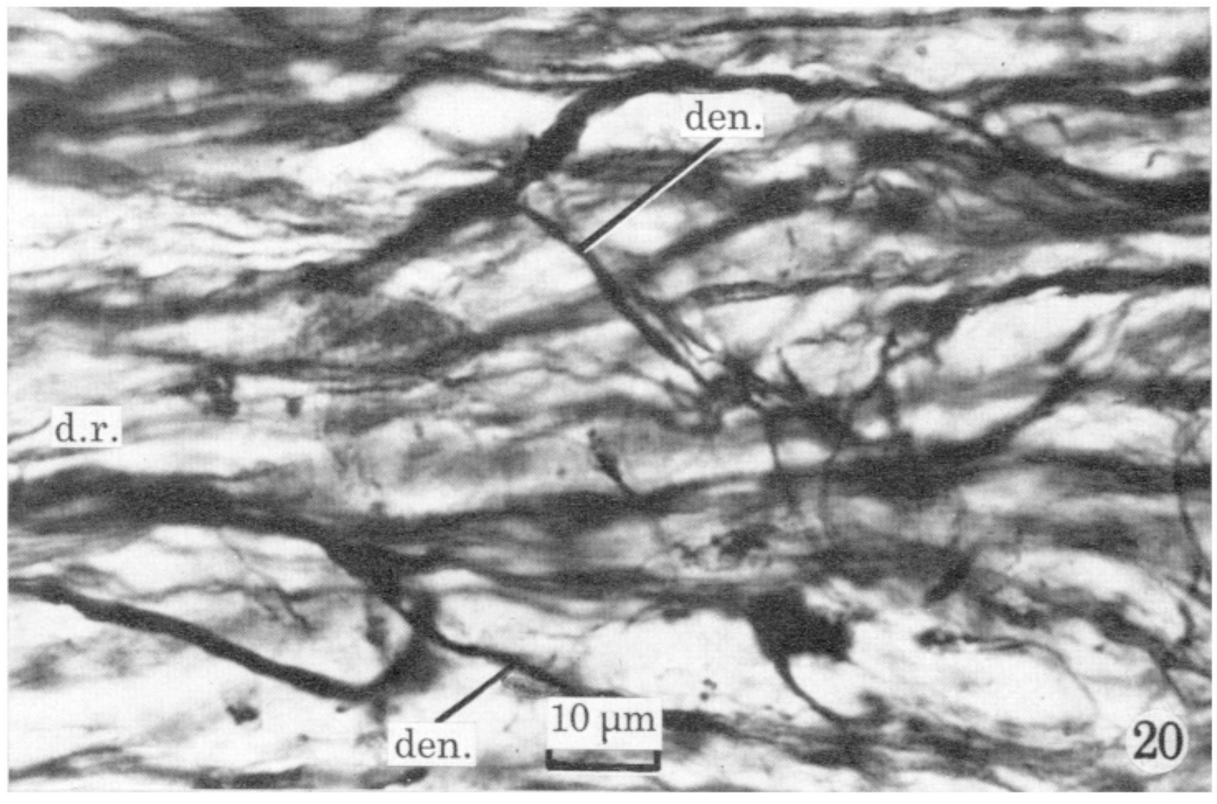

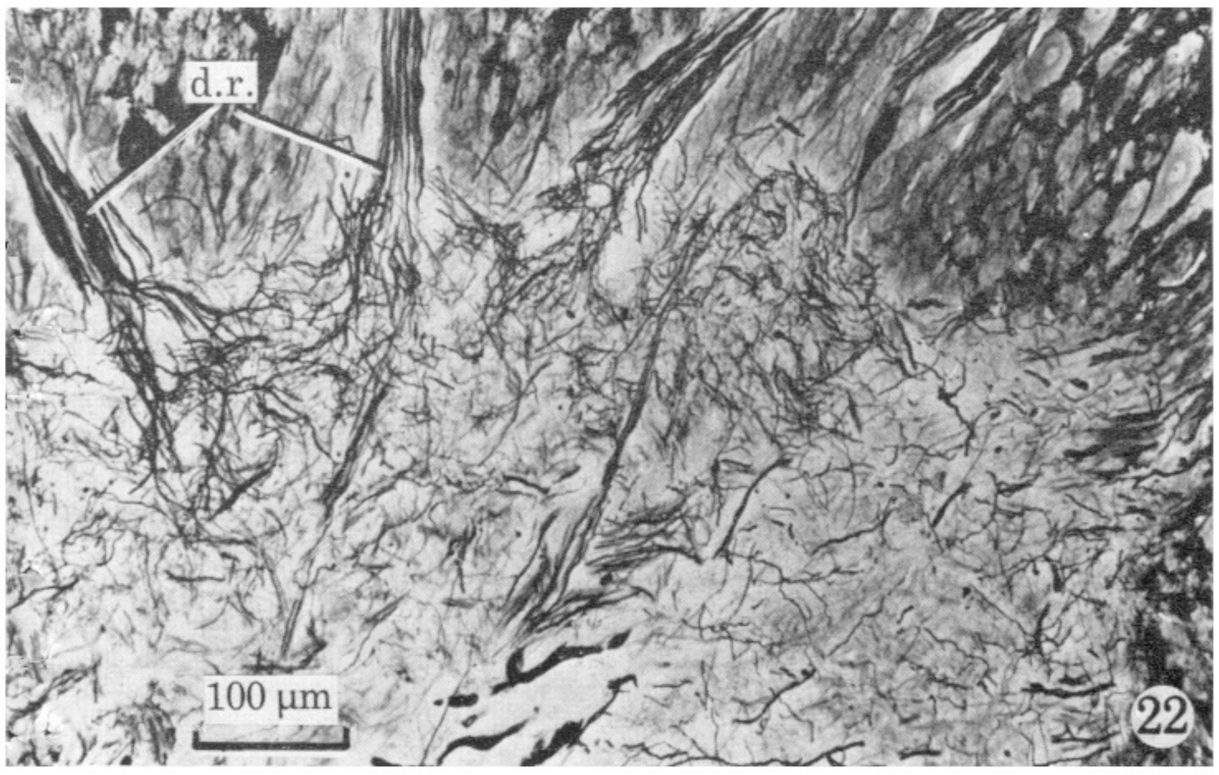

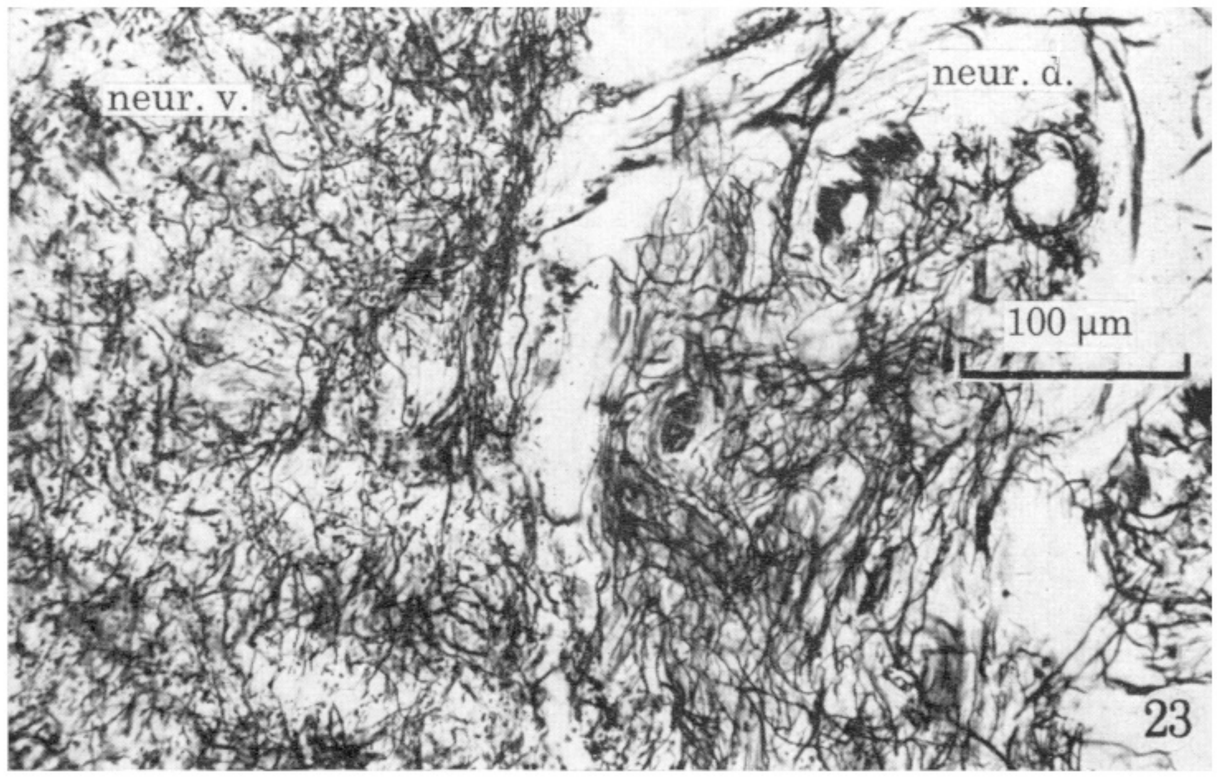

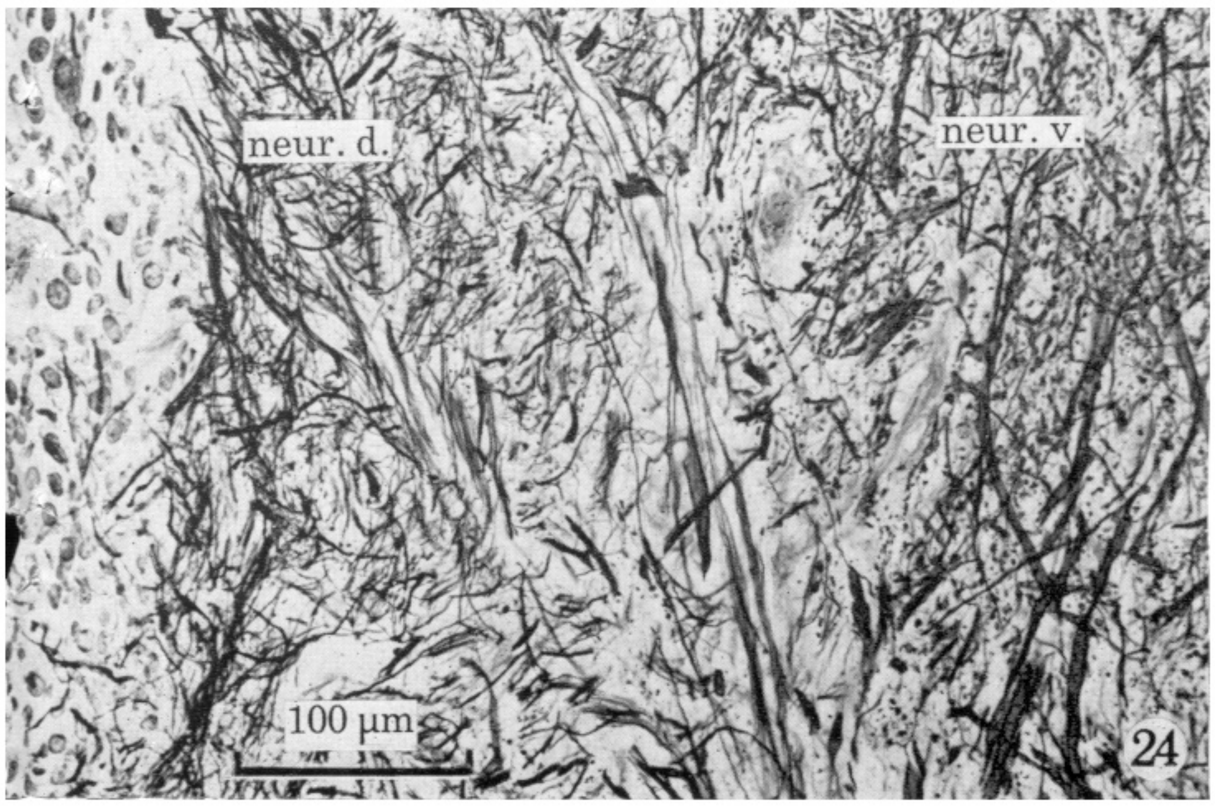

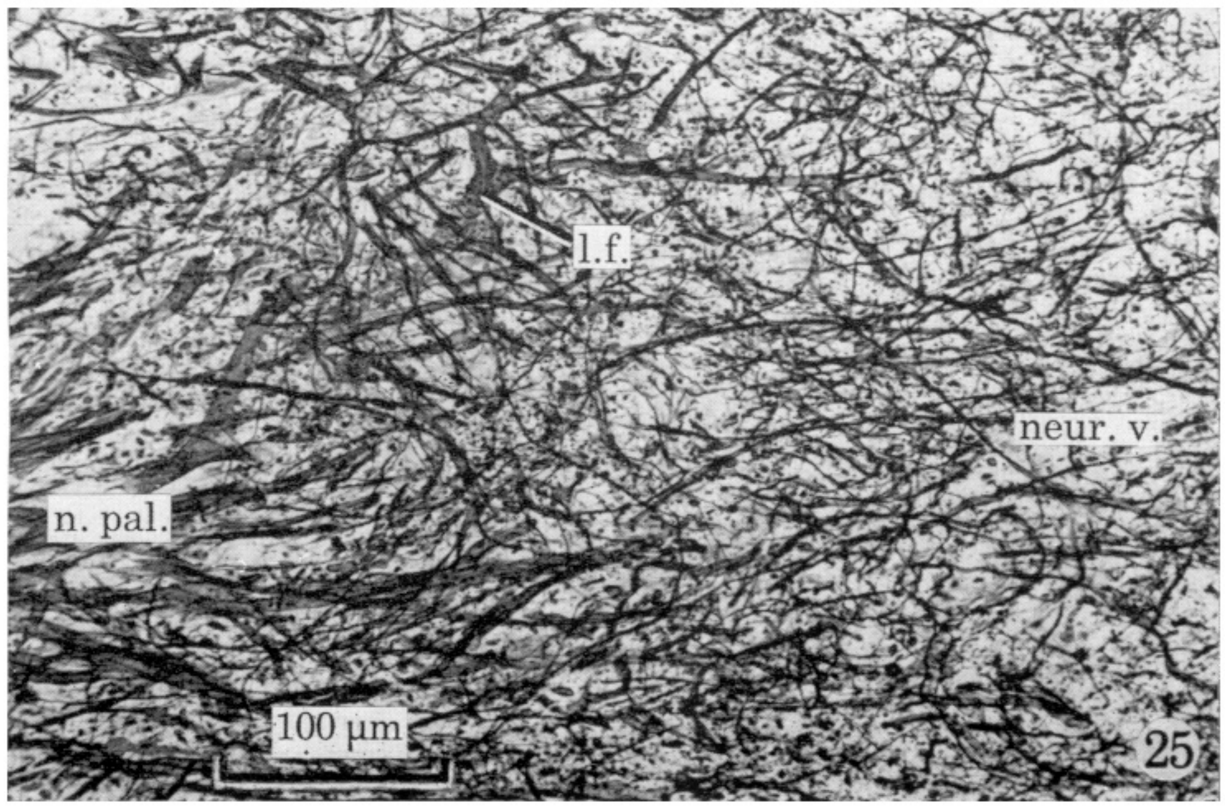

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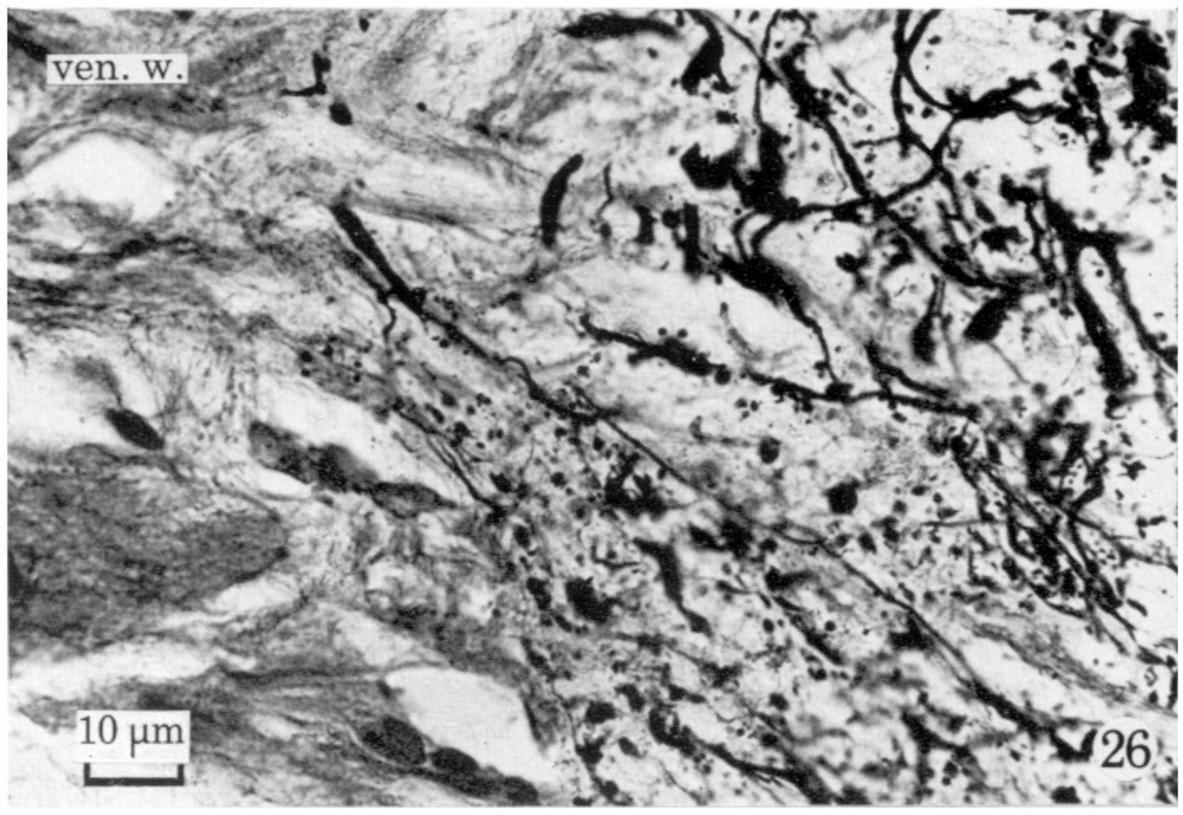
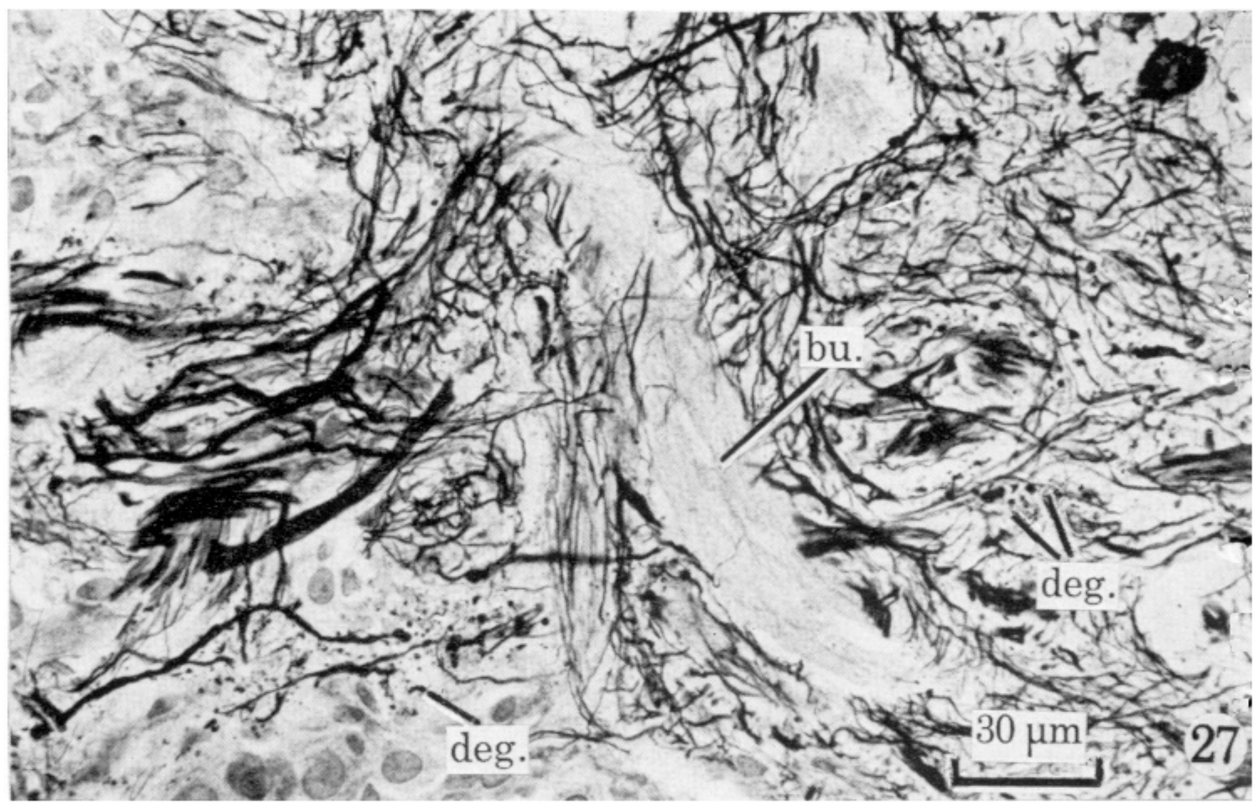
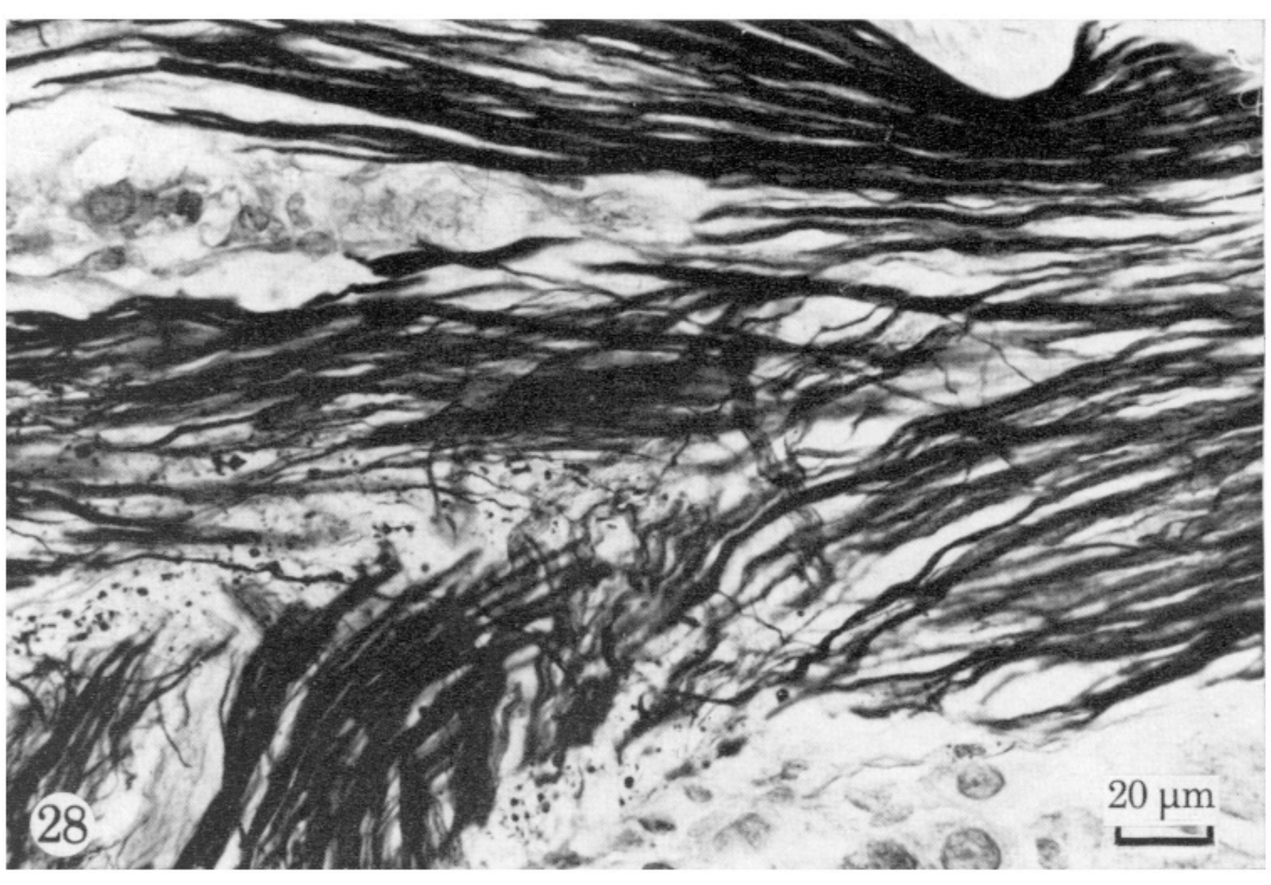
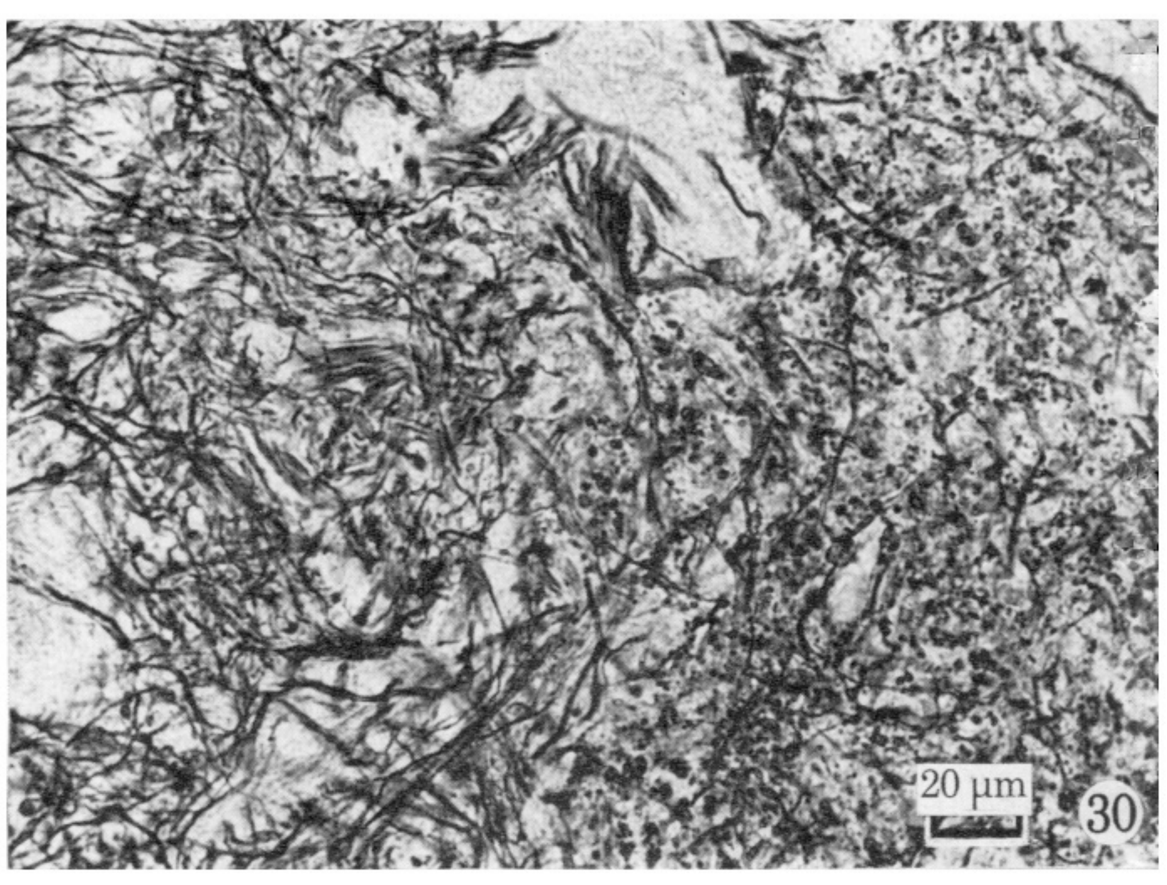
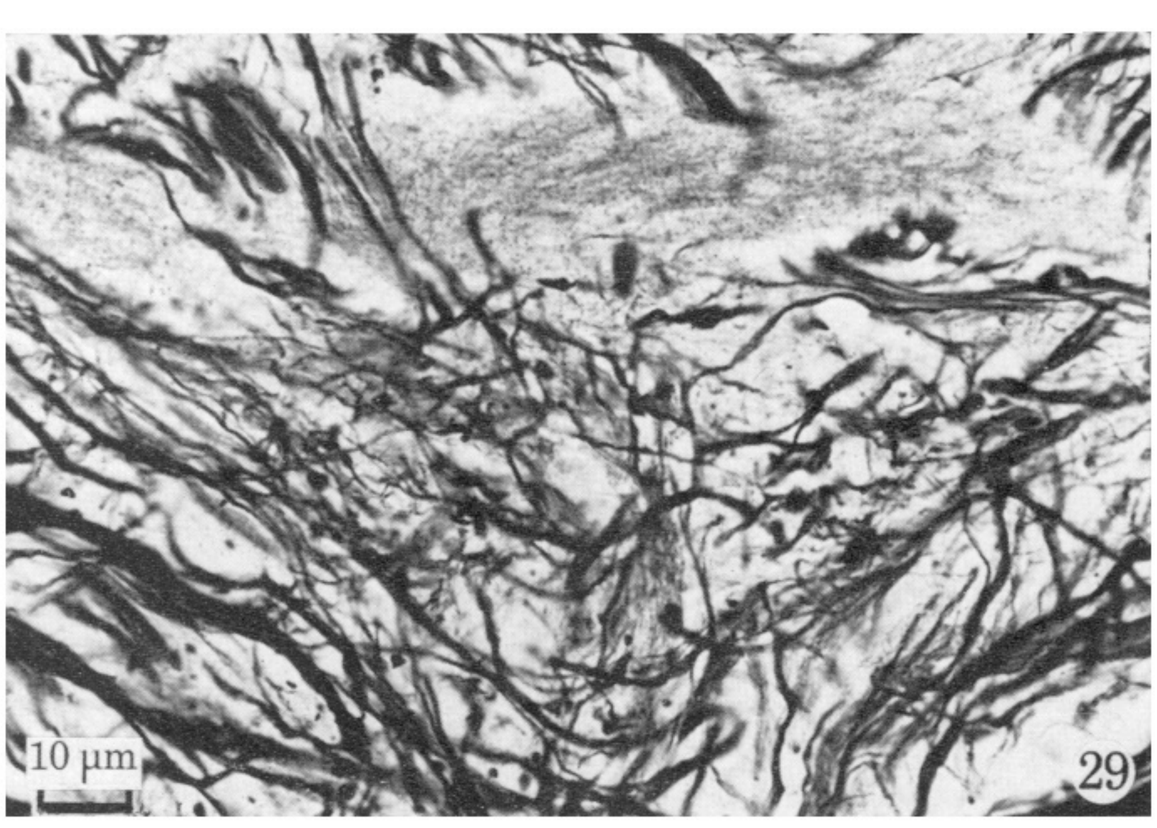
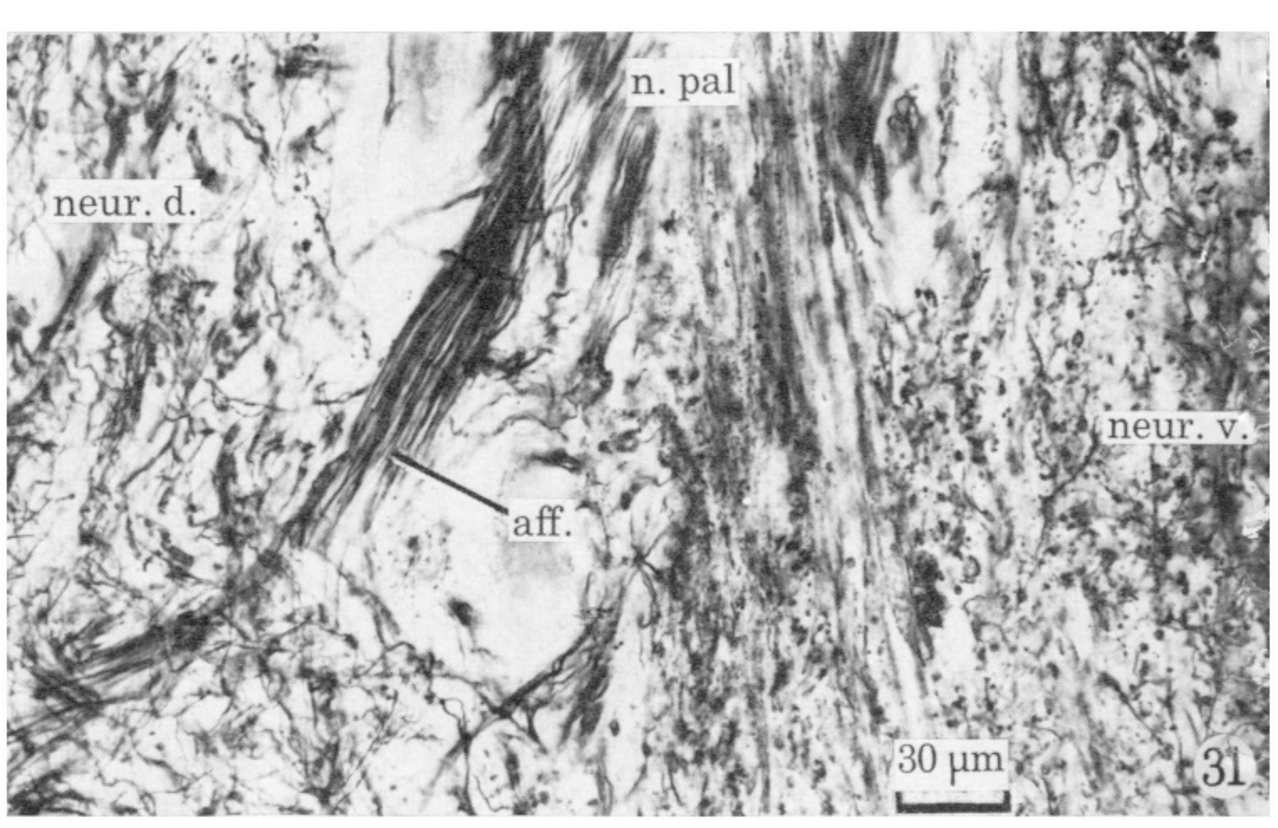


