THE NERVOUS SYSTEM OF *LOLIGO*. V. THE VERTICAL LOBE COMPLEX†

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The vertical lobe system is described in *Loligo* and *Sepia*. It receives inputs from the optic lobes, arms, mouth and skin receptors. These inputs are combined and passed through a system with several superimposed loops. The output includes large neurons reaching to control centres for the arms and mantle, which initiate movements of attack or retreat. Another part of the output passes back to the optic lobes. The vertical lobe system receives no input from the statocyst and has few connections with the basal lobes.

The inferior frontal lobe allows interaction of impulses from the arms, mouth, mantle and skin. Its outputs pass to the buccal mass and arms and upwards to the superior frontal lobe. The latter has two parts comparable to those found in octopods, communicating with the vertical and subvertical lobes. The inferior and superior frontal lobes contain no microneurons with axons restricted to the lobe.

The vertical lobes are strikingly different from those of octopods. They are not divided into lobules, they have many large cells and an extensive neuropil. Numerous microneurons, with axons not leaving the lobe, arise in the peripheral parts of the vertical lobe.

The organization of the neuropil differs in the six lobes that make up the system. In the inferior frontal lobe all the inputs can influence any of the cells. In the superior frontal lobe the neuropil is layered and the topology of the optic lobes is probably preserved. In the vertical lobe large neurons are scattered throughout the neuropil among the processes of the microneurons. The subvertical and precommissural lobe neuropils allow many influences to converge on large output cells, which are also accompanied by microneurons.

1. Introduction

This highest part of the nervous system has never been described in detail for any decapod cephalopod, although its large and complicated centres are no doubt responsible for much of the behaviour of these successful animals. The gross morphology of the lobes has been described by several workers (see Bullock & Horridge 1965). The connections of some of the parts were described by Young (1938), Sanders & Young (1940) and Thore (1939, 1942). The relative proportions of the lobes in different species were described by Wirz (1959).

The present account is concerned mainly with *Loligo* and *Alloteuthis*, for which the material and methods used have been the same as in the previous papers in this series. There are certainly some differences between the vertical lobe systems of *Loligo* and the smaller form *Alloteuthis*, but these have not been systematically studied.

Some studies of fibre tracts by degeneration experiments in *Sepia* are included. The vertical lobe systems of *Sepia* and *Loligo* are remarkably similar in general organization, although differing in some details. Operations on the brain are difficult in decapods and we have had no success with *Loligo*; *Sepia* survived small operations well. The operations were done at Plymouth after anaesthesia with 1 % urethane. Incisions were made through the cartilage into the vertical lobe of one side and the animals allowed to survive for 2–3 days before fixation and staining with Cajal's silver method (Stephens 1971). Excellent evidence of degeneration was seen (figure 14, plate 2).

2. The inferior frontal lobe

2.1. *Introduction*

The most anterior supraoesophageal lobe of a decapod has been conventionally called the inferior frontal (Thore 1942). We shall keep to this usage, but analysis shows that this region is really more comparable to that called posterior buccal lobe in *Octopus* (Young 1971). The lobe called inferior frontal in the latter is strictly not present at all in decapods. However, there is an interchange system of fibres from the arms here, which may be compared to the median inferior frontal lobe of *Octopus* (p. 350).

In decapods, the paired inferior frontal lobes receive fibres from the lips and mouth, from the arms and mantle and from the vertical lobe system. They send fibres into the vertical lobe system and out to the regions that control the actions of the buccal mass and of the arms (figure 76). The neuropil contains a complicated tangle of fibres by which the inputs from the various sources are all brought together to act upon the output fibres and also to send signals upwards to the vertical lobe system.

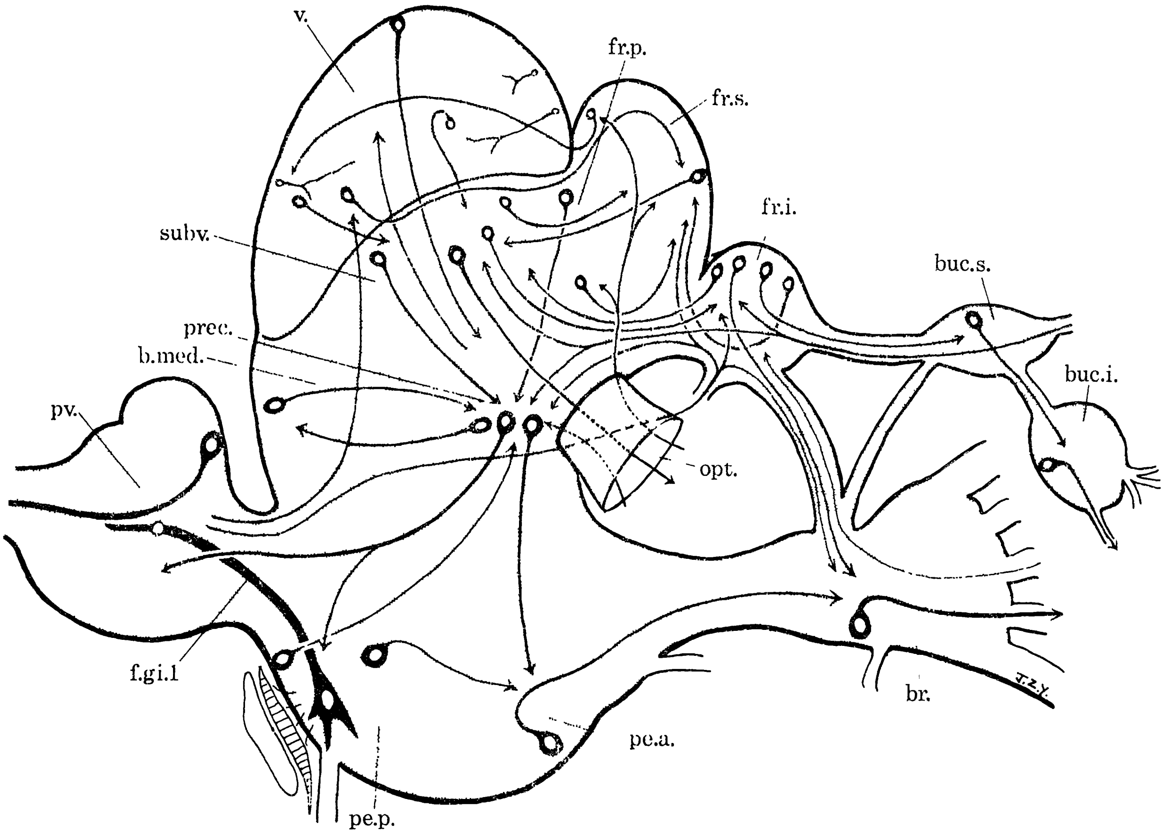


FIGURE 76. General diagram of the inputs and outputs of the tracts of the vertical lobe system of *Loligo*.

Each lobe is joined by four major trunks carrying fibres in both directions and one trunk that only carries fibres away. The four are the cerebro-brachial connective, the cerebro-buccal connective, the cerebral tract and the inferior frontal to median basal tract. The purely outgoing pathway is the inferior frontal to superior frontal lobe tract.

2.2 *Position, relations and cell types*

The inferior frontal lobes of the two sides are joined in the mid-line, where there is much interchange of fibres. The lobes occupy the lower part of the front of the supraoesophageal lobe (figure 6, plate 1). They are thus related to the oesophagus below, to the anterior basal lobe behind and below, and to the superior frontal lobe behind and above. The lobes are narrow in front but broaden out behind (figures 1 and 5). The cell walls of the lobes are uneven, thicker in front, behind and above and thinner at the sides. They contain numerous smaller cells with axons proceeding to the superior frontal lobe. Larger cells, mainly at the front and back, send axons to the brachial and buccal lobes, also some to the subvertical lobe and perhaps to the median basal lobes.

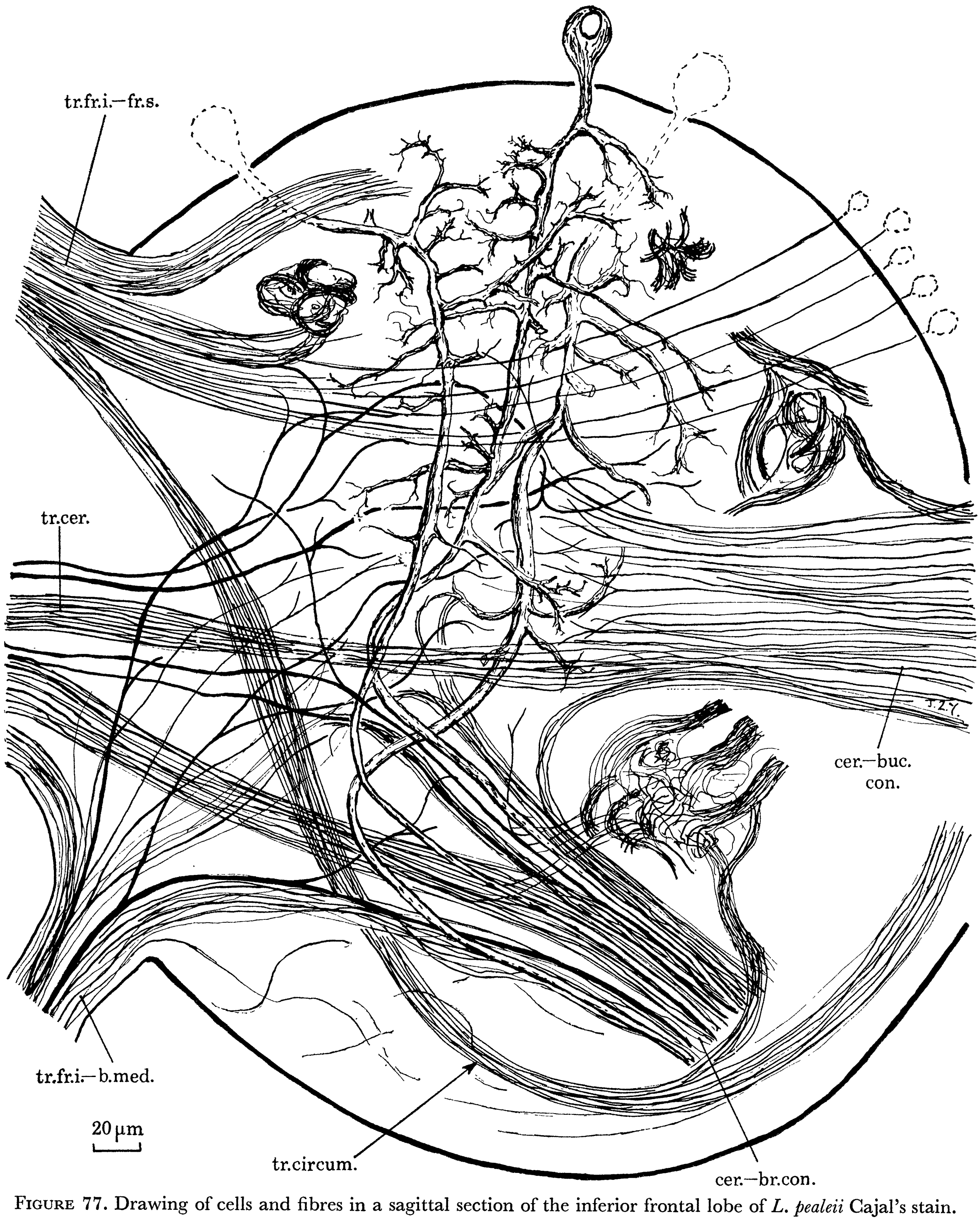


FIGURE 77. Drawing of cells and fibres in a sagittal section of the inferior frontal lobe of *L. pealeii* Cajal's stain.

At the back the walls have ten or more irregular inner layers of small cells (figure 2). They are not graded in size from the outside inwards and probably all send their axons to the superior frontal lobe. None of them seem to be microneurons† ending within the inferior frontal lobe. They are not so regular in arrangement as the cells of either of the parts of the superior frontal lobe nearby (figure 2 and figure 15, plate 2). The nuclei of these inner layers are of irregular oval outline, 5–10 μm in diameter in a young adult *L. pealeii.*

At the outside of the lobe there is a small number of much larger cells. Their nuclei are up to 15 μm in diameter with one or two large nucleoli (figure 2). The cell body measures up to 50 μm in transverse diameter and no doubt more in a large squid. These are the cells that give rise to the fibres passing mainly to the brachial and superior buccal lobes. Most of them lie in the outer part of the cell wall but some of the largest are in the middle of the cell layers and these are then pear shaped. This may be a distinct type of cell. It is not known whether the cells sending fibres to the various destinations arise in separate parts of the inferior frontal lobes.

2.3 *Input to the inferior frontal lobe*

2.3.1 *The cerebro-brachial connectives*

These connectives join the lobe from below, at the sides (figure 3). They contain some large fibres running in both directions (up to at least 15 μm in diameter) and many smaller ones. The ascending fibres are mostly small and they divide at the front of the lobe to make an elaborate plexus in the transverse plane (figures 3 and 78). This plexus of interweaving fibres has the effect of mixing the fibres from the different arms and distributing influences from each arm to a large selection of the cells of the lobe. In this respect the plexus resembles that of the median inferior frontal lobe of octopods (see p. 350).

This plexus at the front of the lobe resolves behind into a number of vaguely defined bundles, perhaps one for each arm or tentacle (figure 4). These bundles are also joined by fibres from the cerebro-buccal connectives, cerebral tracts and inferior frontal to median basal tracts. All the four sources of input to the lobe are thus joined in these plexuses. This is the gateway through which impulses from many parts of the body enter the vertical lobe system.

Some of the ascending fibres of the cerebro-brachial connective pass through the inferior frontal lobe directly to the cerebral tract and to the inferior frontal to median basal tract (figure 77). Some of these are fibres that also give branches within the inferior frontal lobe. Other fibres ascending in the cerebro-brachial connective end only in the inferior frontal lobe, giving branches and short collateral twigs throughout a wide volume (figure 78). The finer branches carry frequent swellings, often showing short terminal twigs when stained by the Golgi method.

2.3.2. *The cerebro-buccal connectives*

These connectives enter near the mid-line and many of their fibres join the plexus of fibres from the cerebro-brachial connectives (figure 1). Others pass on direct to the cerebral tract (figures 5 and 77). A small bundle joins this connective with the cerebro-brachial connective but the direction of these fibres is not known (figure 77).

† The term microneuron is used here for cells whose processes all end within the lobe in which they arise. Some of these have distinct short axons (Young 1977*a*). Those without any obvious axon are called amacrines, for instance in the vertical lobe (p. 335). The distinction is not always easy to draw microscopically but may be functionally important. Local circuit neuron is a term equivalent to microneuron.

2.3.3. *The inferior frontal to median basal lobe tracts*

Fibres in these tracts are an important means of communication between the front and back of the animal. The tracts leave the inferior frontal from behind, run down in front of the anterior basal lobe and then above the oesophagus, beneath the supraoesophageal mass (figure 9, plate 2). The tracts contain fibres running in both directions. Some of those running backwards certainly end in the median basal lobe (Young, 1977*a*). The forward-running fibres may include some from the palliovisceral lobe, perhaps afferents from the mantle.

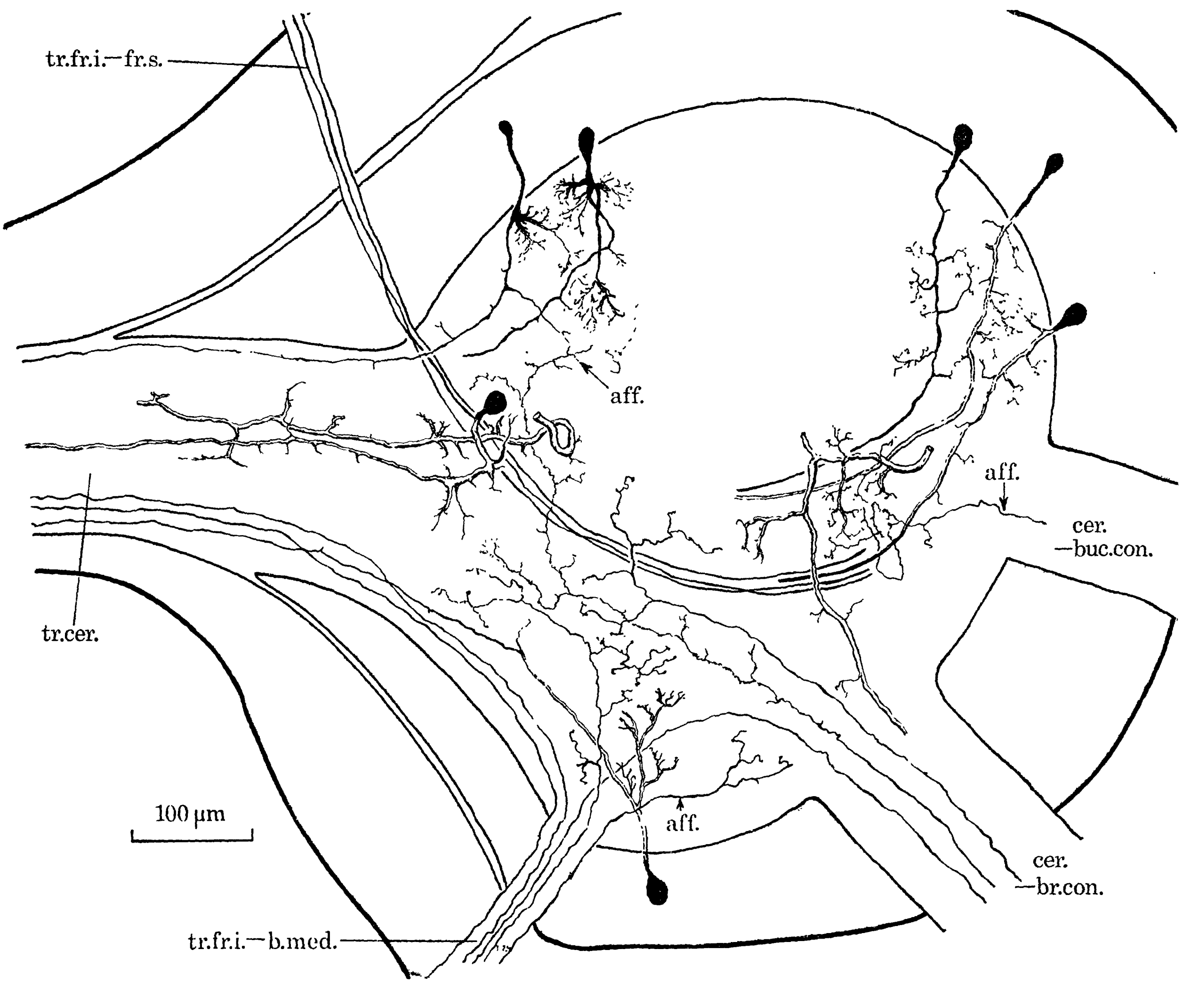


FIGURE 78. Drawing of a sagittal section of the inferior frontal lobe, showing incoming afferents, cells and fibre tracts of *L. vulgaris* (Golgi stain). Details combined from three sections 200 µm thick.

Some of these ascending fibres end within the inferior frontal lobe (figure 78). Others, also presumably ascending, turn back into the cerebral tract (figures 6, 77 and 78). A third set of these ascending fibres sends branches forward, which may reach to the brachial lobes (figure 76). In post-larval *Loligo*, about ten of them appear, all with similar distributions. Each turns forwards in an arc, giving a series of branches that pass upwards to end in the neuropil of the inferior frontal lobe. The main trunk then continues into the cerebro-brachial connective (figure 78). These large fibres thus distribute their influence both to the vertical lobe system and to the brachial ganglia. They may perhaps bring nocifensor signals from the skin of the mantle.

2.3.4. *Cerebral tracts*

Many fibres of the cerebral tracts run forward to end in the inferior frontal lobe (figures 6 and 77). These are presumably the axons of cells of the precommissural lobes (and perhaps subvertical lobes), carrying output signals from the vertical lobe system. They may thus serve as a command system to the arms and buccal mass. Their endings in the inferior frontal lobe also allow a reverse loop back into the vertical lobe system. The bundles running between the cerebral tracts and the other three input channels to the inferior frontal lobe may also contain forward running fibres but there is no direct evidence of this.

2.4 *Output of the inferior frontal lobe*

2.4.1. *Cerebro-brachial tract*

Large cells in various parts of the lobe send axons to the brachial lobes, perhaps directly to the arms. These cells have large trunks that run curved courses though the centre of the neuropil (figure 77). They collect at the ventral side and pass to the cerebro-brachial connectives. They give lateral dendritic branches at all levels, some short, others proceeding to distant regions of the lobe. These dendrites break up at their ends into very complex synaptic bushes (figures 77 and 78). Each cell must receive signals from various parts of the neuropil, perhaps from all the four inputs.

2.4.2. *Cerebro-buccal tract*

The cerebro-buccal connectives contain some large fibres presumed to be axons of large cells of the lobe. It has not been possible to show details of these cells and fibres. It is not known whether they occupy special regions of the lobes or make special connections.

2.4.3. *Inferior frontal to subvertical tract*

Some of the cells at the back of the lobe send axons to the cerebral tract (figure 78). They presumably end in the subvertical and/or precommissural lobes. This pathway can thus carry onwards signals from the combination of influences reaching the inferior frontal lobes, in addition to the fibres that pass directly to these upper lobes from the various input zones.

2.4.4. *Inferior frontal to superior frontal tract* (= *interfrontal tract*)

This is one of the main output pathways of the lobe. It is made up from bundles of the fine fibres arising from the smaller cells of all parts of the lobe (figure 78). Many of these bundles run circumferentially as conspicuous tracts round the neuropil before joining to form the inferior frontal to superior frontal tracts (figures 8 and 78).

2.4.5. *Inferior frontal to median basal tract*

The course of this tract is described on page 317 and is seen in figure 9. It was shown in a previous paper that some of its fibres end in the median basal lobe (Young 1977*a*).

2.5. *Summary of the neuropil and connections of the inferior frontal lobe*

The neuropil has an irregular tangled appearance different from that of any other part of the brain and no doubt reflecting its functions (figure 8). It allows for fibres from the arms, lips, mouth and mantle to influence the descending output cells whose axons pass to the arms and buccal mass. At the same time the smaller cells of the lobe send signals to the vertical lobe system, which in turn can influence the inferior frontal lobe cells through the subvertical lobe and cerebral tract. In spite of its small size the lobe evidently has a central part to play in the whole feeding system.

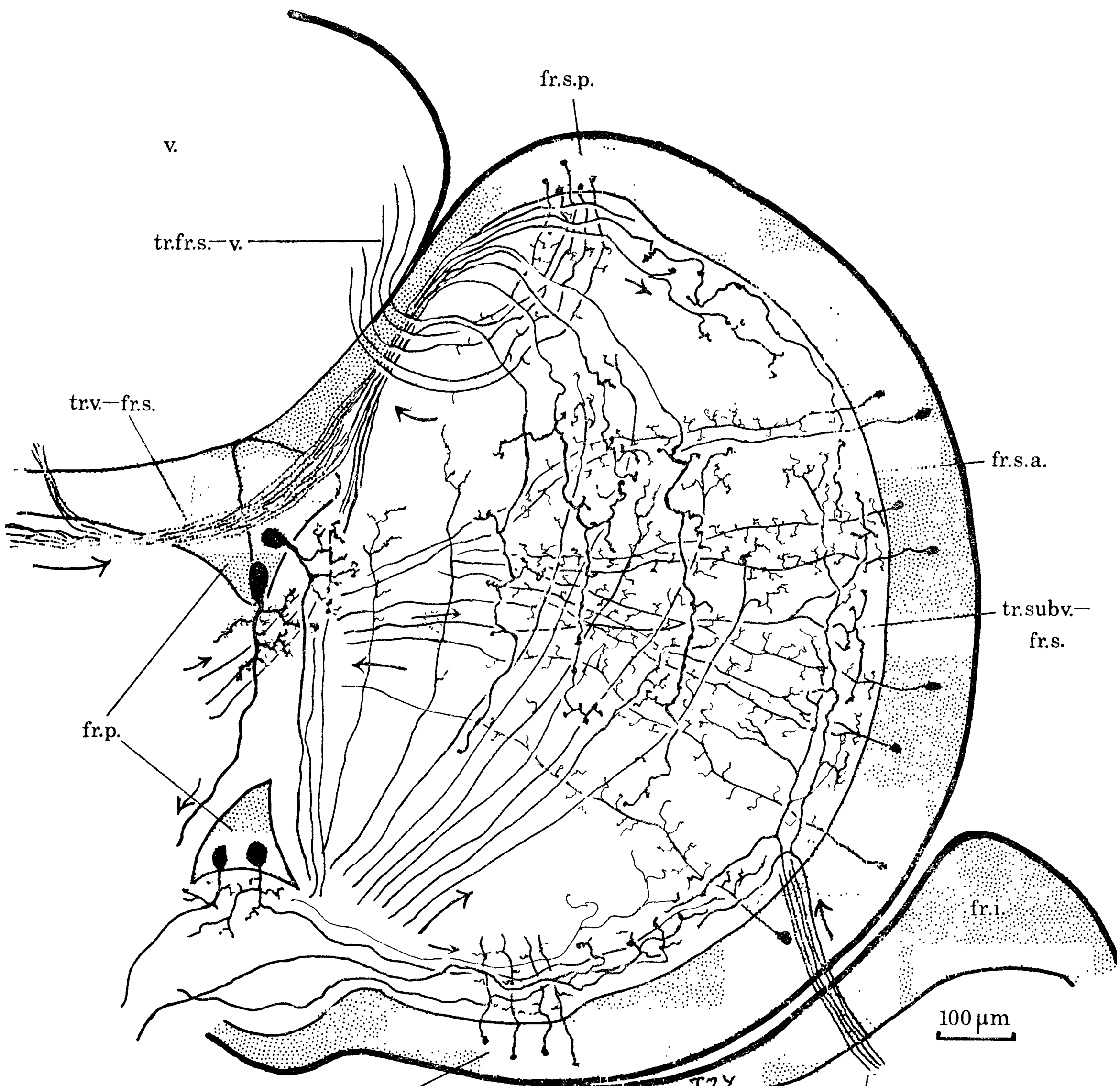


FIGURE 79. Sagittal section of the superior frontal lobe of *L. vulgaris*. Features from four thick sections are shown, somewhat diagrammatically. Arrows show the directions of conduction (Golgi stain).

There is no indication that the neuropil contains separate areas to mediate any special combinations of these inputs and outputs. Rather it has the appearance of a system arranged to allow all the inputs to influence all the outputs. It is provisionally assumed that this is the situation.

3. The superior frontal lobe

3.1. *Position and relations*

This occupies the front of the supraoesophageal mass, above the back of the inferior frontal lobe. It is related to the optic tracts laterally, to the cerebral tract and anterior basal lobe below and to the vertical and subvertical lobes behind (figures 6 and 7). Around the back of the superior frontal lobe is a ring of rather large cells and fibres, arranged as lobules, circular in sagittal section (figures 11 and 79). They will be called the postfrontal lobes and are described separately (page 327).

The cell walls and neuropil of the superior frontal lobe show two distinct parts, with different inputs and outputs. The more anterior part has larger cells and sends fibres to the subvertical lobe and perhaps beyond. The more posterior part sends all its axons to the vertical lobe. The anterior and posterior parts thus correspond to the lateral and median superior frontal lobes of *Octopus* (Young 1971). It is not possible to use those same terms for decapods because of their relative positions. The posterior part surrounds the anterior, which occupies the whole front face of the lobe in the mid-line (figure 17, plate 3).

Description of plate 1

All sections were stained by using Cajal's silver method of preparation.

Figure 1. *L. vulgaris*. Horizontal section of inferior frontal lobe, showing entrance of cerebro-brachial connectives.

