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THE NERVOUS SYSTEM OF *LOLIGO*
III. HIGHER MOTOR CENTRES: THE BASAL SUPRAOESOPHAGEAL LOBES

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[Plates 1–9]

CONTENTS

The three main basal lobes are orientated in different planes set approximately at right angles. The components of each are similar and based on an organization reminiscent of a cerebellum, like that of the peduncle lobes. They all have large cells and fibres ventrally and numerous small cells dorsally. Each of the two parts of the anterior basal lobe contains a region with numerous very fine parallel fibres, similar to the 'spine' of the peduncle lobes. The dorsal basal lobes contain a similar system, but less regular.

The three main parts of the basal lobe system all send fibres to the oculomotor centres of the lateral pedal lobes. The two parts of the anterior basal lobe also send fibres to the centres controlling arm movements in the anterior pedal lobe. The median basal lobe sends large tracts to the posterior pedal lobe, controlling movement of the funnel and fins. It also sends a large tract to the region of the first order giant cell, initiating the jet. There is a further massive system of descending fibres from all the basal lobes (and the precommissural lobe) sending branches to all parts of the magnocellular and palliovisceral lobes.

The functional organization of the basal and peduncle lobes can be understood as follows. They all receive visual and static inputs and send large outputs to the oculomotor centre and back to the optic lobes. The oculomotor centre also receives direct inputs from the statocyst. The control of eye movements is thus organized in cephalopods in the same way as it is in vertebrates: there is a direct static input to the oculomotor centre, which also receives indirect static influences combined with visual ones, by way of the cerebellum in vertebrates, or basal and peduncle lobes in cephalopods.

The basal and peduncle lobes show further similarity to the cerebellum in the presence of the numerous parallel fibres of various diameters, some very fine. These lobes receive dorsal and ventral sets of visual fibres and a set from the magnocellular lobes. The dorsal visual fibres follow the topology of the optic lobes and it is suggested that they provide a tracking system. The numerous fibres passing back from the basal lobes to the optic lobes, allow for a 'corollary discharge' ('efference copy'). The ventral set of large fibres from the optic lobes to the basal lobes may serve to promote the final attack, after the smaller fibres have produced the preliminary tracking movements. The system of large fibres from the magnocellular to the basal lobes are perhaps concerned with avoiding reactions. Each of the large fibres of both of these sets gives branches to all parts of the basal lobes.

All the basal lobes contain many microneurons with trunks limited to the lobes. Some of these are very short amacrines. The median basal and dorsal basal lobes contain especially numerous small cells, perhaps neurosecretory and related to reproduction by way of the optic gland, whose nerve arises nearby.

1. Introduction

This series of papers aims to provide a description of the organization of a squid's brain as shown by light microscopy. The present analysis of the basal lobes is much more complete than was possible in *Octopus* (Young 1971). The large size of many of the fibres in squids has allowed patterns of connection to be established that had not been suspected before. Moreover, the significant features of the parts are becoming more clear as information accumulates showing the similarities and the differences between the brains of various cephalopods (Young 1976*c*). These higher motor centres of the basal lobes have been in some ways the most difficult to analyse. They presumably cooperate with the still higher parts of the brain in reaching 'decisions' as to what action is to be taken and also with the lower parts in the execution of such acts. We have little understanding in any animal of how such functions are performed. There are now indications that these lobes in cephalopods have some similarities to the vertebrate cerebellum, which occupies a comparable position in the hierarchy of the brain. Information about their organization may help to reach an understanding of the principles that are involved in decisions about action, and in the organization of motor activities.

The analysis of these higher motor centres is greatly helped by the fact that it has already been possible to resolve the lower motor centres of the suboesophageal lobes of decapods into their functional components (Boycott 1961; Young 1976*a*). This has been done by stimulation experiments and by tracing the relevant connections anatomically. We can thus proceed to investigate how the higher members of the hierarchy that are considered in this paper are related to the motor centres, for example the oculomotor nuclei and the giant cell system.