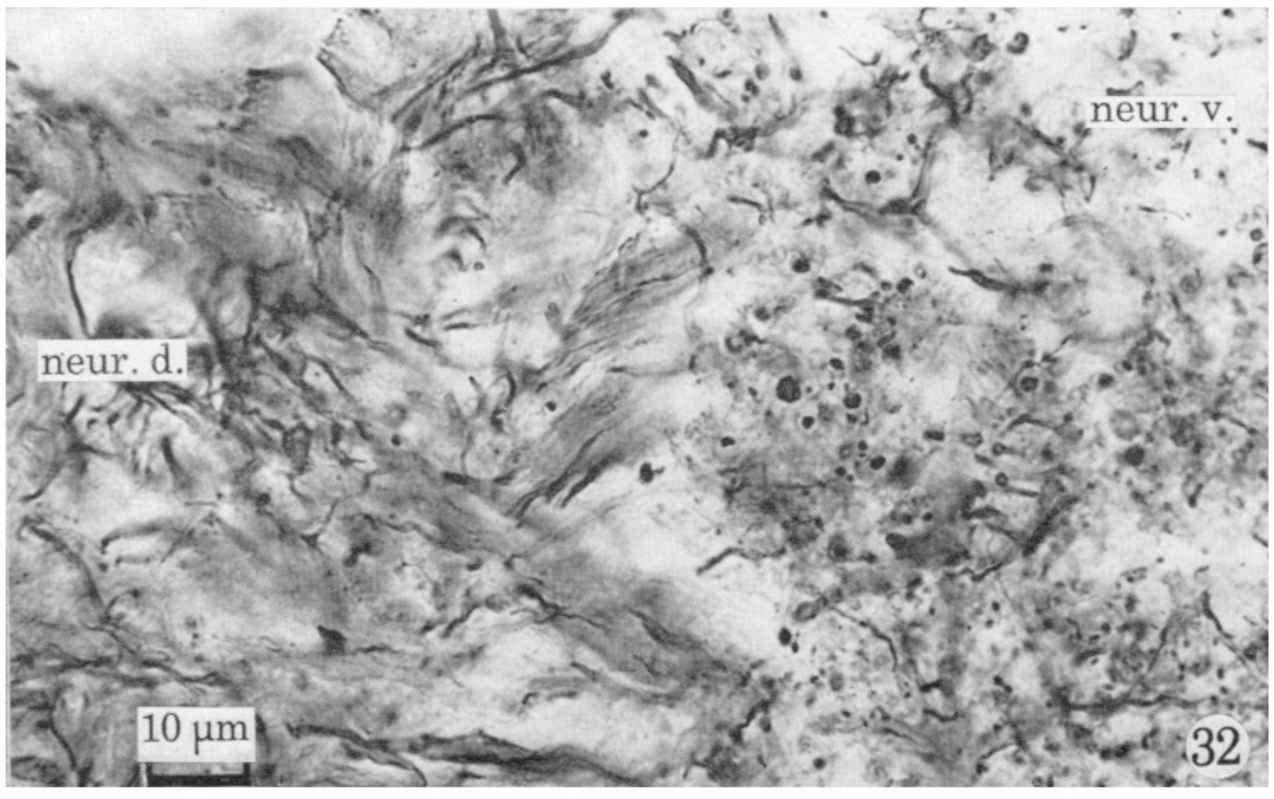


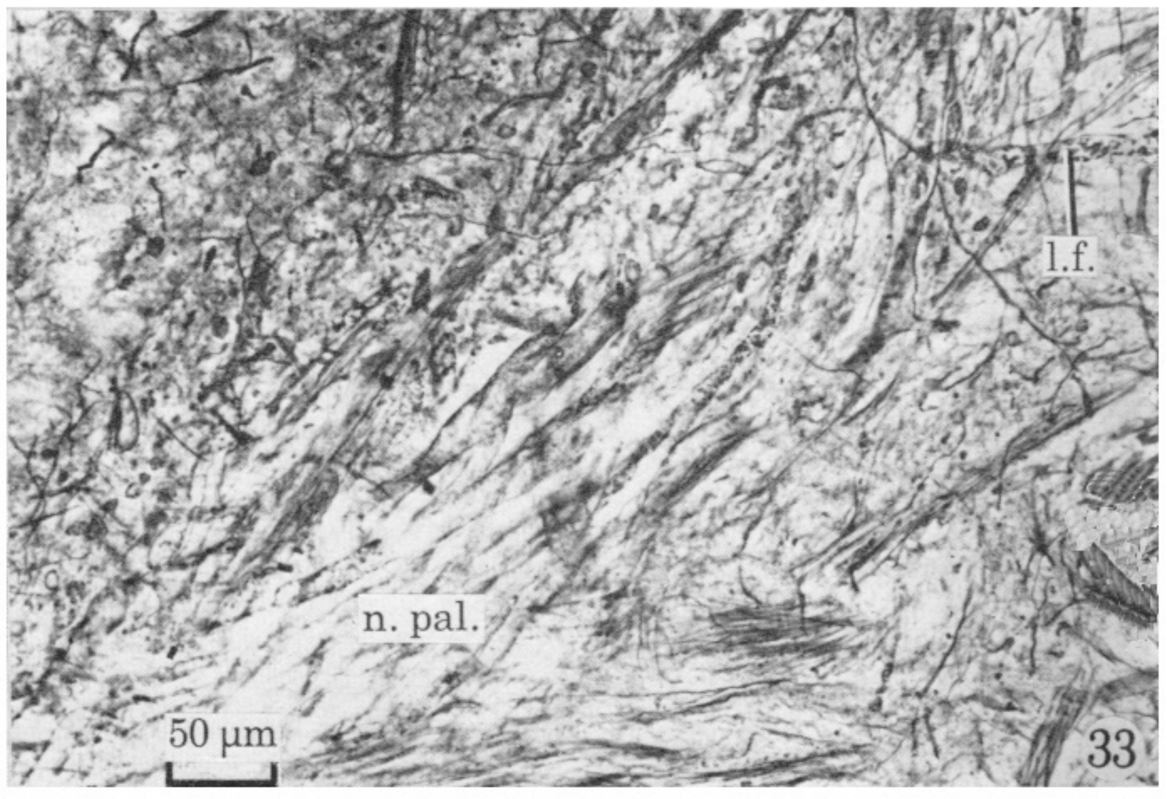




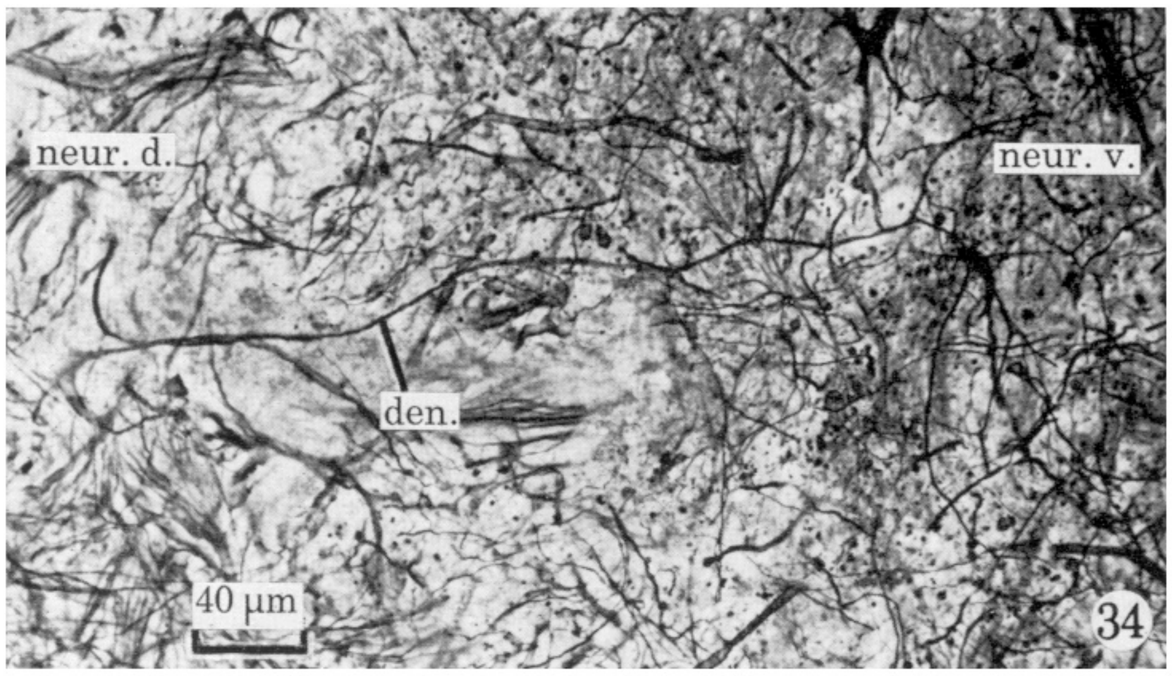


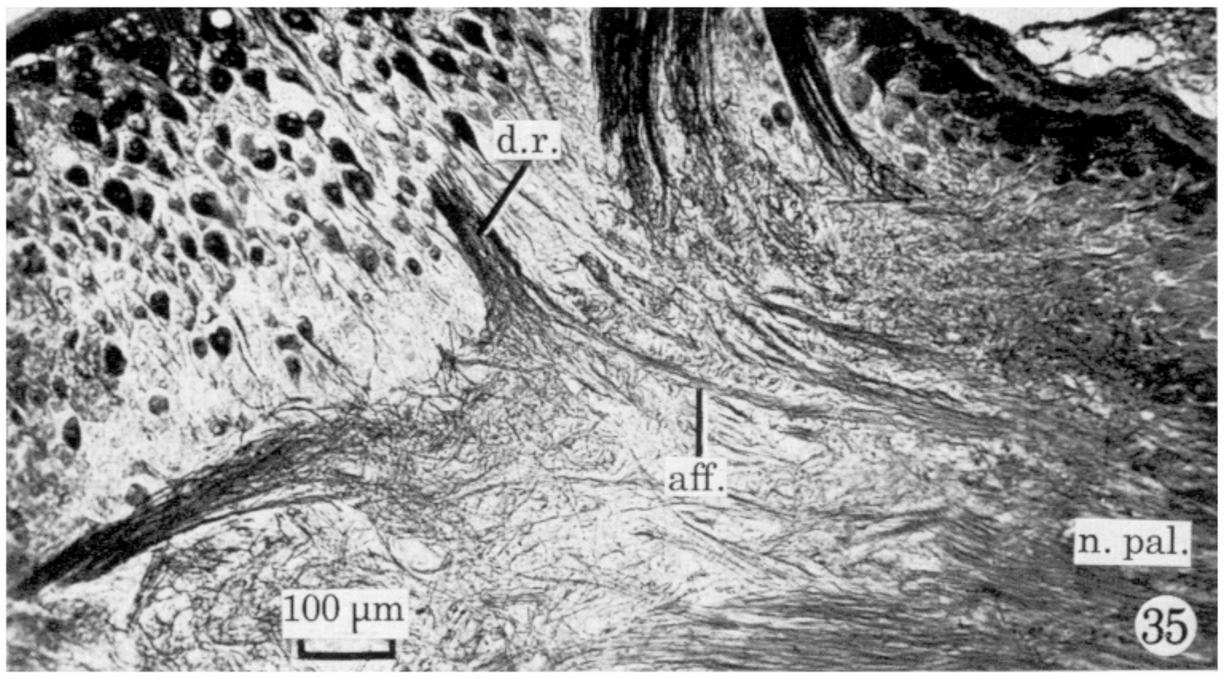


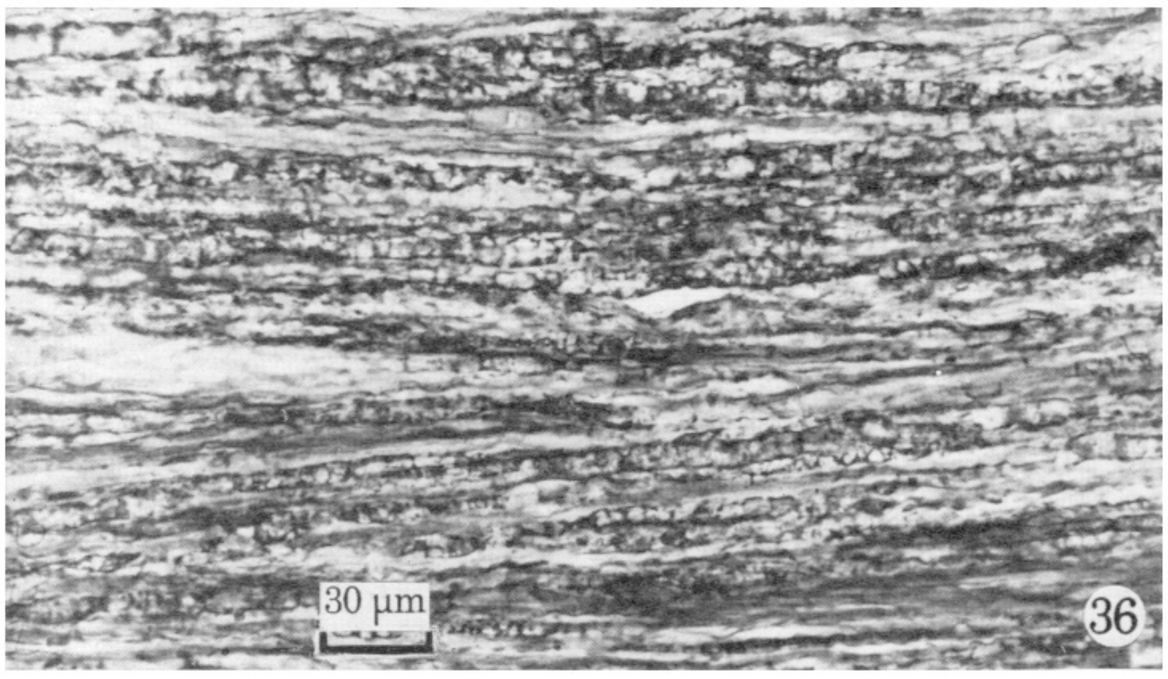


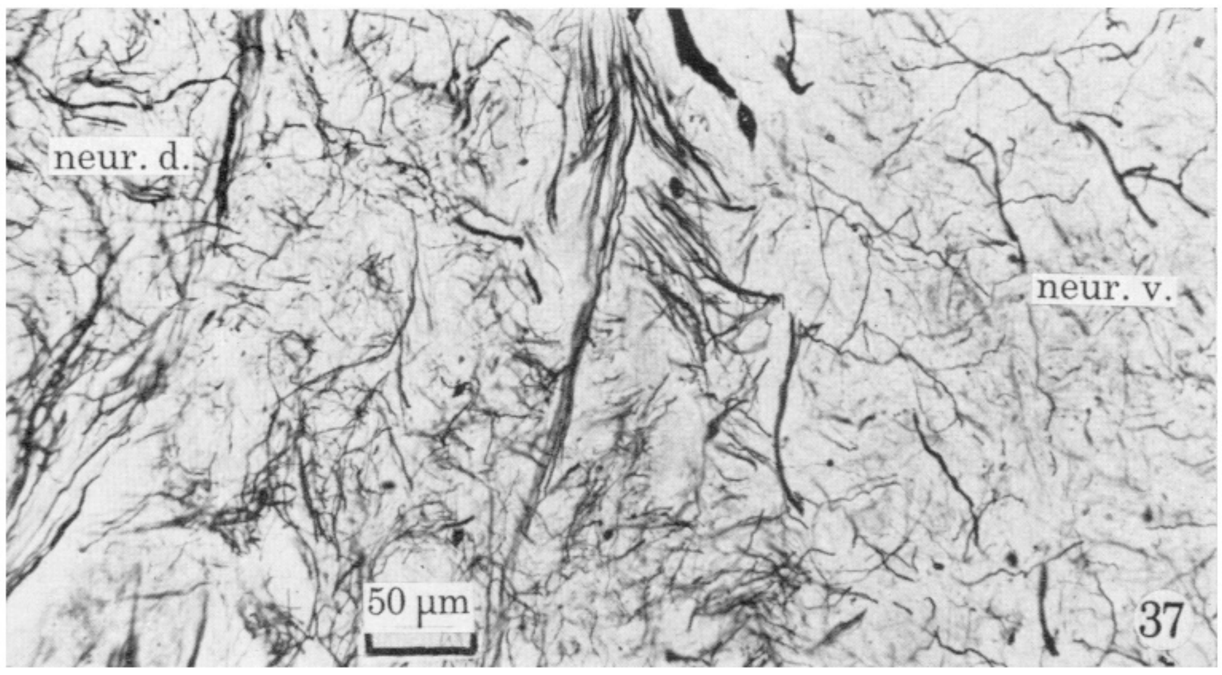


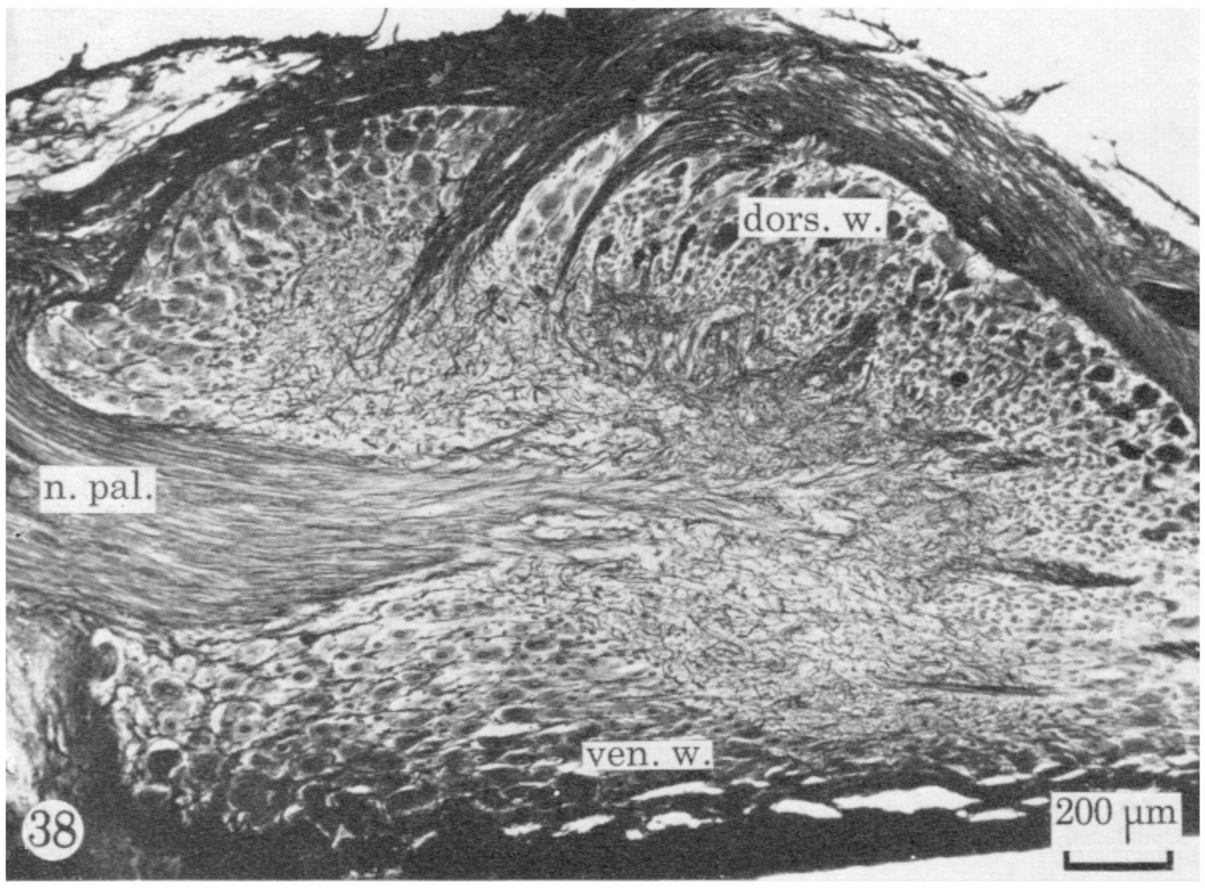
FIGURES 26 to 33. For legends see facing page