Figure 2. *L. vulgaris*. Sagittal section showing back of inferior frontal lobe and the two parts of the superior frontal lobe. This specimen (*Loligo* JB) was a young individual with a mantle length of about 5 cm. The cell sizes can therefore be compared with those shown in the similar animal JA of Young (1976) which was fixed and processed at the same time.

Figure 3. *L. vulgaris*. Transverse section of the front of the inferior frontal lobe, showing interweaving dorsal bundles, comparable to the median inferior frontal lobe of octopods.

Figure 4. *L. vulgaris*. Transverse section of the inferior frontal lobe.

Figure 5. *L. vulgaris*. Horizontal section more ventrally than in figure 1.

Figure 6. *L. pealeii*. Sagittal section of inferior frontal, superior frontal and precommissural lobes.

Figure 7. *L. pealeii*. Sagittal section of the supraoesophageal lobes; showing the connections of the inferior frontal lobe.

Figure 8. *L. pealeii*. Sagittal section of the inferior frontal lobe showing bundles of fibres running circumferentially.

Description of plate 2

All of the sections were stained by using Cajal's silver method of preparation.

Figure 9. *L. pealeii*. Sagittal section of a young animal showing the whole course of the inferior frontal to median basal lobe tract.

Figure 10. *L. pealeii*. Sagittal section of the superior frontal and post-frontal lobes.

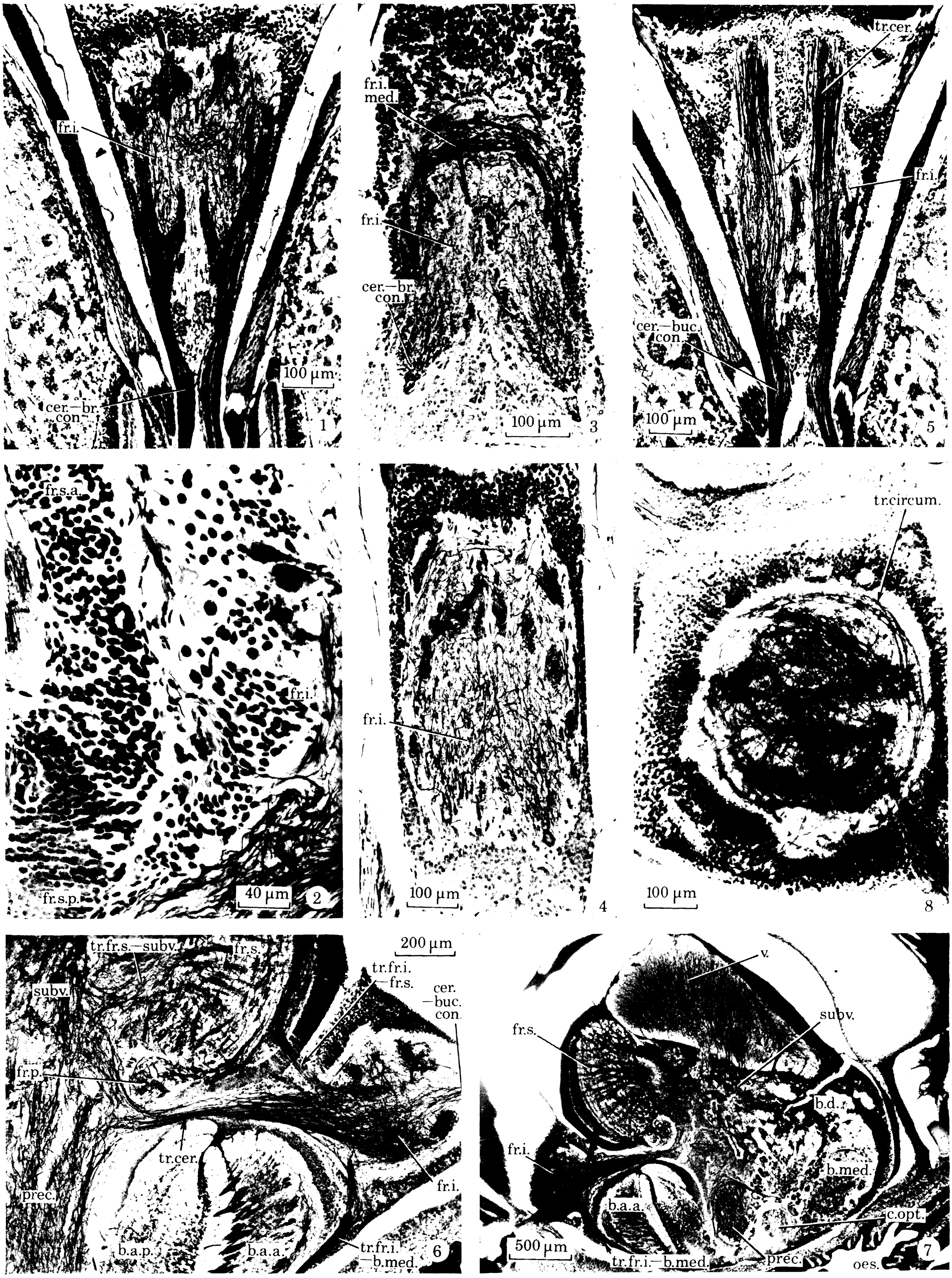
Figure 11. *Alloteuthis*. Sagittal section near mid-line, showing vertical to superior frontal lobe tract and the layer of post-frontal cells at the back of the superior frontal lobe.

Figure 12. *L. pealeii*. Transverse section of the front of the superior frontal lobe, showing the bundles of fibres entering from the inferior frontal lobe below and the vertical lobe above.

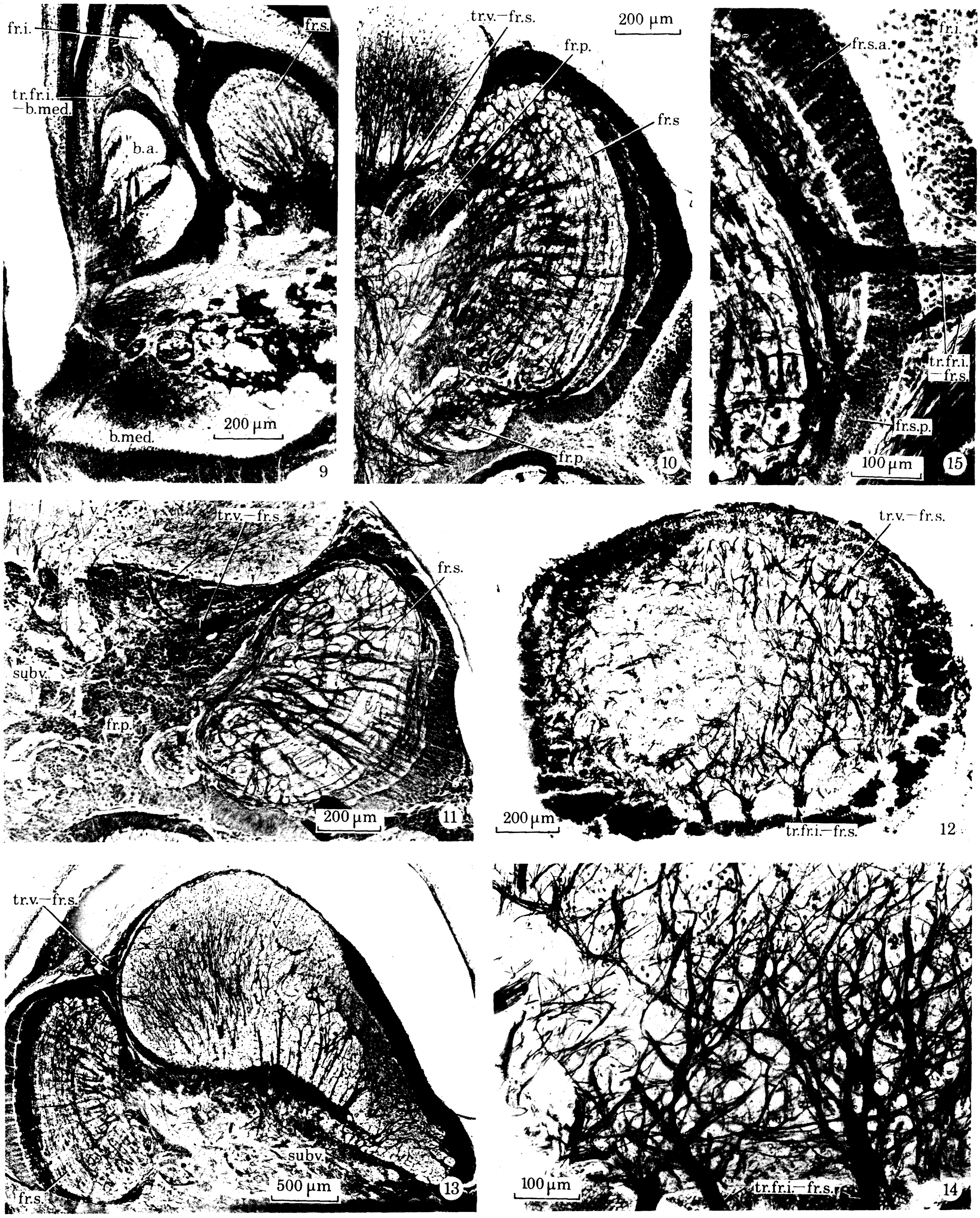
Figure 13. *Sepia officinalis*. Sagittal section showing fibres of the vertical to superior frontal lobe tract entering from above as well as from below.

Figure 14. *Sepia officinalis*. Transverse section of an animal in which the vertical lobe was damaged 42 hours previously. Degenerating fibres of the vertical to superior frontal lobe tract, entering from above, mingle with intact fibres of the inferior frontal to superior frontal lobe tract.

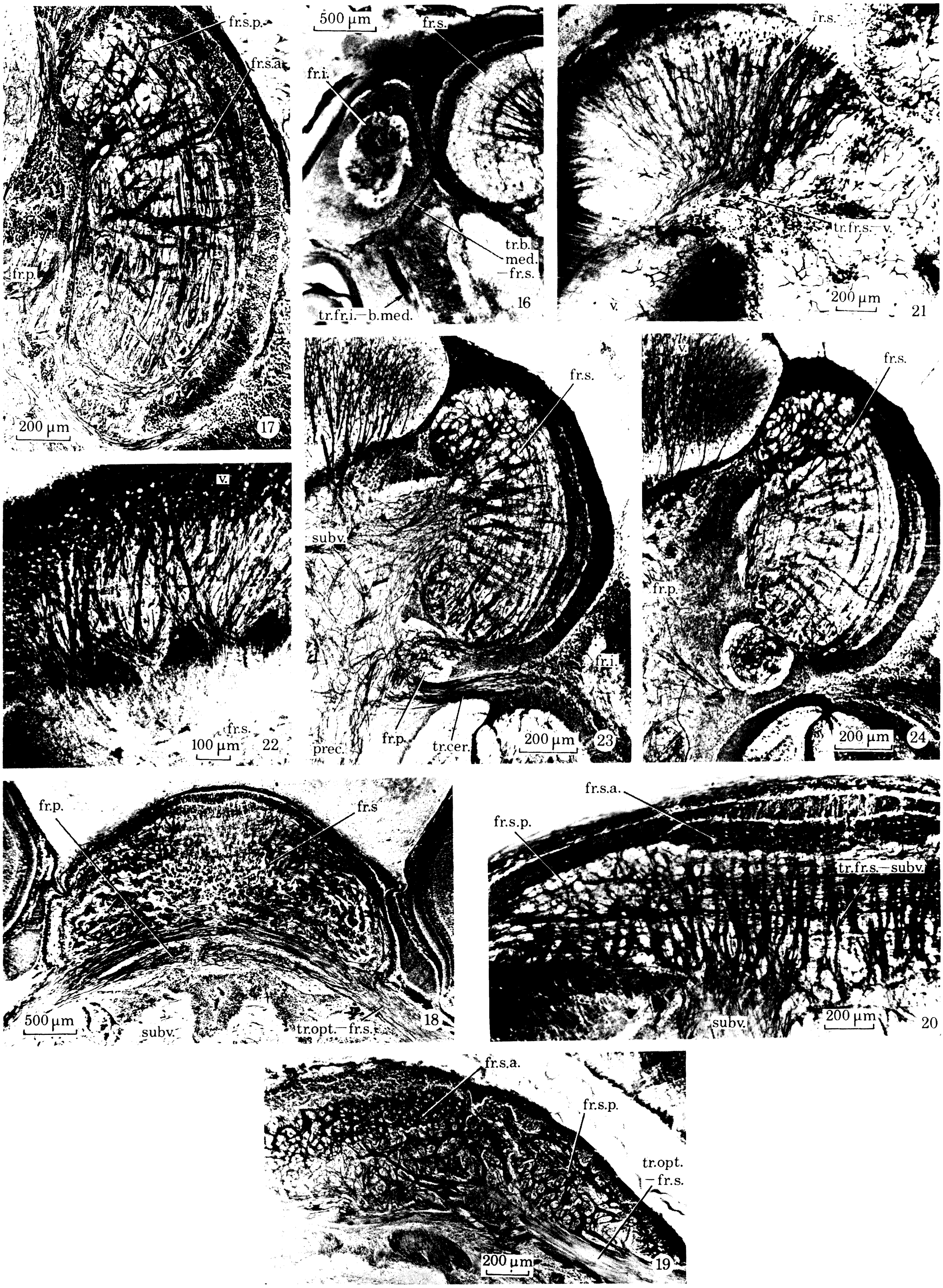
Figure 15. *L. pealeii*. Sagittal section showing the layers in the neuropil at the periphery of the superior frontal lobe.



FIGURES 1–8. For description see opposite.



FIGURES 9–15. For description see p. 320.



FIGURES 16–24. For description see p. 321.

FIGURES 25–33. For description see opposite.

3.2. *Cell types*

The cell wall of the anterior part consists of numerous densely packed layers of cells, about 10 cells deep (figure 2). The cells have round or slightly oval nuclei with diameters 10 × 5 μm (in a small adult *Loligo*). The cells do not decrease regularly in size passing inwards and some of the largest are found close to the neuropil. The nuclei have a homogeneous internal structure, with no distinct large nucleoli.

The wall of the posterior superior frontal lobe is covered by 15 or more layers of cells, smaller and more uniform than those of the anterior part, with nuclei of about 6 μm (figure 2). The boundary between the two regions is sharp. The larger size and greater variety of the cells of the anterior part is presumably reflected in the lengths of their axons, which reach to the subvertical and perhaps precommissural lobes.

The trunks of the cells of the two parts are similar. Each sends a single main fibre towards the hilum of the lobe, giving off lateral dendritic twigs that make contact with the various layers of incoming axons (figures 79 and 80). The dendrites are all rather small and short (up to 50 μm). Many are unbranched twigs but the longer ones carry a few terminal branches. The

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Description of plate 3

Except where otherwise stated, all sections were stained by using Cajal's silver method of preparation.

Figure 16. *Sepia officinalis*. Sagittal section showing fibres of the median basal to superior frontal lobe tract.

Figure 17. *L. vulgaris*. Sagittal section showing the two sorts of neuropil of the superior frontal lobe and the cells of the post-frontal lobe.

Figure 18. *Sepia officinalis*. Horizontal section showing fibres of the optic tracts joining the superior frontal and post-frontal lobes.

Figure 19. *L. vulgaris*. Transverse section showing the optic tract fibres joining the two sorts of neuropil of the superior frontal lobe.

Figure 20. *Sepia officinalis*. Horizontal section showing the two parts of the superior frontal lobe and the superior frontal to subvertical lobe tracts.

Figure 21. *L. vulgaris*. Sagittal section of fibres of the superior frontal to vertical lobe tract (Golgi stain).

Figure 22. *Sepia officinalis*. Transverse section of the front of the vertical lobe showing the interweaving fibres of the superior frontal to vertical lobe tract.

Figure 23. *L. pealeii*. Sagittal section showing superior frontal to subvertical and precommissural lobe tracts.

Figure 24. *L. pealeii*. Section medial to figure 23, showing layer of post-frontal cells lying behind the superior frontal in the mid line.

Description of plate 4

Except where otherwise stated, sections were stained by using Cajal's silver method of preparation.

Figure 25. *Sepia officinalis*. Transverse section showing the ventral part of the post-frontal lobe.

Figure 26. *L. pealeii*. Transverse section showing the vertical and subvertical lobes.

Figure 27. *L. pealeii*. Sagittal section showing two parts of the vertical lobe.

Figure 28. *L. vulgaris*. Horizontal section showing the superior frontal, vertical and subvertical lobes.

Figure 29. *L. vulgaris*. Sagittal section showing cells of the peripheral vertical lobe.

Figure 30. *L. vulgaris*. Sagittal section at the back of the vertical lobe showing cells and two sorts of neuropil.

Figure 31. *L. vulgaris*. Dendrites of the large cells of the vertical lobe and terminations of afferent fibres entering from below (Golgi stain).

Figure 32. *L. pealeii*. Sagittal section of the centre of the vertical lobe showing the loops of the dendritic collaterals of the large cells.

Figure 33*a*, *b*. *L. vulgaris*. Terminations of the dendritic collaterals of the large cells (Golgi stain).

dendrites continue to the centre of the lobe, becoming shorter more peripherally. Each cell thus samples a cylinder of neuropil up to 100 μm in diameter extending through the various input layers. The lack of widespreading dendrites suggests that each cell receives a distinct specific combination of inputs. There may be differences in the number of dendritic branches, some cells may have fewer than are shown in figures 79 and 80.

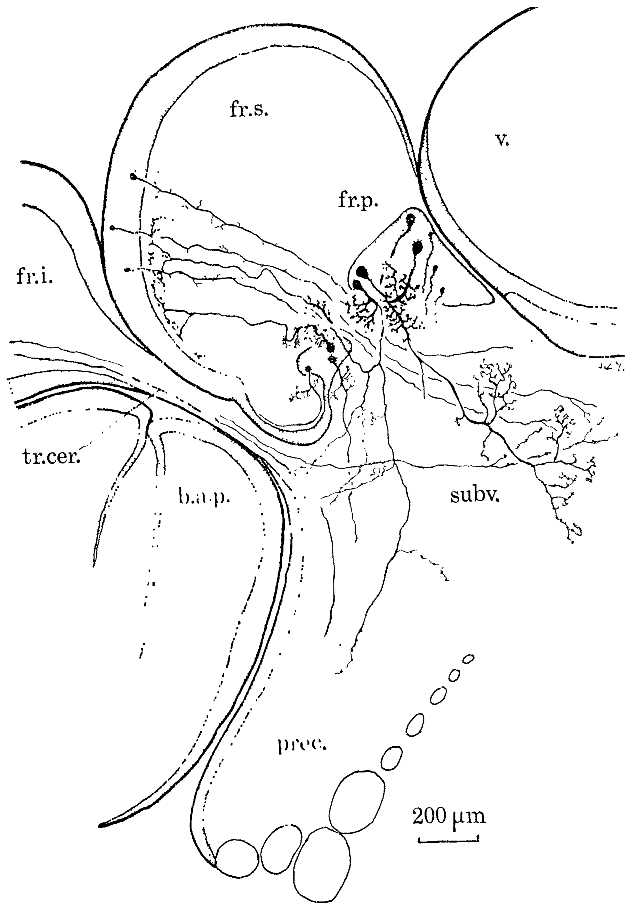


FIGURE 80. Sagittal section showing cells of the post-frontal lobe of *L. vulgaris* (Golgi stain).

3.3. *Input to the superior frontal lobe*

The organization of the neuropil is basically similar in the two parts of the lobe but shows some differences. Both parts receive large optic inputs, the differences are in the relative contributions of the influences from the inferior frontal, vertical, subvertical and post-frontal lobes. Fibres from these latter four sources run round tangential to the surface, across the backward running trunks of the cells of the lobe. They thus make a series of layers as seen in sagittal section (figure 10, plate 2). They will be described beginning at the periphery.

3.3.1. *The vertical to superior frontal tract*

The outermost layer of the neuropil nearest to the cell bodies is composed of fibres of the vertical to superior frontal lobe tract. In *Loligo* and *Alloteuthis* these fibres leave below the vertical lobe and enter the superior frontal from above as a series of bundles (figures 11 and 79). They spread out and interweave, passing downwards to reach to all parts of the lobe (figures 79, 81 and 83). Many of the fibres remain close to the cell layer but others turn in to the centre of the lobe, making conspicuous tracts of darkly staining fibres. In *Sepia* this tract consists of two parts. Some fibres run forward over the dorsal surface of the vertical lobe, whereas the major part leaves, as in *Loligo*, from below (figure 13). The fibres of this tract can be seen in *Sepia* in degeneration after a lesion to the vertical lobe (figures 12 and 14). They interweave in an elaborate manner, forming a plexus partly superficial to the network of fibres of the inferior frontal to superior frontal tract, although fibres of the two sets may run in the same bundles (figure 14). In *Octopus*, degeneration experiments showed that the majority of the fibres of the corresponding tract end near the cell layer of the lateral superior frontal lobe (Young 1971). In decapods there is a similar situation. The degeneration seen in figure 14 does not extend into the posterior part of the superior frontal lobe, which corresponds to the median superior frontal lobe of *Octopus*. The absence of fibres from the vertical lobe in this posterior part explains the difference in appearance of the outer band of fibres in the two parts of the superior frontal lobe (figures 10, 15 and 20). Thus the posterior superior frontal lobe sends fibres to the vertical lobe but does not receive from it. The anterior superior frontal receives fibres from the vertical lobe but does not send any to it (see page 352).

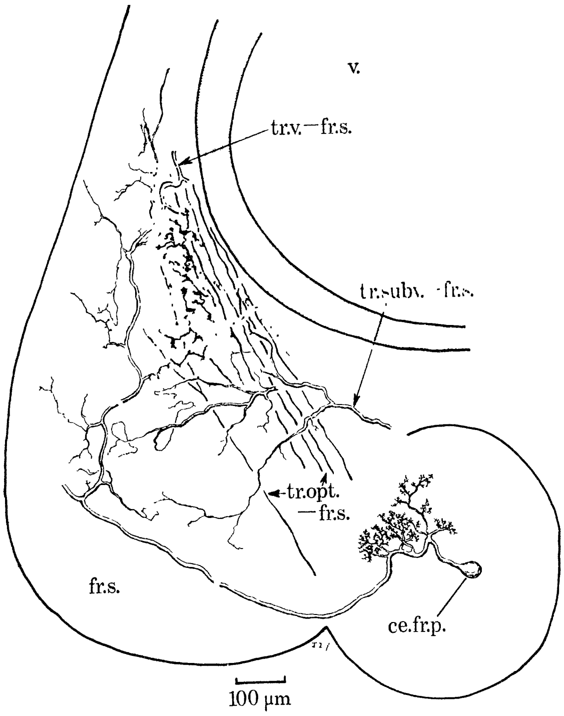


FIGURE 81. Sagittal section of *L. vulgaris* showing a single cell of the ventral post-frontal lobe sending its axon to the superior frontal lobe. Also fibres of the vertical and subvertical to superior frontal lobe tracts (Golgi stain).

The bundles of the vertical to superior frontal tract make a complex plexus, probably allowing fibres from any one part of the vertical lobe to reach back to any part of the anterior superior frontal and vice versa (figure 12). These fibres are characteristically stained black in the Cajal preparations. In Golgi preparations most of them can be seen to run circumferentially round the lobe, some in to its centre (figure 79). Many of them are relatively thick (2–3 μm) and they give repeated branches forming an elaborate mesh, especially close to the surface of the neuropil. These terminal branches carry repeated swellings, some covered with minute spines that are probably synaptic (figure 81). The branches turn and twist following a generally downward direction. Although the main part of the plexus is at the surface, similar endings are also found deeper in the neuropil and some degeneration was also seen there after vertical lobe lesions in *Sepia*. In *Octopus* the corresponding degeneration was mostly limited to the outer region of the neuropil.

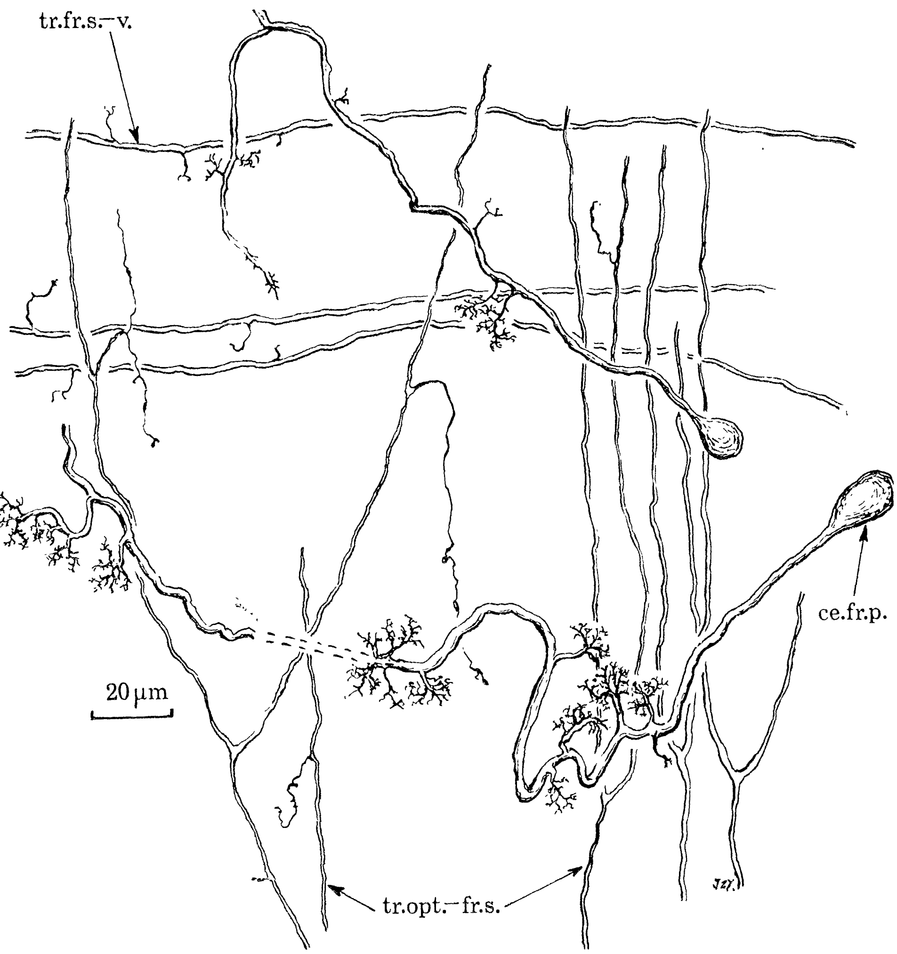


FIGURE 82. Sagittal section of superior frontal lobe of *L. vulgaris* showing the optic tract input fibres and two cells of the post-frontal lobe with axons running to the superior frontal lobe (Golgi stain).

3.3.2. *The inferior frontal to superior frontal (interfrontal) tracts*

The fibres running from the inferior frontal to the superior frontal lobe enter from below and pass around central to those of the previous tract (figure 15). They reach over the whole surface of the lobe making a plexus that probably gives full opportunity for fibres from cells of all parts of the inferior frontal lobe to reach to any part of both sections of the superior frontal lobe (figures 12 and 14). This tract is also joined by a small bundle of ascending fibres from the inferior frontal to median basal tract (figure 16). These may come from the pallio-visceral lobe or beyond, bringing signals from the hinder part of the body directly to the vertical lobe system, perhaps including nociceptive (pain) signals.

The fibres of the interfrontal tract divide as they enter the lobe, one branch running to the anterior superior frontal and the other to the posterior part (figures 15 and 79). They then proceed to divide further and give short collateral branches with small swellings and terminal synaptic spines. The terminations of these fibres form less complex networks than those of the vertical to superior frontal tracts and the swellings on them are smaller. Some branches from these fibres proceed in to the centre of the lobe.