It is remarkable that the basal lobes considered here have no direct connections with the vertical lobe system, although this lies anatomically directly above them. These basal lobes receive a major part of their input from the optic lobes and to avoid artificial separation it is better first to consider together all the lobes between the optic and the suboesophageal centres. The lobes on the optic tract (peduncle and olfactory lobes) have in the past usually been treated separately and will indeed be described in this series in a separate paper (Messenger 1977). But first we should consider all the lobes together, and these are, on each side:

peduncle lobes olfactory lobes	optic tract lobes
dorso-lateral lobes subpedunculate lobes dorsal basal lobes median basal lobes lateral basal lobes	posterior basal lobe
anterior anterior basal lobes posterior anterior basal lobes	anterior basal lobes

Naming of these lobes would perhaps ideally be in terms of the actions they control. But knowledge of function is imperfect and following Dietl (1878), recognition on a basis of position has been usual, and will be retained (see Young 1971). The lobes are mainly arranged across the supraoesophageal mass and down at the sides. This provides the opportunity for important commissural connections. The question of whether this plan is the result of ancestral conditions is discussed on page 391.

There is a primary division into anterior basal and posterior basal lobes, but both of these are complex and are here sub-divided. The anterior basal lobe consists of two distinct parts, both in the transverse plane, but one extended largely dorso-ventrally and the other transversely. Each contains the same component features. The posterior basal lobe is set in an oblique near-horizontal plane and its median basal and dorsal basal parts show some of the same 'cerebellar' features. However, it is more complex and contains in addition other lobules concerned with various functions (p. 376).

In this paper, a description is given of some of the features of the various parts of the anterior and posterior basal regions of *Loligo* and the closely related but smaller squid *Alloteuthis*. The material and methods used were those described in the first two papers of this series (Young 1974, 1976*a*).

2. Plan of organization of the basal lobes

The main parts of the basal lobe system constitute three separate but similar units, two of them in the anterior basal lobe and one in the posterior basal lobe, all concerned with the control of movement of the eyes and of the whole animal. All three are organized on a similar plan, including sets of fine parallel fibres, but they are extended in different directions approximately at right angles to each other. The peduncle lobes are organized on the same plan and

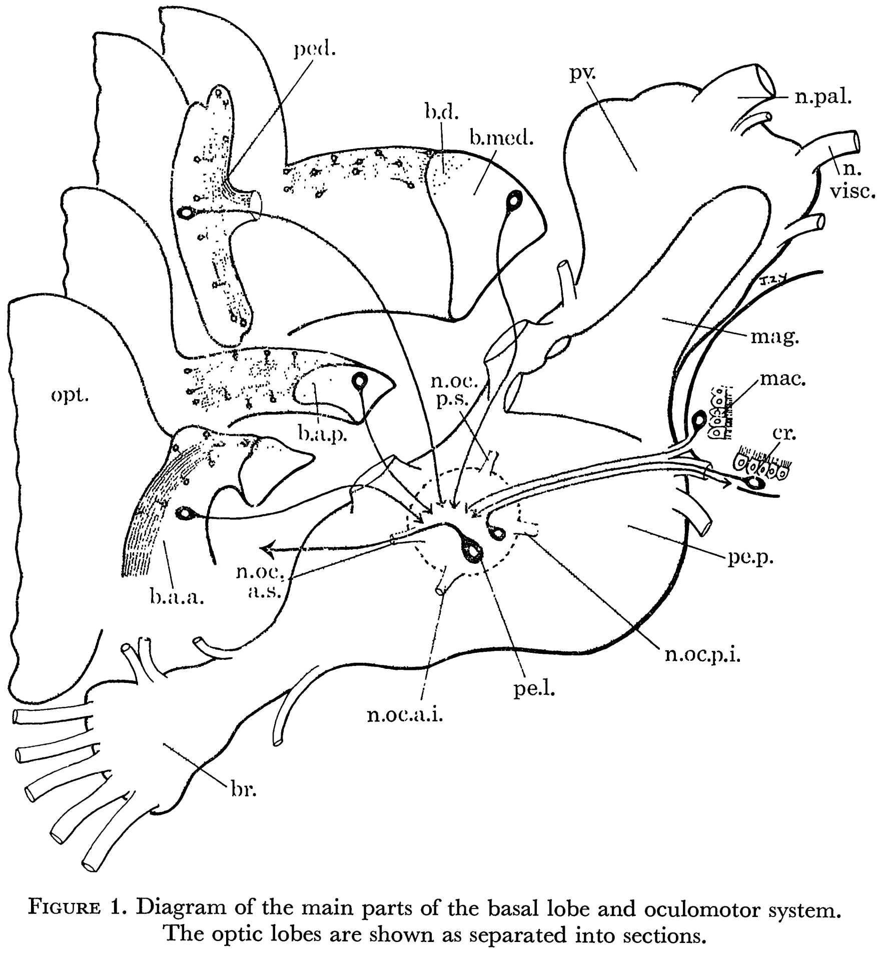

FIGURE 1. Diagram of the main parts of the basal lobe and oculomotor system. The optic lobes are shown as separated into sections.