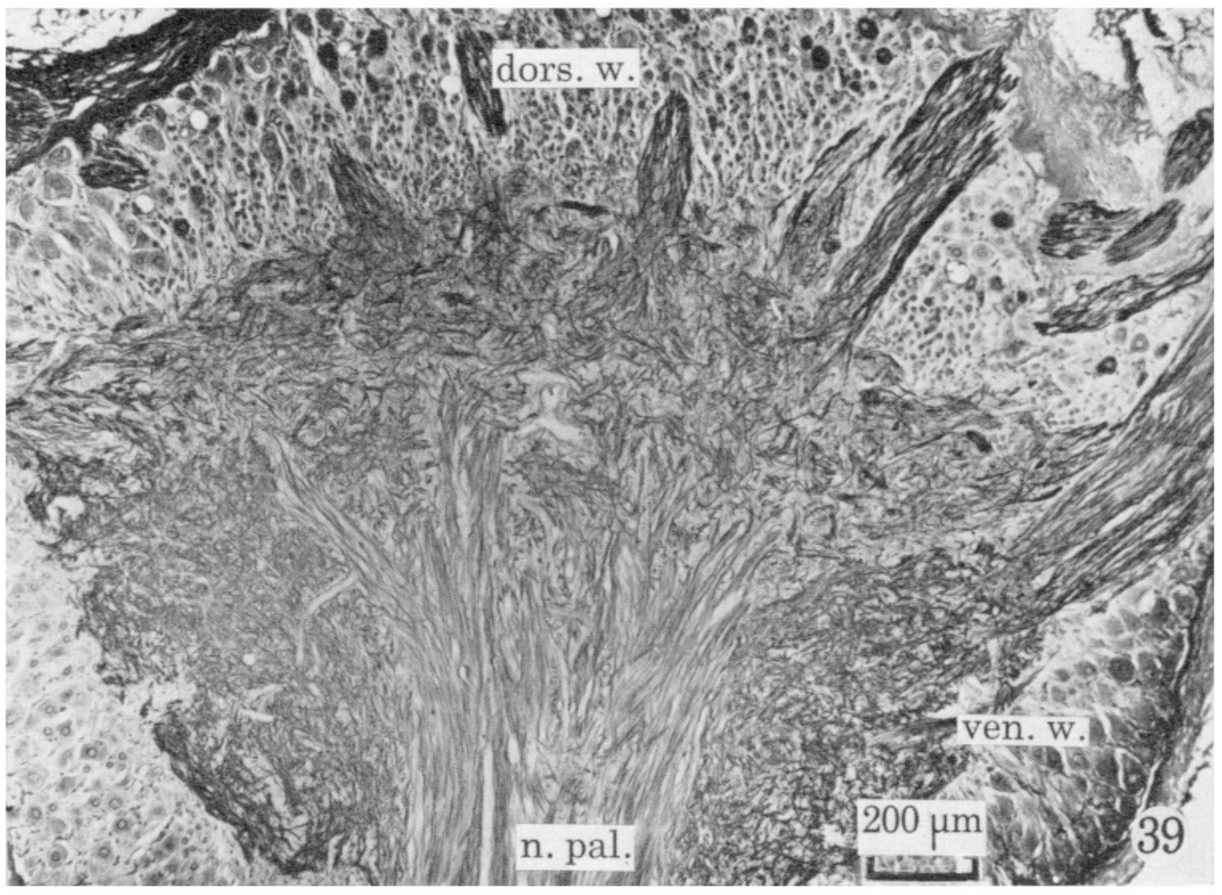


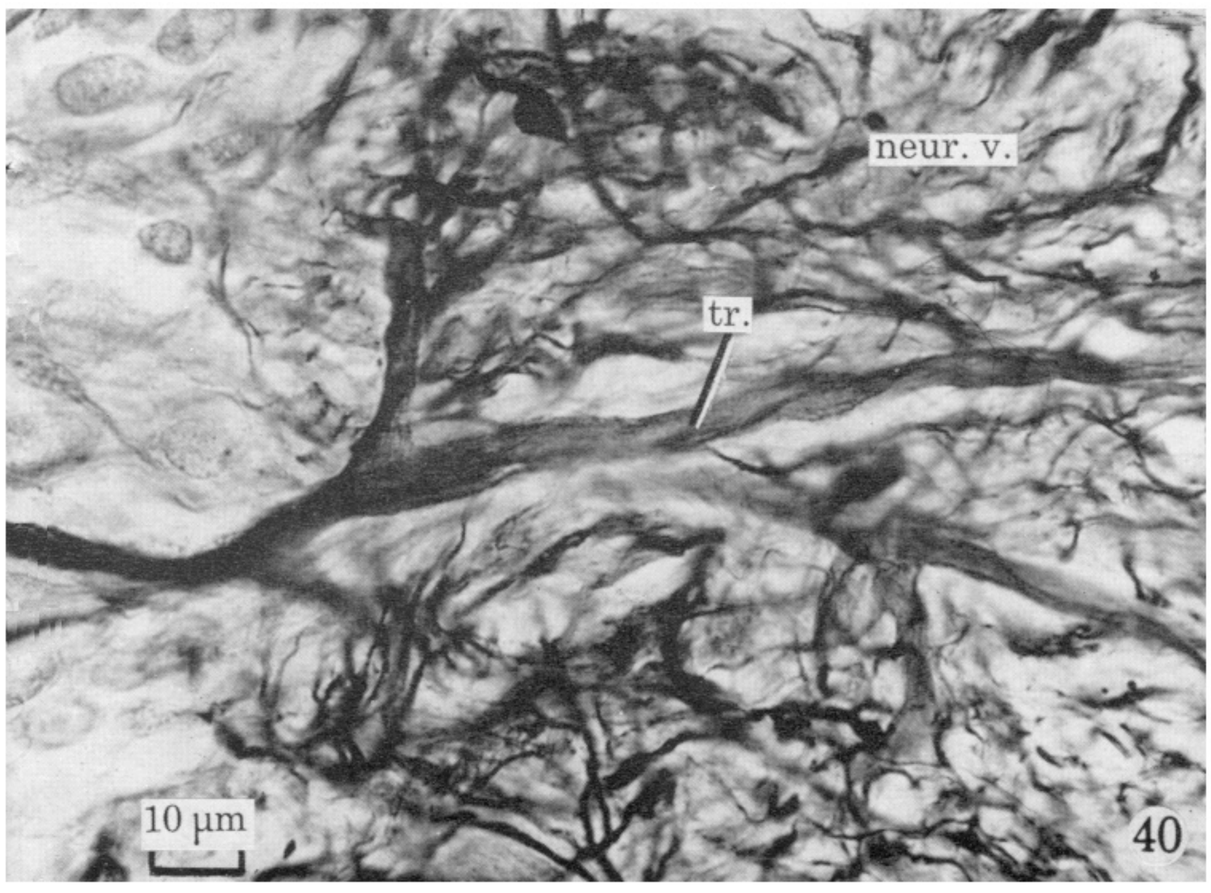


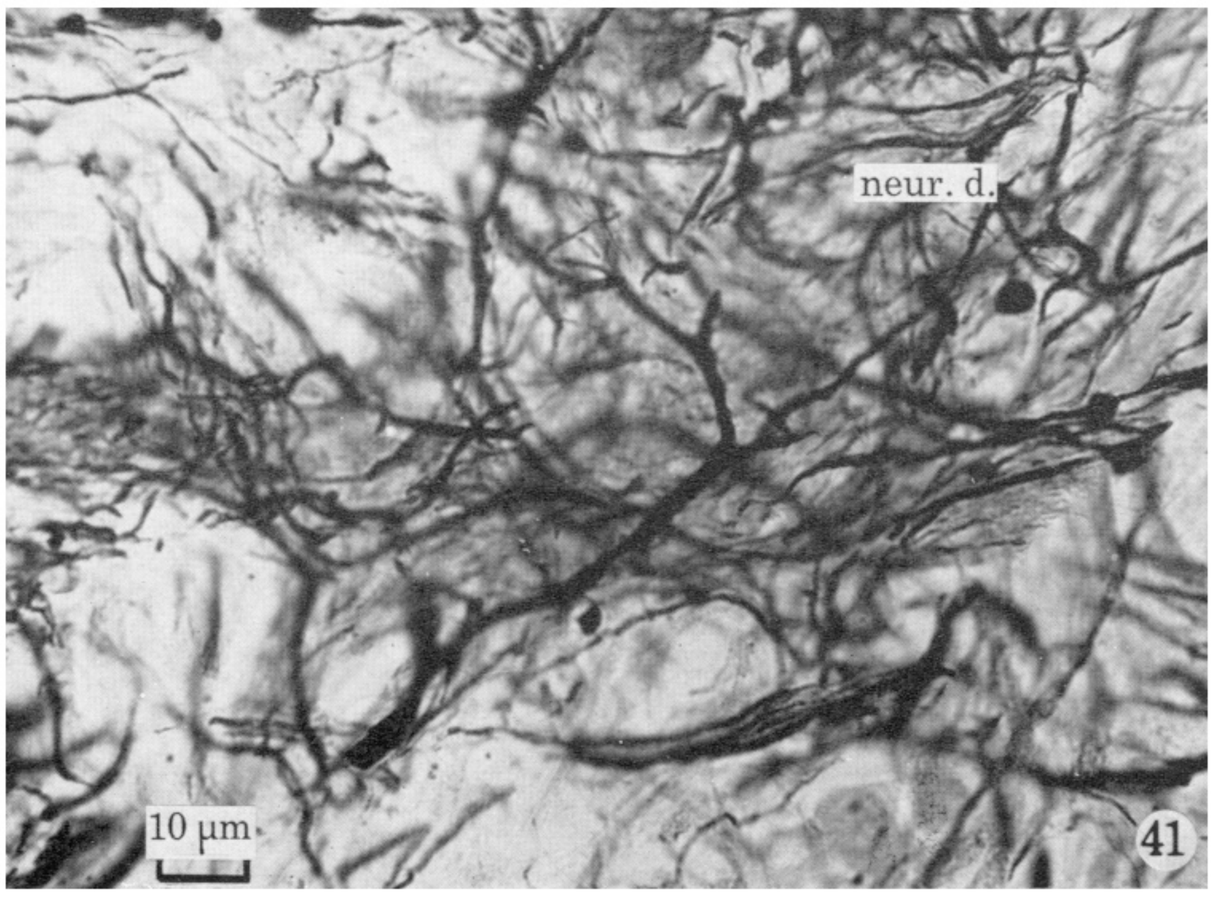




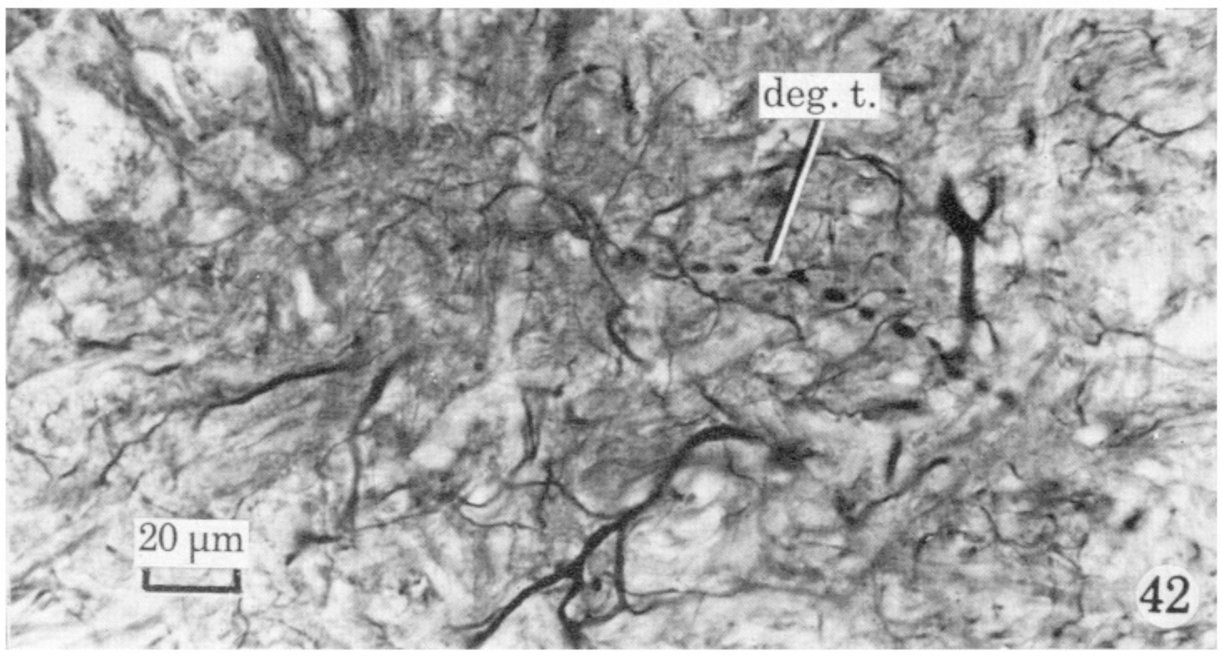


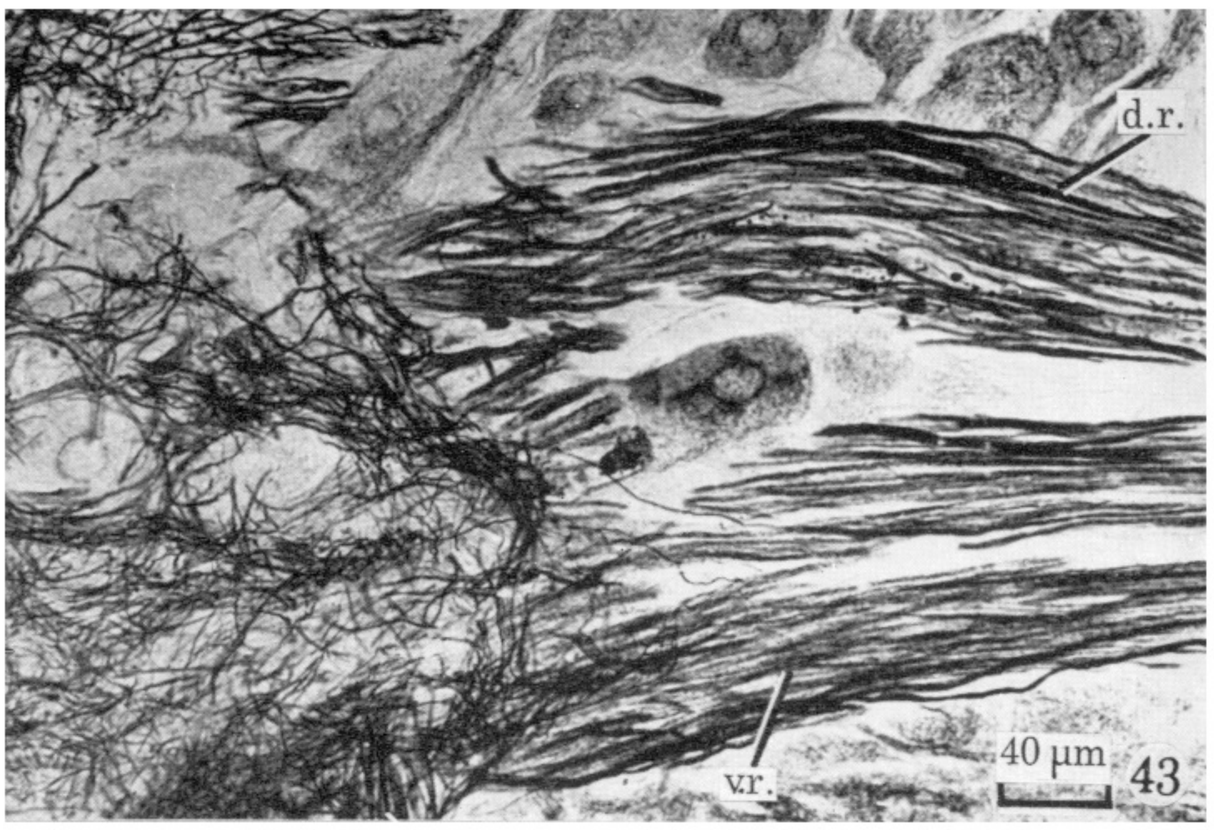


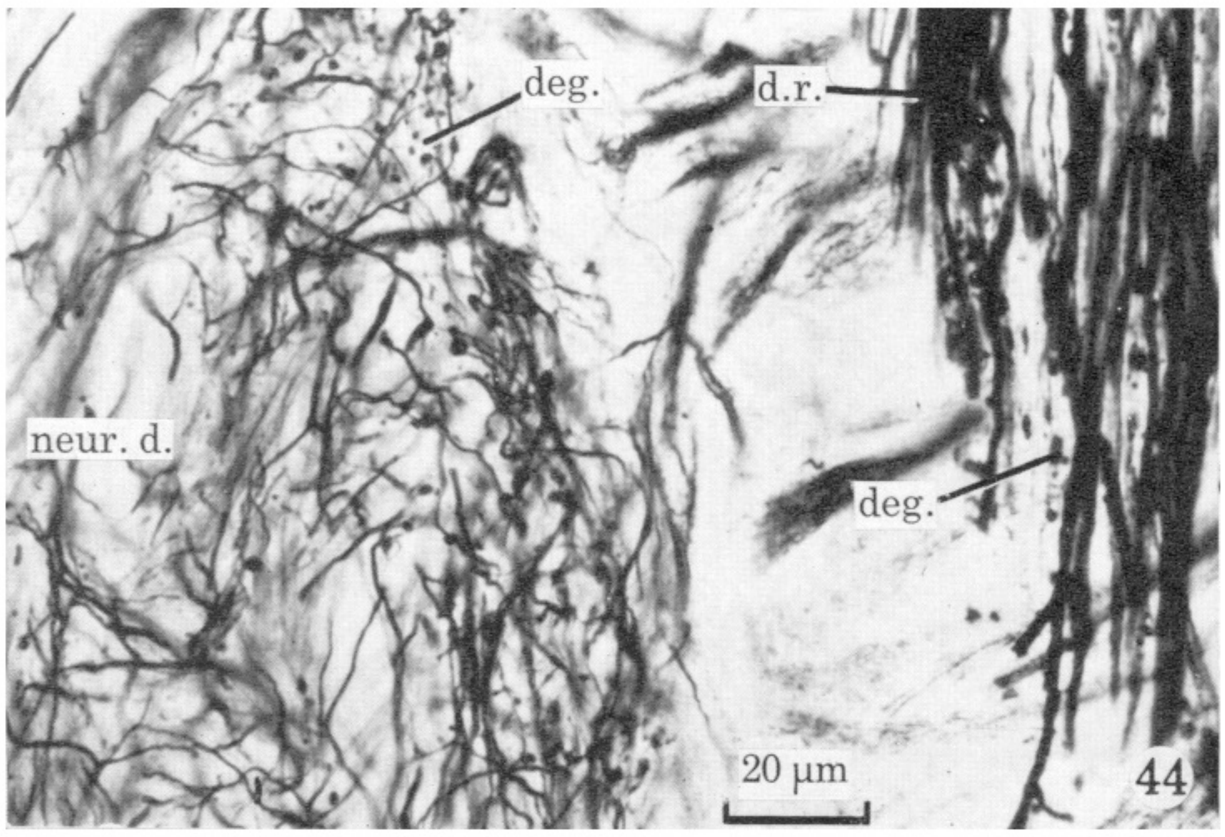


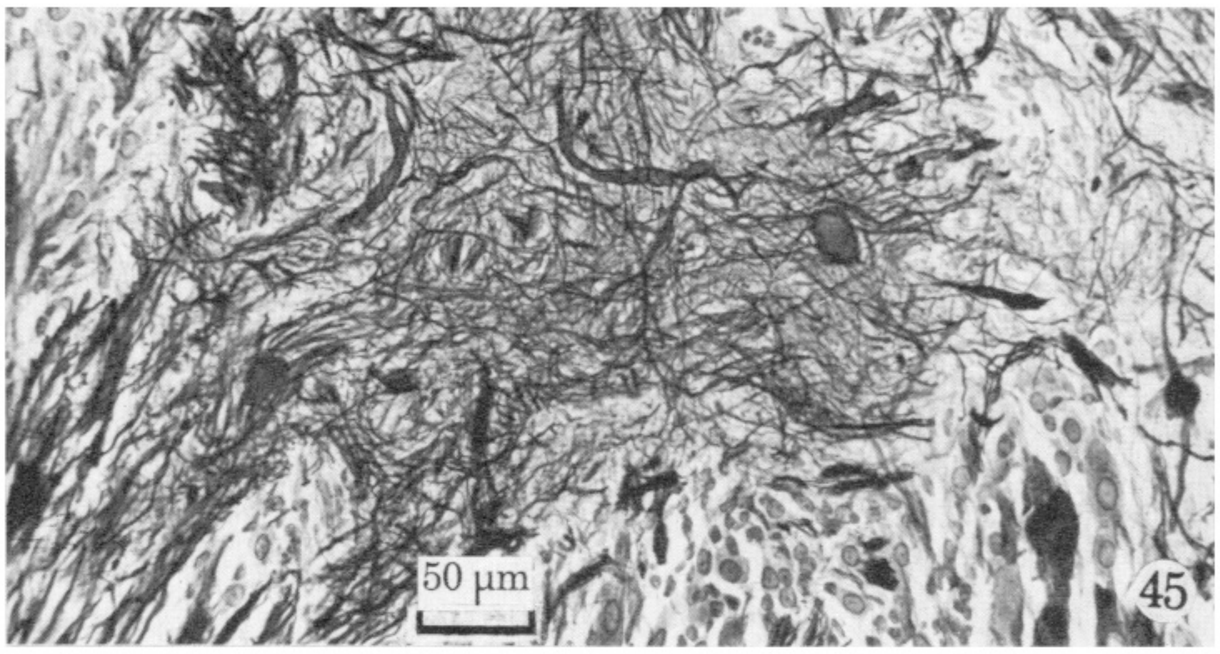


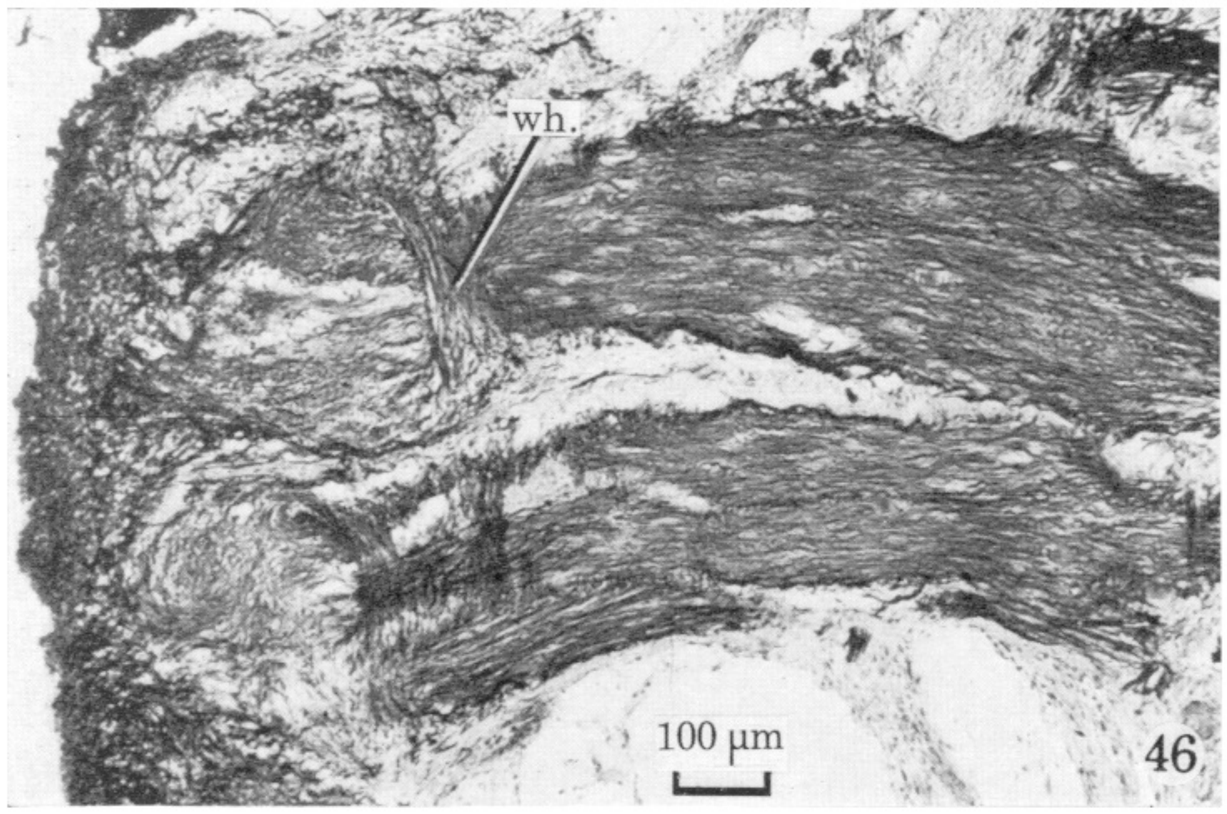
FIGURES 34 to 41. For legends see facing page