3.3.3. *Subvertical and post-frontal to superior frontal tracts*

These are probably distinct systems but they are difficult to separate. The main bulk of the fibres enters from below, forming the third layer beneath the surface of the lobe (figures 10 and 15). They divide and form endings over the whole surface of the lobe (figure 79). Some of these are the axons of cells of the post-frontal lobe (figure 81). Fibres from the subvertical lobe enter not only from below but also at the hilum of the lobe and from above (figures 79 and 81). This last set joins the vertical to superior frontal tract and is accompanied by fibres that run from the post-frontal across the hilum of the lobe (figures 17 and 79).

3.3.4. *Optic to superior frontal tract*

The fibres from the optic lobes enter by three pathways (figure 18). Those for the anterior division form large bundles passing towards the mid-line, from which smaller bundles separate (figure 19). These make a conspicuous set when seen in cross sections, the bundles of fibres being usually more lightly stained with silver than others in the lobe.

The fibres for the posterior division of the lobe enter as a series of separate bundles at the front of the optic tract (figure 18). Although the two parts receive distinct bundles, it has not been decided whether or not individual fibres reach to both. The optic fibres make ten or more partly distinct layers running across the centre of the lobe. There is much interweaving between the bundles, as has been confirmed by the degenerating fibres after section of the optic tract in *Sepia*.

The individual fibres of the optic to superior frontal lobe tract mostly run for long distances within the lobe without dividing. They give only a few collateral twigs, but the details of the final terminations have not been seen satisfactorily (figures 81–83). Each fibre probably influences a considerable volume of neuropil.

The third source of optic input to the superior frontal lobe is through the post-frontal lobe which receives a direct set of fibres from the optic tract (figure 18). However, fibres from these bundles probably also reach forward to the superior frontal lobe itself.

3.4. *Output of the superior frontal lobe*

3.4.1. *Superior frontal to vertical lobe tract*

The trunks of the cells leave the cell layers in rather compact bundles and these proceed radially towards the hilum (figures 21 and 22). On the way, the bundles interchange fibres and at the hilum there are elaborate plexuses. The outputs of the anterior and posterior divisions are probably quite distinct. The fibres of the superior frontal to vertical tract certainly arise mainly, and probably wholly, from the posterior division. It is difficult to be certain that the anterior division does not contribute any fibres to this tract, but it is assumed not to do so. The interweaving bundles of the superior frontal to vertical tract are the most lateral output from the lobe. They pass upwards and backwards over the surface of the vertical lobe, just within the cell layer (figure 21 and figure 27, plate 4). They interweave in a further plexus as they pass back, reaching to the extreme hind end of the vertical lobe (figure 28). This tract is thus similar to the median superior frontal to vertical lobe tract of octopods (Young 1971).

3.4.2. *Superior frontal to subvertical and post-frontal lobe tracts*

The output of the anterior superior frontal lobe proceeds to the subvertical lobe and neighbouring regions (figures 20 and 23). These tracts lie medial to the superior frontal to vertical tracts. Their endings are described on page 342. Some fibres also pass to the post-frontal lobe (figure 23).

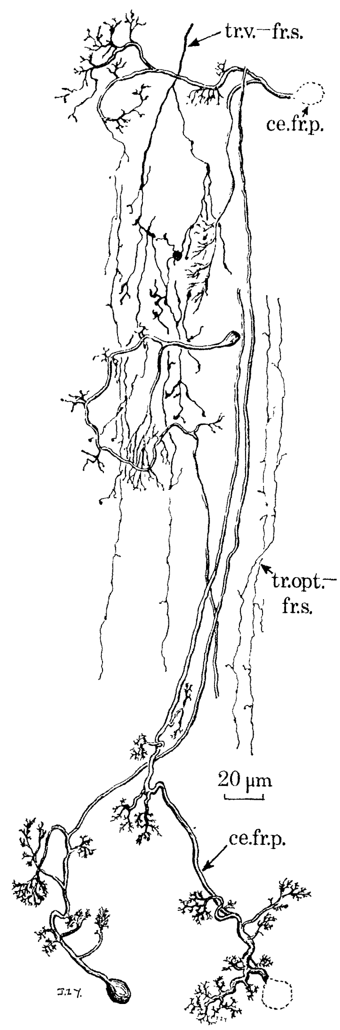


FIGURE 83. Sagittal section of post-frontal region of *L. vulgaris* showing cells above and below with trunks going in opposite directions (Golgi stain).

3.4.3. *Superior frontal to precommissural lobe tract*

Many fibres pass down towards the cerebral tract and precommissural region (figure 23, and figure 65, plate 7). They appear to be descending fibres but it is difficult to be sure of their direction (without degeneration experiments) or whether they end in the precommissural lobe or reach to the suboesophageal lobes.

These output fibres of the anterior superior frontal region form simple plexuses while still within the superior frontal neuropil, but not after they have left it. The arrangements for mixing are perhaps less complete than in the superior frontal to vertical tract. There is indeed a difference between the neuropils of the anterior and posterior divisions of the lobe. The former shows a more regular arrangement of tangential input fibres and radial output ones. The posterior superior frontal region contains more irregular interweaving bundles (e.g. figures 19 and 20).

4. The post-frontal lobe

4.1. *Position and cell types*

This is a set of cells grouped around the hilum of the superior frontal lobe. Some of the cells are large and have characteristic bushy dendrites not seen either in the superior frontal lobe itself or in the subvertical lobe nearby (figures 80–83). We may consider this ring of cells in three parts.

1. Ventrally, below the back of the superior frontal lobe, there is a distinct separate lobule of outer cells and central neuropil (figures 24 and 25). Its cells are larger than those of the superior frontal lobe and more nearly resemble those of the precommissural lobe, with which it is continuous below (figures 57 and 65, plate 7). Most of the cells have nuclei of about 10 μm diameter, but some have large oval ones (20×30 μm). These large cells have the characteristic bushy dendrites and some of them send an axon forwards to break up in the plexus near the surface of the superior frontal lobe (figures 80 and 81). Others send a fibre down to divide up into terminal branches in the precommissural lobe (figure 79, 80, 95 and 98).

2. In the mid-line, the cells of the walls of this inferior part of the post frontal lobe are continuous with a sheet of cells extending up between the superior frontal and subvertical lobes (figure 24). These cells are similar to those of the inferior lobule and some of them have bushy dendrites and an axon proceeding forwards to the superior frontal lobe.

3. Over the dorsal margin of the superior frontal to subvertical tracts lies a group of large and small cells. The larger ones have bushy dendrites some of which extend forwards, radially into the superior frontal lobe (figures 79 and 83). They presumably receive synapses from the optic and other input sources. The axons of these cells pass downwards to spread widely in the subvertical and perhaps precommissural lobes (figure 98).

These post-frontal cells around the back of the superior frontal lobe thus seem to collect influences by dendrites extending among the fibres passing between the superior frontal lobe and the subvertical lobe. The cells then distribute their axons widely, some forwards to the superior frontal lobe, others back to the subvertical lobe or down to the precommissural lobe. A group of large cells in this position has also been recognized in *Octopus* (Barlow 1971), but their connections were not reported.

4.2. *Connections of the post-frontal lobes*

The inferior post-frontal lobule exchanges bundles of fibres with the neuropil of the neighbouring regions. The direction of these fibres is not known but they include (*a*) an optic to post-frontal tract (figure 18); (*b*) a subvertical to post-frontal tract, perhaps including connections with the vertical lobe; (*c*) a post-frontal to precommissural tract (figure 65, plate 7); (*d*) an inferior frontal to post-frontal tract and (*e*) a superior frontal to post-frontal tract. These connections are mostly shown in figure 23. It is not known whether the upper parts of the post-frontal region are also connected with these other regions.

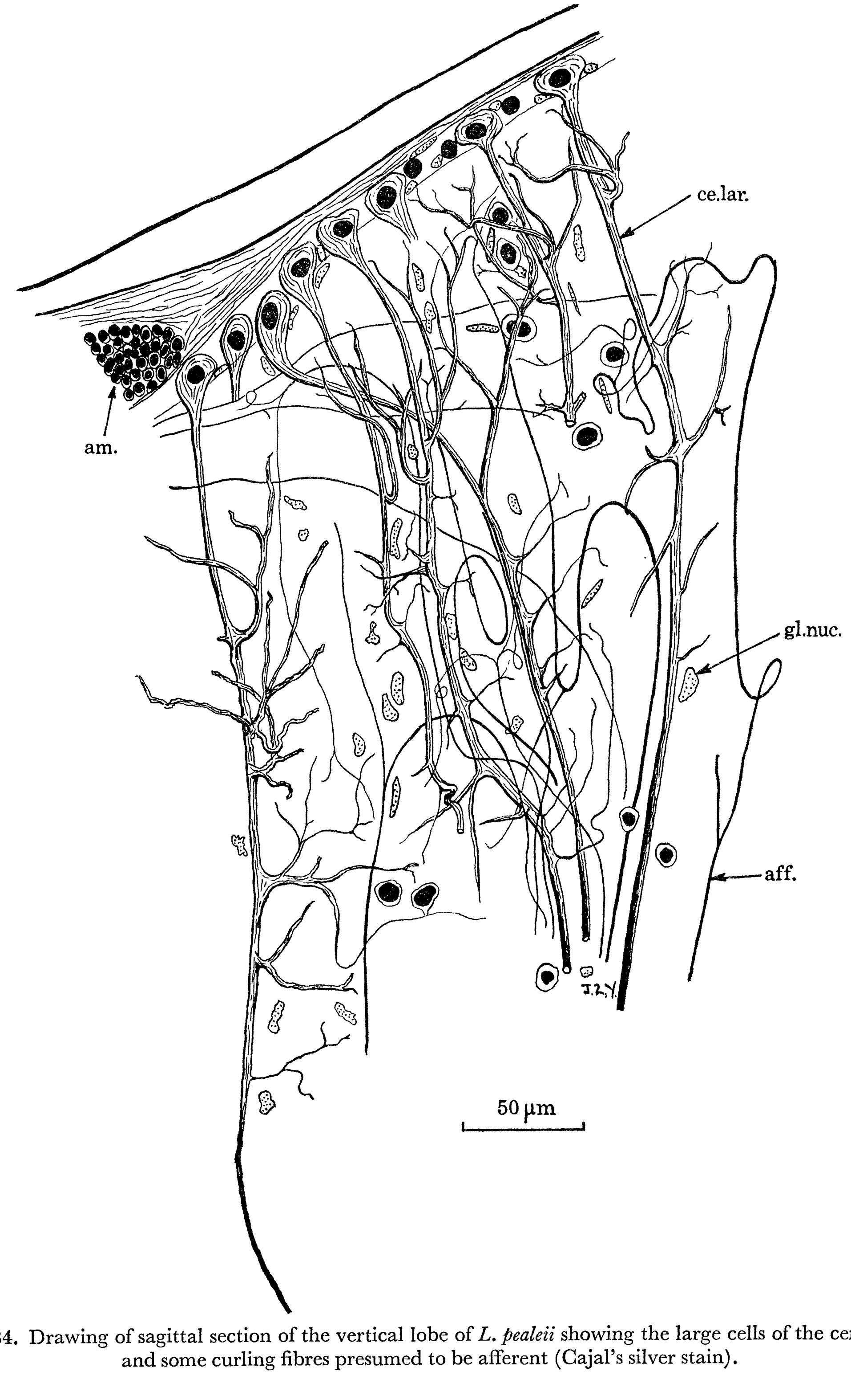


FIGURE 84. Drawing of sagittal section of the vertical lobe of *L. pealeii* showing the large cells of the central zone and some curling fibres presumed to be afferent (Cajal's silver stain).

5. The vertical lobe

5.1. *Position and relations*

The vertical lobe is a conspicuous paired, dome shaped structure at the top of the brain (figures 26, 27 and 28). Each half consists of two parts with different structures, yet with the neuropils widely continuous and probably forming one functional whole. The peripheral vertical lobe has a thick cell wall including many small amacrine cells and a few large cells.

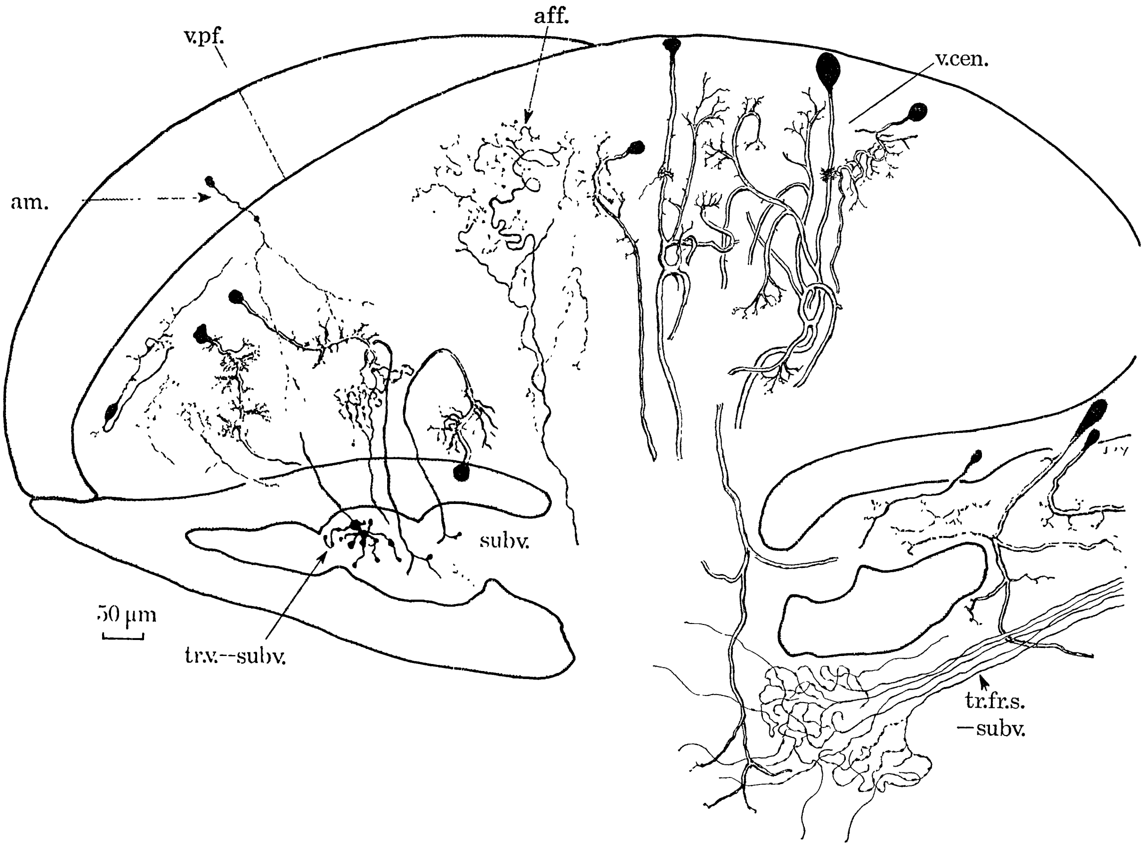


Figure 85. Drawing of the vertical and subvertical lobes of *L. vulgaris* showing the various types of cells and fibres (Golgi stain).

There are a few neurons scattered throughout its neuropil. It receives the superior frontal to vertical lobe tract and also an input of fibres from below. The central vertical lobe occupies the whole middle part of the dome. It has only a very thin outer cell layer composed of a single row of very large cells (figures 27, 84 and 85). Its centre is filled with a mass of neuropil among which many further medium and large neurons are dispersed. This central neuropil receives processes from the small amacrine neurons of the peripheral region. In addition, it receives afferent fibres from below, but probably none directly from the superior frontal lobe. The 'central' type of tissue continues posteriorly beneath the peripheral zone (figure 27). The two parts are here separated by a row of large cells that is continuous with the thin layer covering the top of the dome (figure 30). There is also an extension of the central type of tissue down to the base of the lobe close to the mid-line on each side (figure 26 and figures 55 and 56, plate 6).

The whole vertical lobe of each side is related to the subvertical lobe below, which itself has two main parts, anterior and posterior (page 340). The only other relation of the vertical lobe to nervous tissues is with the superior frontal lobe anteriorly. The upper surface is close to the cranial cartilage, from which it is only separated by a venous sinus (figure 55, plate 6).

5.2. *Distribution of cells in the vertical lobe*

The lobe contains three main types of cells, (*a*) large cells round the edge, whose trunks pass down through the neuropil to give axons running to relatively distant destinations in the superior frontal and subvertical lobes; (*b*) smaller cells mainly scattered throughout the neuropil, whose axons end in the upper part of the subvertical lobe; and (*c*) amacrine cells, with axons restricted to the vertical lobe. The structure of the two parts shows sharp differences. The cell layer of the peripheral part consists of a thick outer mass composed mostly of uniform small cells, 25 or more layers deep (figure 29). Their nuclei are about 5 μm in diameter and stain uniformly in the Cajal preparations, without conspicuous nucleoli. There is no gradation in size with depth, in fact they are a typical homogeneous population of amacrine microneurons. Their trunks pass into the neuropil of both parts of the lobe, but probably none of them proceed beyond it (page 335).

There are some larger cells in this peripheral part of the lobe, both within the cell layers, in the outer part of the neuropil and also within it (figure 29). The nuclei of some are round, up to 10 μm in diameter and with several nucleoli. Other nuclei, especially of the neurons lying in the neuropil, are oval in shape and up to 12×5 μm in size. The axons of these large cells proceed to the subvertical lobe and constitute the only direct output of the peripheral vertical lobe other than to the central part.

There are relatively few glial nuclei in the cell layers and neuropil of the peripheral vertical lobe. The glial cells are very large and each of them presumably serves a large territory, but their nuclei are small (figure 84 and page 339).

In the central part of the vertical lobe neurons are scattered throughout its whole extent. There is thus no sharp division between neuropil and cell layers – a most unusual condition for an invertebrate animal. The cells are of two types. There is a single layer of very large cells round the edge, with nuclei of various shapes and up to 16 μm in diameter (figure 84). The cell body may be 25 μm or more in transverse diameter. The cells at the centre of the lobe are mostly smaller. They are distributed quite uniformly through all parts (figures 34 and 35, plate 5). There is also a layer of large cells along the lower edge of the lobe (figure 86).

5.3. *Structure of the cells of the vertical lobe*

5.3.1. *The largest cells of the central zone*

The large cells of the central region have a very interesting and characteristic structure, with extensive branched, curving dendritic trunks (figures 85–87). The first part of the trunk is smooth and the first dendrites may take the form of a small tuft of numerous, fine collaterals, sometimes attached to a coarser stem (figure 87). Somewhat more distally the main trunk branches, giving thick collaterals at right angles, from which further branches then arise. These run in various directions and angles (figure 31). Some are recurrent and reach nearly to the surface. Others curve in remarkable loops, sometimes down to the base of the lobe, and then back upon themselves (figures 86 and 87). Branching is usually dichotomous but otherwise very irregular. Sometimes the two products are of equal size and length. Distances between branches are also very irregular. The branches are themselves large and have a mainly smooth surface, and are therefore presumably not synaptic. Many proceed for long distances in various directions. They often make large regular curves, giving the neuropil a very characteristic appearance (figures 32 and 84).

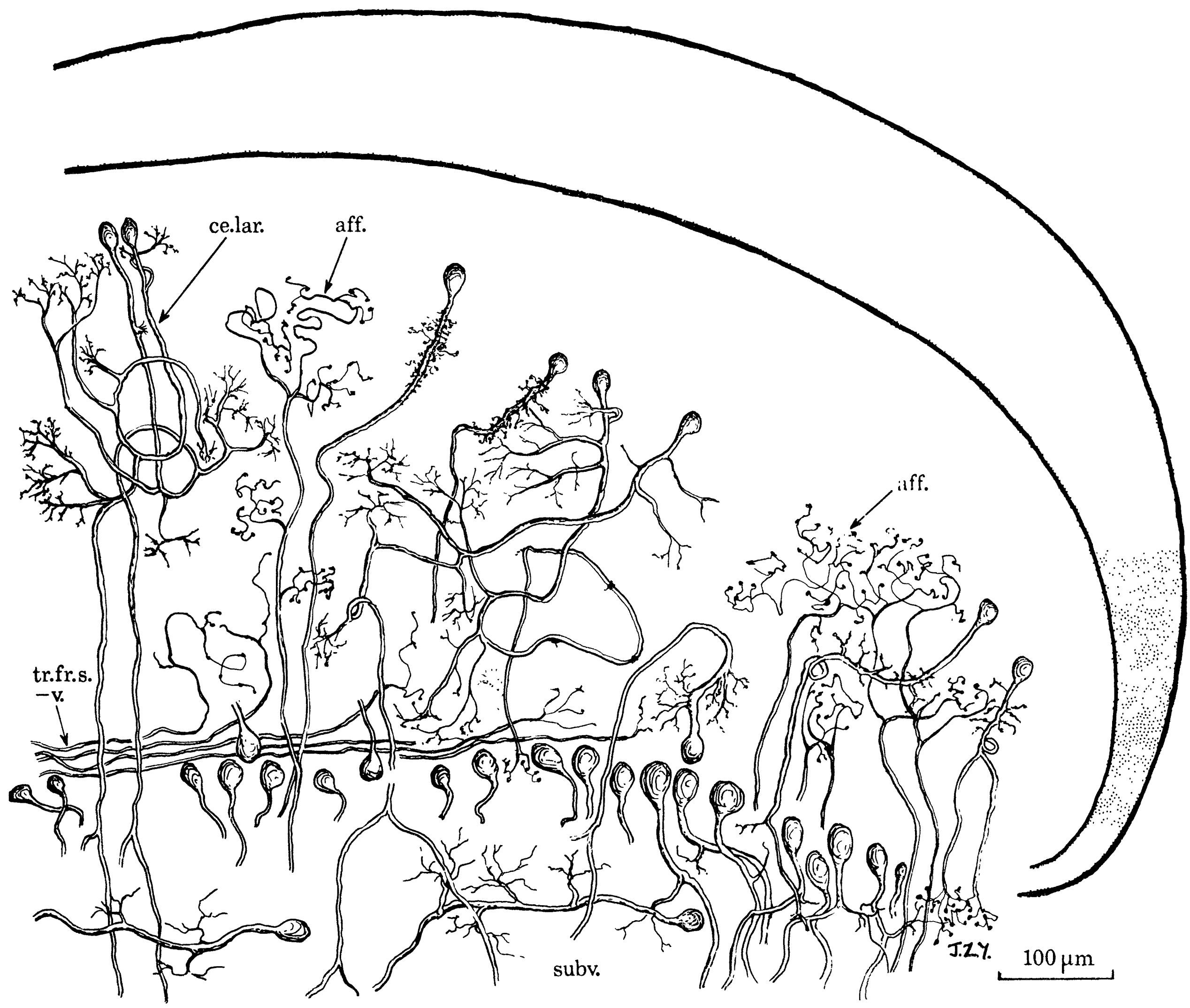


FIGURE 86. Drawing of sagittal section of back part of the vertical and subvertical lobes of *L. vulgaris* showing cells and fibres (Golgi stain).

Each dendritic trunk branches several times and finally ends in rather localized synaptic tufts (figures 33*a*, *b* and 87). These are formed by repeated further branching but the resulting minor trunks are mostly straight. They have few swellings and are not pitted. They make a few small lateral twigs, presumably synaptic, and finally taper to thin points without terminal swellings. They thus differ sharply from the dendrites of the inner and peripheral cells of this region (page 333). They seem to provide for localized collection of influence from a number of widely dispersed areas. Moreover, the influence must be produced by relatively small areas of synaptic contact. This is unexpected in view of the large diameter of the parent trunks. Although the terminal dendritic branches are straight, the afferents entering from below are as much curled here as elsewhere in the lobe (page 338). The main trunks of these large cells eventually pass through the cell layer to reach the subvertical lobe. They may either break up there or turn forwards to the superior frontal lobe. It has not been possible to follow the axons of individual cells to decide whether they branch in the subvertical lobe *as well as* proceeding to the superior frontal lobe. The details of the branches within the subvertical lobe are considered later (pages 342, 344).

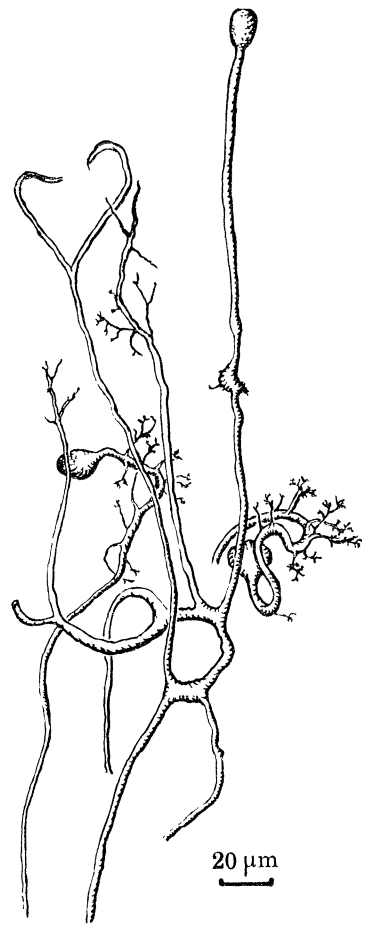


FIGURE 87. Drawing of two types of large cell of the vertical lobe of *L. vulgaris* showing endings of the dendrites (Golgi stain).

5.3.2. *Other cells of the central zone*

The numerous neurons with cell bodies within the central mass of the central area have dendrites very different from those of the large outer cells (figures 34, 35 and 87). Here the initial unbranched trunk is short. The branches occupy a relatively short length of the main trunk and proceed much less far from it than do the branches of the large cells. The dendrites thus occupy a restricted volume close to the cell body. The thick, main trunks of the dendrites are relatively little-branched, but are varicose, with many spines attached to the swellings. They end without any special terminal branching. They may arise from the cell body, at more than one point (figure 37). The main trunk of the cell often proceeds upwards for a short distance and then forms a loop and passes downwards. There may be more than one axon passing to the subvertical lobe (figure 86). Other cells in this neuropil have dendrites of yet another type, extending over a longer stretch of the main trunk (figures 38, 89 and 90). The part of the trunk that carries dendrites is roughened by thousands of small indentations and protrusions, presumably occupied by incoming terminals. At irregular intervals along the length of the trunk, branches of very varied diameter and length are given off. Many are tiny spines, each capped with a knob, others are longer trunks with many bifurcations and secondary twigs. These secondary trunks are also pitted and may have swellings along their length. All the branches end in minute terminal knobs; these are often rather more lightly stained than the parent trunk in Golgi preparations.

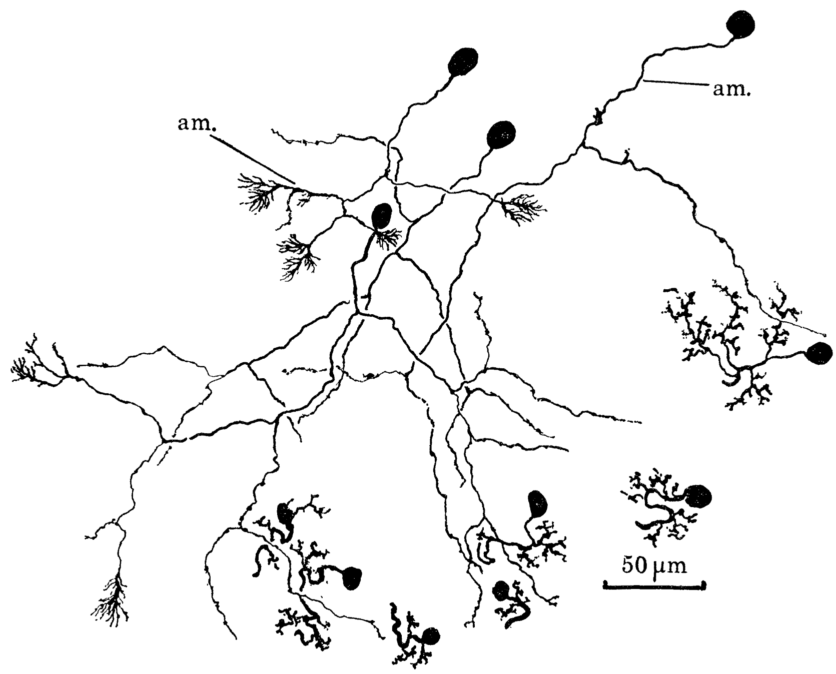


FIGURE 88. Drawing of amacrine cells and some other cells in the neuropil of the vertical lobe of *Alloteuthis*. Note the endings of the amacrine cells (Golgi stain).