there are therefore four lobes with this 'cerebellar' type of organization on each side (figure 1, above). They are concerned with producing responses to combined visual and statocyst inputs, providing appropriate orientation in relation to the movement of fellow squids (in schooling) or to food or enemy objects. The squid, like most other cephalopods, depends largely upon the eyes for its tracking movements and a large part of the output from these basal lobes proceeds to the oculomotor centres and another part back to the optic lobes, providing a 'corollary discharge' or 'efference copy' (Sperry 1950; v. Holst 1973).

Each of the basal and peduncle lobes is elongated and contains sets of fibres and cells of a graded series of sizes (Messenger 1971; Woodhams 1975; Messenger & Woodhams 1976). The largest fibres and cells occupy a region at one end, which has been called basal in the peduncle lobe, while the finest parallel fibres and smallest cells occupy the other end, the 'spine' (figures 2 and 3, plate 1). We can therefore recognize a plane and direction of elongation for each lobe. The planes are hard to describe exactly because the whole orientation of the optic lobes and brain is oblique with reference to the principal axes of the animal (Young 1974, 1976*a*). This obliquity has probably itself a functional significance related to the fact that when these squids move forwards the head is held higher than the tail and conversely when swimming backwards. It is not easy to define the horizontal plane of the brain, since the oesophagus does not run in that plane. However, the floor of the supraoesophageal mass is approximately horizontal (figure 3, plate 1). The optic lobe is set at an angle of about 60° to the horizontal anatomical plane of the body, with the higher end in front. The peduncle and basal lobes are also set at this angle, with the higher ends in front for the anterior basal and behind for the median basal lobe (figure 3, plate 1). We shall however use the terms 'vertical' and 'horizontal' to indicate the approximate planes of orientation. The orientations of these various parts of the system are probably important functional features. The projections of the optic lobe maintain the topographical relations of the retina. It seems likely that the peduncle and basal lobe systems reflect the same topology and serve to translate the information into appropriate instructions to the muscles that produce eye-movements and locomotion.

Each of the lobes has large cells ventrally, with axons proceeding to the motor centres of the pedal lobe, including fibres to the eye muscle centres of the lateral pedal lobe. Other cells send axons back to the optic lobes of the same and the opposite sides. Most dorsally each of the lobes

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Description of plate 1

All are of sections stained with Cajal's silver method unless otherwise stated. All figures are mounted with the dorsal side upwards or the anterior end below (unless stated otherwise).

Figure 2. Horizontal section showing the peduncle lobe and the three parts of the basal lobes of a young *L. pealeii.*

Figure 3. Sagittal section near the mid-line to show the basal lobes. *L. pealeii.*

Figure 4. Section laterally in the sagittal plane, showing the lateral anterior basal lobe. *L. pealeii.*

Figure 5. (*a*) Transverse section of the anterior anterior basal lobe, re-touched to show the efferent fibres and the large afferent fibres of the ventro-lateral optic to anterior basal tract, some uncrossed (tr.opt.–b.a.ven.), some after crossing (tr.opt.–b.a.ven.cr.). *L. pealeii.*

Figure 7. Sagittal section at the side of the anterior basal lobes to show the two regions of the fine parallel fibres ('spines'). The complete course of a cell of the posterior anterior basal to lateral pedal lobe tract is shown retouched. *L. vulgaris.* Holmes' method.