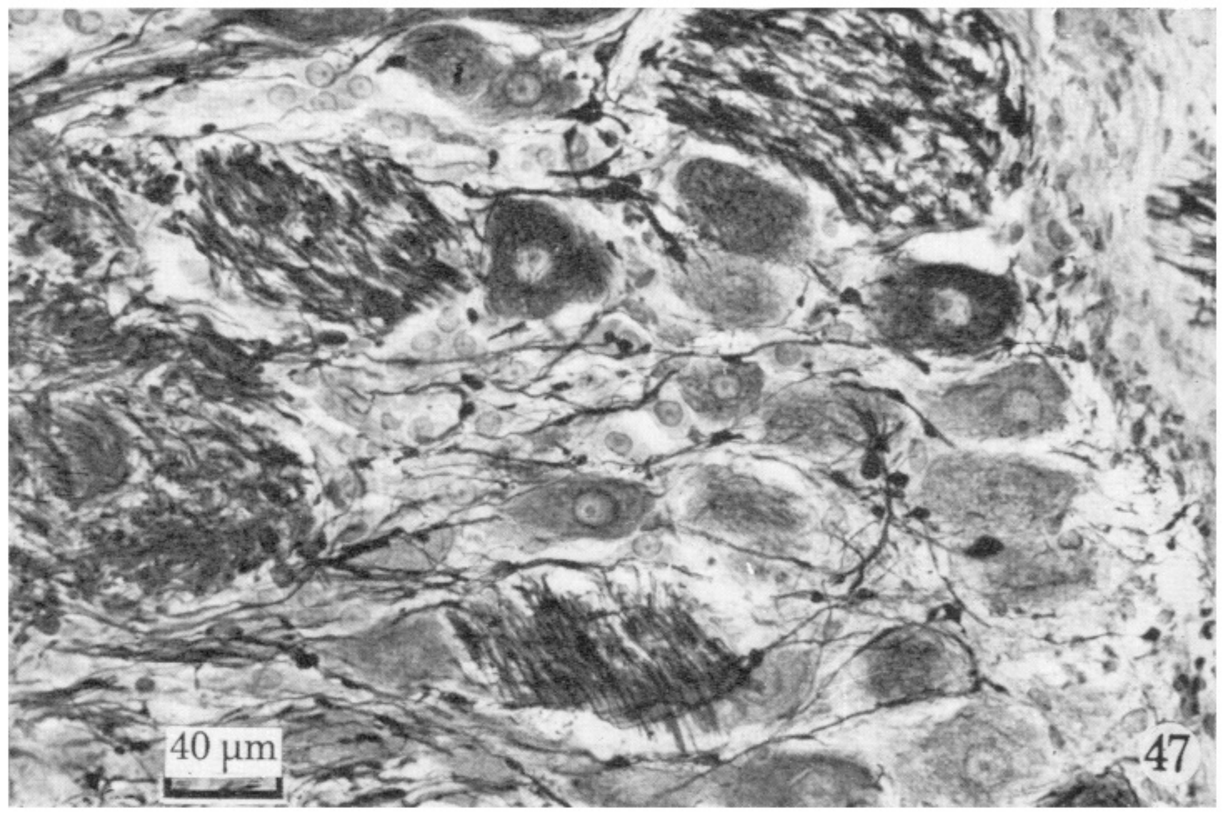


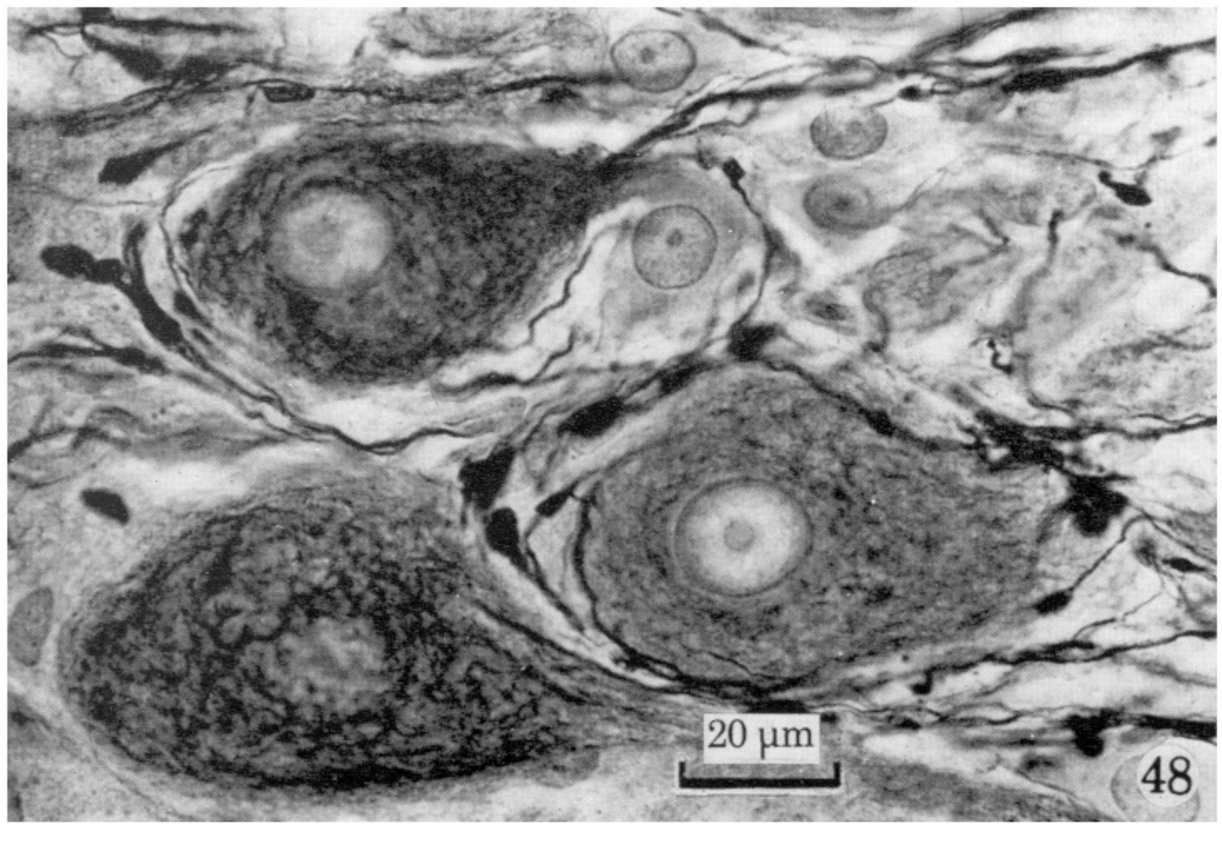


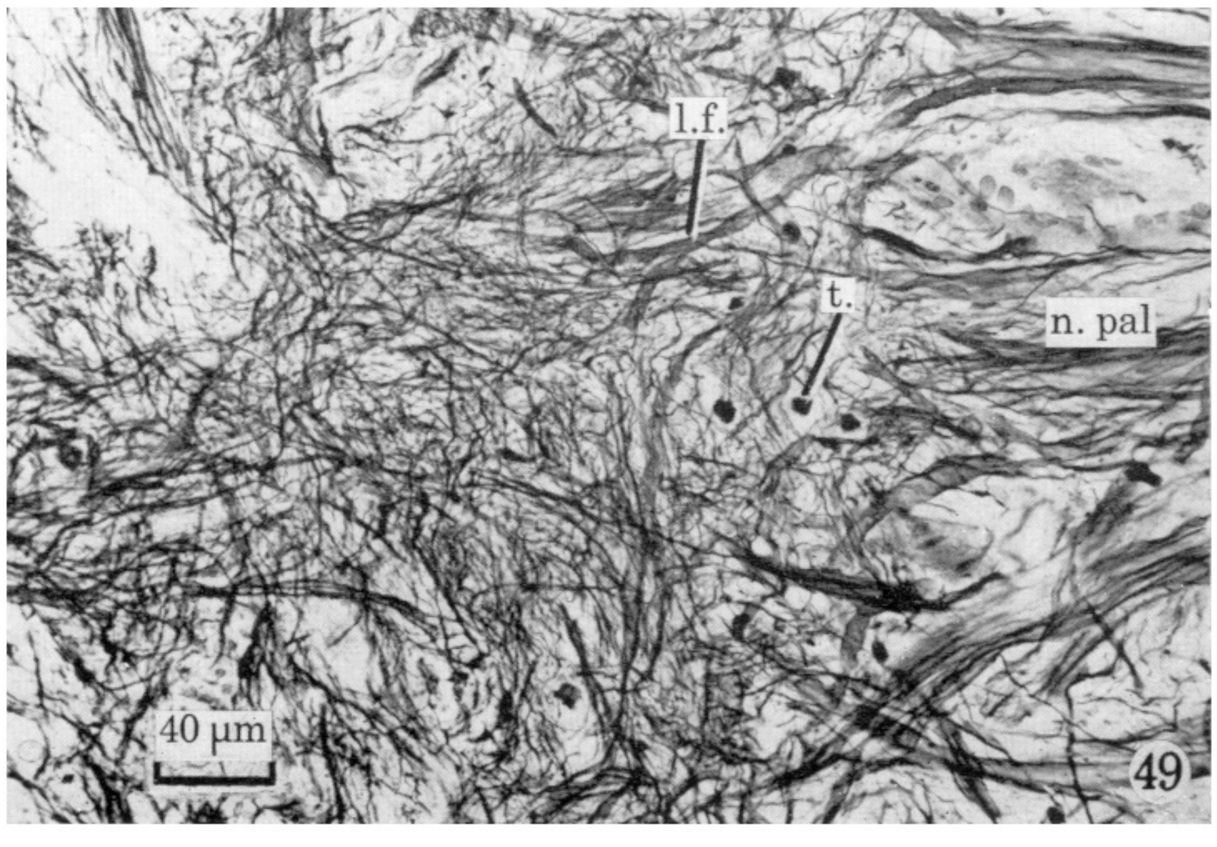




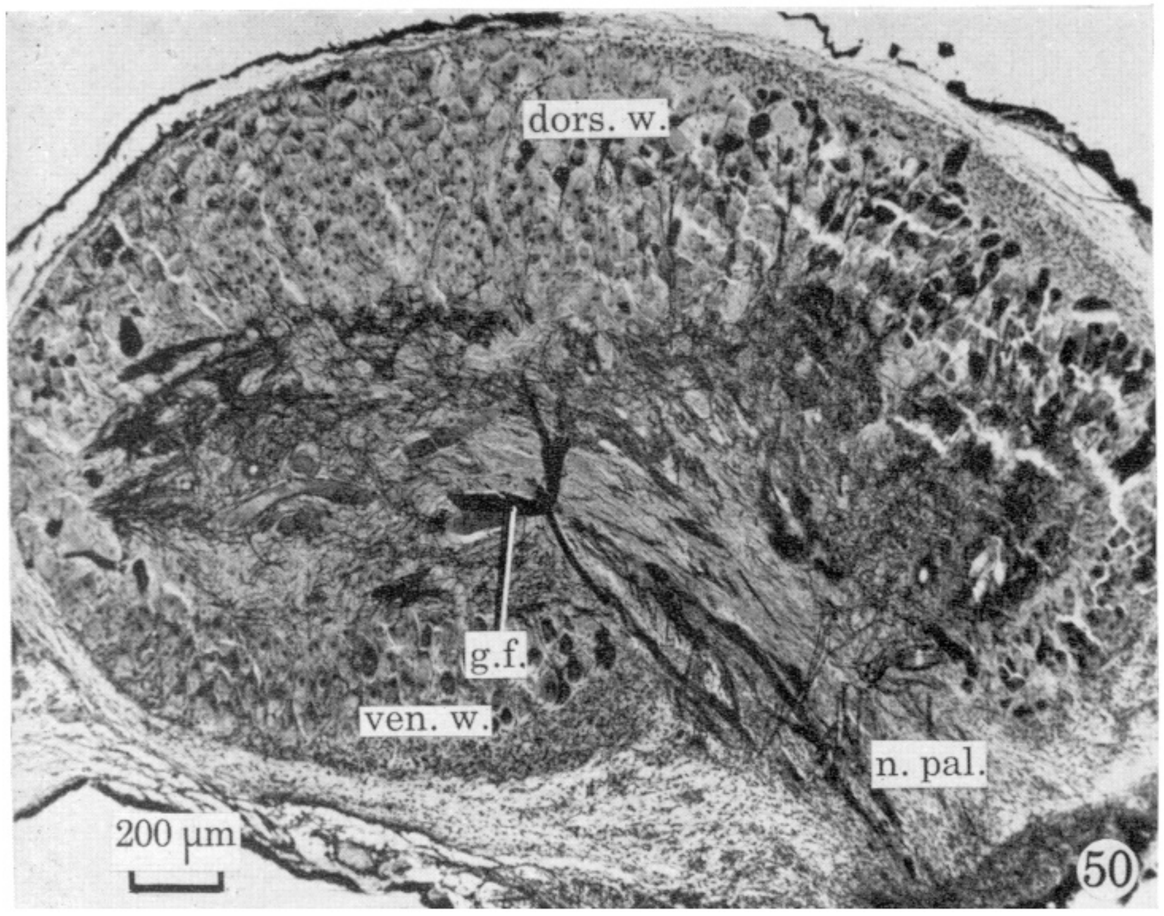


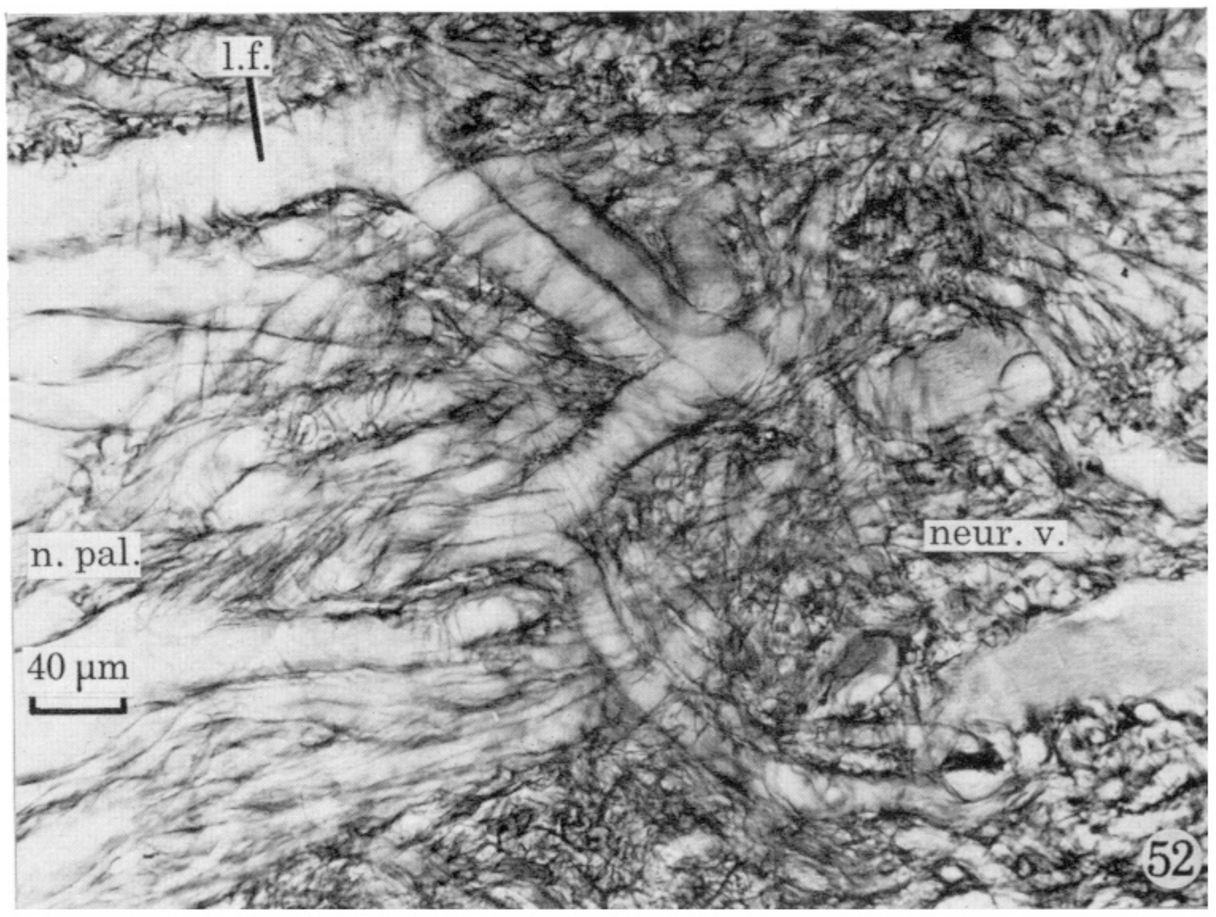


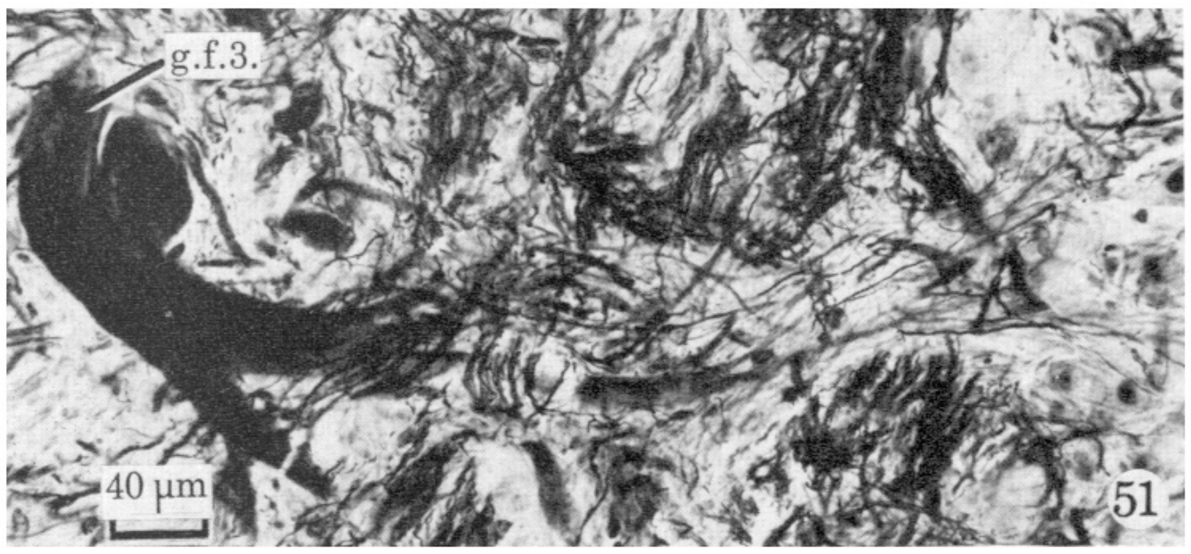


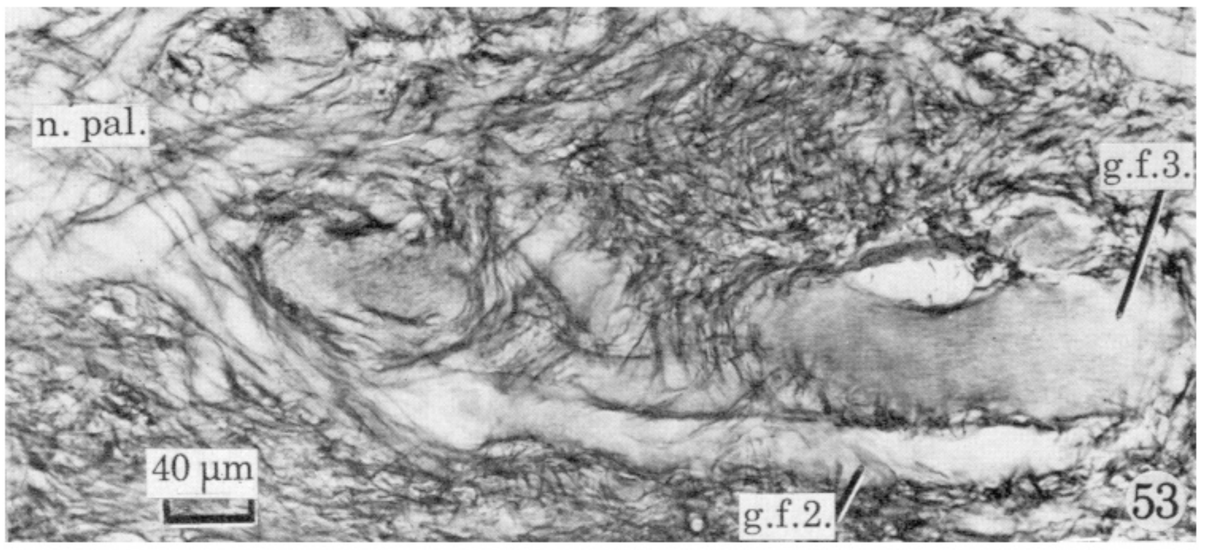


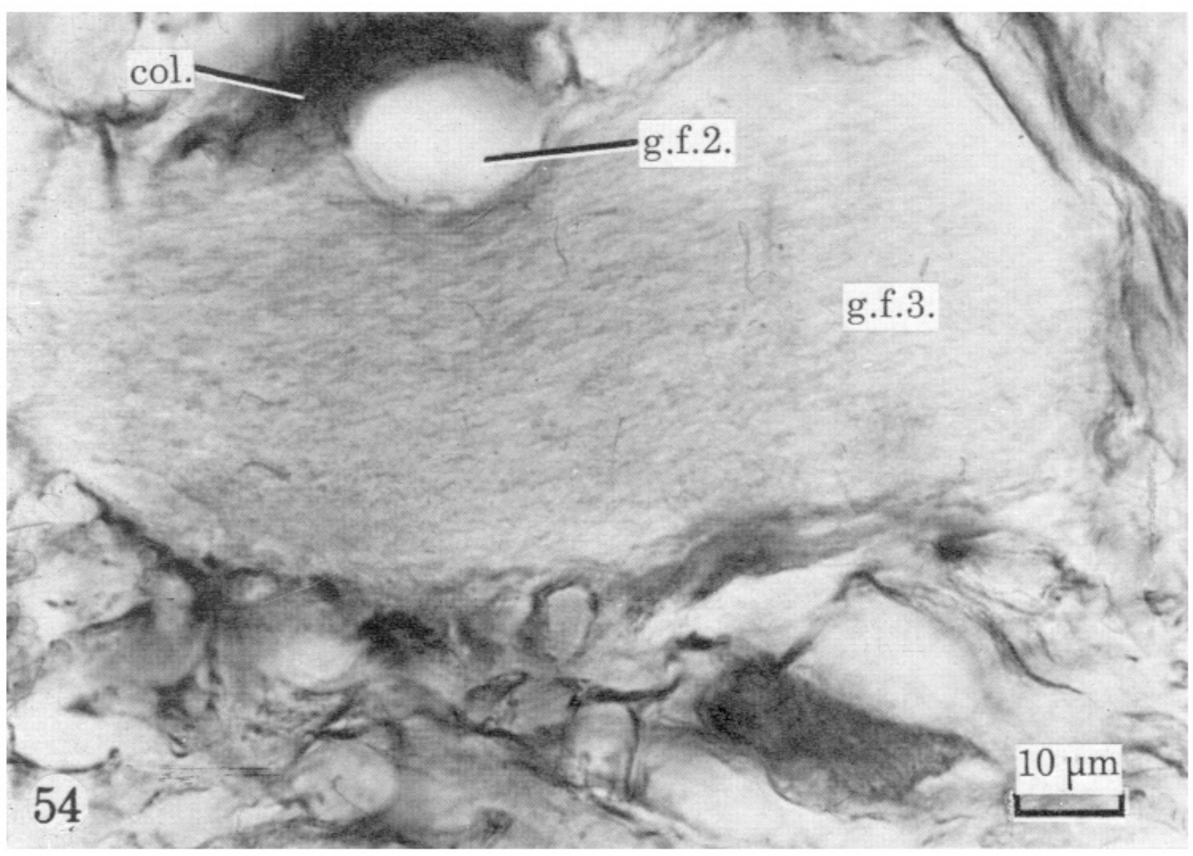
FIGURES 42 to 49. For legends see facing page