Beyond the last of the dendritic branches, the trunk becomes quite smooth (figures 89 and 90). This difference clearly shows that the roughness and indentations are significant features at the synaptic level. The axon curves around upon itself as it gives its branches, but the branches themselves do not curve. The axon finally reaches the subvertical lobe, but details of its further course are unknown.

5.3.3. *Larger cells of the peripheral zone*

These cells are not as large as the largest cells of the central zone; they have dendritic branches which spread less widely through the neuropil (figures 39 and 85). These branches end in fine swellings (figure 40). The cells are less branched than the large cells in the central zone and they thus collect from a smaller volume. Branches begin close to the cell body. Some of the earlier branches are numerous fine threads, making a sort of bush. Those further down often come off at right angles (but not always). Each has relatively few major branches, but many minor ones; there are often small swellings along them. The dendritic distribution is relatively limited, both along the trunk and laterally. The trunk may twist in a complete rather tight loop before it finally proceeds to the posterior subvertical lobe and breaks up there into rather coarse terminal branches of somewhat limited extent (figure 91).

The cells lying along the ventral surface of the vertical lobe are similar to the smaller cells of the peripheral zone and have short dendrites. Their trunks proceed upwards towards the centre of the neuropil and then turn sharply downwards to the subvertical lobe (figures 89 and 90). They give numerous lateral dendritic branches, usually at right angles to the trunk and dividing at once into minor branches, often carrying small swellings. They thus have the same limited dendritic spread as the other medium sized cells of the vertical lobe. The finest branches are multiple sprays of twigs, carrying swellings but often tapered at the tips. In addition to these multiple dendrites, the trunks give off single short lateral branches.

5.3.4. *Bipolar cells*

At the back of the peripheral part of the lobe there are some bipolar cells, just within the neuropil (figure 85). The destination of their axons is not known.

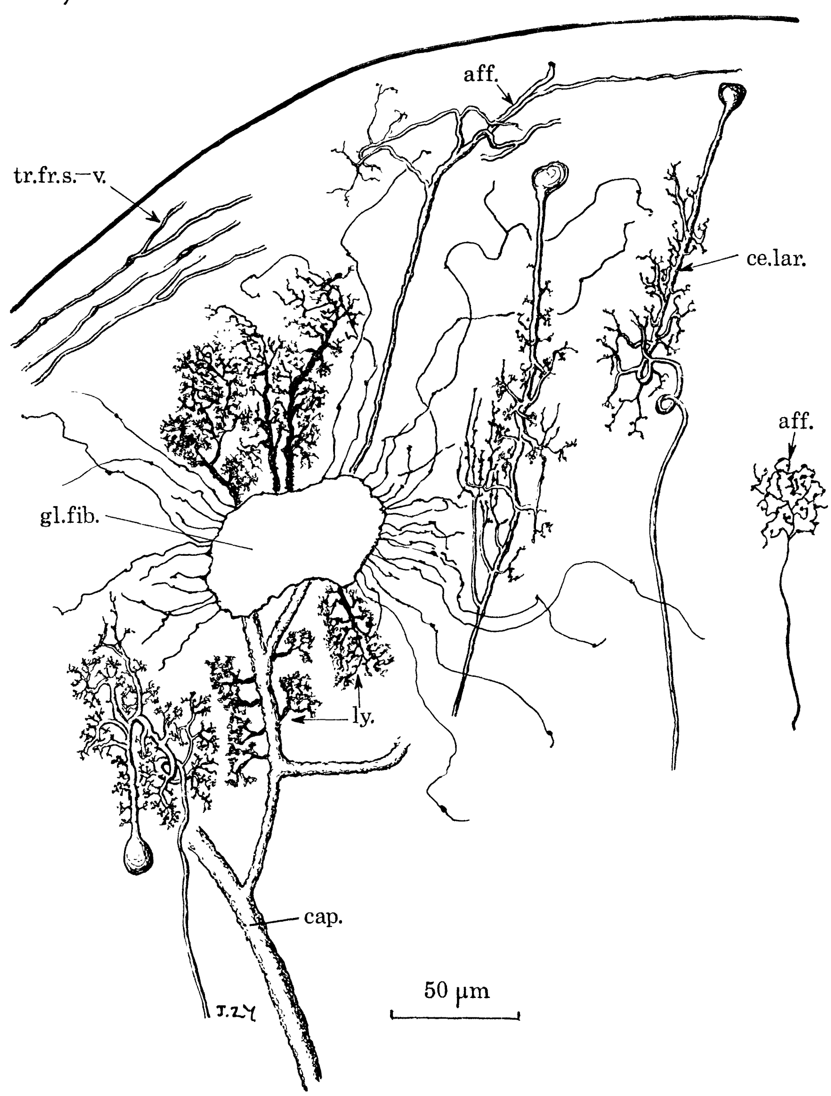
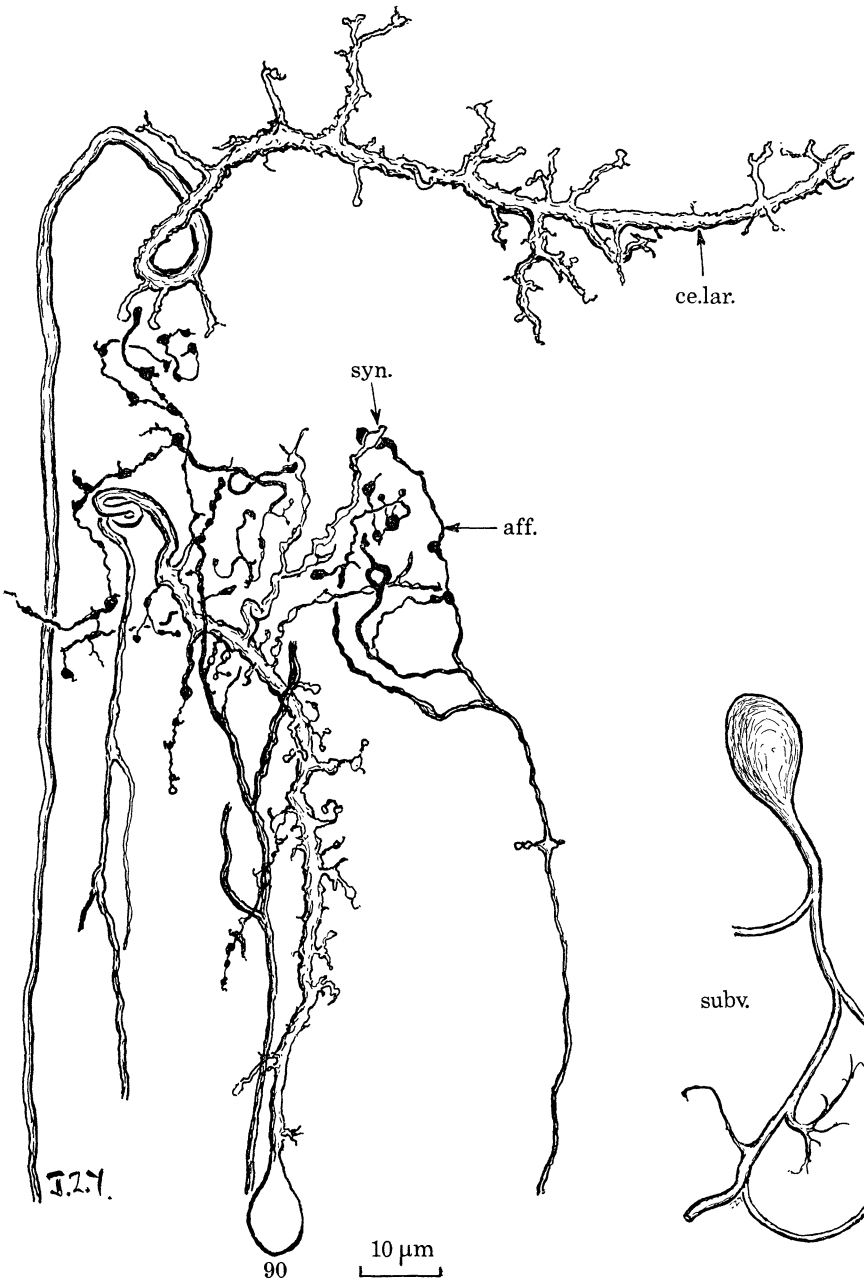


FIGURE 89. Drawing of sagittal section of the vertical lobe of *L. vulgaris* showing a glia cell, large neurons with short dendrites, a capillary, and branching 'lymphoid spaces' (Golgi stain).

5.3.5. *Amacrine cells and the peripheral neuropil*

These are not easy to study because when they do stain in Golgi preparations, large numbers often stain together along with the glia fibres, which are closely similar. The peripheral neuropil is largely made up of processes of the amacrine cells. Their fine interweaving trunks give it a characteristic appearance both with Cajal and Golgi stains (figures 30 and 36).



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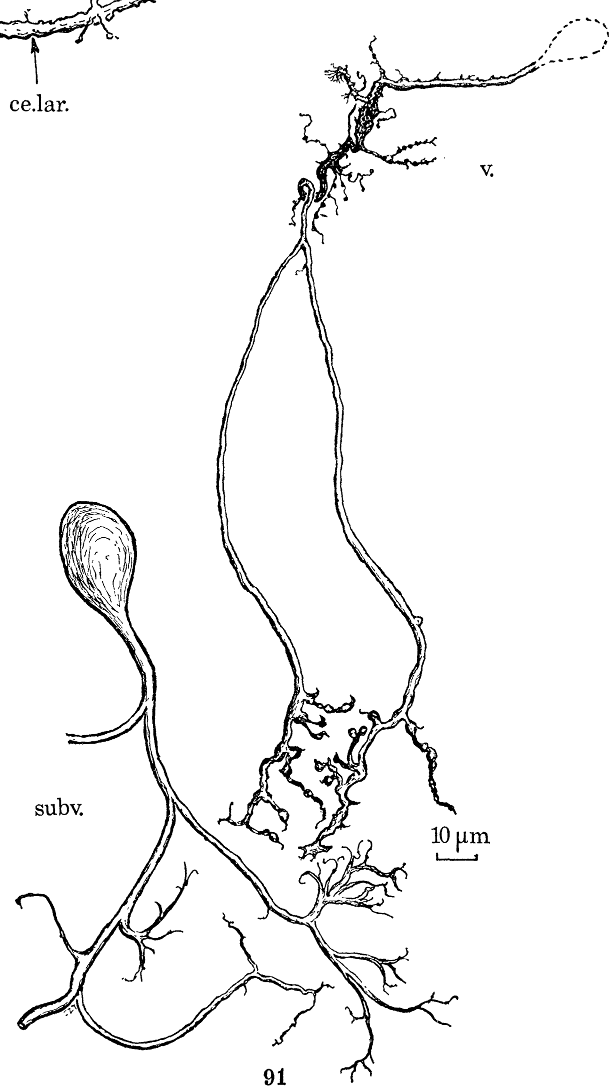

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FIGURE 90. Drawing from sagittal section of vertical lobe of *L. vulgaris* showing short dendrites of a large cell making contact with endings of an afferent fibre entering from below (Golgi stain).

FIGURE 91. Drawing from a sagittal section of *L. vulgaris* showing cell with short dendrites in the vertical lobe and its two axonal trunks ending near the dendrites of a subvei tical lobe cell (Golgi stain).

Shortly after entering the neuropil, each trunk carries a swelling (figures 42 and 92). These come into relation with corresponding swellings on the fibres of the superior frontal to vertical tract. The amacrine swellings have several indentations and small projections and those of the fibres of the tract show several short branches. Each amacrine usually carries only one swelling at this level but may have two. It is therefore perhaps stimulated only by a single incoming fibre. Some of them, however, have roughened main stems, as if perhaps they are in contact with many incoming fibres (figure 43).

Passing towards the centre of the neuropil the amacrine trunks have a smooth outline, but with distinct swellings at intervals. They branch, sometimes quite early, but not very frequently (figures 88 and 92). Towards the ends they give collateral dendritic branches and finally taper to terminal twigs. The ends may be slightly dilated compared to the main trunk and carry a brush of some 20 or more fine terminal twigs (figures 44 and 93). Each of these twigs carries only minute granules, and often tapers away beyond the limit of resolution. No branches of these cells have ever been seen to leave the lobe.

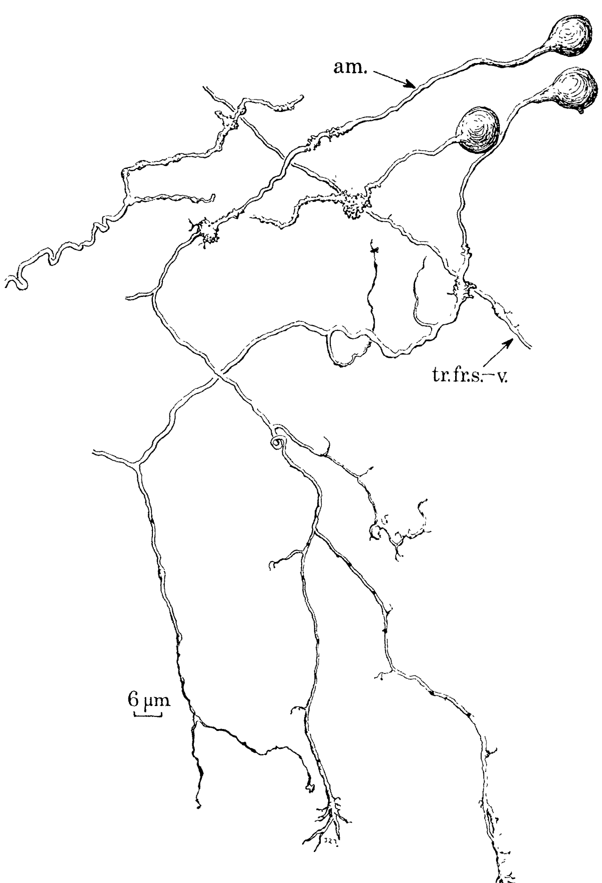

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FIGURE 92. Drawing of sagittal section showing the whole course of two amacrine cells of the vertical lobe of *L. vulgaris*. Note the proximal swellings and fine branching terminals (Golgi stain).

FIGURE 93. Detail of one of the terminals of an amacrine cell seen in figure 92.

The amacrine trunks run in a generally radial direction towards the centre of the lobe. But they proceed irregularly, crossing each other and not forming obvious bundles. Some of them terminate after one or two hundred micrometres, others run for considerable distances (figure 94). They make a dense network throughout the neuropil, interwoven with the dendritic branches of the larger cells of the lobe and with many glia fibres. The latter, like the amacrine trunks, have a smooth outline with swellings. Presumably they actually accompany the amacrine trunks and are complementary to them. It is remarkable that there are two systems including so many long fibres, running approximately straight. The glia fibres are mostly rather thicker than the amacrines, but not sufficiently so to allow the two sorts to be distinguished for certain unless they are followed to the cell body (figures 45, 89). Other long fibres of a class different from any of those yet described, have been seen running close to the surface of the lobe (figure 48). They may be the trunks of the bipolar cells (figure 85).

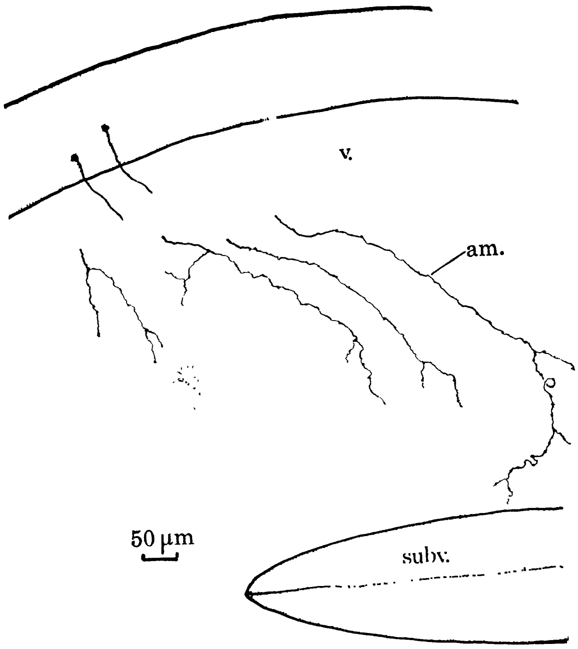


FIGURE 94. Drawing of horizontal section of vertical lobe of *Alloteuthis* to show the great length of some of the amacrine trunks (Golgi stain).

5.4. *Output of the vertical lobe*

The whole output of the vertical lobe goes either to the superior frontal or to the subvertical lobe.

5.4.1. *Vertical to superior frontal tract*

The fibres of this tract arise from all parts of the lobe (figures 10, 11 and 13); they pass through the layer of cells at the base of the lobe and turn forward (figure 79). It is not clear that they arise from any type of cells different from that of the vertical to subvertical tract. Some of them certainly come from cells of the more peripheral parts of the lobe. Their courses in the superior frontal lobe are described on page 322.

5.4.2. *Vertical to subvertical tract*

These fibres also arise from all parts of the lobe and may accompany those of the other tract as they pass through the cell layers. Some of the fibres of the vertical to subvertical tract break up as soon as they have left the vertical lobe, others proceed further. Their endings are described on page 342.

5.5. *Input to the vertical lobe*

5.5.1. *Superior frontal to vertical tract*

The superior frontal to vertical tract enters at the front and runs all round the peripheral part of the lobe immediately central to the layers of small cells (figure 46). The tract does not continue over the central part of the vertical lobe and probably none of its fibres reach there. It is likely therefore that all the connections of this tract are made with the amacrine cells of the peripheral zone. The individual fibres, seen with the light microscope, run with only occasional branching (figure 47). The side branches may terminate in knobs. There are swellings at intervals along the fibres, which are thus making synaptic contacts as they pass (figures 89 and 92). The major knobs occur, however, only at rather long intervals (figure 48). It is difficult to know which of them are true synaptic points, but those that carry small collaterals almost certainly are.

5.5.2. *Subvertical to vertical tract*

The second input to the lobe comes, as in *Octopus*, from below. These fibres show particularly well in Golgi preparations. They constitute the only input to the central zone (except indirectly through the amacrine cells). They run straight up into the central zone, beginning to branch shortly after entering (figures 85 and 86). Dichotomous branching continues right to the top of the lobe. The distances between branch points, and the lengths of the daughter branches, are very irregular. Branches may be much finer than the parent trunk and quickly taper to a fine varicose ending, perhaps with little branching. Or, if they are rather larger, they may diverge, branch again and send fibres up and down to occupy a wide volume. There are occasional lateral twigs, ending without further branching. On the other hand the major trunks often run for considerable distances without dividing and then burst into characteristic terminal formations (figures 49 and 50). These terminations are produced by repeated dichotomous branching at decreasing intervals. The daughter branches, at first, are mostly equal in diameter and length but short collaterals may be formed, especially towards the ends. As they approach the synaptic region of the cells the fibres begin to carry both collateral branches and swellings along their length (figures 51 and 52). There is good evidence that synaptic contacts are made both *en passage* and terminally. The swellings along the lengths of the fibre often carry minute collateral twigs, usually rather faintly stained, and similar twigs are found at the ends of the branches. These terminals are complementary in size and shape to the depressions and branches of the dendrites of the cells of the lobe (page 333). In a few places the two have been seen locked together (figure 90).

The difficulty in interpreting these situations is to distinguish between the two partners. The swellings on the incoming fibres are mostly larger than those on the dendrites, but the difference is not great enough to allow positive identification in doubtful cases. The afferents branch and curl in such a way as to provide potential contacts in large compact regions of neuropil. There is some evidence that any one afferent contacts more than one vertical lobe cell and *vice versa* (figure 90).

It is not easy to unravel the detailed course of the fibres in these terminal nets. The fibres sometimes divide and reunite again to make rings and quite long closed loops are perhaps present. Certainly the majority of the branches finally terminate freely. It may be that the appearance of closed loops is only a result of the remarkable winding courses, which often lead the fibres to cross themselves.

Each incoming fibre thus seems to deliver its major effect to a small number of rather localized zones, but these zones are not all together. Since the large cells of the lobe have such wide dendrites it is difficult to decide whether any one incoming fibre influences one or several large cells – probably several. Conversely, each large cell is almost certainly influenced by more than one afferent, since the branching of the afferents is less profuse than that of the dendrites. Some of these afferents have been seen at the extreme periphery of the neuropil very close to the incoming fibres of the superior frontal to vertical lobe tract (figure 53).

The source of these afferents entering from below is not known. Most of them come up through the subvertical lobe and they may include afferents from the mouth region or arms via the cerebral tracts or from the hinder part of the body. A few afferents seem to enter the vertical lobe from in front, perhaps from the large post-frontal cells (figure 86). The finest endings of these resemble those of the fibres entering from below (figure 52).

5.5.3. *Other endings in the vertical lobe*

Other forms of afferent fibre reach the lobe. Thick fibres run up to the surface from the subvertical lobe giving off fine lateral twigs (figure 89). Some of these reach to the peripheral zone where they branch forming a few rather coarse endings (figure 54). These have been seen only at the back of the lobe. It is uncertain whether they will be found mingled with endings of the superior frontal to vertical lobe tract.

5.6. *Blood vessels and glia of the vertical lobe*

The blood supply reaches the lobe from below. Arterioles come off at right angles from the arteries and after further division, the capillaries rejoin at more acute angles. The venules discharge into sinuses over the surface.

The tissues are drained by a system of lymph channels similar to that described for *Octopus* (figure 89) (Young 1971). The detailed form of these is not certain. Gliovascular cells also occur in the vertical lobe, as elsewhere in the brain (figure 41). The fibrous glia cells have small oval nuclei and very numerous radiating processes (figures 41, 45 and 89).

6. The subvertical lobe

6.1. *Position and relations*

This region contains the neurons that pass the output of the vertical lobe to other parts of the brain and back to the optic lobes. They vary in size according to the distances they must reach, but it is not clear whether those for the different destinations differ in receptor dendrites or in other ways. The subvertical lobe is directly continuous with the precommissural lobe. Clearly the two form a single system distributing influences to the optic lobes and to other centres.

The subvertical lobe is a mass of tissue of irregular shape lying right across the supraoesophageal mass below the vertical lobe and behind the superior frontal lobe (figures 13, 26 and 27). The upper surface is everywhere in contact with the lower side of the vertical lobe. Below, the line of division between subvertical and precommissural lobes is arbitrary, but may be taken as the level of the lowest subvertical commissural fibres (figure 55). The lower border of the posterior part of the subvertical lobe lies above the dorsal basal lobes (figure 57, plate 7). Laterally the subvertical lobe reaches to the edge of the supraoesophageal mass, where the subvertical to optic tracts join the latter (figure 26).

Internally the subvertical lobe may be divided into anterior and posterior parts, with slightly different structures, corresponding to inputs mainly or wholly from the central and peripheral parts of the vertical lobe respectively. The anterior part of the lobe consists of a layer of cells below the vertical lobe which forms the dorsal wall of a well marked lobule, with neuropil at its centre. Below this is a set of irregular islands of cells and fibres (figures 55, 56). Anteriorly the cells form a continuous wall in the mid-line, reaching down to the precommissural lobe. The posterior region of the subvertical lobe has a simpler form, consisting of a wall of several layers of cells around a neuropil (figure 57).

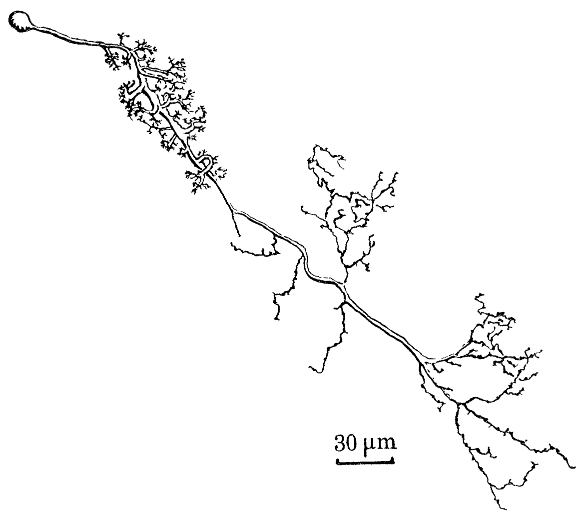


FIGURE 95. Drawing of single cell of the dorsal post-frontal region of *L. vulgaris* showing its bushy dendrites and varicose terminals in the subvertical lobe (Golgi stain).

6.2. *Cell types of the subvertical lobes*

There are some differences between the connections and cells of the anterior and posterior parts of the lobe. The main (anterior) part of the lobe contains cells of various diameters, the largest with oval nuclei 10×5 µm and maximum diameter 15 µm. The smaller cells have nuclei which range down to 2 µm in diameter. The cells of various sizes are irregularly distributed. The very small ones mostly lie in the more dorsal parts. The cells become larger as one proceeds ventrally (figure 56). In the posterior part of the lobe the cells are more uniform and larger, with round nuclei of 15 µm or more and total diameter 30 µm or more. These larger cells have axons proceeding either to the superior frontal, precommissural or optic lobes. Presumably the larger ones run for greater distances but it has not been possible to follow the processes of individual cells to their destinations. We cannot say therefore whether those for each of the three targets arise together or are dispersed throughout the lobe. The axons of the smaller cells of the lobe end within it.

The large cells of the posterior subvertical lobe begin to give dendritic branches shortly after entry to the neuropil (figure 86 and 91). The branches include short collaterals, which then divide again repeatedly to make rapidly tapering terminals. The larger branches spread widely throughout the neuropil and are presumably influenced from many incoming fibres.

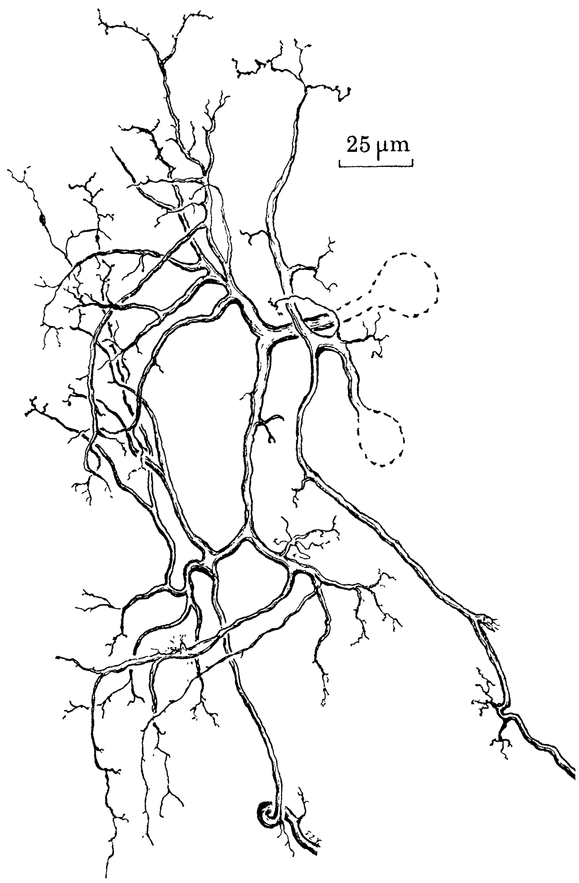


FIGURE 96. Drawing of the branches of the cells of the subvertical lobe of *L. vulgaris* (Golgi stain).