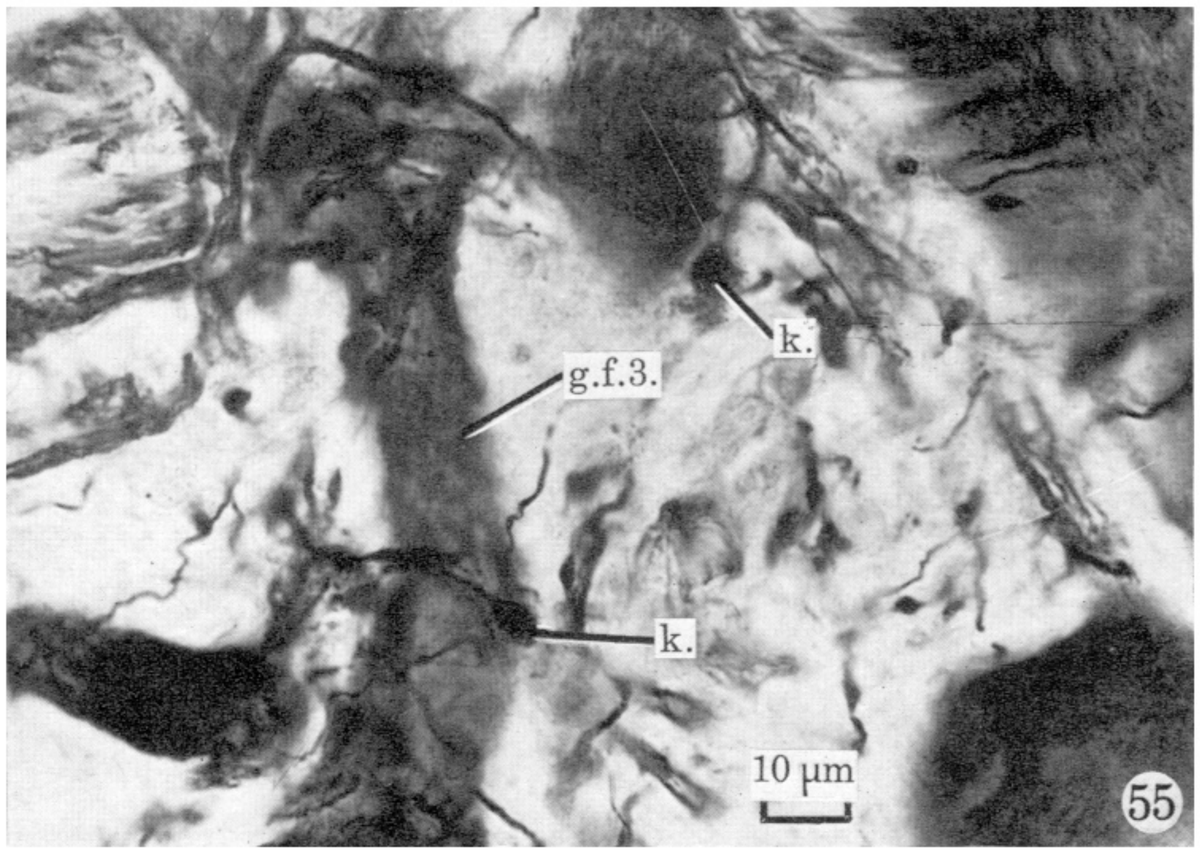


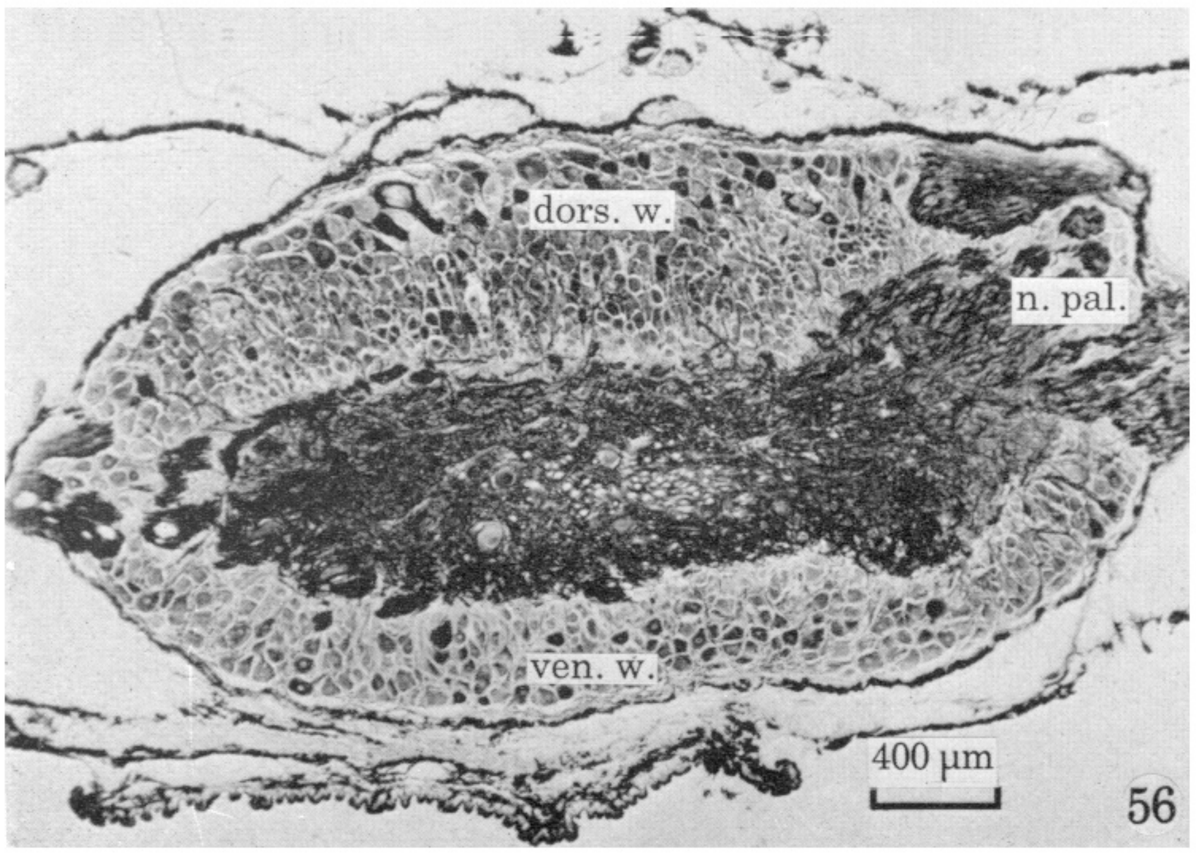


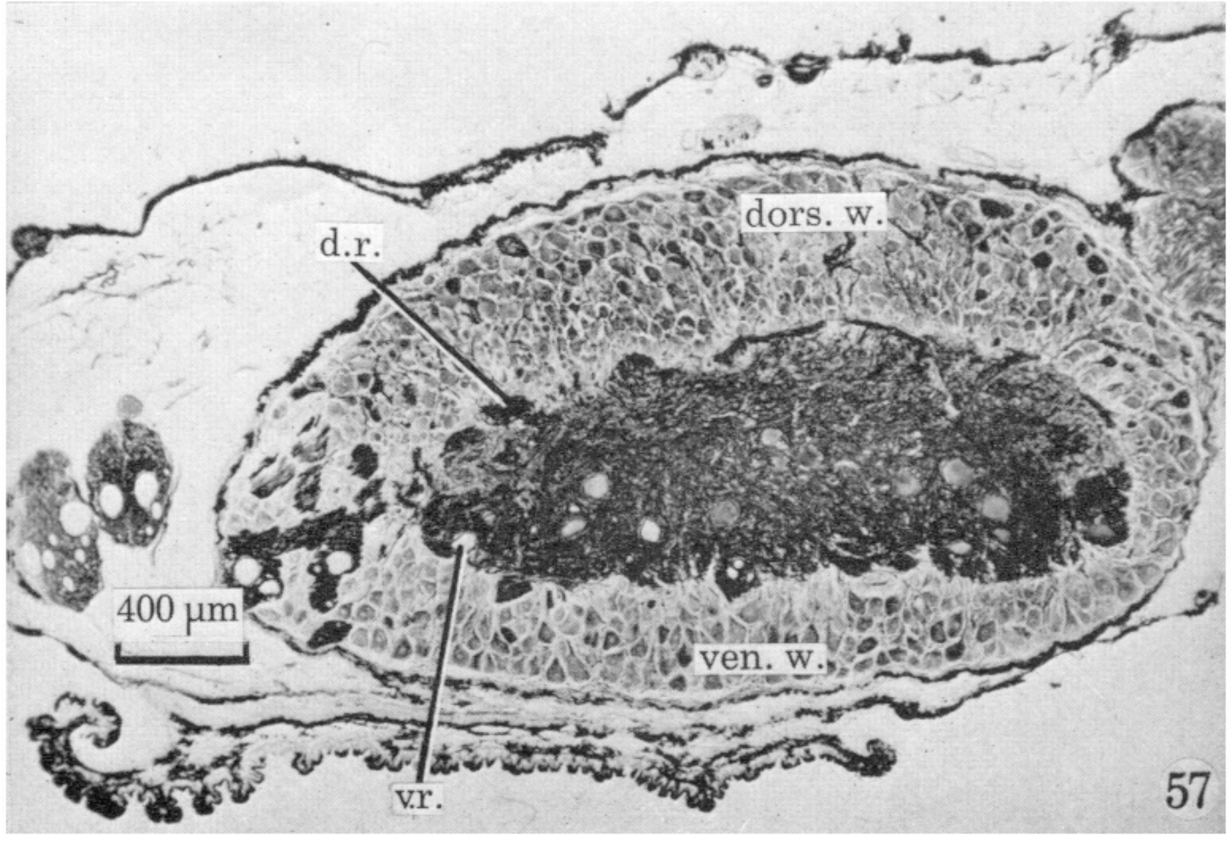




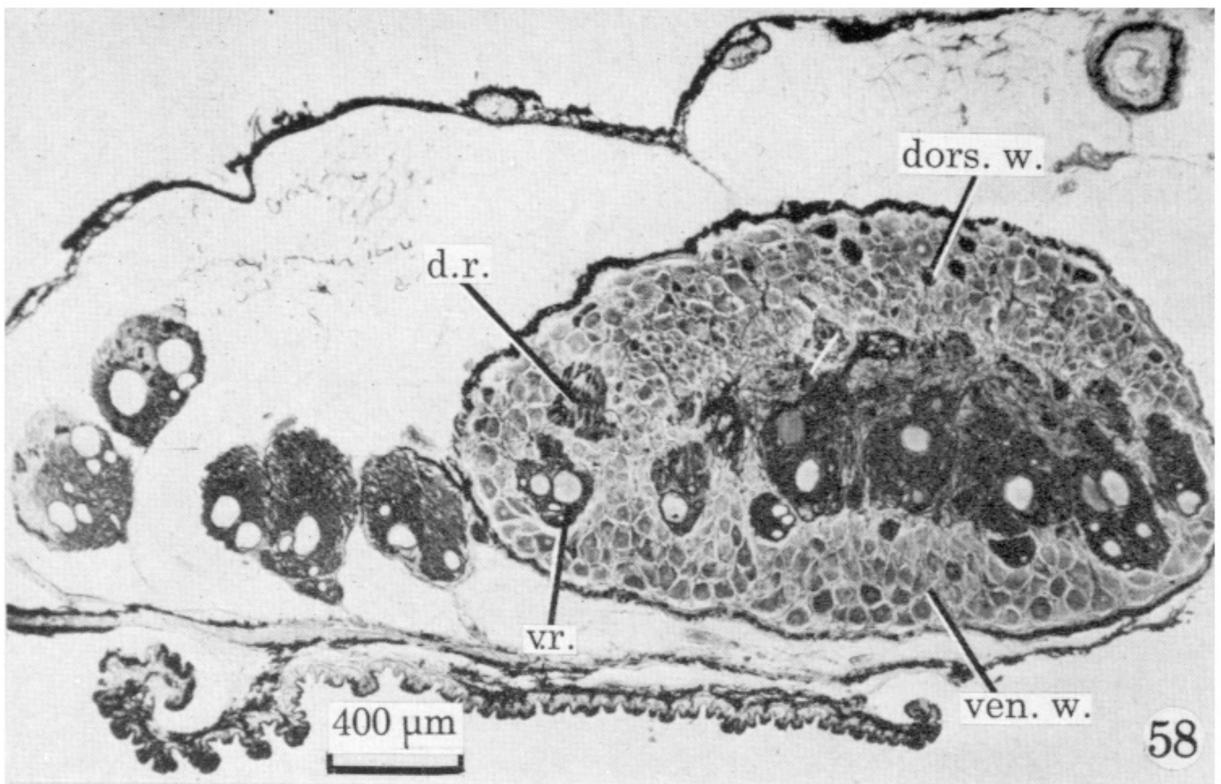


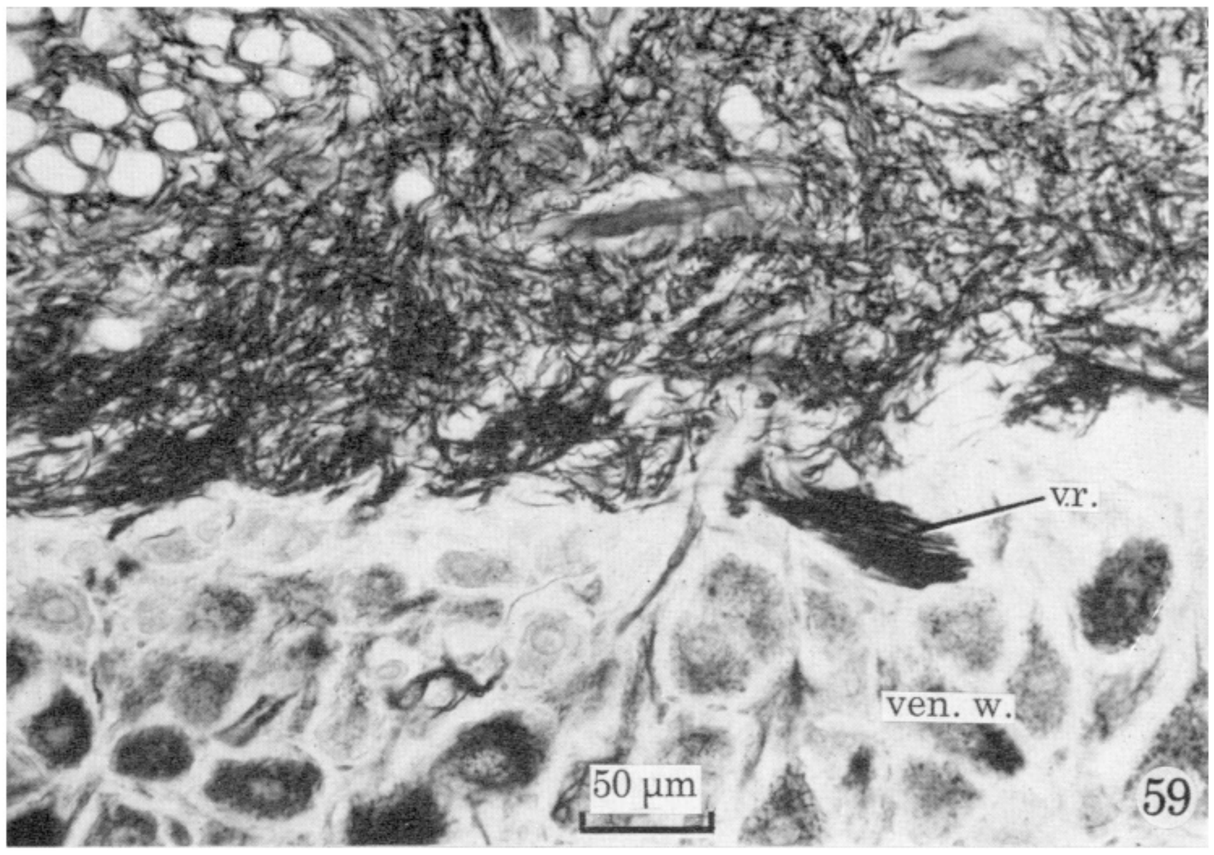


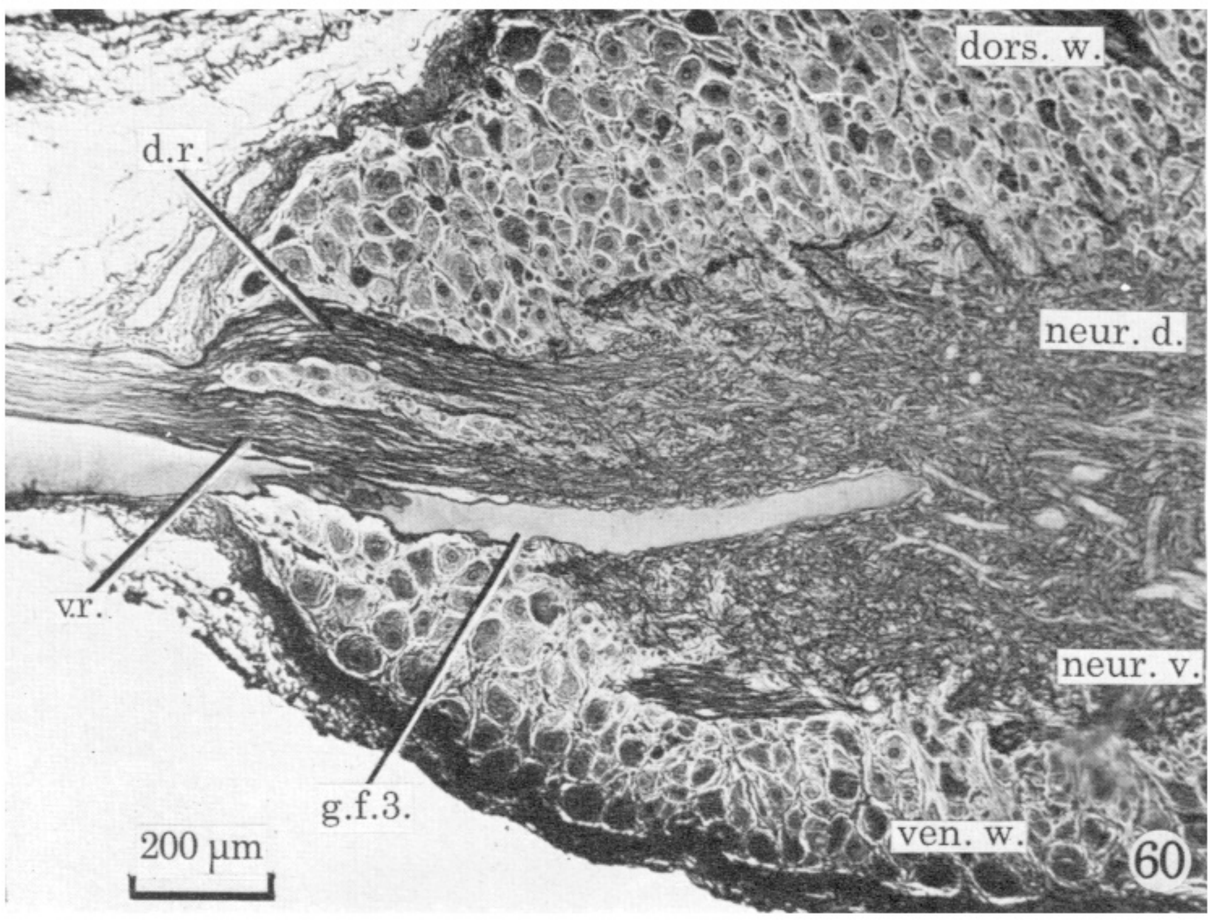


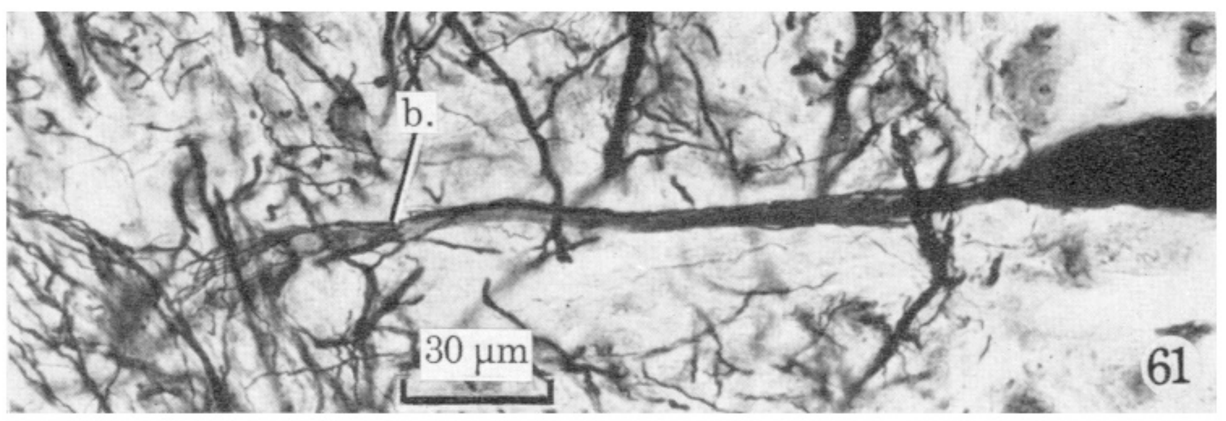


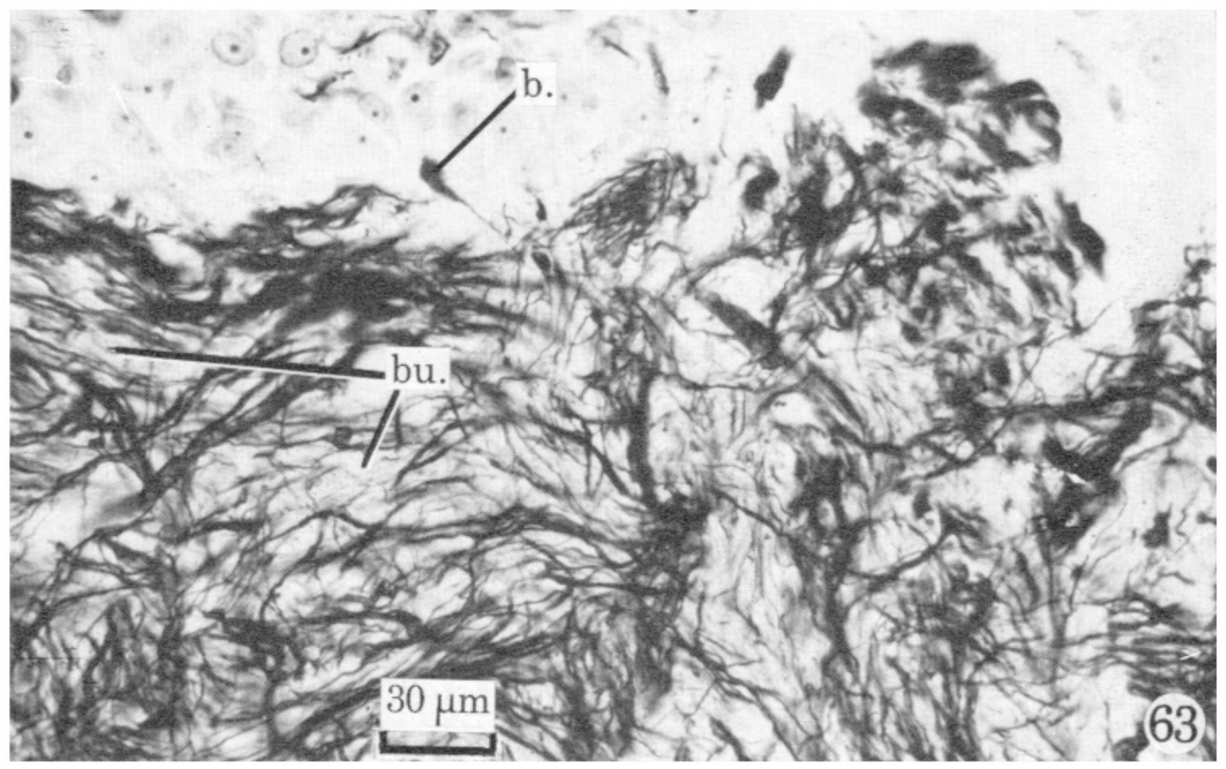
FIGURES 50 to 57. For legends see facing page

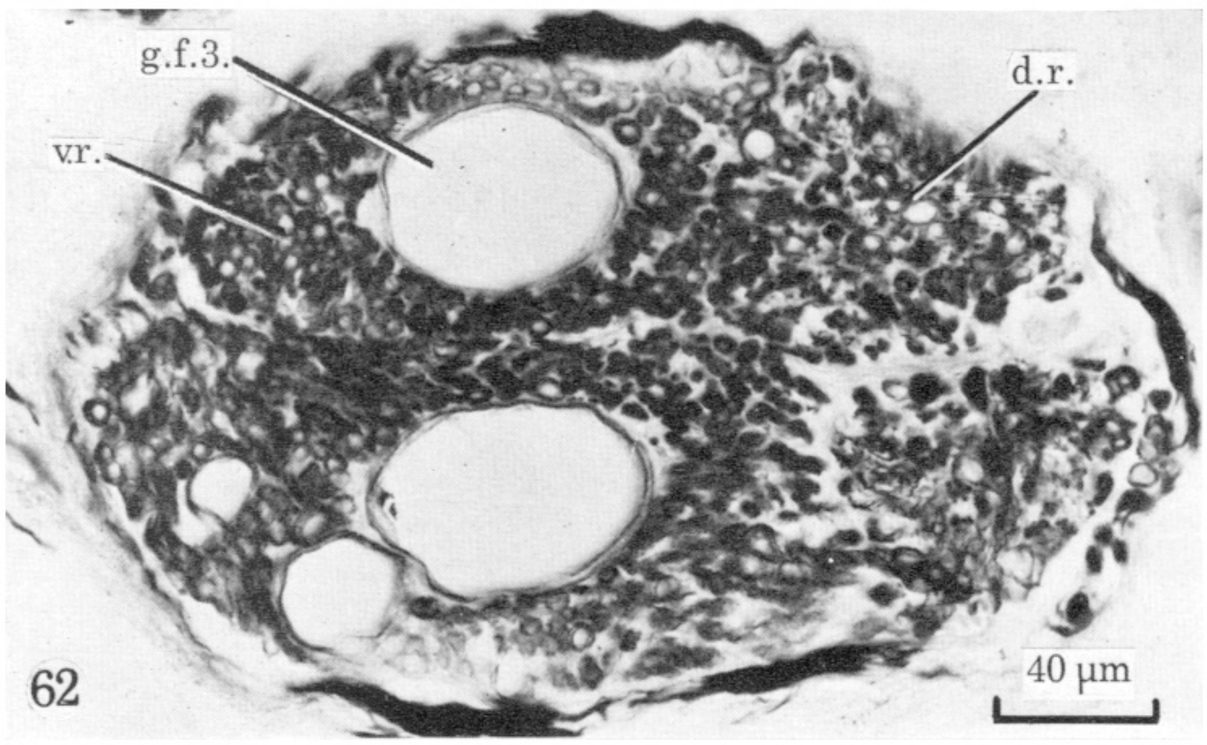


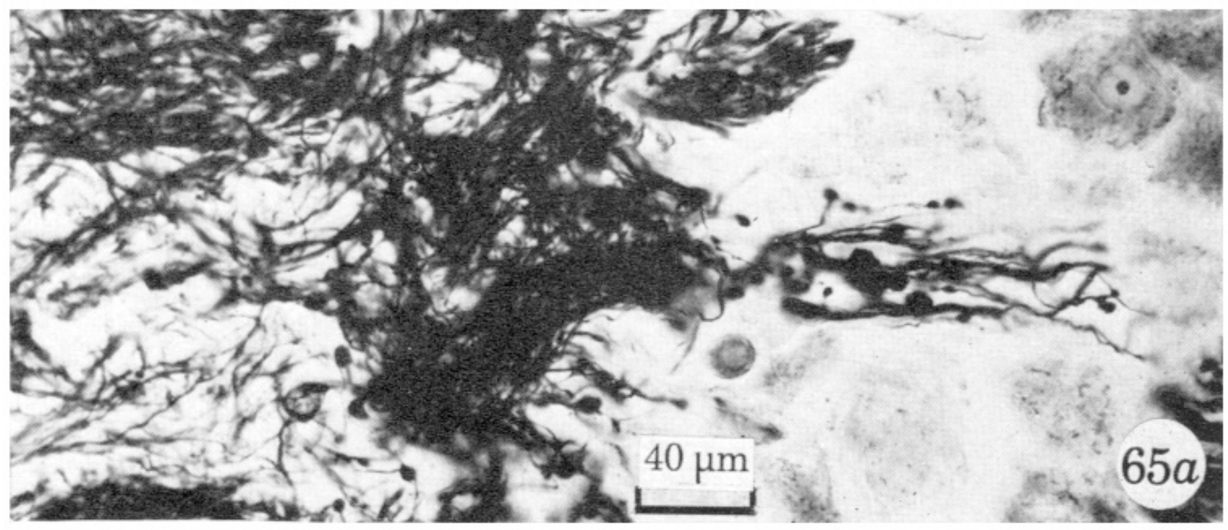


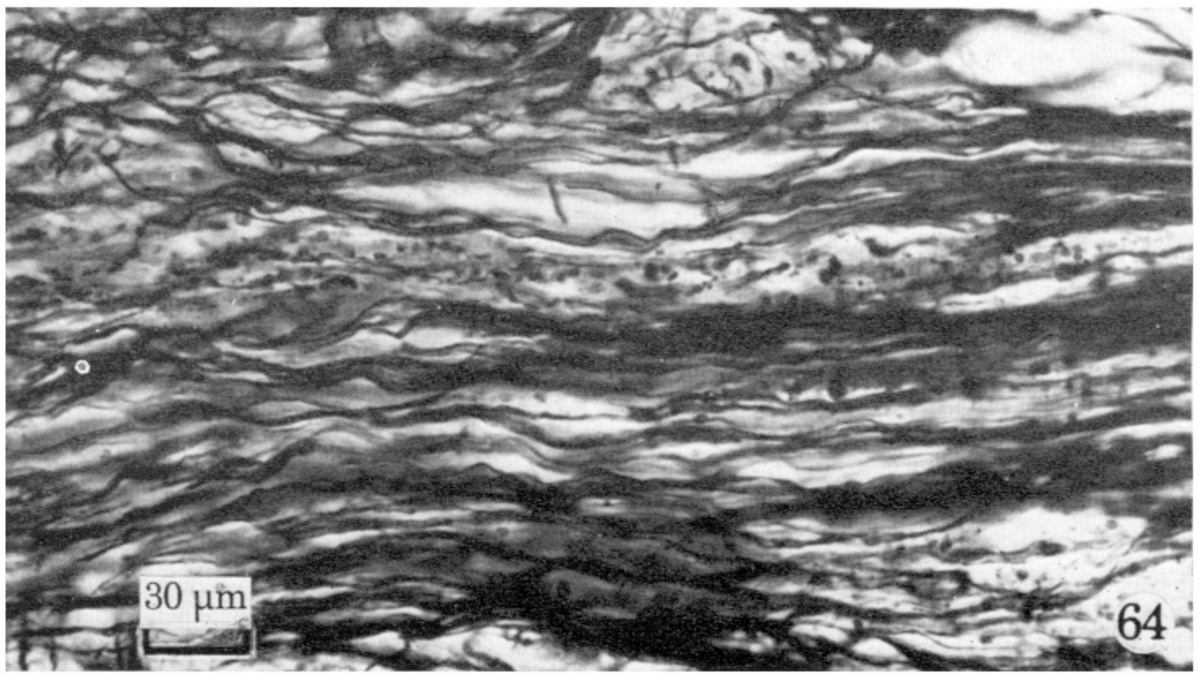


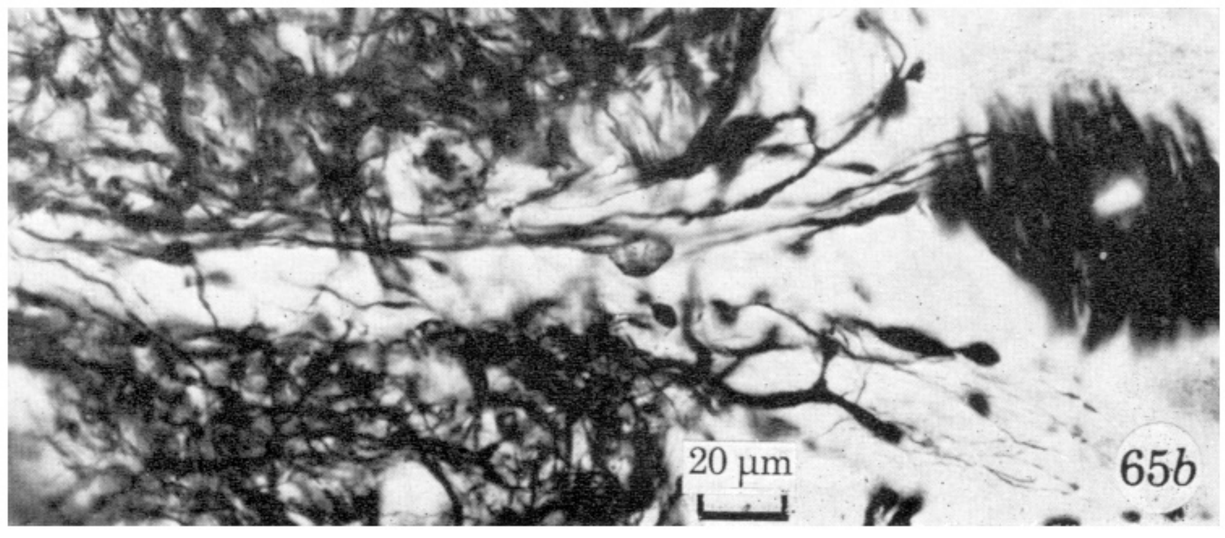




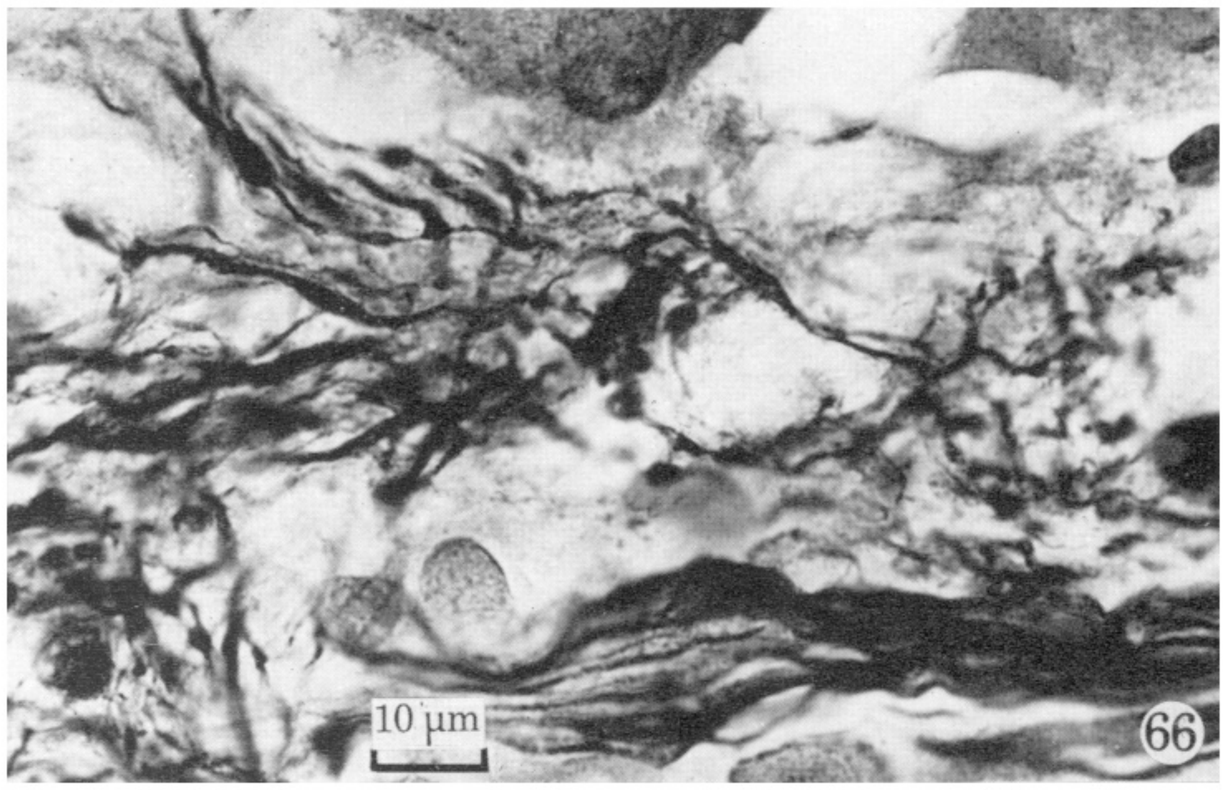


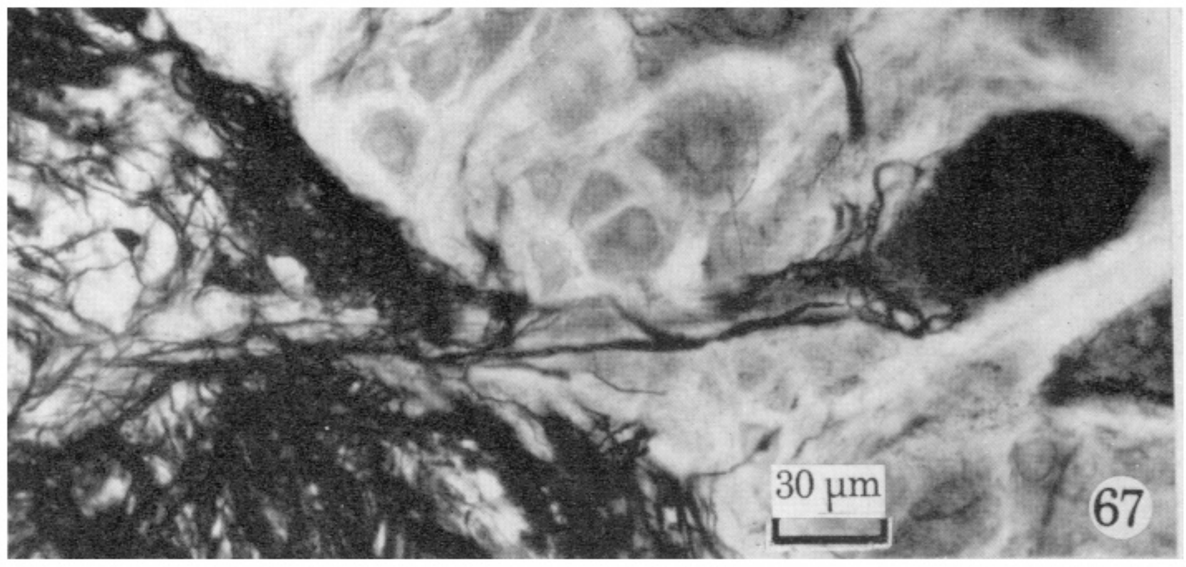


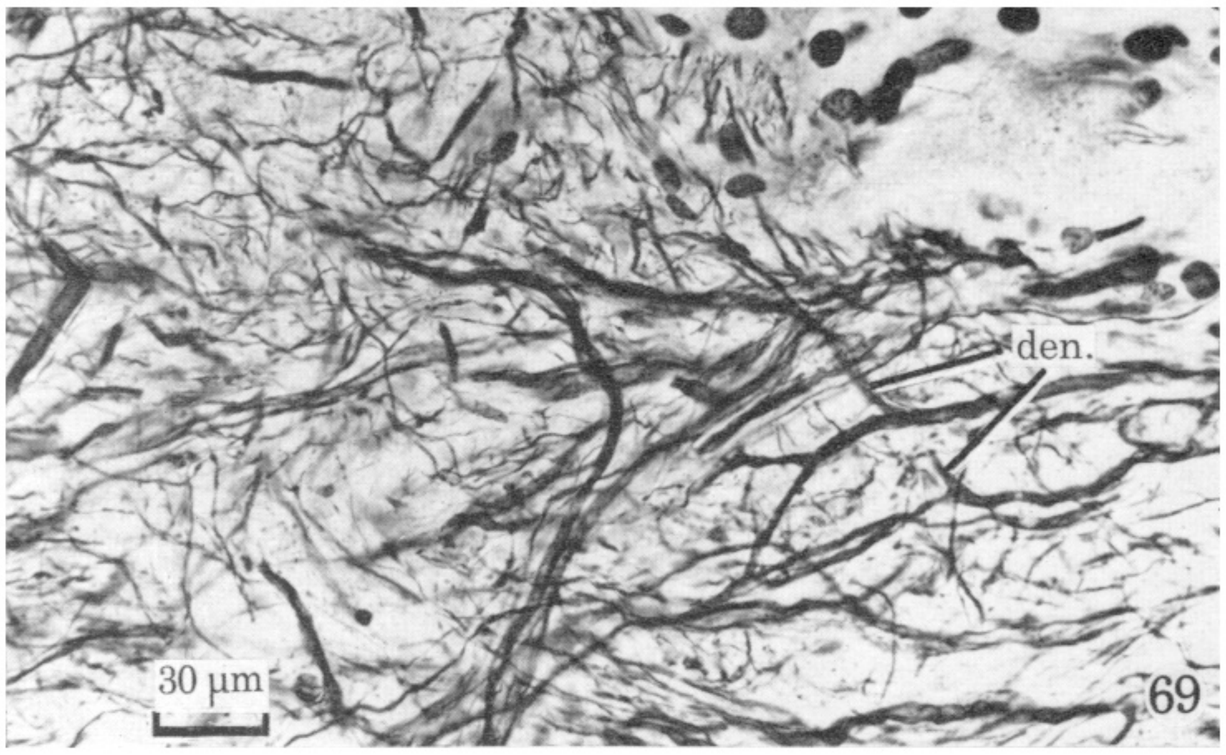


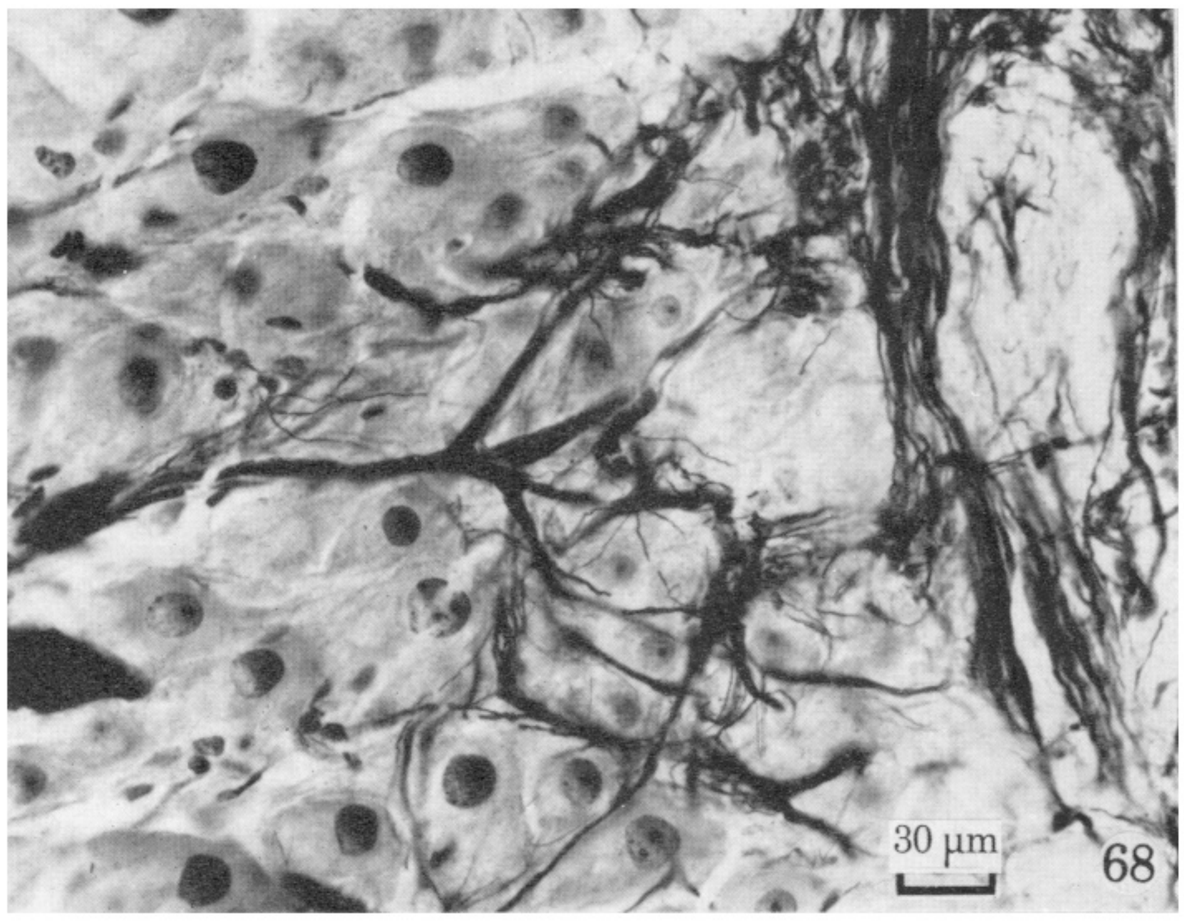


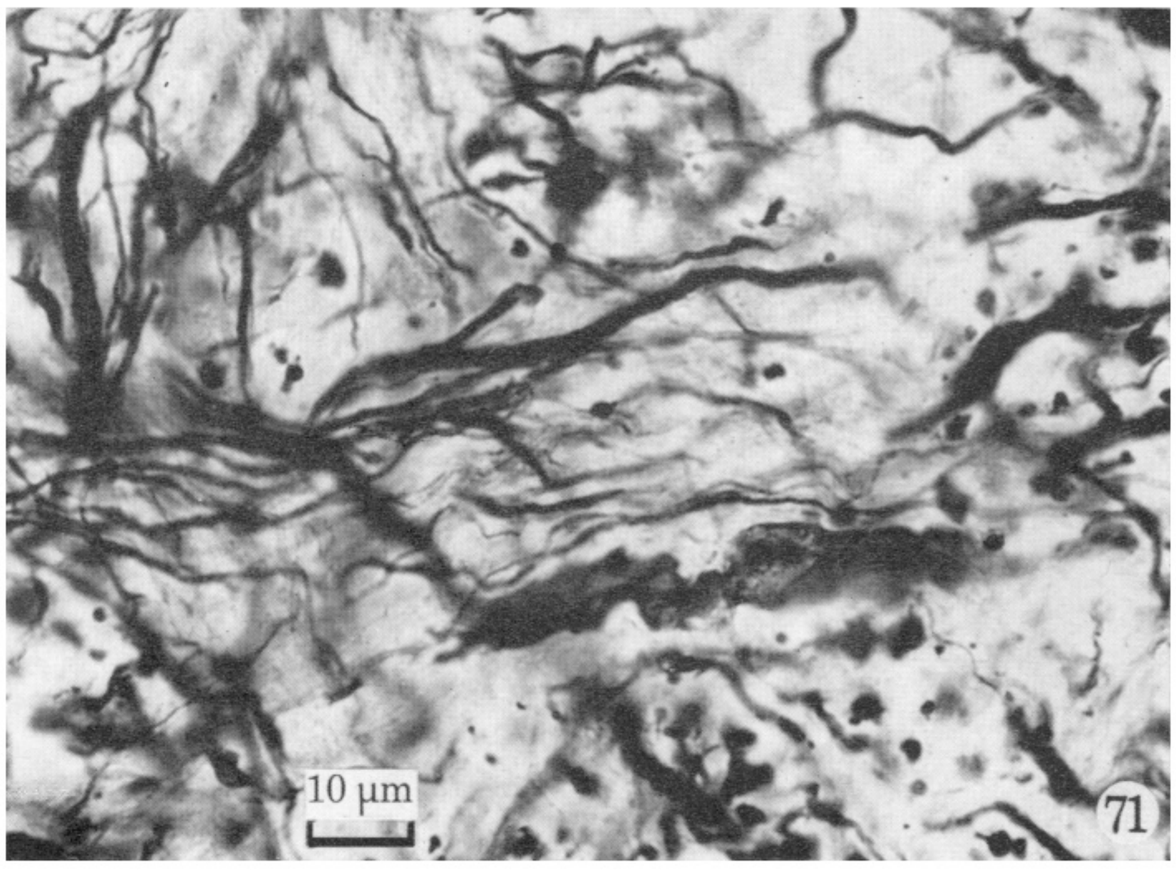
FIGURES 58 to 65. For legends see facing page