The extensive branching systems spread either horizontally or vertically, or both horizontally and vertically. The finer branches give short collaterals and finally taper away to slightly varicose tips (figures 59 and 97). Larger cells from other parts of the subvertical lobe have similar forms. The dendrites extend over a considerable length of the trunk but are mainly rather thin and do not form the bushy masses that are so characteristic of the cells of the post-frontal region (p. 327 and figure 99). The tapering dendrites make a number of fine collateral spines, evidently synaptic. Each large subvertical cell thus samples an irregular volume of neuropil, presumably receiving input from several (or many) vertical lobe cells.

The small cells of the subvertical lobe have a variety of forms. None of them resemble the amacrines of the vertical lobe. Their axons proceed to some other part of the subvertical lobe and break up into rather limited terminals there. Some of these small cells show a series of short collateral twigs and then a profusion of lateral branches, ending in terminals with slight swellings (figures 60 and 99). The trunks of these cells are roughened, with pits and small knobs and the branches end in blunt terminals with little or no swelling (figure 61). These are, as it were, reciprocal to the swollen terminals of incoming vertical to subvertical fibres and it may be that the two are related. Other cells are bipolar. The small cells in the deeper parts of the lobe point in various directions (figure 99). Nothing more definite can be said than that these small cells seem to distribute their influence within the subvertical lobe. It is impossible to be sure which of their axons proceed outside it but certainly some end within it.

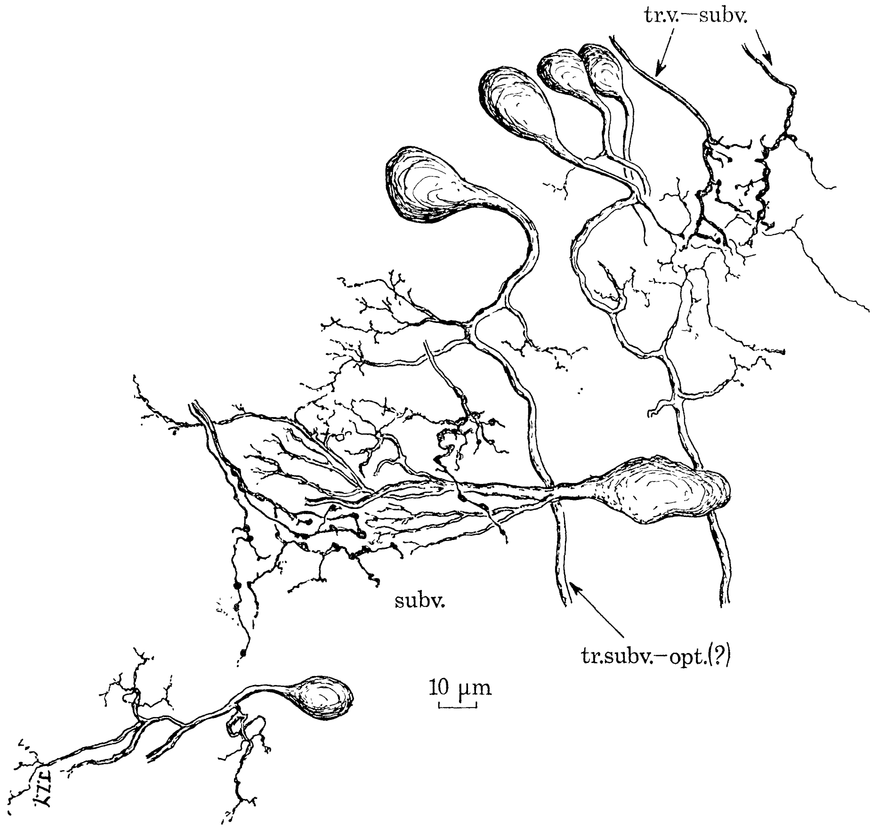


FIGURE 97. Sagittal section of back of subvertical lobe of *L. vulgaris* showing fibres entering from the vertical lobe and cells with axons proceeding downwards (? to the optic or precommissural lobes) or forwards (? to the superior frontal lobe) (Golgi stain).

6.3. *Input to the subvertical lobe*

(1) Vertical to subvertical tract. This consists of the axons of both sorts of large cells. These are relatively large axons, 2 μm or more in diameter. They pass in bundles through the cell layers that separate the lobes and spread out in all directions to make a very complicated interweaving plexus in the subvertical lobe (figure 62).

(2) Superior frontal to subvertical tract. These fibres fan out from in front to all parts of the lobe (figures 23, 85 and 98).

(3) Post-frontal to subvertical tract. Cells from all parts of the post-frontal lobes send axons that divide within the subvertical lobe (figures 80, 95 and 98).

(4) Inferior frontal to subvertical tract. Fibres from the cerebral tract also spread throughout the subvertical lobe (figures 6 and 98). These include fibres running from the lips, arms and hinder part of the body (see figure 76).

(5) Optic to subvertical tract. The bundles connecting the subvertical and optic lobes almost certainly include fibres running towards the subvertical lobe (figure 55). The large fibres from the optic lobe to the precommissural lobe probably also send branches up to the subvertical lobe (figure 69, plate 8); this may be an important pathway to the vertical lobe system.

(6) Dorsal basal to subvertical lobe. The connections between the dorsal basal and subvertical lobes probably include fibres running in both directions.

(7) Magnocellular and palliovisceral to subvertical tracts. There are probably fibres from the magnocellular lobe to the subvertical lobe running through the precommissural lobe. Other fibres taking this course may come from the pallial and visceral nerves, bringing nocicep-

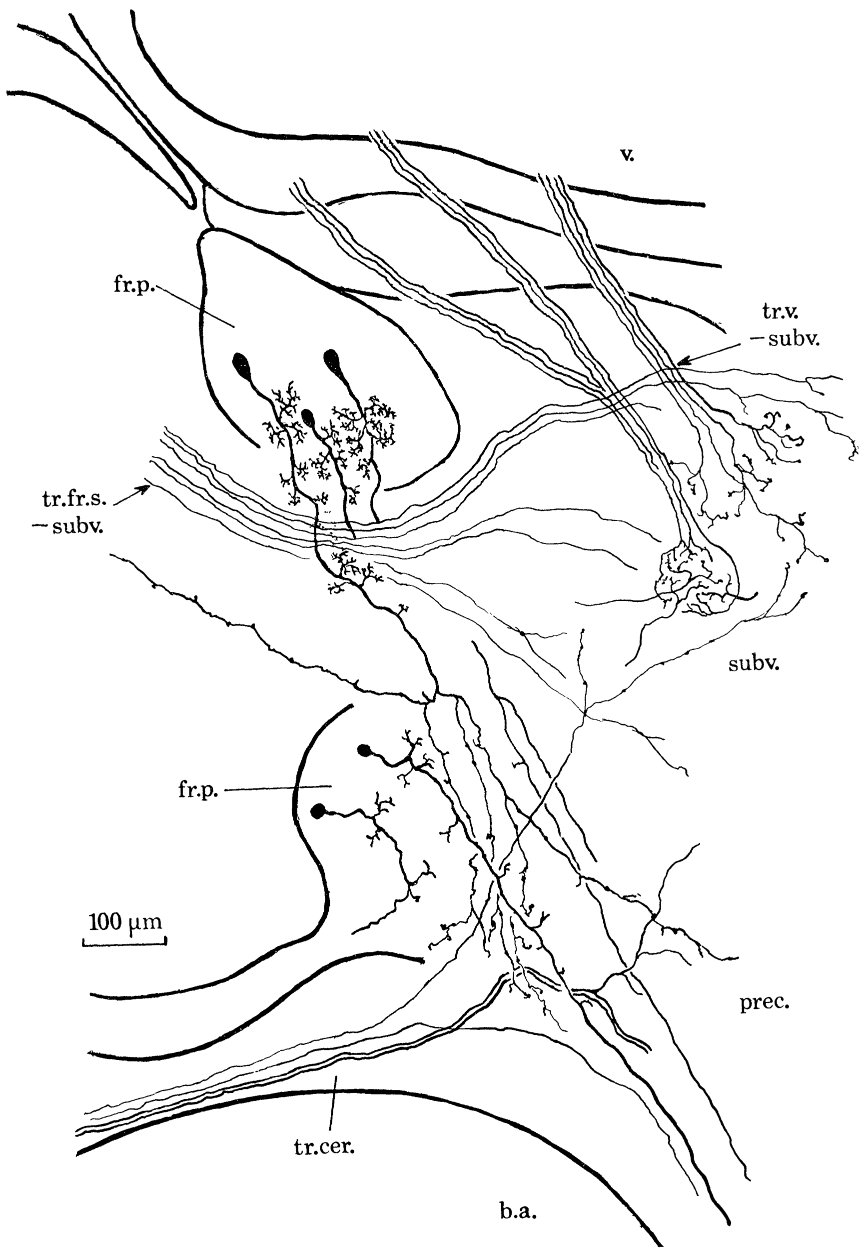


FIGURE 98. Drawing made from two sagittal sections of parts of the subvertical and precommmissural lobes of *L. vulgaris* showing fibres entering them from various sources (Golgi stain).

tive signals from the hinder part of the body. These pathways may continue on into the vertical lobe.

The details of the endings of some of these sets of fibres can be made out as follows:

(1) The larger cells of the peripheral vertical lobe, end in characteristic terminals with large dilatations (figures 63, 64, 86 and 91). On entering the neuropil the fibres begin to give coarsely beaded collaterals. Many, perhaps all of these, carry fine thread-like terminations. The whole terminal tree may occupy a relatively restricted volume, but even so is probably in relation with several of the large and small cells of the subvertical lobe. Each of these in turn must be influenced by several vertical lobe cells.

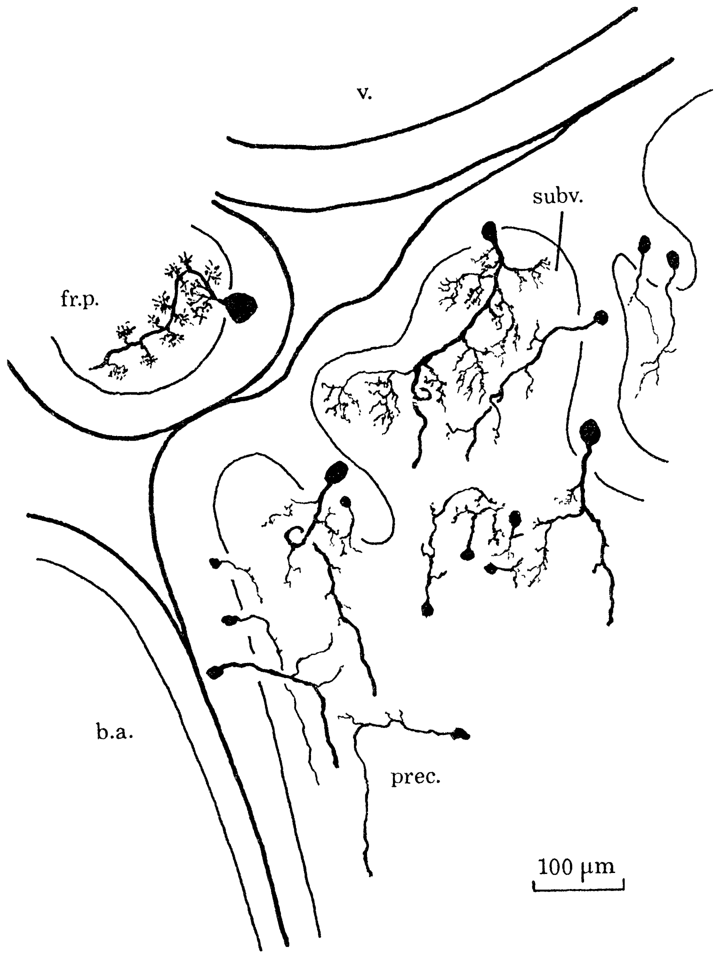


FIGURE 99. Drawing of sagittal section of *Alloteuthis* to show medium and small cells of the subvertical lobe. The smallest have no long axon. A cell of the post-frontal lobe is included to show the different form of its dendrites (Golgi stain).

The very large cells of the centre of the vertical lobe make more widely spread endings in the subvertical lobe (figure 98). These do not end in swollen terminals such as the above. Instead they make rather thin tapering terminals.

(2) Fibres of the superior frontal to subvertical tract running across the subvertical lobe, end as fine simply branched terminals (figures 85, 98) some reaching right to the hind end of the lobe.

6.4. *Output of the subvertical lobe*

(1) Subvertical to optic tract. Bundles proceed downwards and turn laterally in both directions (figure 55). They branch and anastomose so that fibres from one side can reach to either optic lobe.

(2) Subvertical to precommissural tract. The other main output pathway from the vertical lobe leads through the precommissural lobe to suboesophageal centres. The details are described on p. 348.

(3) Subvertical to inferior frontal tract. It is difficult to be sure whether fibres run from the subvertical lobe to the cerebral tract and so to the inferior frontal lobe and perhaps beyond to the brachial and/or superior buccal lobes. Probably they do so.

(4) Subvertical to superior frontal tract. Fibres entering at the hilum of the superior frontal lobe include some that arise in the subvertical lobe. It is not clear whether this represents a pathway functionally distinct from the vertical to superior frontal tract.

(5) Subvertical to vertical tract. The numerous fibres entering the vertical lobe from below may include axons arising from cells of the subvertical lobe as well as others from more distant sources. It was not possible to decide between these alternatives in *Octopus* (Young 1971). This question is important since this is one of the only two sources of input to the vertical lobe. In either case it is probable that the vertical lobe receives influences from all the sources that enter the subvertical lobe.

(6) Subvertical to dorsal basal tract. There are probably fibres running in this direction in *Loligo* as there were shown to be by degeneration in *Octopus* (Young 1971).

7. The precommissural lobe

7.1. *Introduction and relations*

This lobe is the main output pathway from the vertical lobe system, other than the reverse paths to the optic lobes. It has relatively few cells, but some of them are very large and probably function as command neurons producing complex actions. The lobes of the two sides are joined above the oesophagus, where there are large precommissural lobe commissures, containing very large fibres. The lobes diverge below the level of the oesophagus to join the middle suboesophageal mass. Dorsally the precommissural lobes are continuous with the subvertical lobes behind and the inferior post-frontal lobes in front (figure 65). They receive the cerebral tracts from in front and below this they lie behind the anterior basal lobes. The lobes of the two sides are joined in front of the optic commissure and here they extend laterally far into the hilum of the optic lobe, forming partly distinct lateral lobules, containing some very large cells (figure 66). This is apparently comparable to the region called the lateral subvertical lobe in *Octopus*, where there are also large cells (Young 1971). Together with the interbasal and dorsal magnocellular lobes, which are nearby (figure 67), these cells may be responsible for initiating attacks upon prey (page 347). At the sides of the oesophagus the precommissural lobes lie between the anterior basal lobe in front, median basal lobe behind and interbasal lobe laterally (figure 73).

7.2. *Cells and neuropil*

The cells of the lobe mostly lie on the anterior face, forming a thin layer behind the anterior basal lobe (figure 65). There are also some cells along the posterior face and some very large cells at the sides (figure 66). Some of the cell bodies reach 30 μm in diameter and are the largest in the vertical lobe system. Their trunks proceed to the centre of the lobe and turn downwards, giving off dendritic branches. The full form of the larger cells has not been seen. Some of the dendrites are very long (figure 69). Many of them turn upwards and reach to the base of the subvertical lobe and (probably) to the inferior post-frontal region. In the lower part of the precommissural lobe the trunks give off straight dendritic branches backwards (figure 70). It may be that each of the large cells of the lobe has dendrites that reach to all parts of it. The axons of some of these large cells collect together to form a bundle at the front of the lobe passing down to the middle suboesophageal mass (figure 70). Others form bundles passing backwards to the palliovisceral and magnocellular lobes (figure 71; see also figure 74 of Young 1977*a*).

There are many smaller neurons in the lobe but none are very small amacrines. Probably all the cells have axons proceeding to other lobes, the smaller ones going to other supraoesophageal lobes, the larger to suboesophageal destinations.

Description of plate 5

All sections were stained by using Golgi's method of preparation.

Figure 34 and 35. *Alloteuthis*. Cells lying within the neuropil of the vertical lobe.

Figure 36. *Alloteuthis*. Amacrine cells in the neuropil of the vertical lobe.

Figure 37*a*, *b*. *Alloteuthis*. Bipolar cells in the neuropil of the vertical lobe.

Figure 38. *L. vulgaris*. Large cell of the vertical lobe with short dendrites.

Figure 39. *L. vulgaris*. Cell in the neuropil of the vertical lobe.

Figure 40. *L. vulgaris*. Detail of endings of dendrites of the cell in figure 39.

Figure 41. *L. vulgaris*. Neuropil of the vertical lobe, retouched to show branches of one amacrine cell. A large glia cell and a gliovascular cell are also shown.

Figure 42*a*, *b*. *L. vulgaris*. Vertical lobe amacrine cells showing the proximal swellings that make contact with fibres of the superior frontal to vertical lobe tract.

Figure 43. *L. vulgaris*. A single vertical lobe amacrine cell with varicose trunk.

Figure 44. *Alloteuthis*. Branched terminations of an amacrine cell of the vertical lobe.

Description of plate 6

Except where otherwise stated, sections were stained by using Cajal's silver method of preparation.

Figure 45. *L. vulgaris*. Small fibrous glia cell of the vertical lobe (Golgi stain).

Figure 46. *L. vulgaris*. Sagittal section near the surface of the vertical lobe, showing interweaving fibres of the superior frontal to vertical lobe tract.

Figure 47. *L. vulgaris*. Single fibres of the superior frontal to vertical lobe tract, showing few branches (Golgi stain).

Figure 48. *L. vulgaris*. Fibres of the superior frontal to vertical lobe tract, showing occasional swellings. Also the trunk of a bipolar cell (Golgi stain).

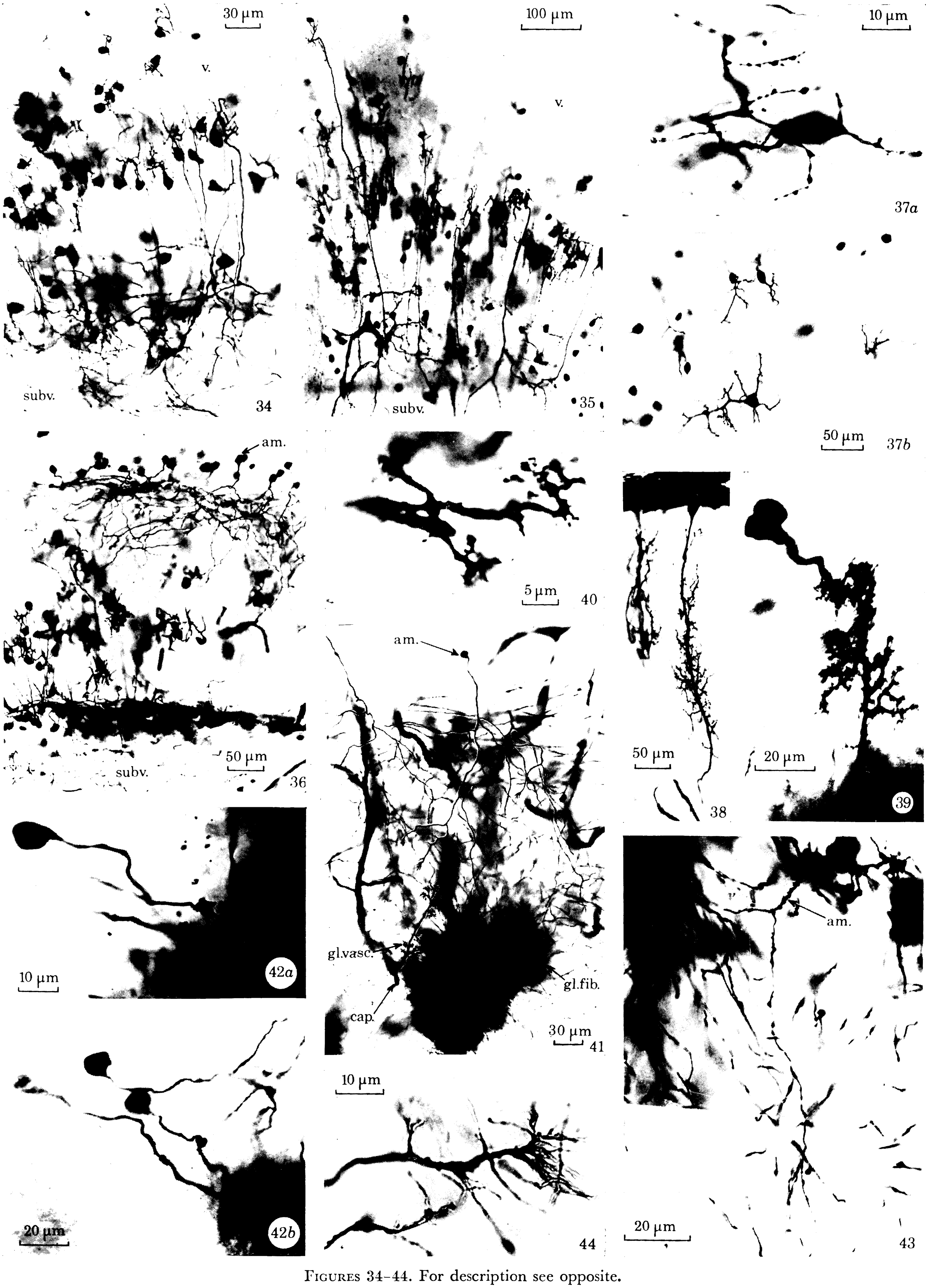
Figures 49 and 50. *L. vulgaris*. Branching fibres entering the vertical lobe from below and ending among amacrine fibres (Golgi stain).

Figures 51 and 52. *L. vulgaris*. Details of terminations of the fibre shown in figure 50 (Golgi stain).

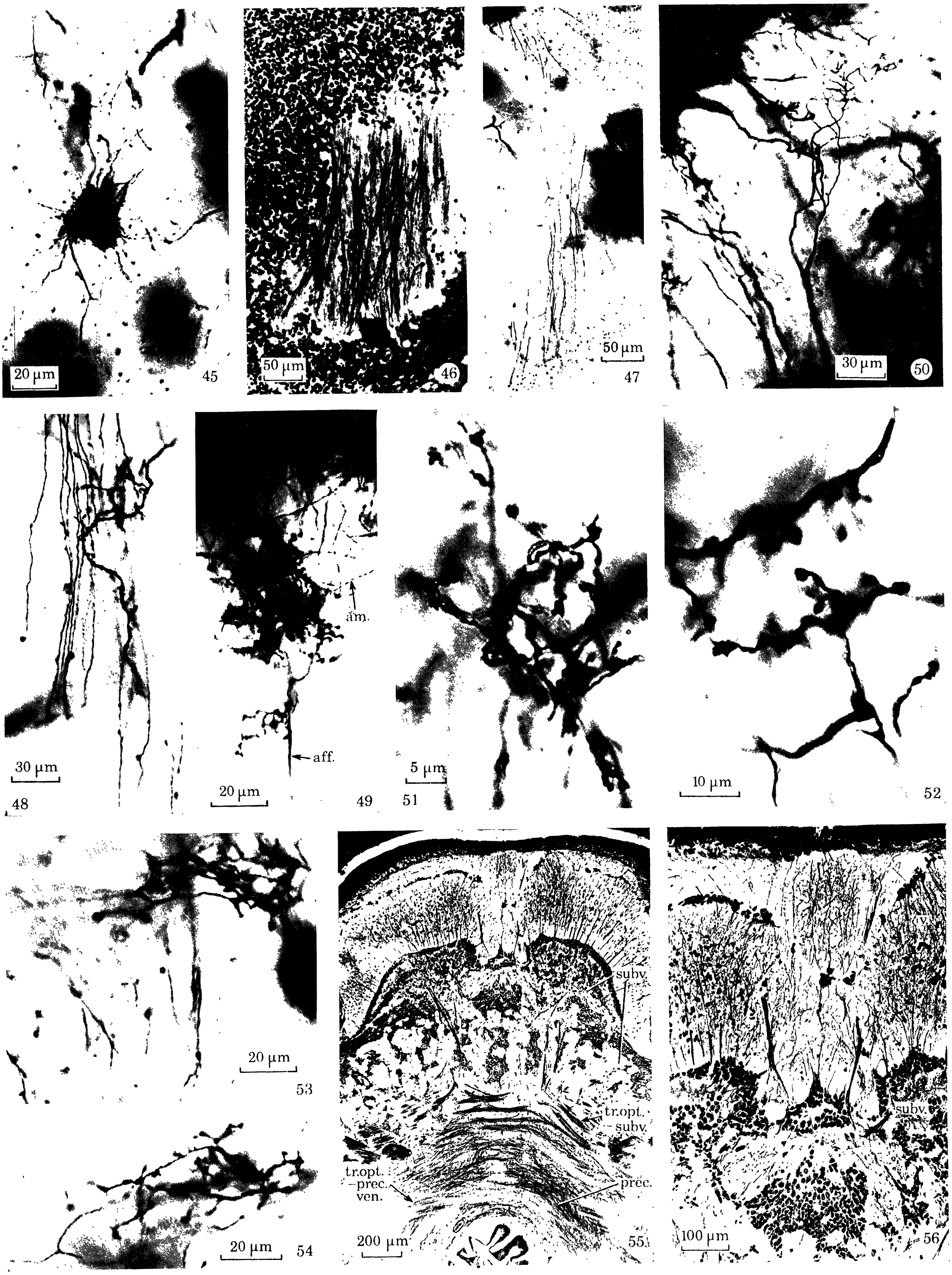
Figures 53 and 54. *L. vulgaris*. Other types of ending seen in the vertical lobe (Golgi stain).

Figure 55. *Alloteuthis*. Transverse section showing the positions of the vertical, subvertical and precommissural lobes.

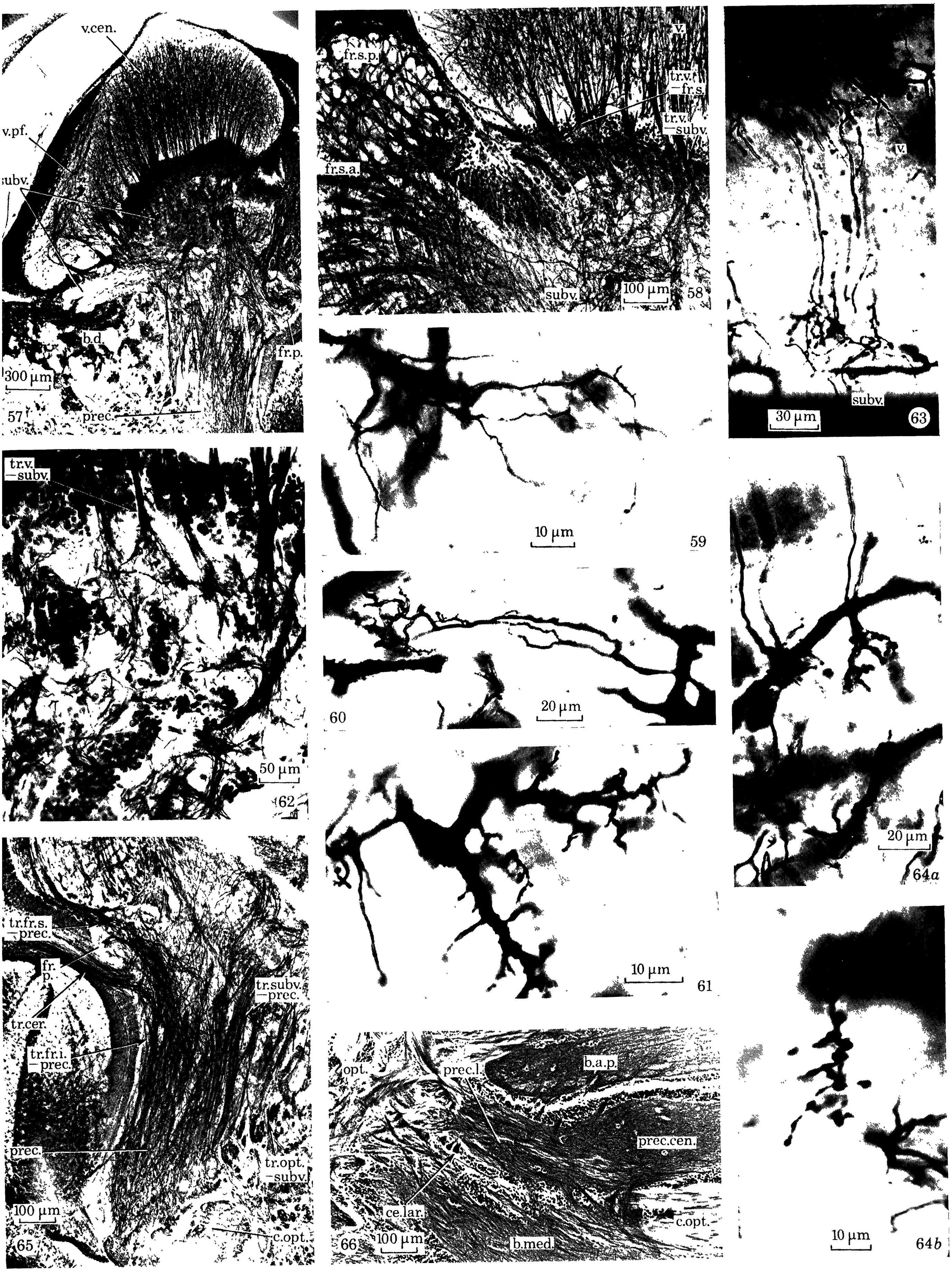
Figure 56. *Alloteuthis*. Transverse section showing large and small cells of the subvertical lobe.



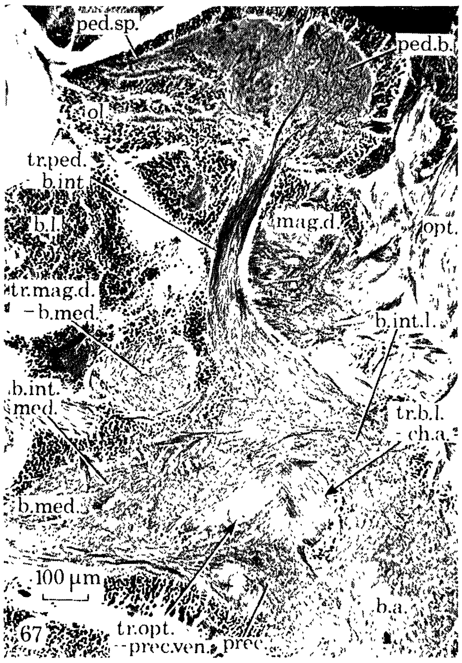
FIGURES 34–44. For description see opposite.

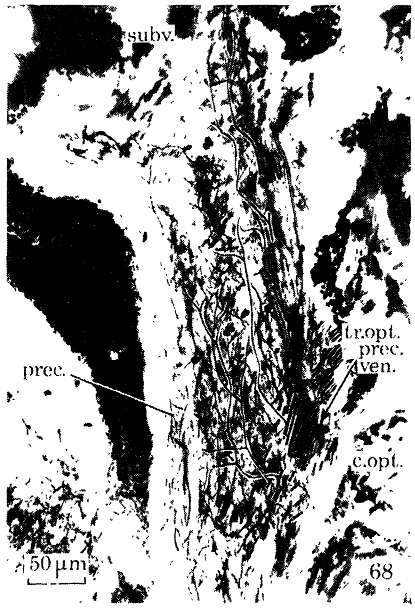


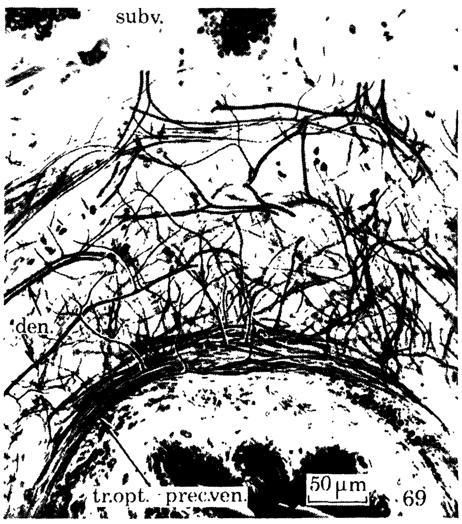
FIGURES 45–56. For description see p. 346.

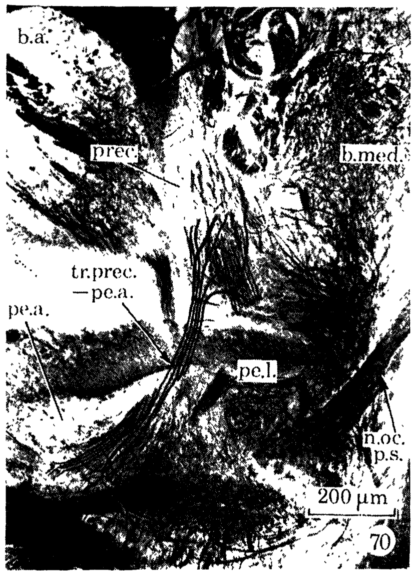


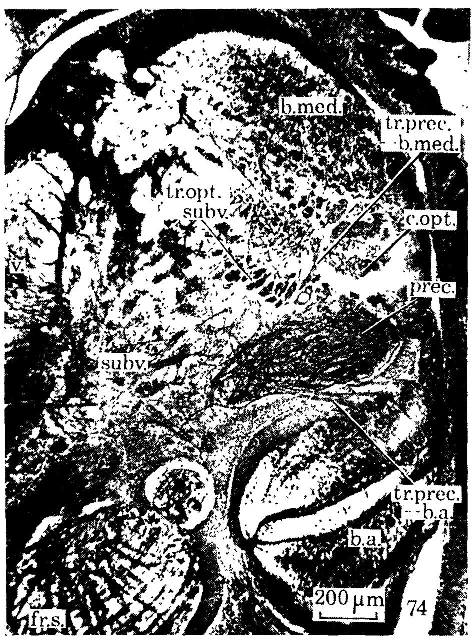
Figures 57–66. For description see p. 347.











FIGURES 67–75. For description see opposite.

7.3. *Efferent pathways of the precommissural lobe*

7.3.1. *Precommissural to anterior pedal tract*

This is a main output pathway from the lobe and contains large fibres. They run forwards across the anterior basal to pedal tract and so to the centre of the anterior pedal lobe (figure 70). This is the most medial of the tracts that run in the anterior division of the posterior cerebro-suboesophageal connective. At the front of the anterior pedal lobe these large fibres then divide up in the region of the dendrites of the large anterior pedal cells whose axons run to the arms (figure 70). There is reason to think that these are part of the system for control of the tentacles in the act of seizure of prey (Young 1977*b*). Some of these large fibres may run on directly into the connectives that unite the anterior and middle suboesophageal mass.

Description of plate 7

Except where otherwise stated, sections were stained by using Cajal's silver method of preparation.

Figure 57. *L. pealeii.* Sagittal section showing connections between the vertical lobe and the subvertical and precommissural lobes.

Figure 58. *L. pealeii.* Sagittal section showing the interconnections of the vertical, subvertical and superior frontal lobes.

Figure 59. *L. vulgaris.* Dendritic branches of a cell of the subvertical lobe (Golgi stain).

Figure 60. *L. vulgaris.* Dendritic branches of a cell of the subvertical lobe (Golgi stain).

Figure 61. *L. vulgaris.* Detail of endings of dendritic branches of cells of the subvertical lobe (Golgi stain).

Figure 62. *L. pealeii.* Transverse section showing plexus of fibres of the vertical to subvertical lobe tracts.

Figure 63. *L. vulgaris.* Individual fibres of the vertical to subvertical lobe tract (Golgi stain).

Figures 64*a*, *b*. *L. vulgaris.* Detail of endings of fibres of the vertical to subvertical lobe tracts (Golgi stain).

Figure 65. *L. pealeii.* Sagittal section to show precommissural lobe near the mid-line and its connections with the inferior frontal and subvertical lobes.

Figure 66. *L. pealeii.* Horizontal section to show the full lateral extent of the precommissural lobe and its very large cells.

Description of plate 8

All sections were stained by using Cajal's silver method of preparation.

Figure 67. *L. vulgaris.* Horizontal section to show the relation of the precommissural lobe with the interbasal and peduncle lobes.

Figure 68. *L. pealeii.* Sagittal section of a juvenile specimen, retouched to show the branches of the large fibres of the optic to precommissural lobe tract.

Figure 69. *L. pealeii.* Transverse section of a juvenile specimen, retouched to show the large fibres of the optic to precommissural lobe tract crossing in the commissure and giving branches to the lobe.

Figure 70. *L. pealeii.* Sagittal section retouched to show the large fibres of the precommissural to anterior pedal lobe tract.

Figure 71. *L. pealeii.* Sagittal section retouched to show the large fibres of the precommissural to pallioviscera lobe tract and their collateral branches to the magnocellular lobe.

Figure 72. *L. vulgaris.* Sagittal section with large fibres of the precommissural to palliovisceral lobe tract retouched.

Figure 73. *L. pealeii.* Sagittal section of a juvenile showing the relation of the precommissural and interbasal lobes.

Figure 74. *L. pealeii.* Sagittal section near the mid-line to show the connections between the precommissural lobes and the anterior basal and median basal lobes.

Figure 75. *L. pealeii.* Transverse section of a juvenile showing the ventral optic to precommissural lobe tract.

7.3.2. *Precommissural to magnocellular and palliovisceral tract*

This is part of a remarkable set of fibres and has already been described (Young 1977*a*). They form the most medial bundles of the posterior part of the posterior cerebro-suboesophageal connective (figures 71 and 72). They run backwards from all of the basal lobes, giving collateral branches to the posterior pedal and magnocellular lobes and passing on to end in the centre of the palliovisceral lobes. It may be that they provide input to the jet mechanism at the moment of prey seizure by the tentacles.

7.3.3. *Precommissural to interbasal tract*

Many fibres run between the precommissural lobe and the medial interbasal region, a place where many bundles of fibres enter the brain (figures 67 and 73). These probably include fibres running in both directions. There is some evidence that the interbasal region is concerned in the initiation of seizure of prey (Young 1977*a*).

7.3.4. *Precommissural to anterior basal and median basal tracts*

Fibres arising from small cells are seen leaving the precommissural lobe in bundles running forwards and backwards joining it to the anterior and median basal lobes (figure 74).

7.3.5. *Other possible outputs from the precommissural lobe*

No fibres have been seen running from this lobe to the optic lobes but they cannot be excluded. It is assumed that the lobe does not itself send fibres from its cells upwards to the subvertical or post-frontal lobes, but large fibres from the ventral optic tract pass through the precommissural lobe on their way upwards (see below) (p. 349). Some of the fibres that run between the precommissural lobe and the cerebral tract appear to pass forwards (p. 318) and a tract running in this direction has been shown experimentally in *Octopus* (Young 1971).

7.4. *Input to the precommissural lobe*

7.4.1. *Subvertical to precommissural tract*

Numerous fibres pass down from the cells of the subvertical lobe to spread out in the precommissural lobe (figure 65). These fibres come from all parts of the subvertical lobe, forming irregular bundles, without any obvious topological arrangement. It is assumed that they all come from the subvertical lobe, but it cannot be excluded that some arise in the vertical lobe. It is also assumed that all the fibres of this tract end in the precommissural lobe and that none proceed to suboesophageal destinations. The details of the endings have not been seen, but the fibres divide within the precommissural lobe and branches proceed downwards in different directions. Probably each influences many cells of the lobe.

7.4.2. *Inferior frontal to precommissural tract*

These fibres have been described on page 318. Some of them probably come from the brachio-cerebral tract, perhaps from the arms, others perhaps from the buccal mass and lips. Within the lobe they turn down and spread across the trunks of the cells probably reaching to all parts (figure 65).

7.4.3. *Magnocellular to precommissural tract*

This is part of a large bundle of fibres lying laterally, which sends branches to all the basal lobes (Young 1977*a*). They include many large fibres arising near the giant cell and each giving branches to several of the basal lobes. The branches to the precommissural lobe enter ventrally and divide as they spread upwards.

7.4.4. *Superior frontal to precommissural tract*

Bundles of fibres from the hilum of the anterior superior frontal lobe pass down to the precommissural lobe and spread out there (figure 65).

7.4.5. *Post-frontal to precommissural tract*

The large connections between these lobes contain descending fibres, probably including those from the larger cells (page 327) (figures 65, 80 and 98).

7.4.6. *Anterior and median basal to precommissural tracts*

Fibres pass in both directions between the precommissural and the basal lobes (figure 74) (Young 1977*a*). Some turn up and down within the precommissural lobe and end there.

7.4.7. *Optic to precommissural tracts*

Large fibres arising from the ventral part of the optic lobe reach to the precommissural lobe as well as to the anterior and median basal lobes (figure 75) (Young 1977*a*). The fibres run to the mid-line above the oesophagus and then send abundant branches curling upwards to all parts of the precommissural lobe (figure 69). The characteristic darkly staining fibres may perhaps pass on to the subvertical and post-frontal lobes. This very conspicuous set of fibres may provide the system that initiates attacks on prey (page 347).

7.4.8. *Interbasal to precommissural tract*

The neuropils of these two lobes are continuous and presumably exchange fibres in both directions (figures 67 and 73).

8. Discussion

8.1 *The inferior frontal lobe*

This is very much less complicated in *Loligo* and other decapods than in octopods. Chemotactile functions are less developed in the arms of decapods, and probably the inferior frontal lobes do not contain specific tactile memory systems (Young 1965). Cuttlefish can learn not to attack objects seen through glass (Sanders & Young 1940, Messenger 1973), but there is no evidence that they have powers of tactile discrimination. One function of the small inferior frontal lobe is presumably to regulate the operations of the buccal mass, through the tracts leading to the buccal ganglia. The separation of these latter from the rest of the brain is a characteristic feature of decapods and presumably indicates that they operate largely independently.

The other major function of the inferior frontal lobe is as a gateway to the vertical lobe system. It brings inputs from the arms, lips and mouth and from the hind part of the body. It carries outputs to the arms and buccal mass. It is not a mere conduction pathway, since impulses are sent on to the superior frontal lobe largely by cells that arise in the inferior frontal lobe. The various sources of input therefore interact in their excitation of these cells. Correspondingly the large descending output cells of the inferior frontal are probably influenced not only by descending fibres from the subvertical lobe but also by the other inputs.

The mixing of influences within the inferior frontal lobe is achieved by the tangles of fibres seen in figures 3 and 8. These have a certain similarity to the plexiform arrangements in the median inferior frontal lobe of *Octopus* (Young 1971). That lobe might have been evolved from the dorsal part of the inferior frontal lobe as seen in figure 3.

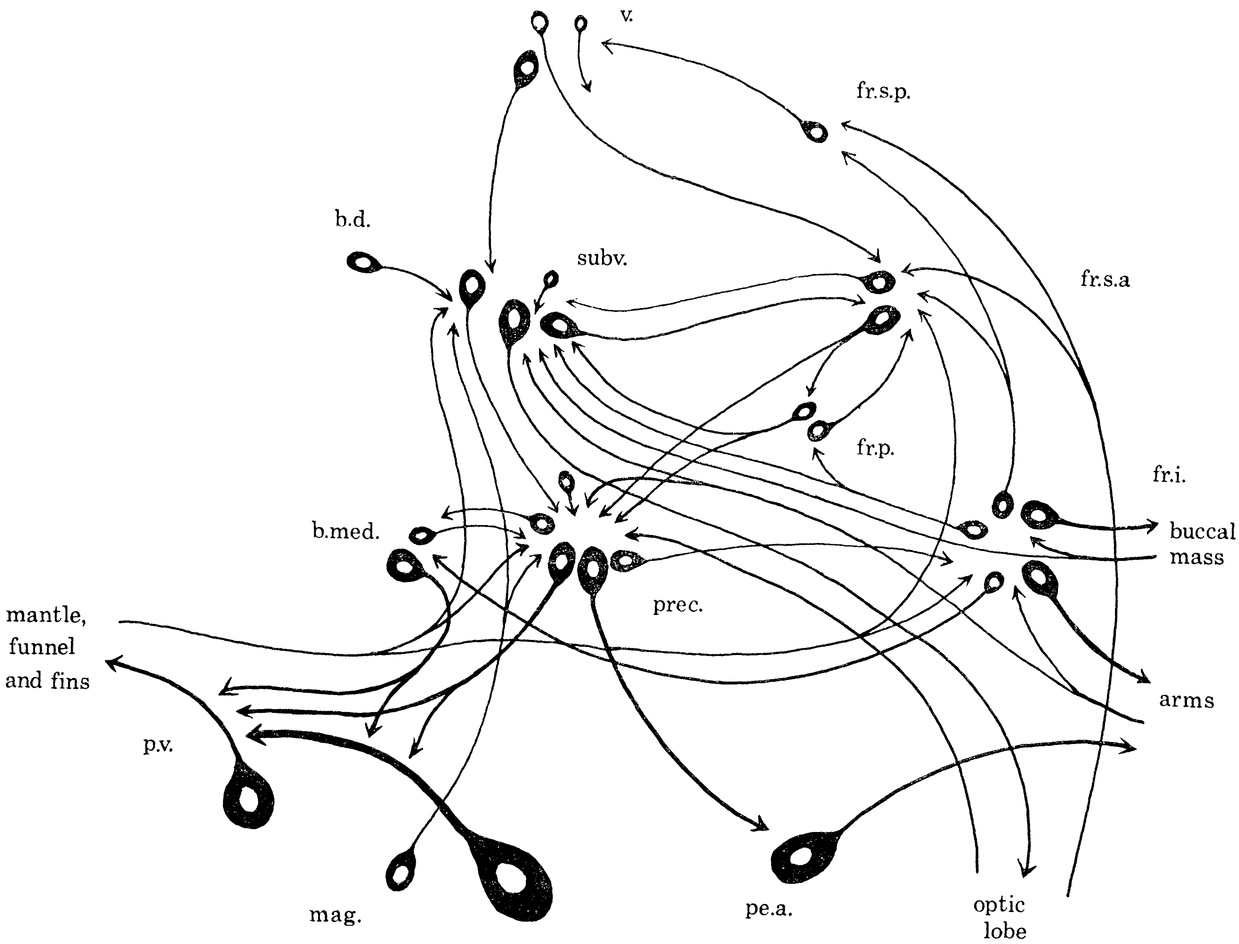


FIGURE 100. Diagram showing the circuits and pathways of the vertical lobe system.

8.2. *Different forms of neuropil*

The six lobes that make up the vertical lobe system show striking differences in organization. The inferior frontal lobe neuropil is obviously arranged to allow interactions of the inputs. In both parts of the superior frontal lobe the fibres are strikingly orientated. The trunks of the cells of the lobe run radially to the hilum across two sets of tangential fibres. The bundles of incoming optic fibres run transversely and the other inputs vertically. Moreover there is some segregation of these other inputs, with those from the inferior frontal and vertical lobes entering the neuropil more peripherally. It is not certain whether their influences remain more closely limited to the outer neuropil than those of the optic fibres; such a difference might be important.

The regular arrangements in the superior frontal lobe suggest that the topology of events in the optic lobe may be retained, and this may be an important part of the system concerned with discrimination of visual forms (Young 1974).

The neuropil of the vertical lobe is quite different from that of any of the others and from the vertical lobe of *Octopus* (see below). The great extent of the neuropil is itself a striking feature in contrast to *Octopus*. Here spreading dendrites of the large cells can receive signals from a great number of fibres, both from the superior frontal lobe and from below. Each large cell also receives influences from the processes of many amacrine cells. It is difficult to believe that a regular topology is preserved here. But perhaps different sets of the large cells may be activated by particular combinations of inputs.

The neuropil of the subvertical lobe is again different from the others, but is hard to interpret. It receives inputs from the vertical and superior frontal lobes and also from the optic lobes, the arms and mouth, and perhaps other sources. There are many small microneurons with axons restricted to the lobe; these are different from the amacrines of the vertical lobe. The neuropil of the subvertical lobe shows no obvious regularity and its large cells send signals probably mainly back to the optic lobes perhaps also down to the precommissural lobe. The latter is certainly a command centre and its neuropil shows no layers or other regularities. Its tangled appearance is similar to that of the motor lobes of the suboesophageal centres. The inputs it receives from the optic and vertical lobe systems and from other lobes, operate upon the spreading dendrites of the very large cells whose axons reach to suboesophageal centres.

8.3. *Amacrine cells* (*Local circuit neurons*)

There are no microneurons in the inferior frontal, superior frontal or precommissural lobes. All the cells of these lobes pass to other lobes. The vertical and subvertical lobes on the other hand contain many cells whose branches end within the lobe. The amacrines of the vertical lobe have several long branches. There is a synapse with a superior frontal fibre close to the cell body and more peripheral synapses at the ends of the branches. This is quite a different arrangement from the amacrines of the suboesophageal lobes, whose synapses are distributed along them (Young 1976*a*). The amacrines of the subvertical lobes are different again, and often much shorter (page 342).

The amacrines are the most numerous cells in the lobes where they occur. We can say little more about their function than was guessed nearly forty years ago. 'That masses of nervous tissue such as the neuropil of these lobes function by giving local rather than propagated responses...serving to change the thresholds of the efferent fibres which issue from the mass.' (Sanders & Young 1940).

8.4. *Comparison of* Loligo *with* Octopus

The general arrangement of the vertical lobe system is strikingly similar in all coleoids and suggests that they are monophyletic. The differences in the inferior frontal lobe system have been discussed (page 349) and are due to the use of the arms in the benthic habitat of the octopuses. The superior frontal lobes are alike even in the detailed division into two parts and in their connections, though these occupy different positions. The vertical lobes, however, show some striking differences. The five lobules in an octopus seem designed to allow a maximum of surface, and hence of cells, and a minimum of neuropil (connections). In *Loligo* we have the opposite. There is no folding, part of the surface has no small cells, and there is a huge neuropil. The octopod condition seems to favour a large number of small cells, the decapod a large number of large cells. The large cells are numerous even within the neuropil. These differences are very striking and call for further knowledge of fine structure and experiments on function.

8.5. *Recurrent loops in the vertical lobe system*

The presence of potentially self re-exciting chains of neurons has earlier been reported in *Sepia* (Young 1938, Sanders & Young 1940). The loop there referred to was between the superior frontal and vertical lobes. This is actually a circuit within the larger circuit provided by the system optic lobe → posterior superior frontal → vertical → subvertical → optic lobe (figure 100). Another parallel circuit omits the vertical lobe, passing from optic lobe → anterior superior frontal → subvertical → optic. There is also the possibility of a shorter circuit from anterior superior frontal → subvertical → anterior superior frontal. The connection plan of these circuits is still obscure because of uncertainties about the relations of the two parts of the superior frontal lobe. It is not clear whether the return pathway from the vertical lobe to the anterior superior frontal lobe links up with the forward pathway through the posterior superior frontal lobe. A similar doubt exists in *Octopus* where, after injury to the vertical lobe, there is degeneration in the lateral but not the median superior frontal lobe (Young 1971).

In addition to these circuits involving optic impulses there are also connections that would allow self re-excitation by the inferior frontal → superior frontal → vertical → subvertical (or precommissural) → inferior frontal circuit.

8.6. *The functioning of the vertical lobe system*

It remains to be discovered whether any or all of these circuit systems provide for recursive functional operations. The whole vertical lobe complex presumably somehow enters into the process of making decisions between possible lines of behaviour, perhaps in the light of information that has been learned. It was shown that in *Sepia* removal of the vertical lobe does not prevent the animal from learning not to attack a prawn behind a glass window (Sanders & Young 1940). There was a clear loss of the restraint learned before the operation, but this was soon re-learned.

The vertical lobe system receives a wide selection of inputs from the eyes, arms, mouth and all parts of the body. It may serve to allow varied associations of input combinations. The effects of these on the motor system are then produced through the large precommissural neurons, while copies are sent back from the subvertical lobe to the optic lobes. It is significant that the different input sources converge on the vertical lobe from two opposite directions. They all enter in front through the inferior frontal–superior frontal complex. Fibres from the *same* sources also come together from below in the subvertical lobe and pass on upwards to the vertical lobe. This anatomical arrangement may somehow provide the basis for decisions in the light of the information from these sources and from the memory store.

The present study has shown for the first time the anatomical details of the precommissural and interbasal regions and the motor paths by which the vertical lobe system can control behaviour (page 347). There are large fibres from the precommissural lobe both to the arm centres in the pedal lobe and to those for swimming in the magnocellular and palliovisceral lobes. These pathways can be activated either through the vertical lobe system or directly by the large ventral optic to precommissural lobe tract or from the arms through the cerebral tract (pp. 318, 348). At the same time the large reverse pathway from the subvertical to the optic lobes carries what may be an efference copy of the command (Sperry 1950, von Holst 1973). This may be the means by which appropriate adjustments of the eyes and other parts are made from the optic lobes, acting through the peduncle lobe and basal lobes, with their 'cerebellar' capacities (Young 1976*b*, Messenger 1978). These lobes (and the statocysts) have only small and indirect connections with the vertical lobe system. It seems therefore that there is a rather sharp division between the parts of the brain concerned with deciding upon lines of behaviour and those that regulate the details. Nevertheless the small connections between the basal lobes and the precommissural lobe may provide for some important function. In particular the interbasal region is evidently an important motor pathway that requires further investigation. Much remains to be done but perhaps with this series of papers we are approaching a situation in which it can be said that we have some picture of the combined operations of all parts of the nervous system of a squid in its daily life.