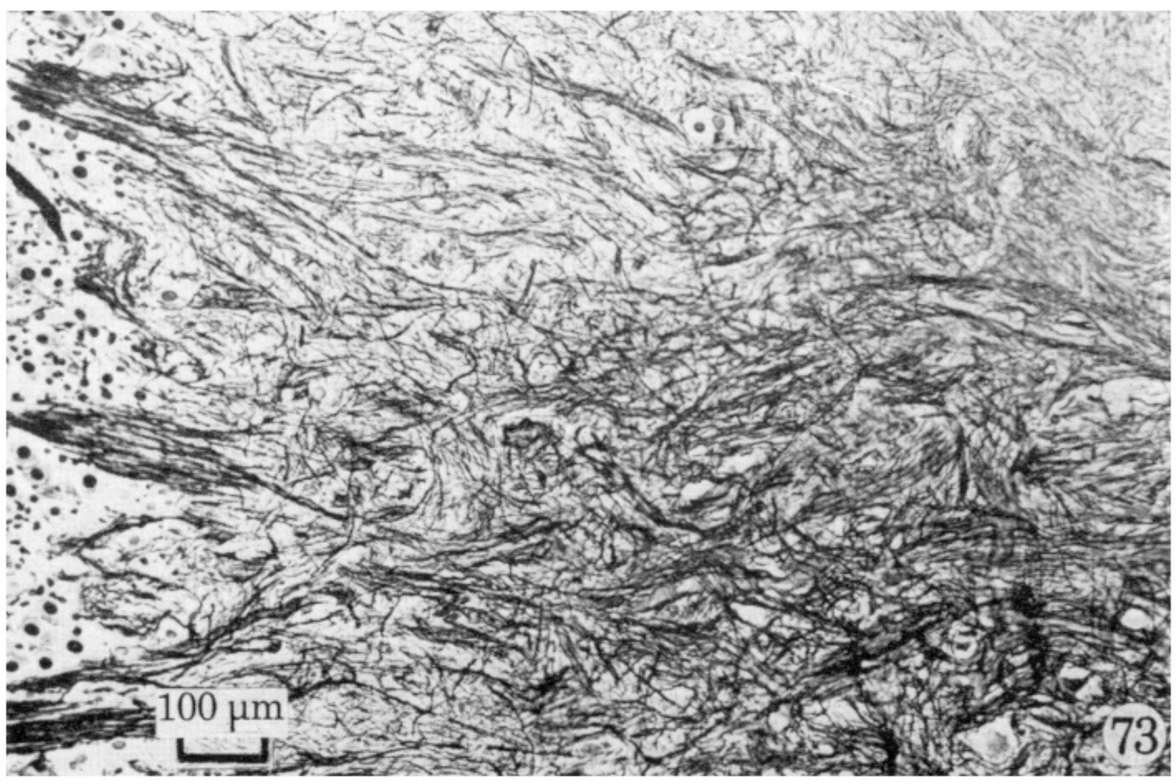




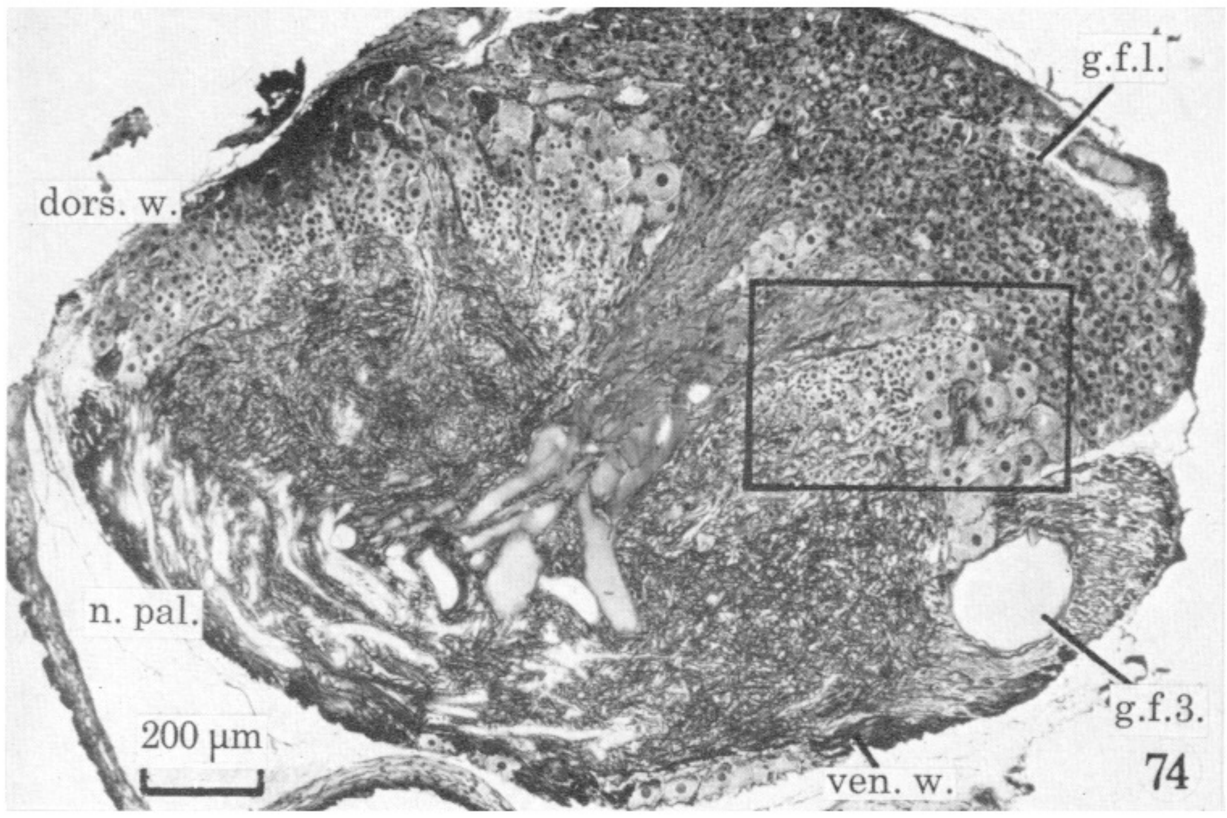


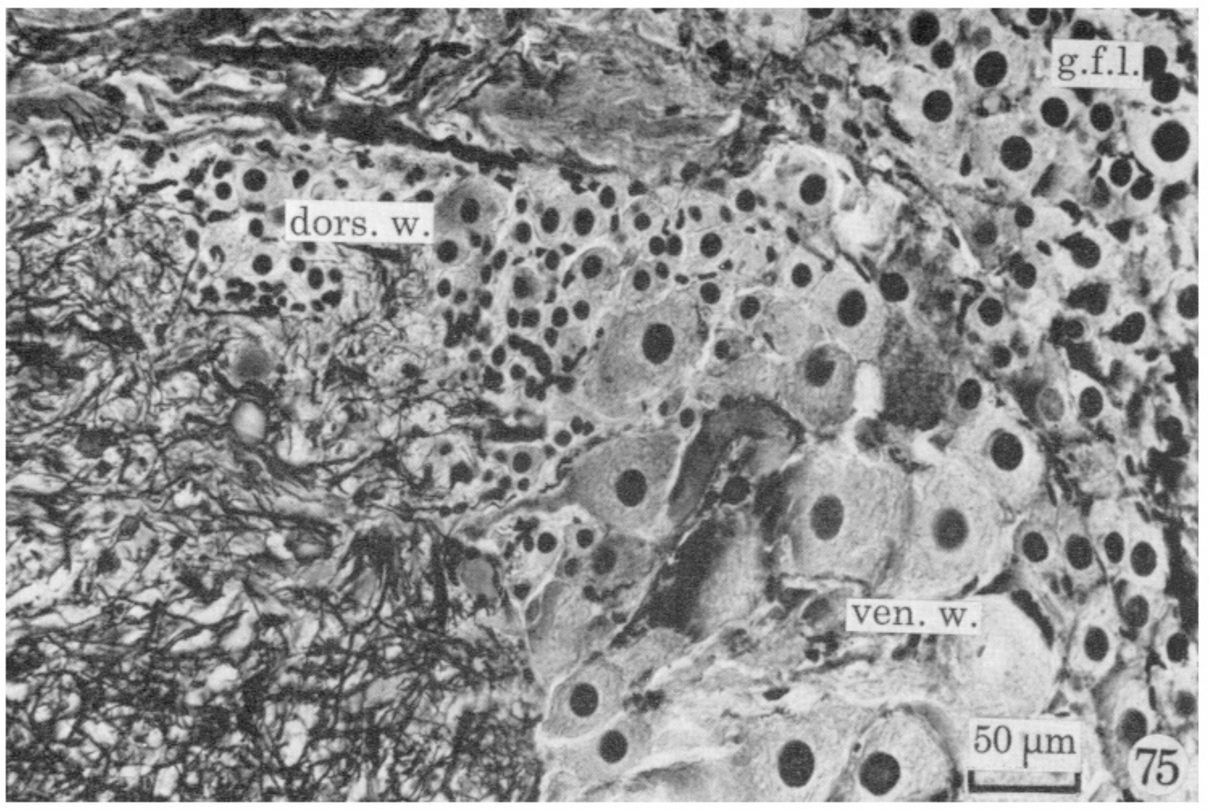


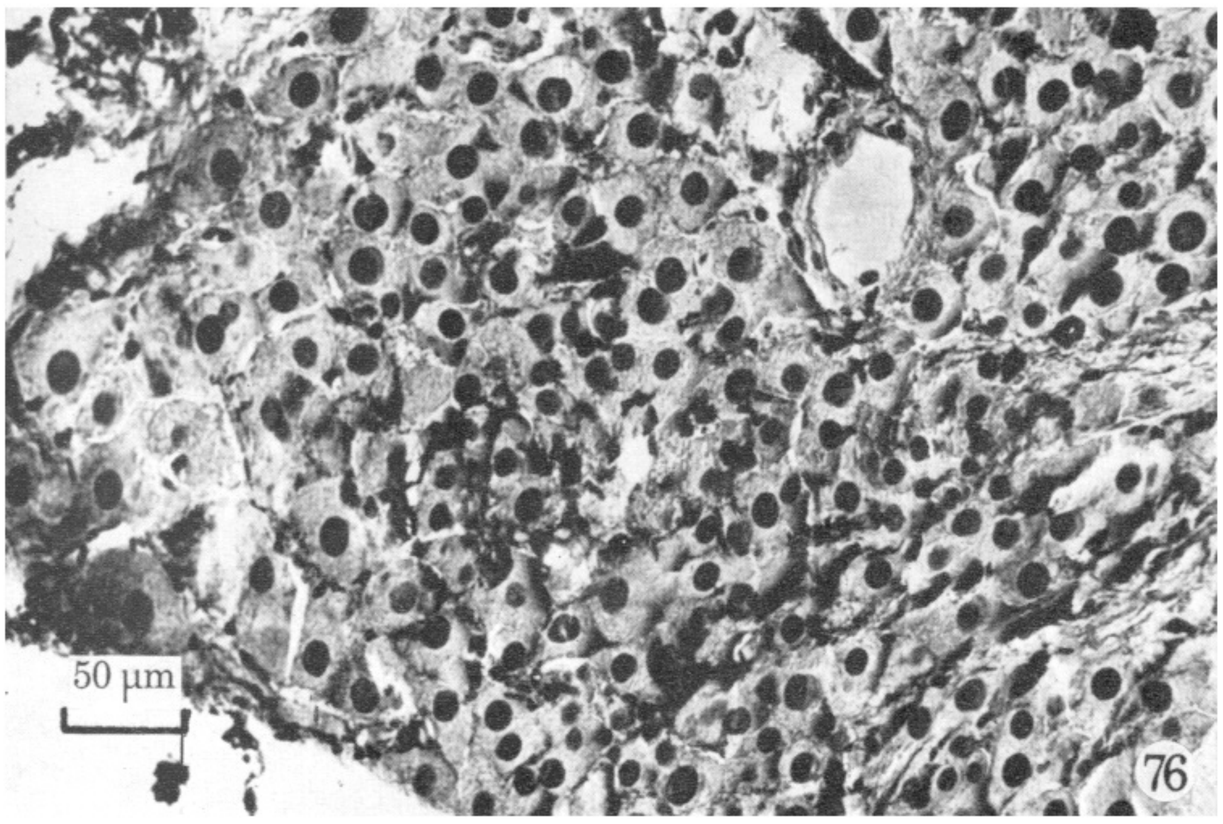


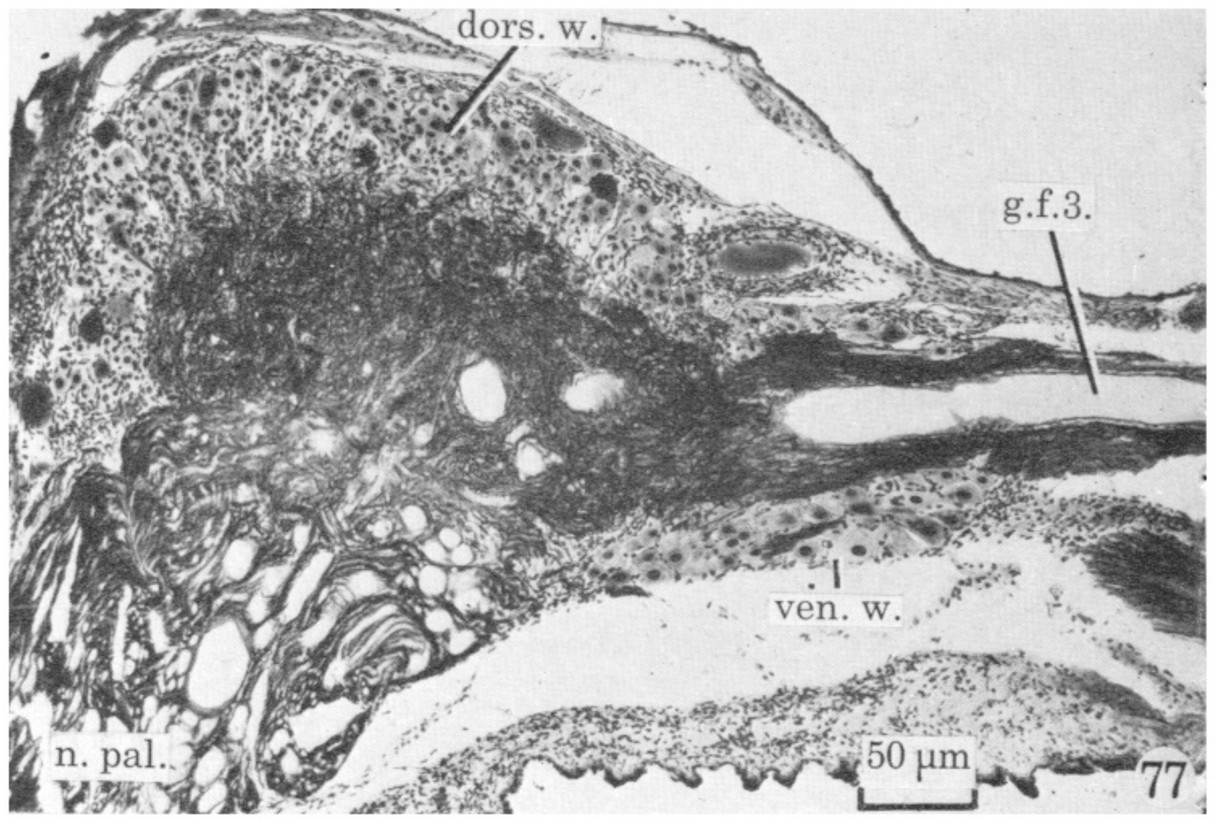


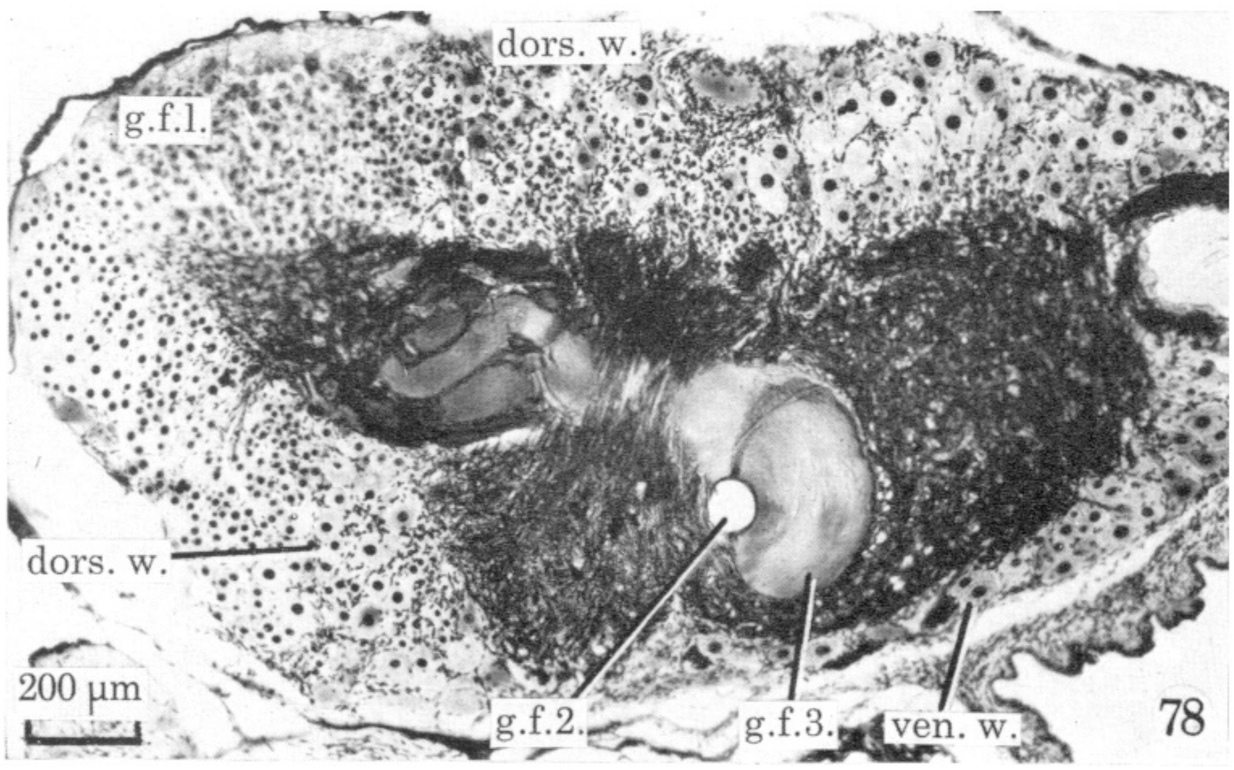
FIGURES 66 to 73. For legends see facing page