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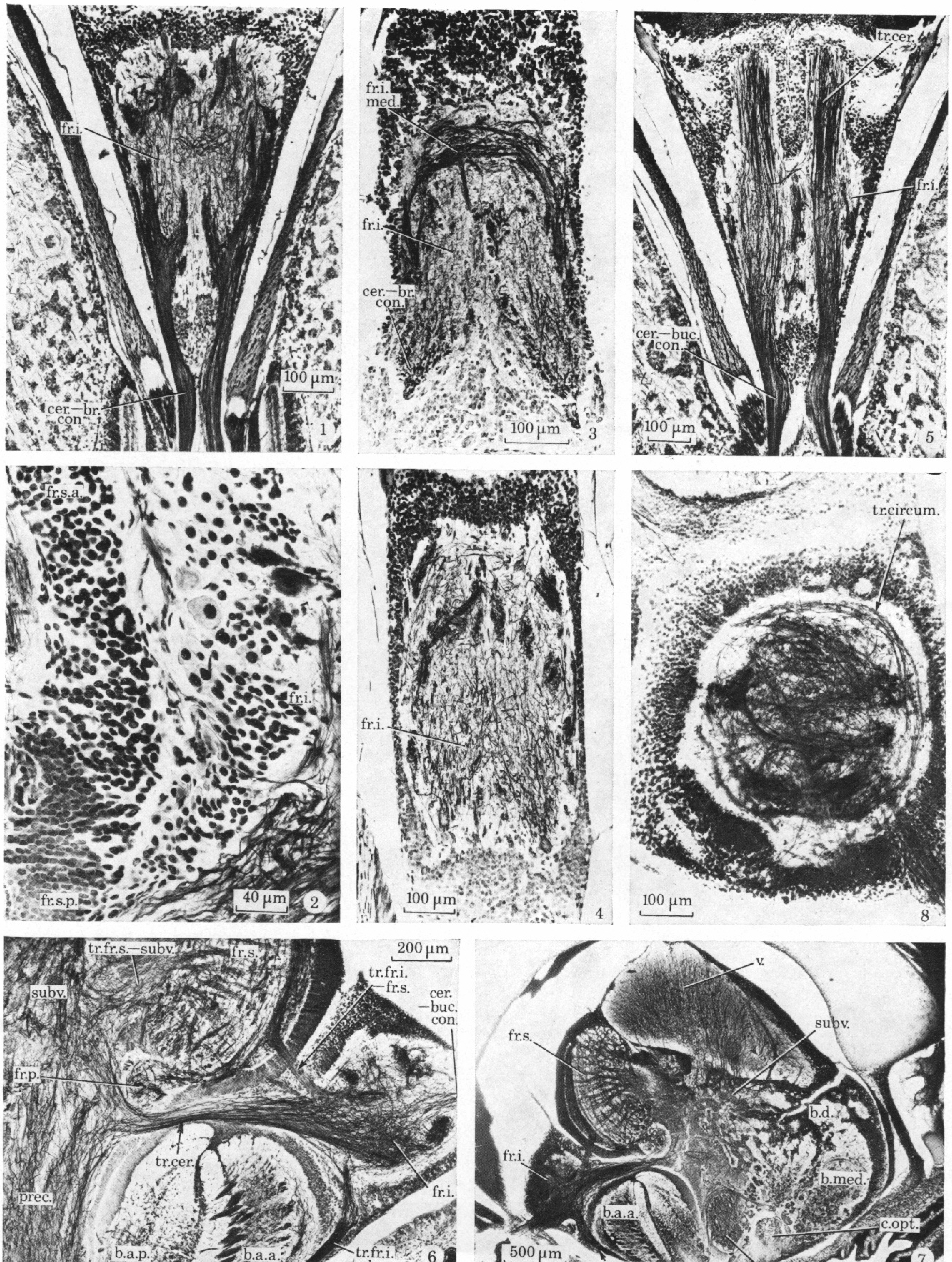
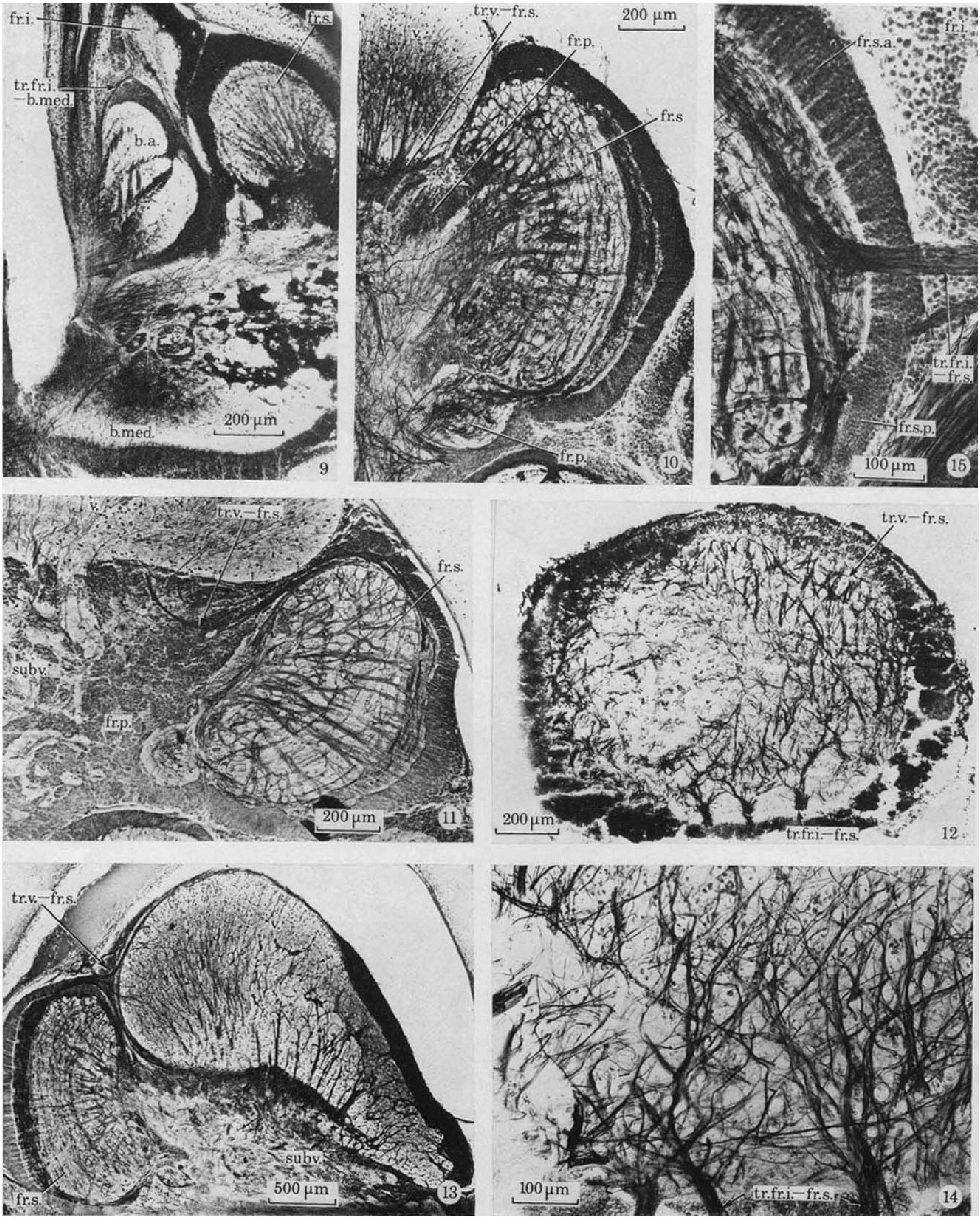
Explanation of abbreviations used in figures

aff.	afferent fibre
am.	amacrine cell
b.a.	anterior basal lobe
b.a.a.	anterior anterior basal lobe
b.a.p.	posterior anterior basal lobe
b.d.	dorsal basal lobe
b.int.	interbasal lobe
b.int.l.	lateral interbasal lobe
b.int.med.	median interbasal lobe
b.l.	lateral basal lobe
b.med	median basal lobe
br.	brachial lobe
buc.i.	inferior buccal lobe
buc.s.	superior buccal lobe
c.opt.	optic commissure
c.prec.	precommissural commissure
cap.	capillary
ce.fr.p.	cell of posterior frontal lobe
ce.lar.	large cell
cer.-br.con.	cerebro-brachial connective
cer.-buc.con.	cerebro-buccal connective
den.	dendrite
f.gi.1.	first order giant fibre
fr.i.	inferior frontal lobe
fr.i.med.	median inferior frontal lobe
fr.p.	posterior frontal lobe
fr.s.	superior frontal lobe
fr.s.a.	anterior superior frontal lobe
fr.s.p.	posterior superior frontal lobe
gl.fib.	fibrous glia
gl.nuc.	nucleus of glial cell
gl.vasc.	gliovascular cell
ly.	lymph channel
mag.	magnocellular lobe
mag.d.	dorsal magnocellular lobe
n.oc.a.s.	superior anterior oculomotor nerve
n.oc.p.s.	superior posterior ocular nerve
n.op.p.s.	superior posterior ophthalmic nerve
oes.	oesophagus
ol.	olfactory lobe
opt.	optic lobe
pe.a.	anterior pedal lobe
pe.l.	lateral pedal lobe
pe.p.	posterior pedal lobe
ped.b.	basal region of peduncle lobe
ped.sp.	spine of peduncle lobe
prec.	precommissural lobe
prec.cen.	central region of precommissural lobe
prec.l.	lateral region of precommissural lobe
p.v.	palliovisceral lobe
subv.	subvertical lobe
syn.	synapse
tr.b.l.-ch.a.	lateral basal to anterior chromatophore lobe tract
tr.b.med.-fr.s.	median basal to superior frontal lobe tract
tr.cer.	cerebral tract
tr.circum.	tract around inferior frontal
tr.fr.i.-b.med.	inferior frontal to median basal lobe tract
tr.fr.i.-fr.s.	inferior frontal to superior frontal lobe tract
tr.fr.i.-prec.	inferior frontal to precommissural lobe tract
tr.fr.int.	interfrontal tract
tr.fr.s.-prec.	superior frontal to precommissural lobe tract
tr.fr.s.-subv.	superior frontal to subvertical lobe tract
tr.fr.s.-v.	superior frontal to vertical lobe tract
tr.mag.d.-b.med.	dorsal magnocellular to median basal lobe tract
tr.opt.-fr.s.	optic to superior frontal lobe tract
tr.opt.-prec.ven.	ventral optic to precommissural lobe tract
tr.opt.-subv.	optic to subvertical lobe tract
tr.pe.p.-fl.	posterior pedal to fin lobe tract
tr.ped.-b.int.	peduncle to interbasal lobe tract
tr.prec.-b.a.	precommissural to anterior basal lobe tract
tr.prec.-b.med.	precommissural to median basal lobe tract
tr.prec.-pe.a.	precommissural to anterior pedal lobe tract
tr.prec.-pv.	precommissural to palliovisceral lobe tract
tr.subv.-fr.s.	subvertical to superior frontal lobe tract
tr.subv.-opt. (?)	subvertical to optic lobe tract (?)
tr.subv.-prec.	subvertical to precommissural lobe tract
tr.v.-fr.s.	vertical to superior frontal lobe tract
tr.v.-subv.	vertical to subvertical lobe tract
v.	vertical lobe
v.cen.	central region of vertical lobe
v.pf.	peripheral region of vertical lobe

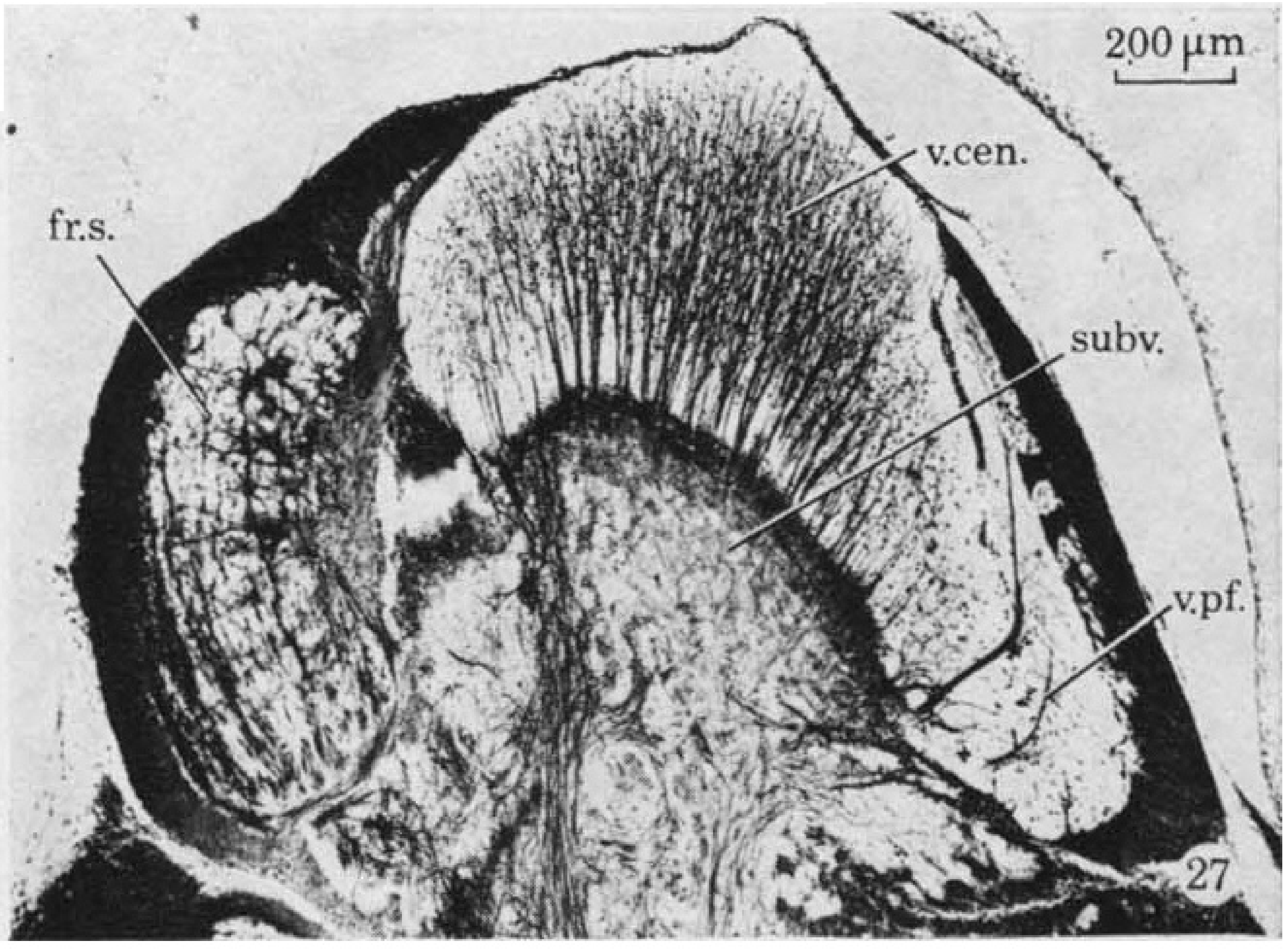


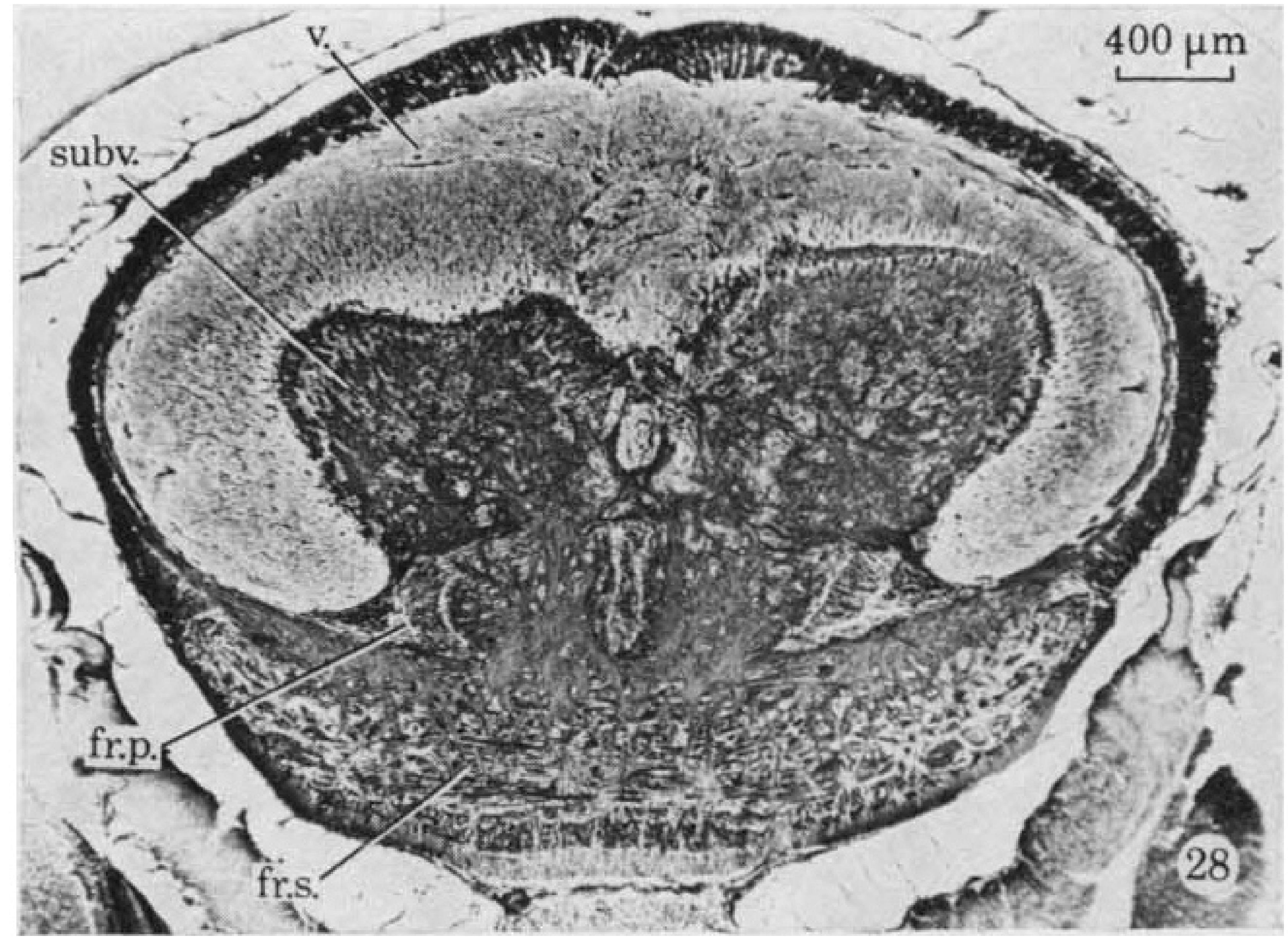
FIGURES 1–8. For description see opposite.

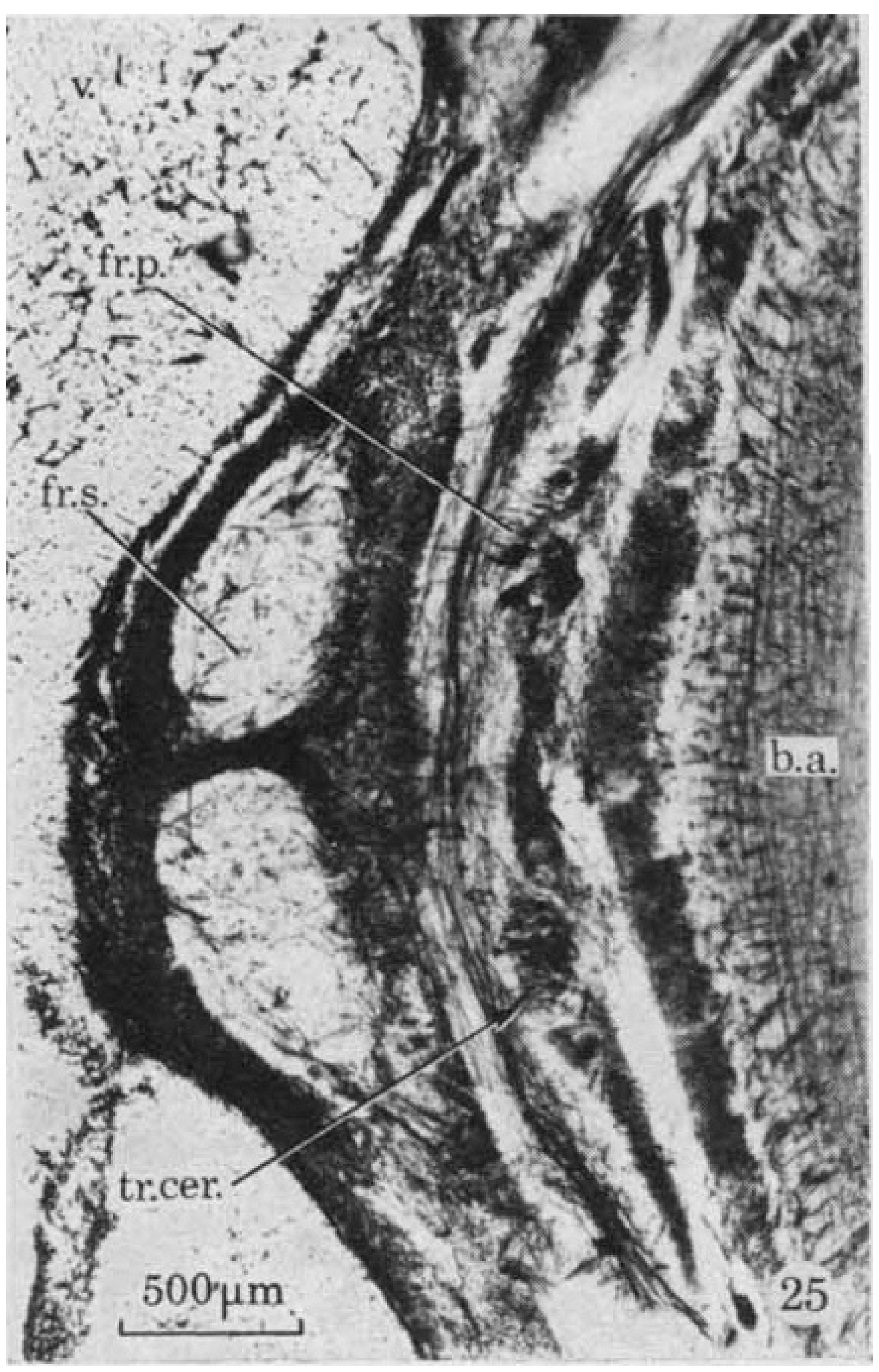


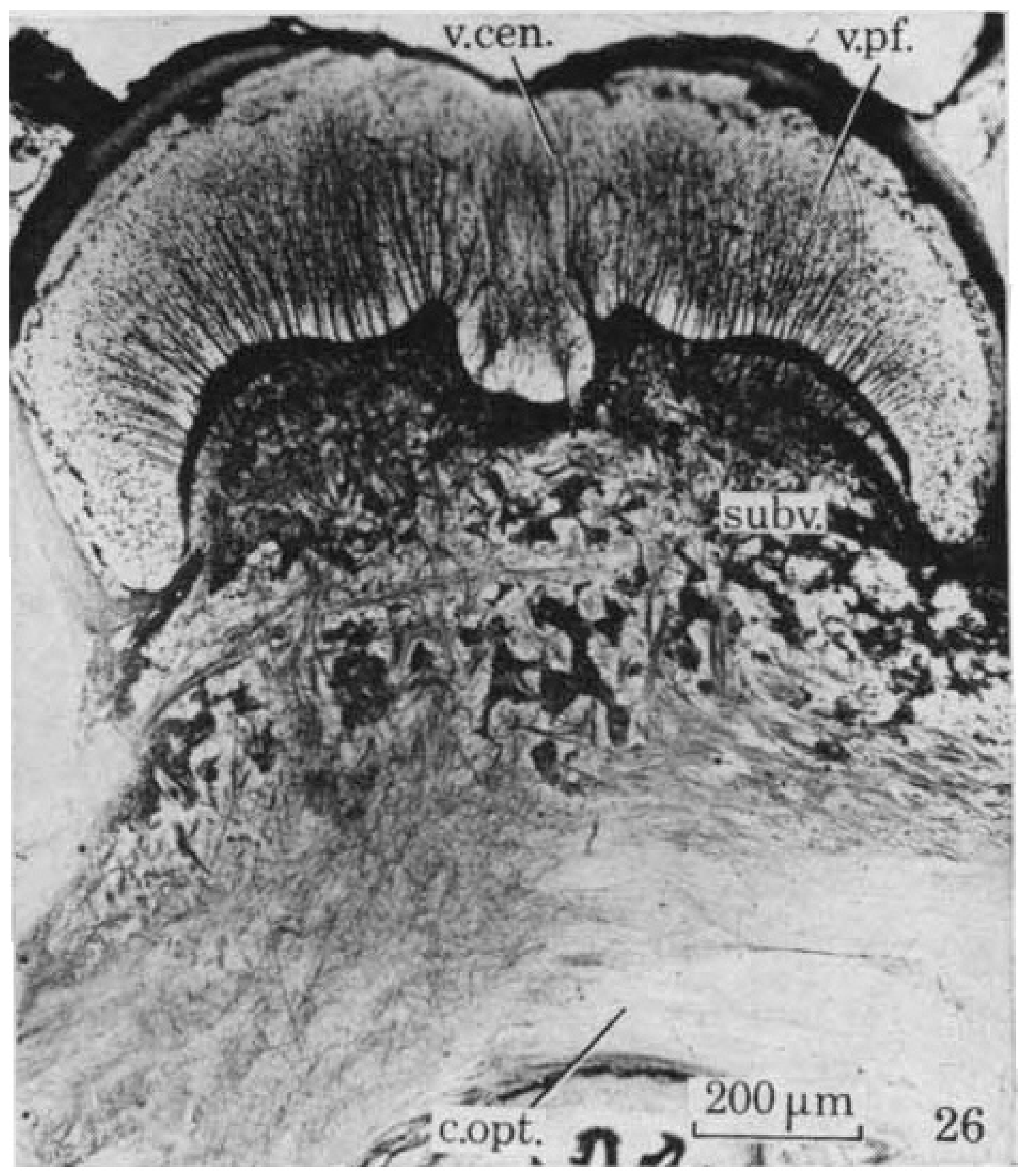
Figures 9–15. For description see p. 320.

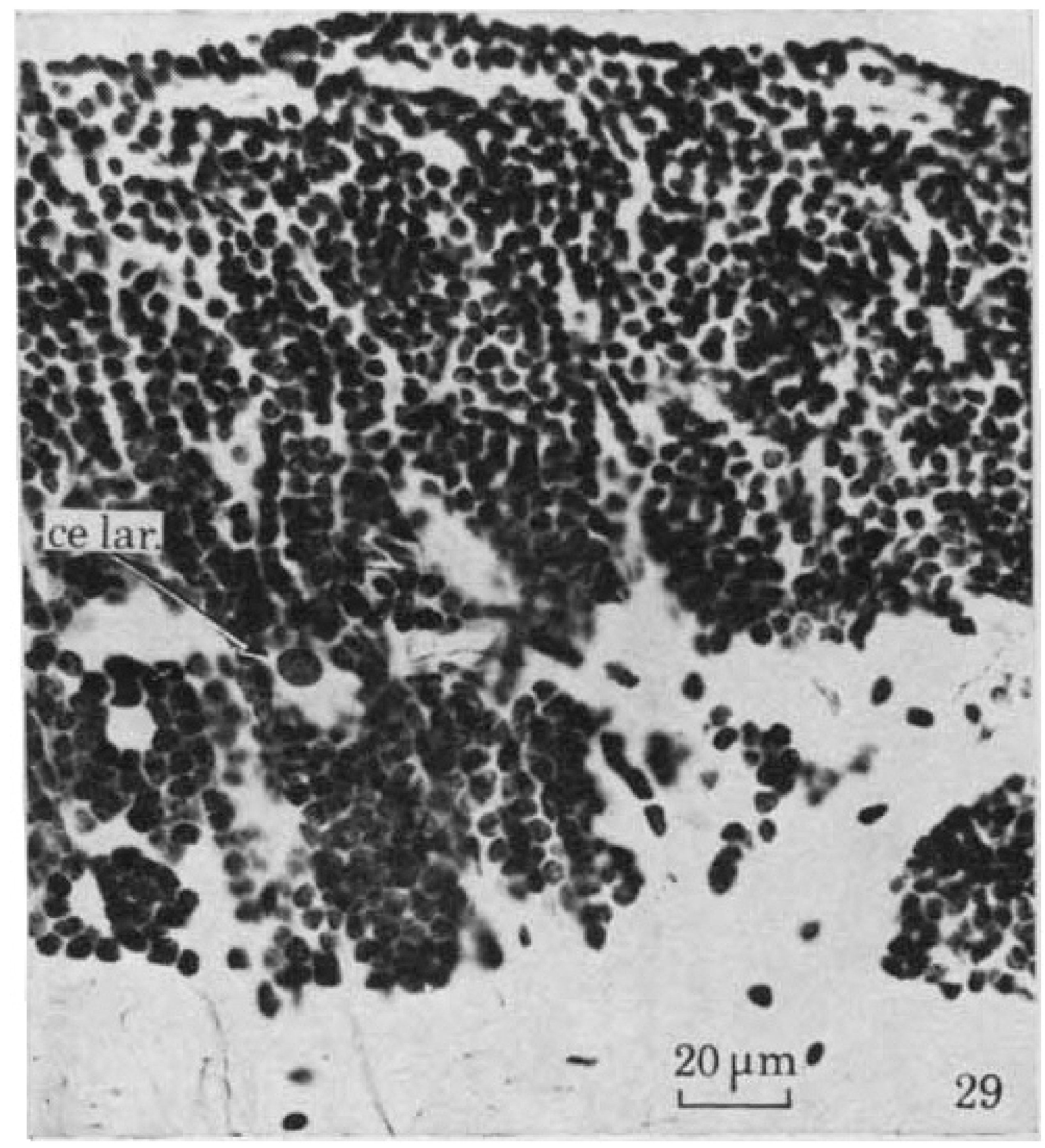
FIGURES 16–24. For description see p. 321.

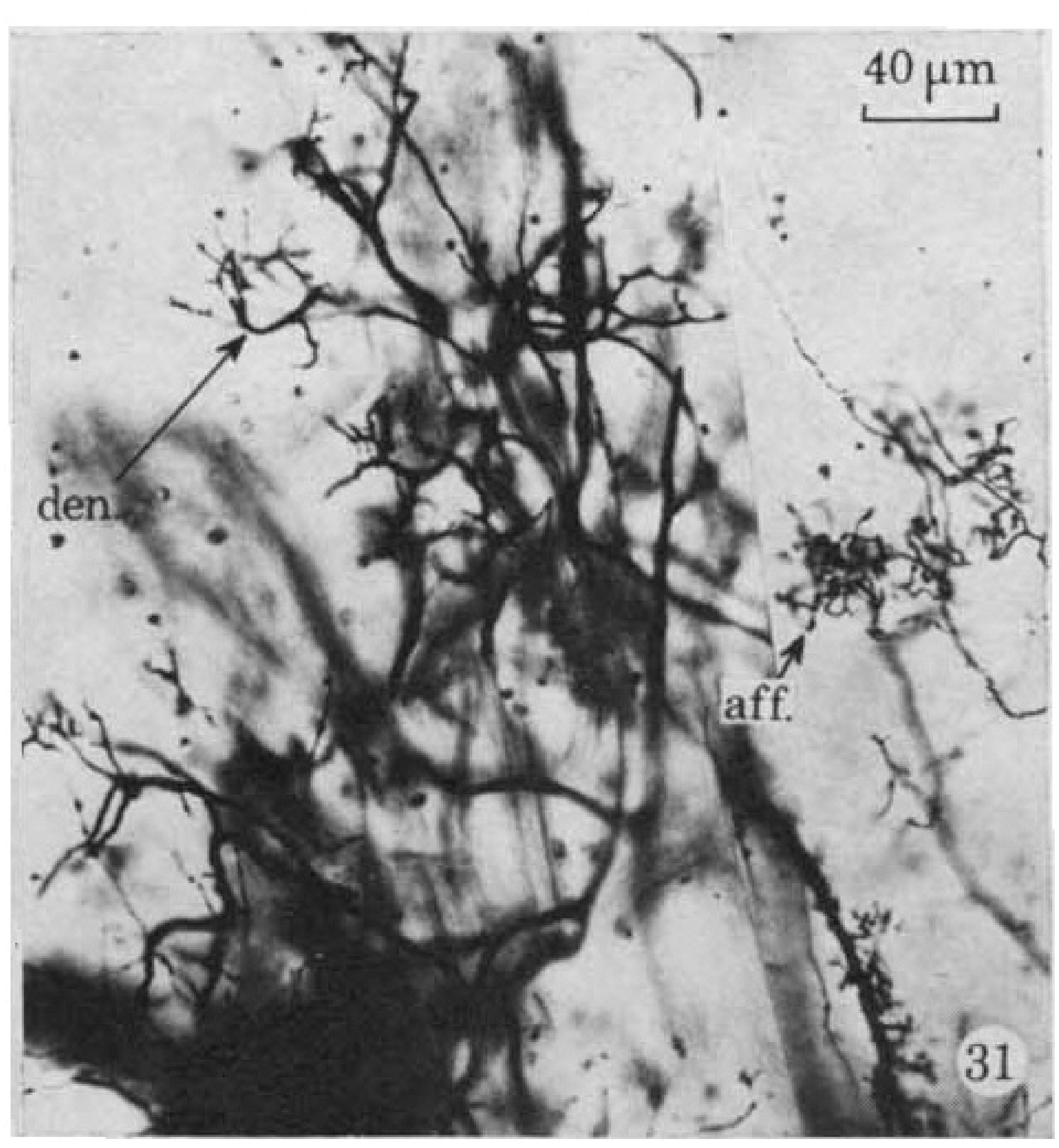


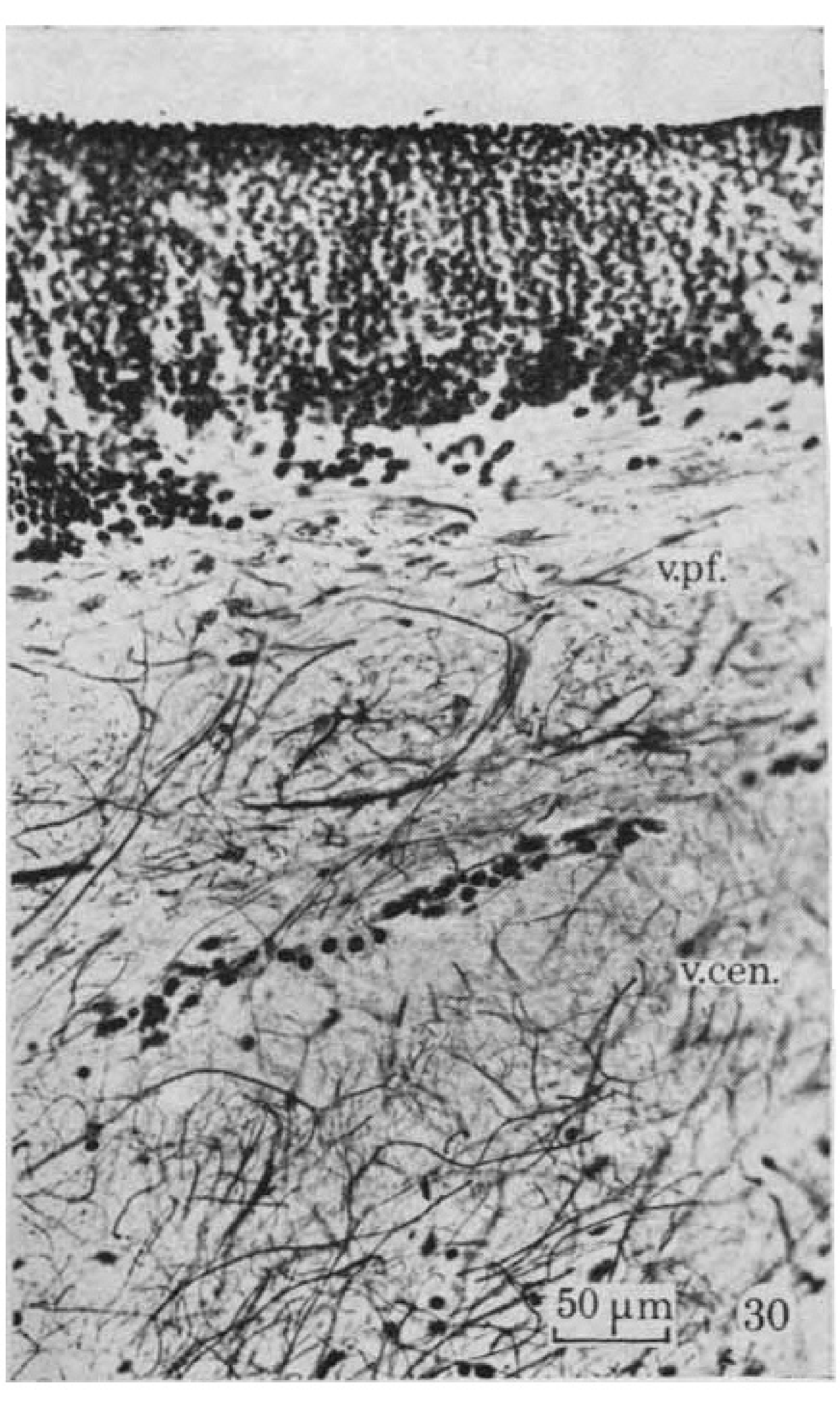


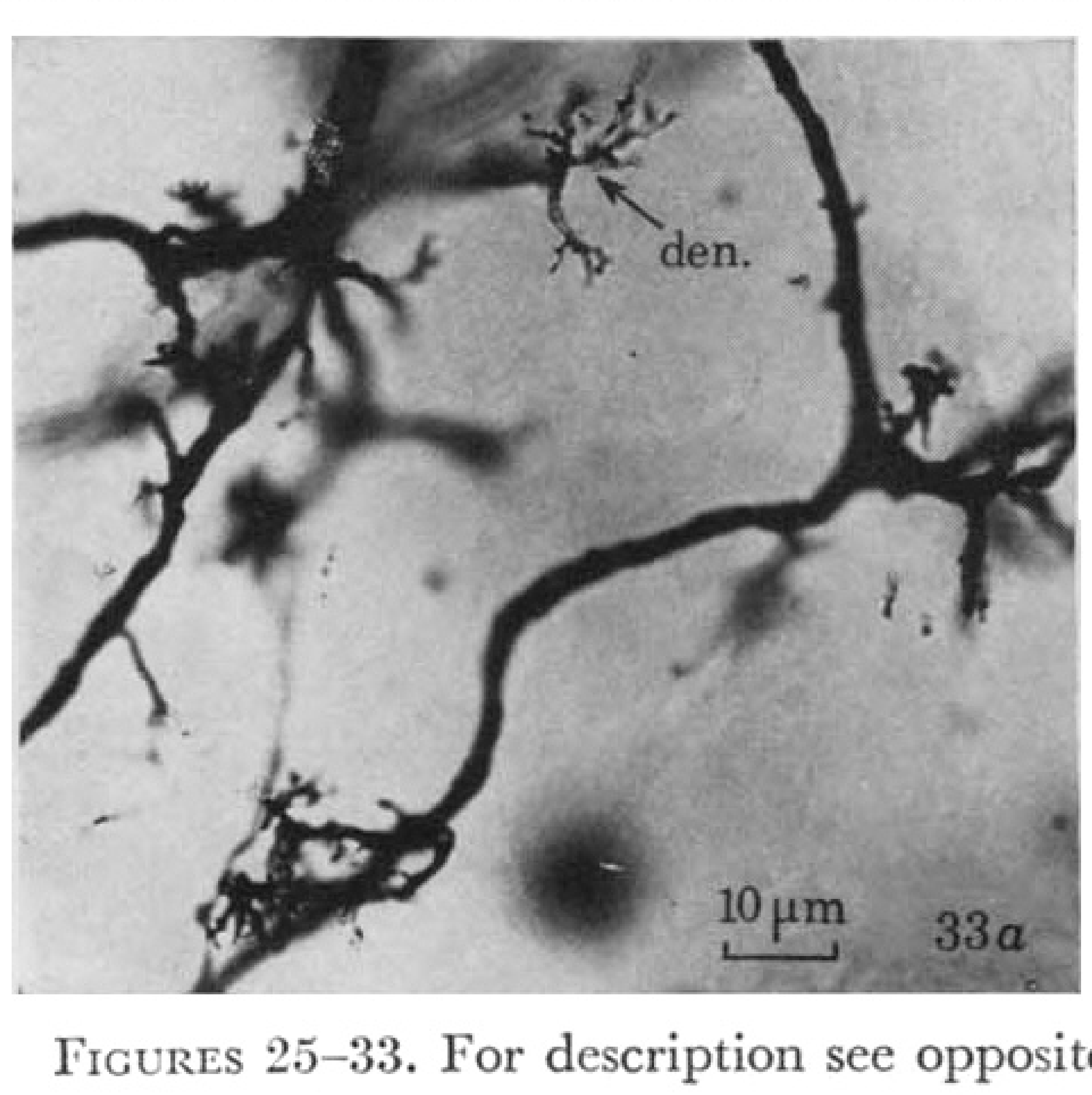


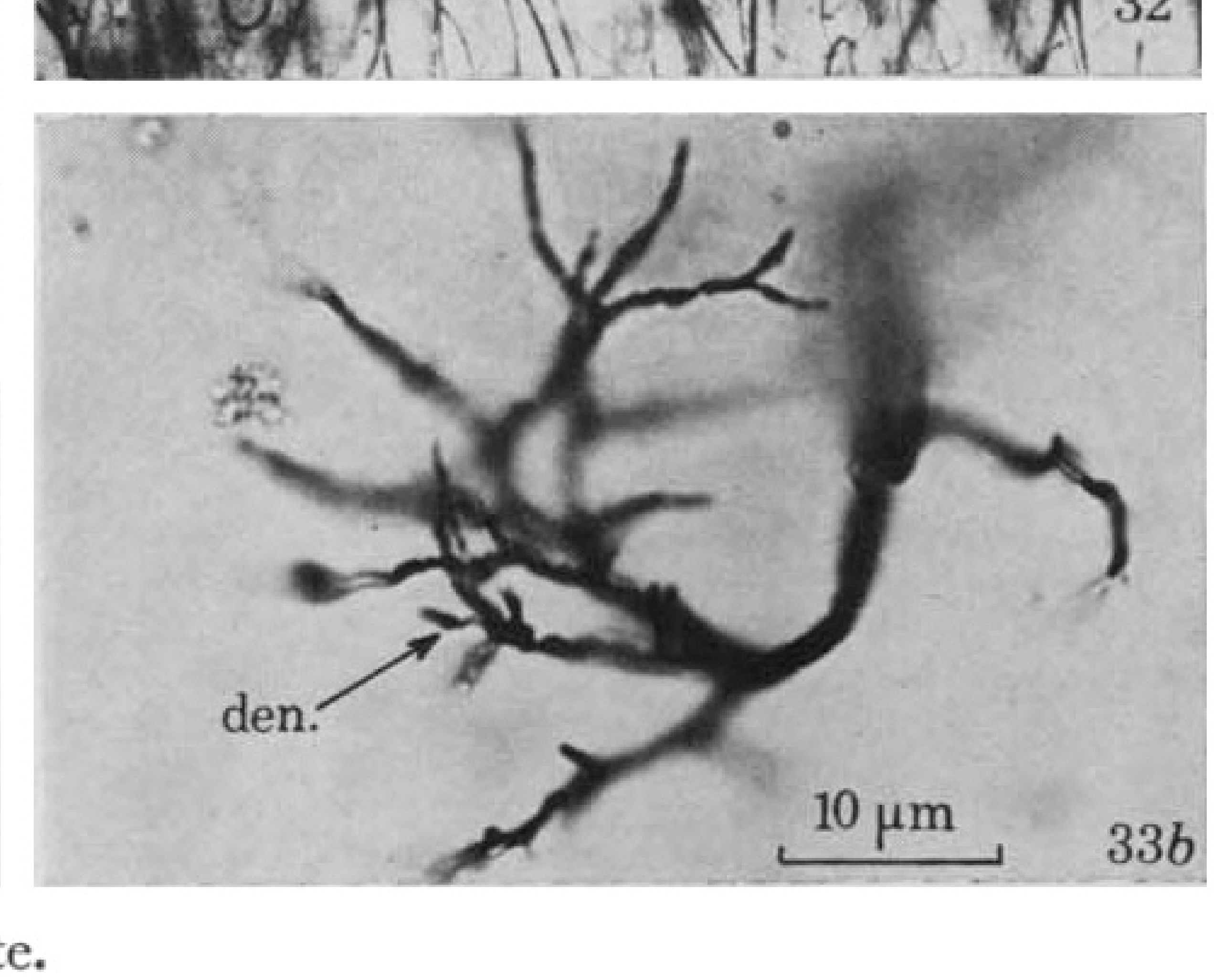




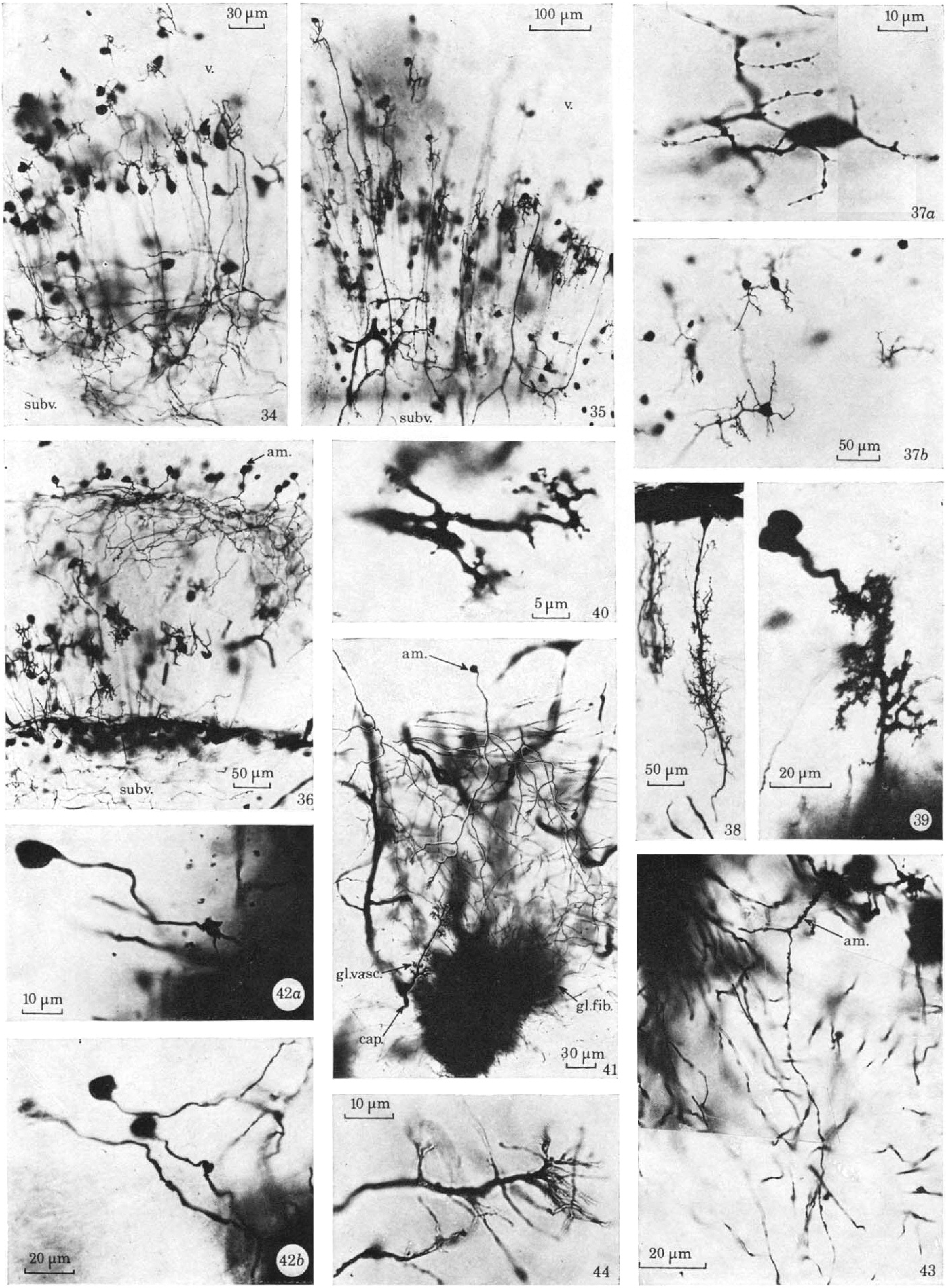




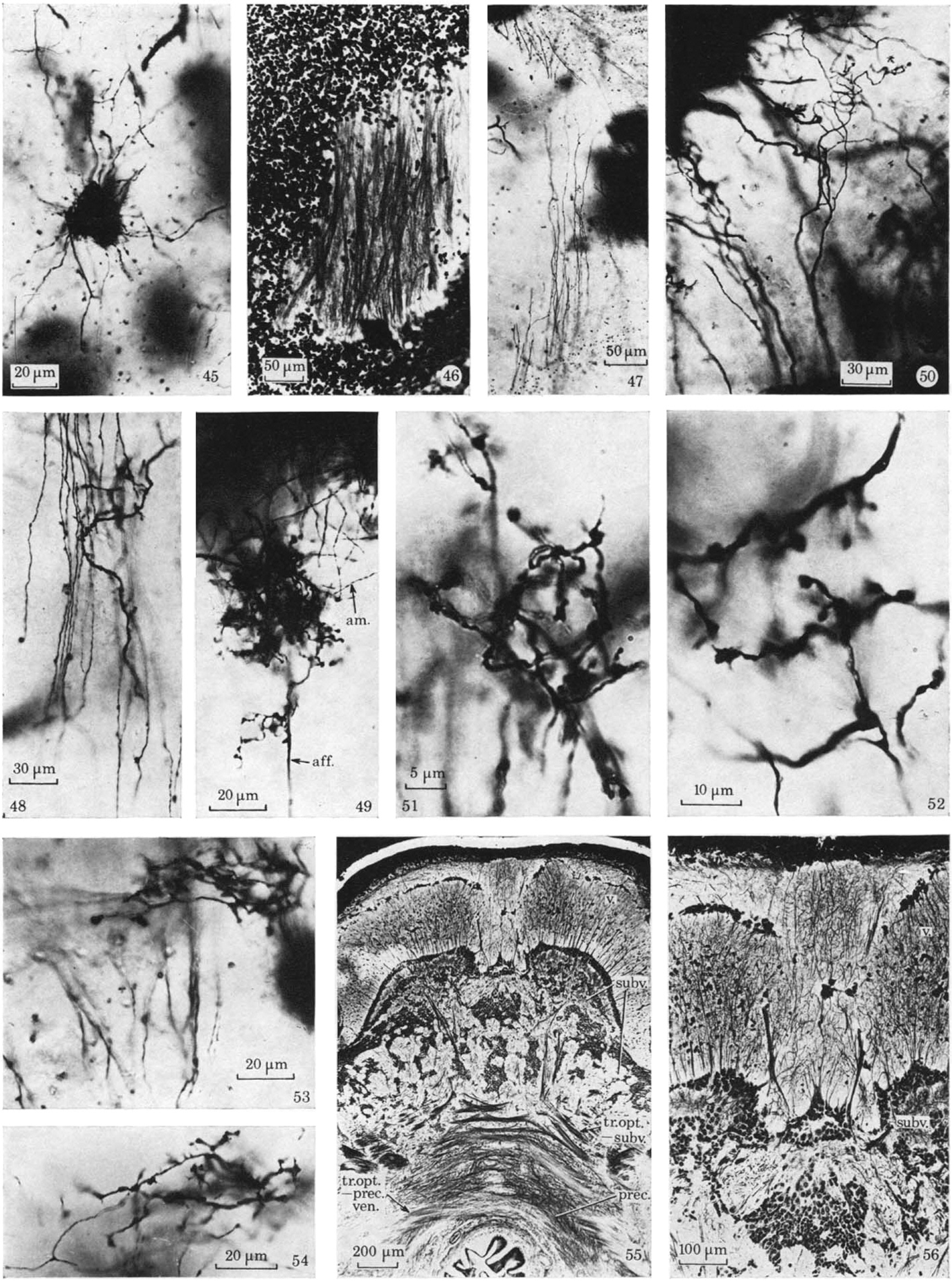




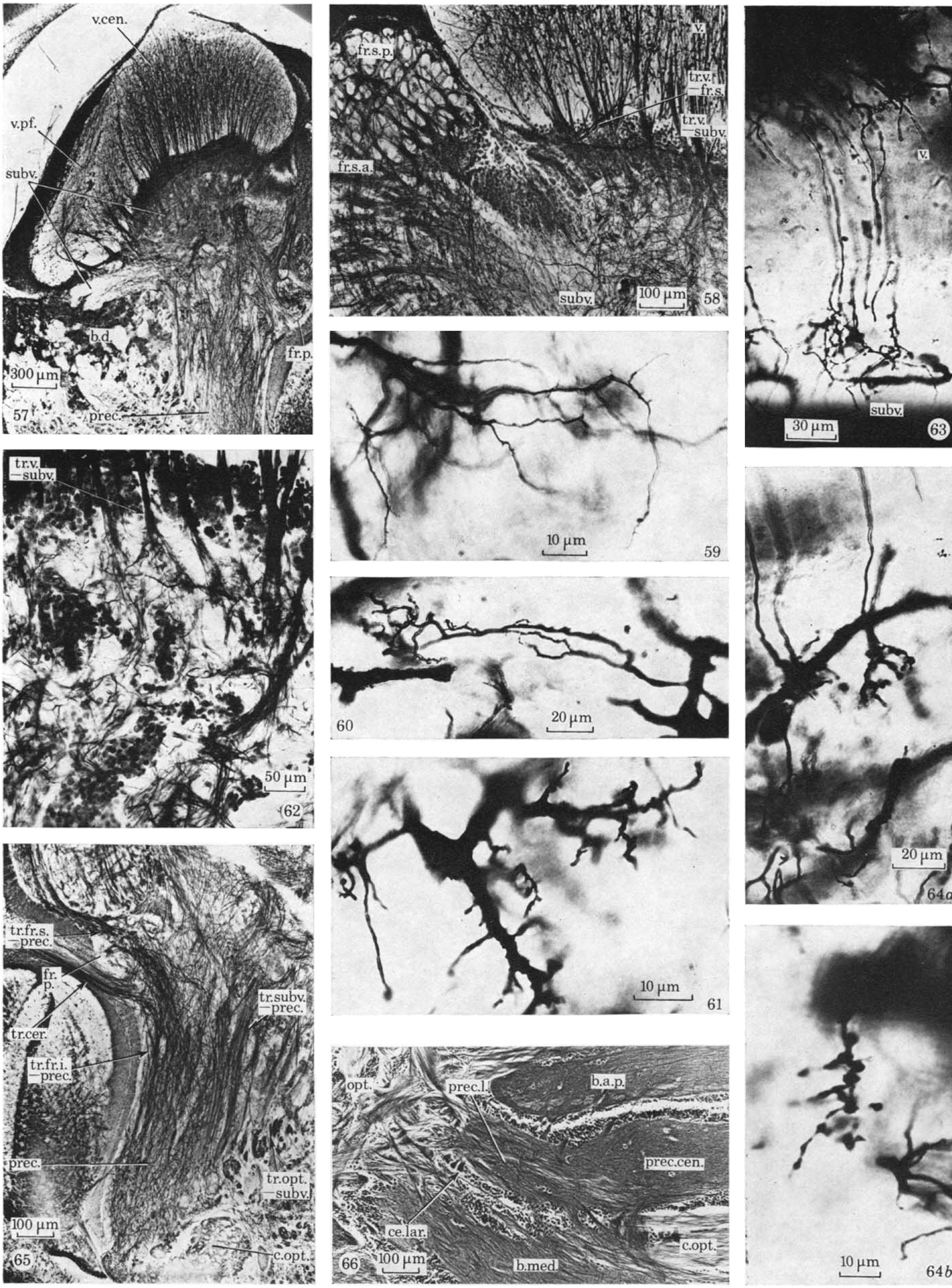
FIGURES 25–33. For description see opposite.



Figures 34–44. For description see opposite.



FIGURES 45–56. For description see p. 346.



FIGURES 57–66. For description see p. 347.

Figures 67–75. For description see opposite.