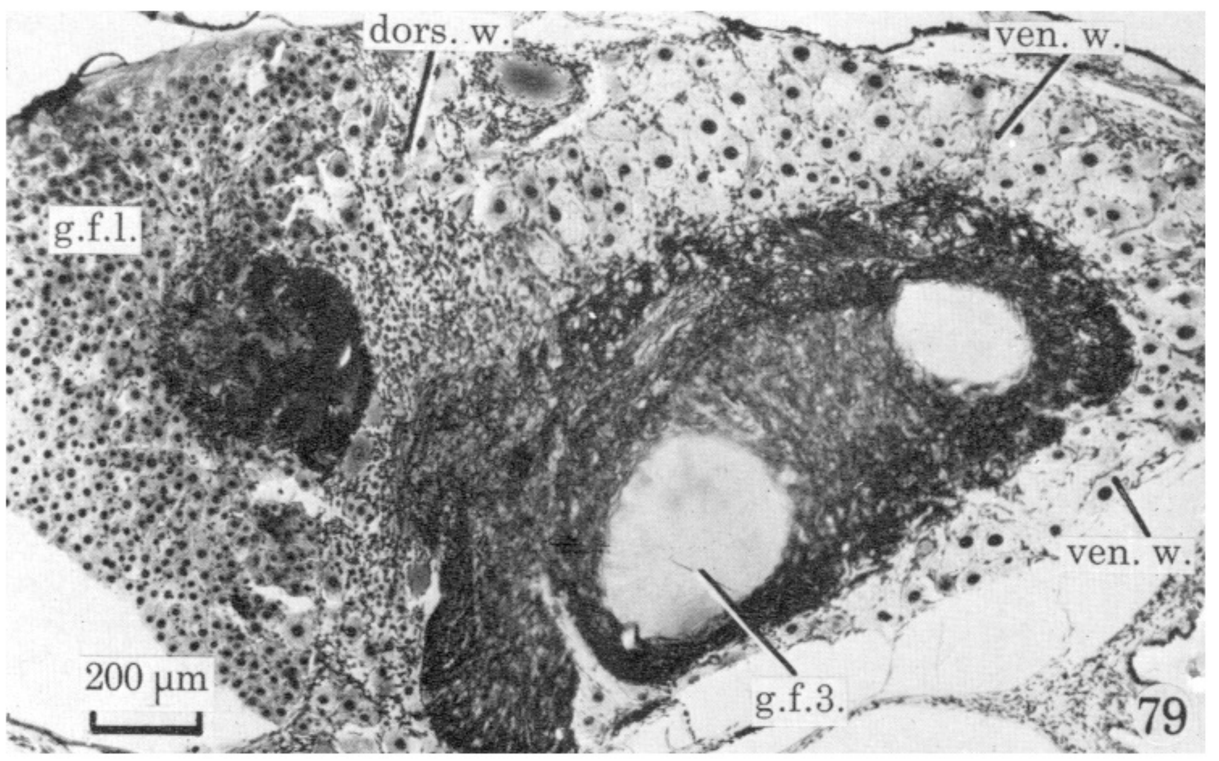


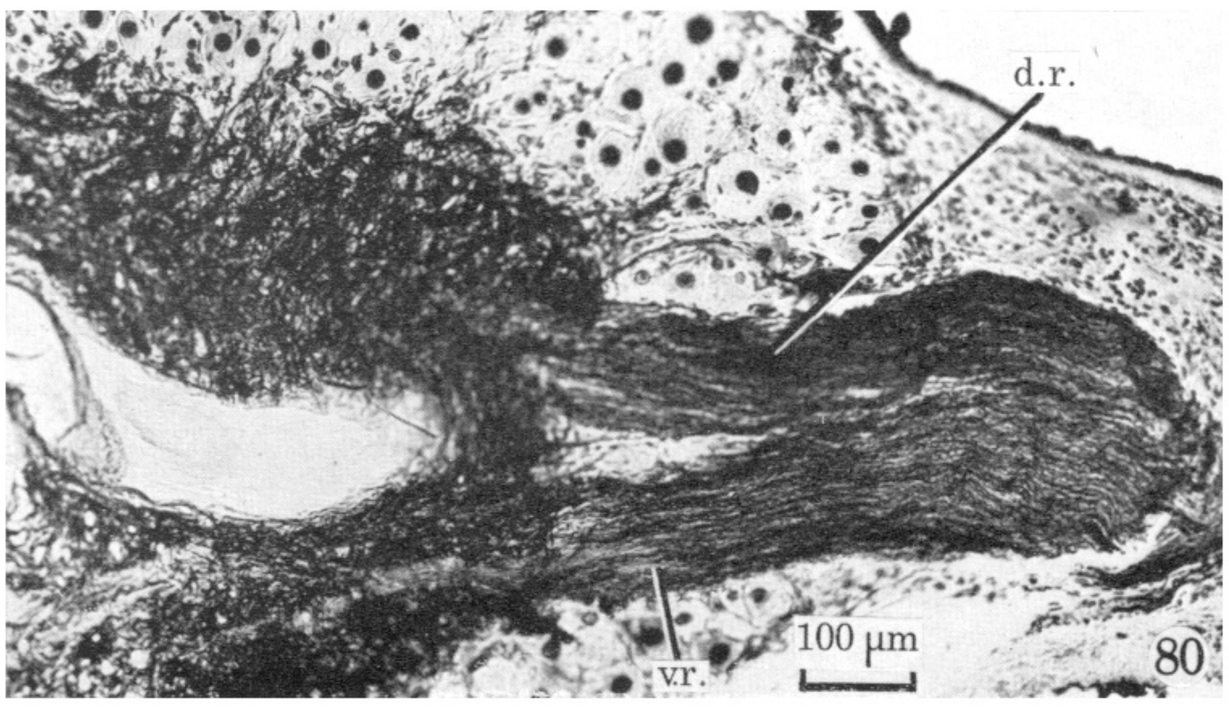


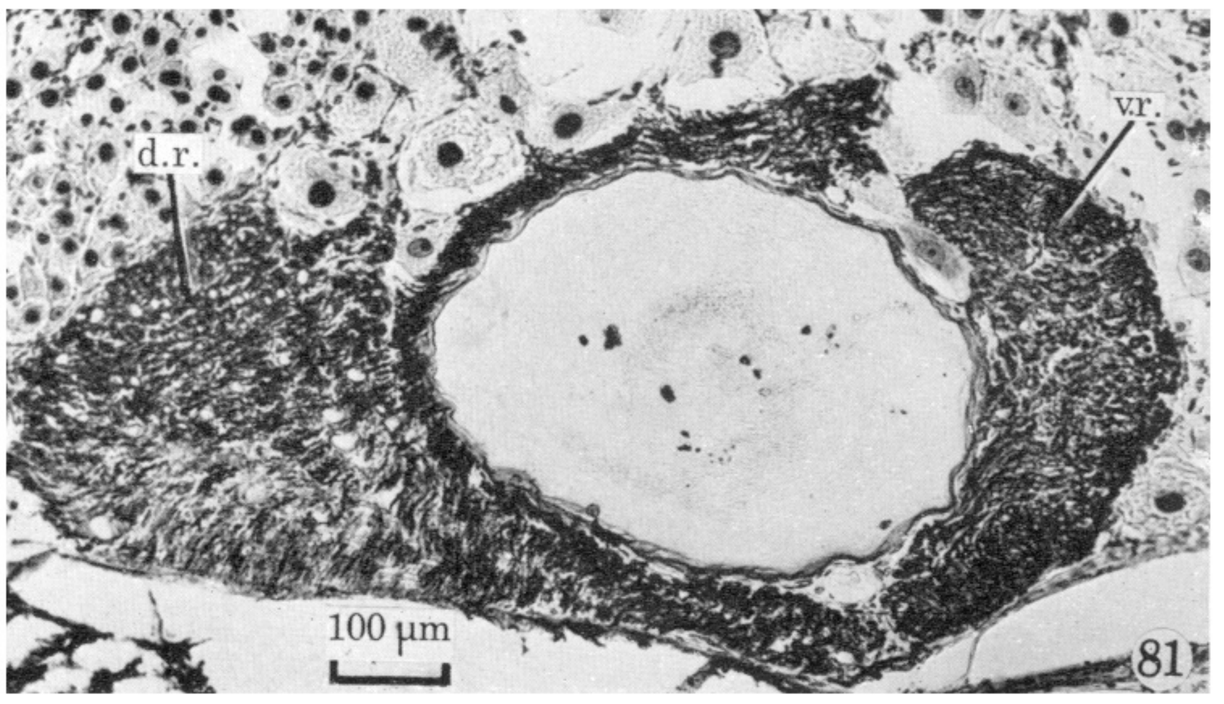




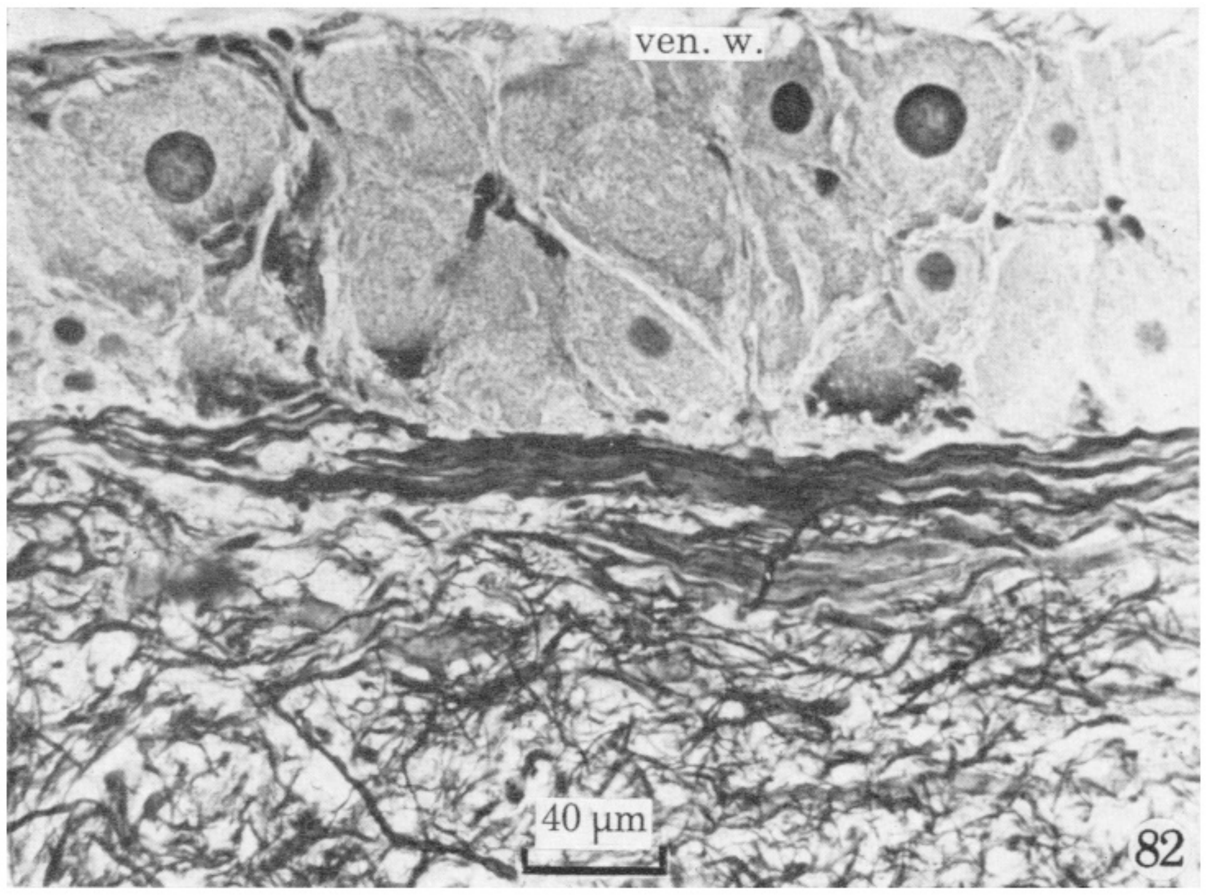


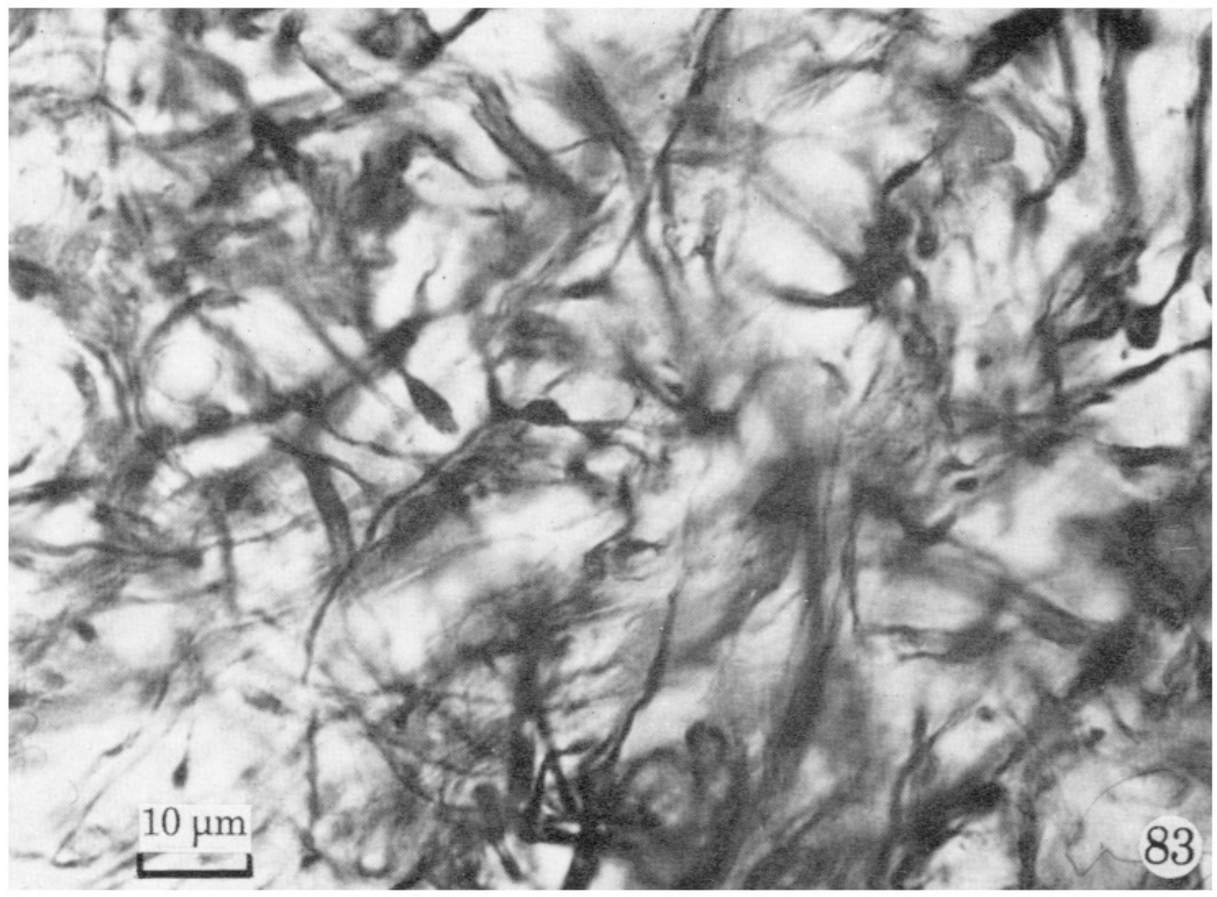


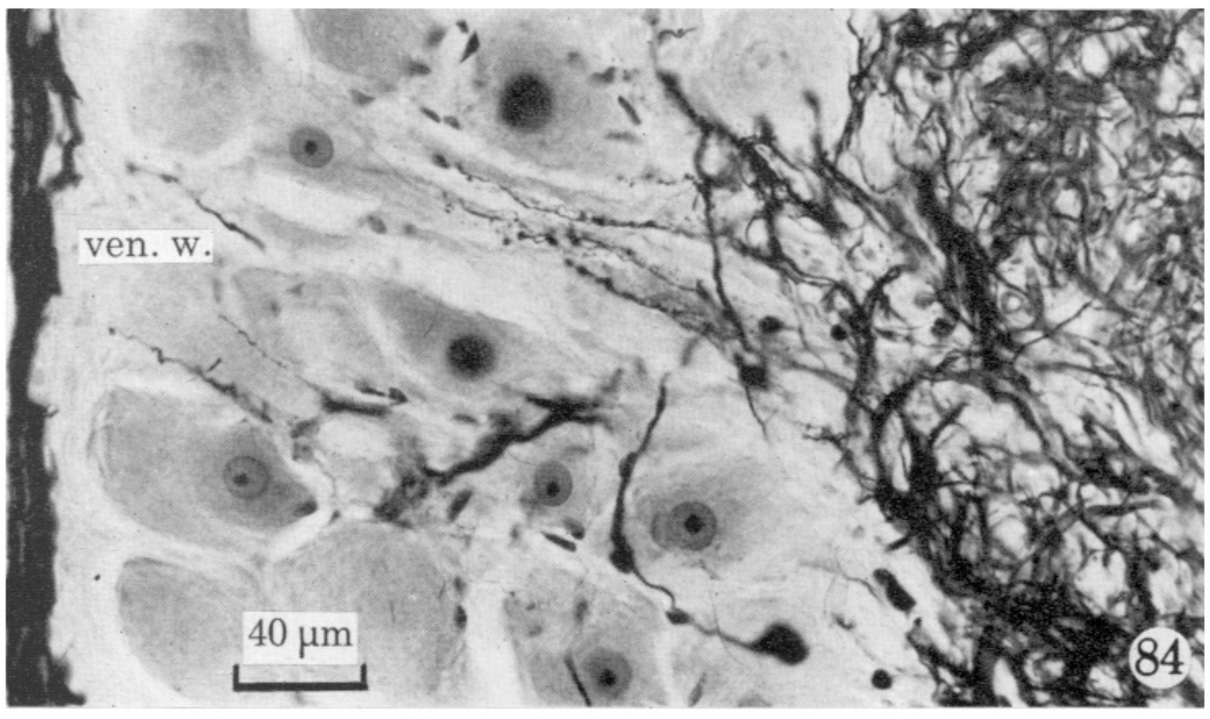


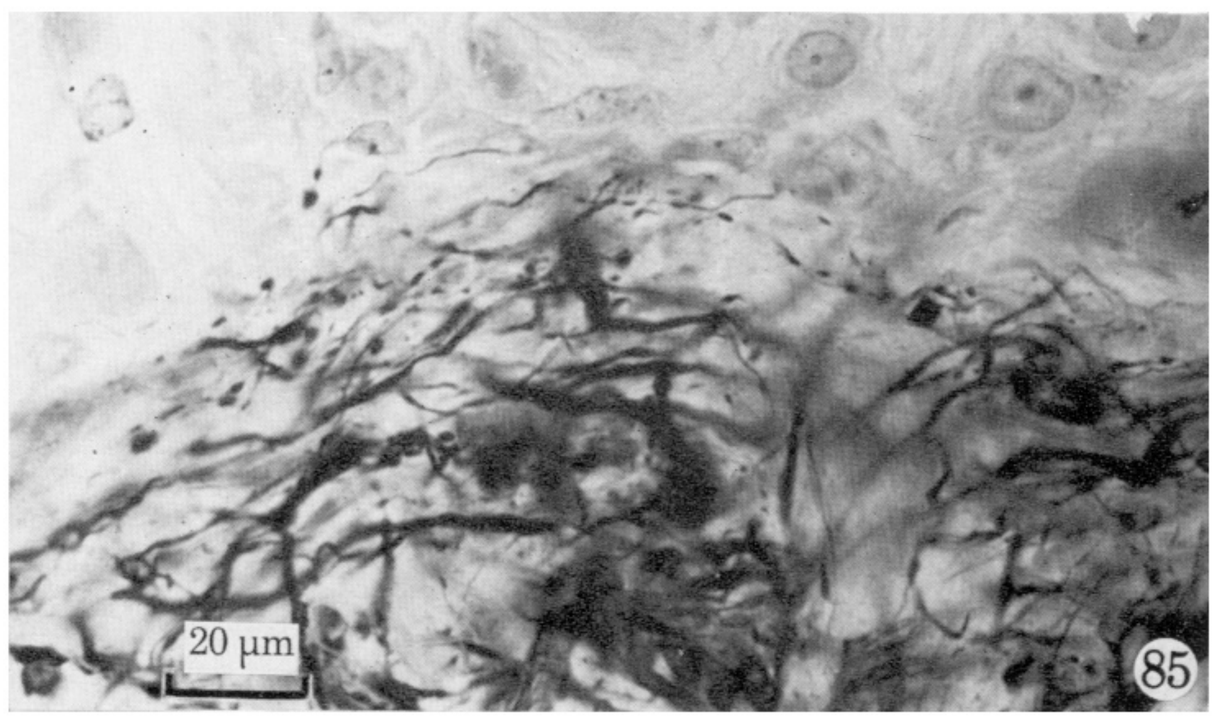


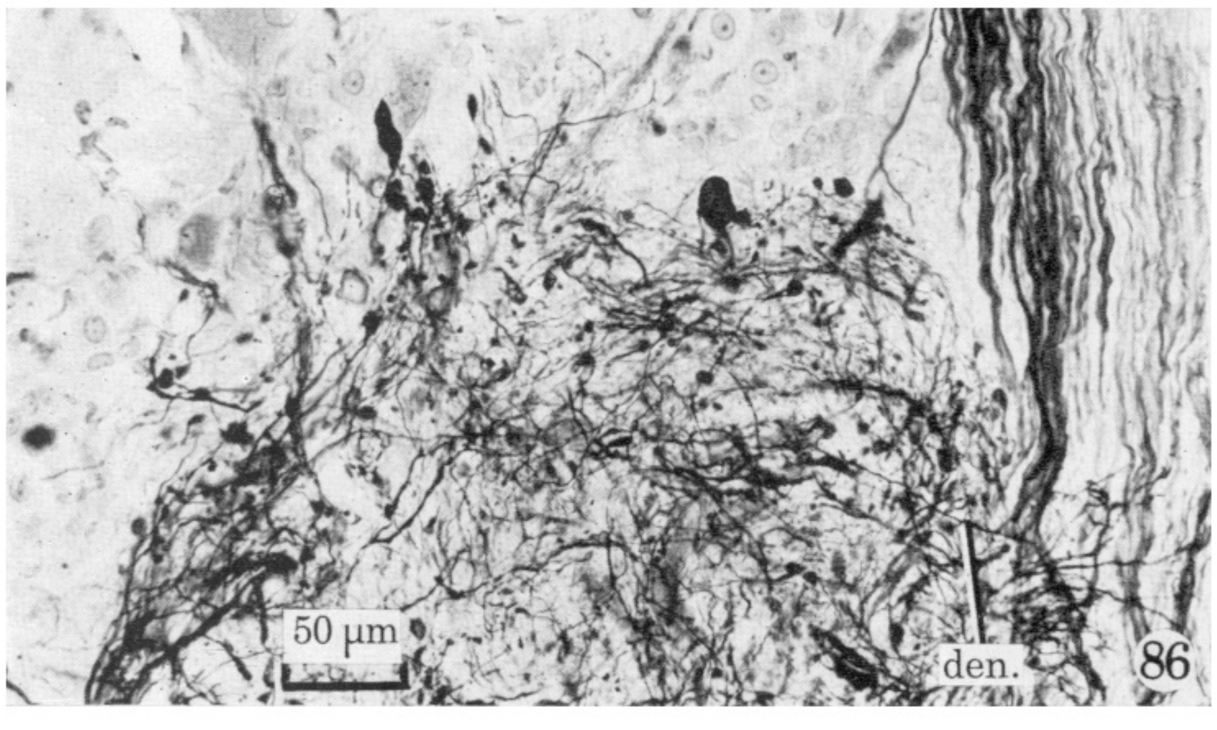
FIGURES 74 to 81. For legends see facing page

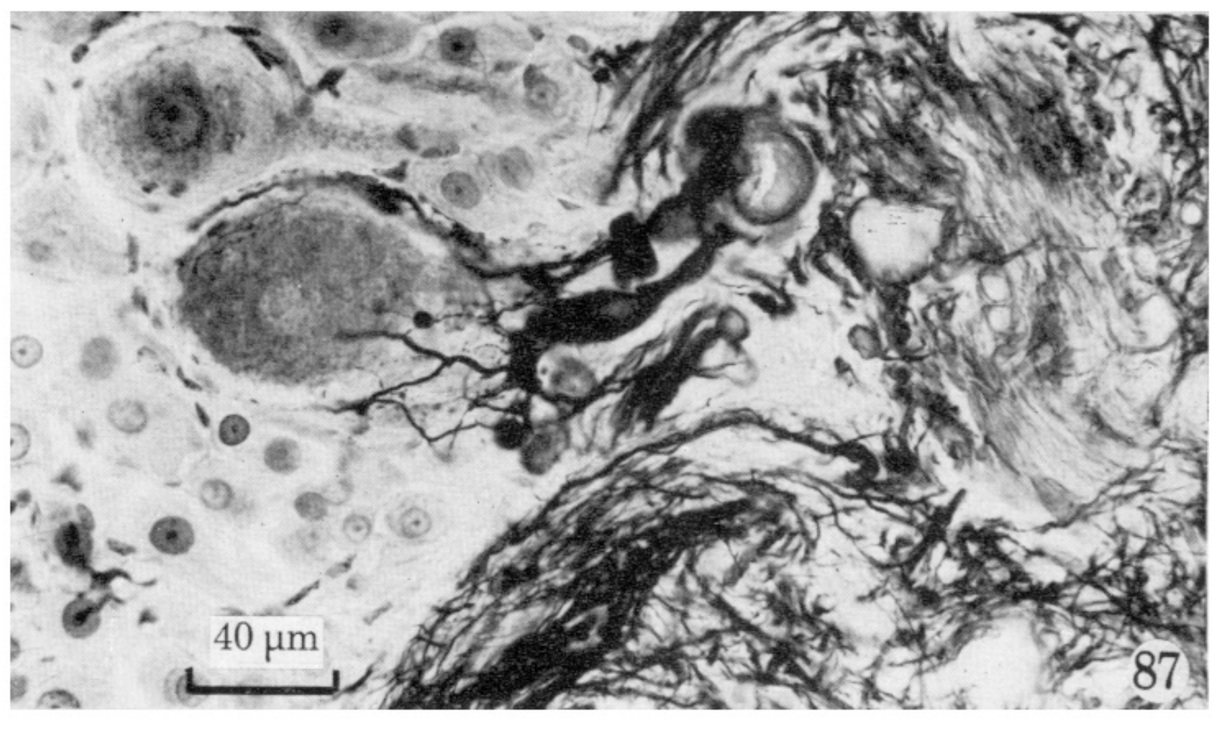


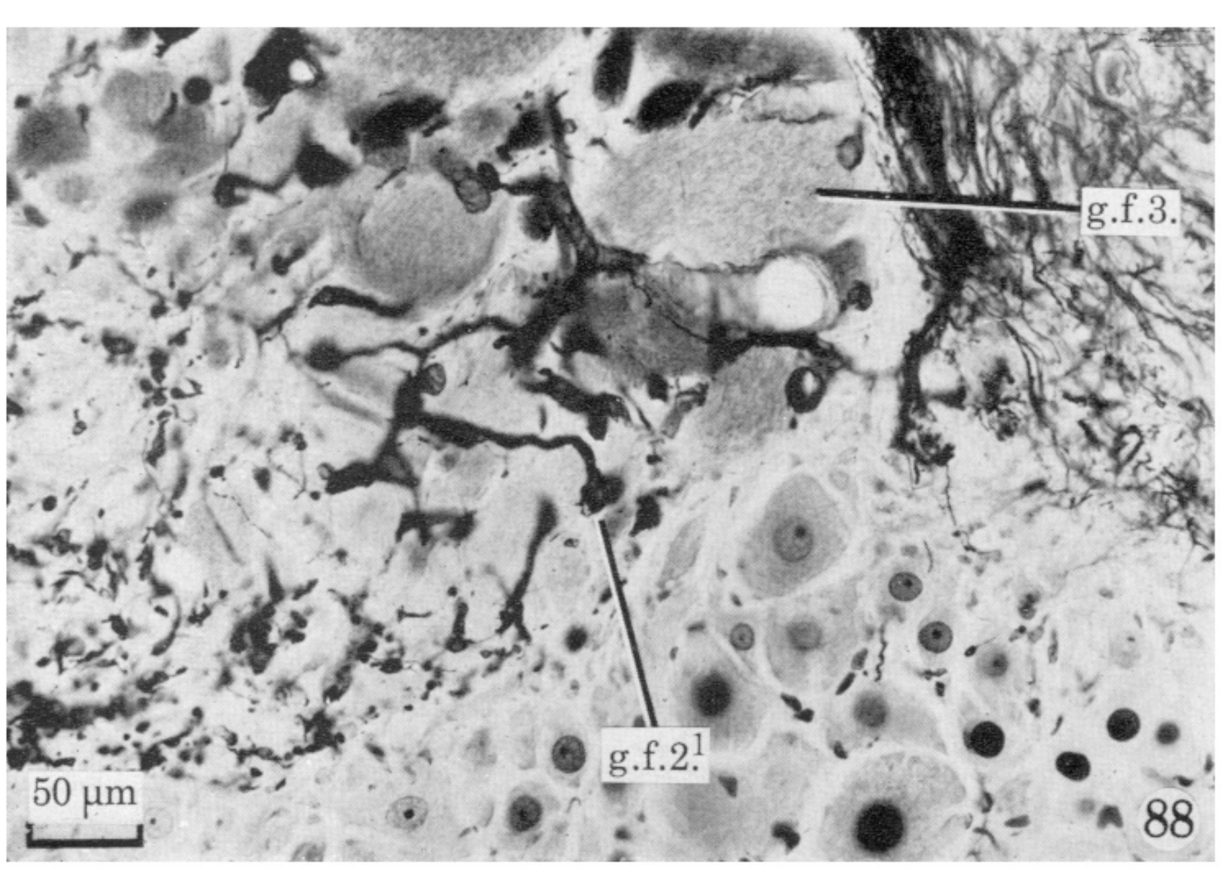


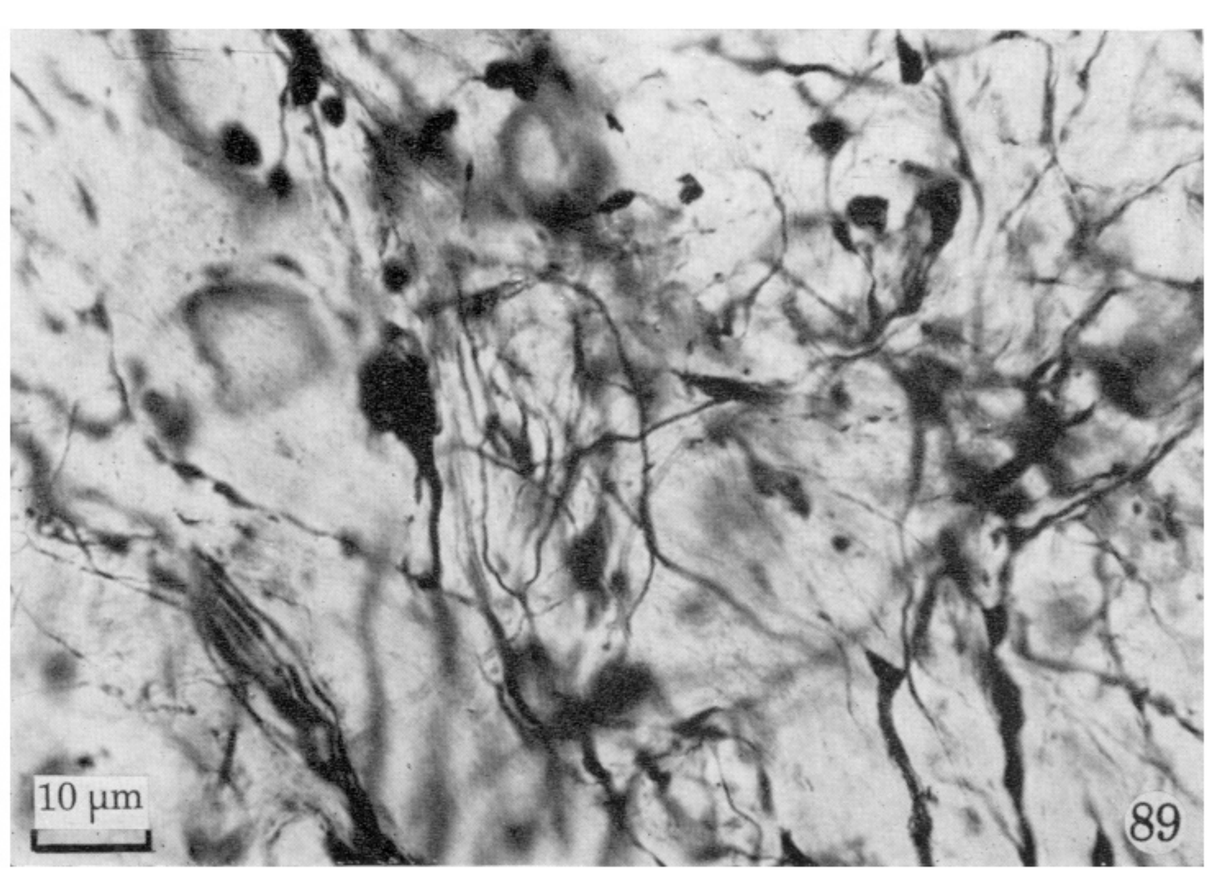












FIGURES 82 to 89. For legends see facing page