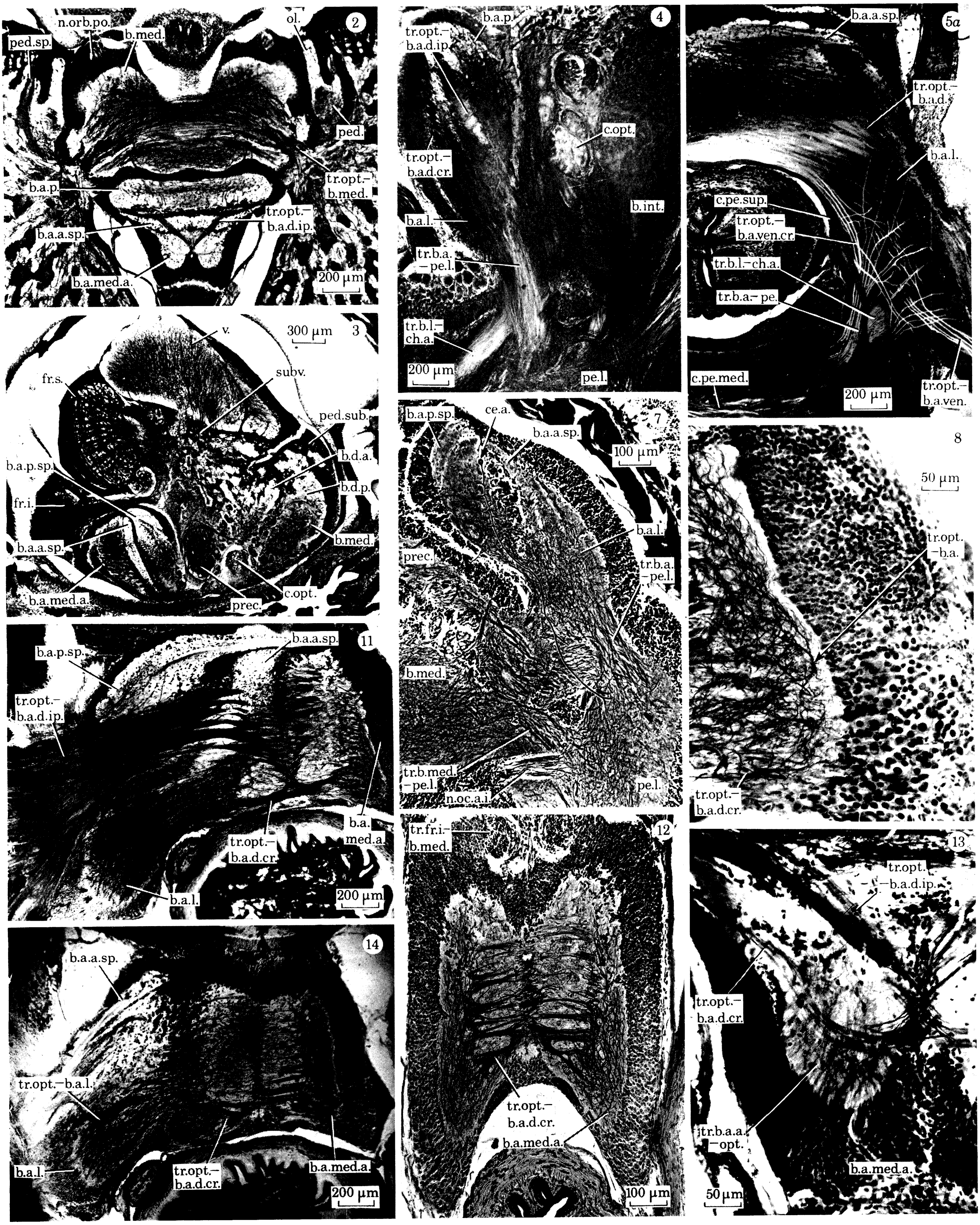
Figure 8. Transverse section of the antero-median lobule, showing cell sizes decreasing from ventral to dorsal, with a sharp decrease where the 'spine' region begins. Fibres of the optic to anterior basal tracts run across the trunks of cells of the lobe (see figure 32, plate 3). *L. pealeii.*

Figure 11. Oblique transverse section at the front of the anterior anterior basal lobe to show the dorsal optic to anterior basal tract and its crossings. *L. pealeii.*

Figure 12. Transverse section at the front of the antero-median lobule. Note the cell-sizes decreasing from ventral to dorsal, also the crossings of bundles of the dorsal optic to anterior basal tract and fibres of the lateral optic to anterior basal tract ascending vertically. *L. vulgaris.*

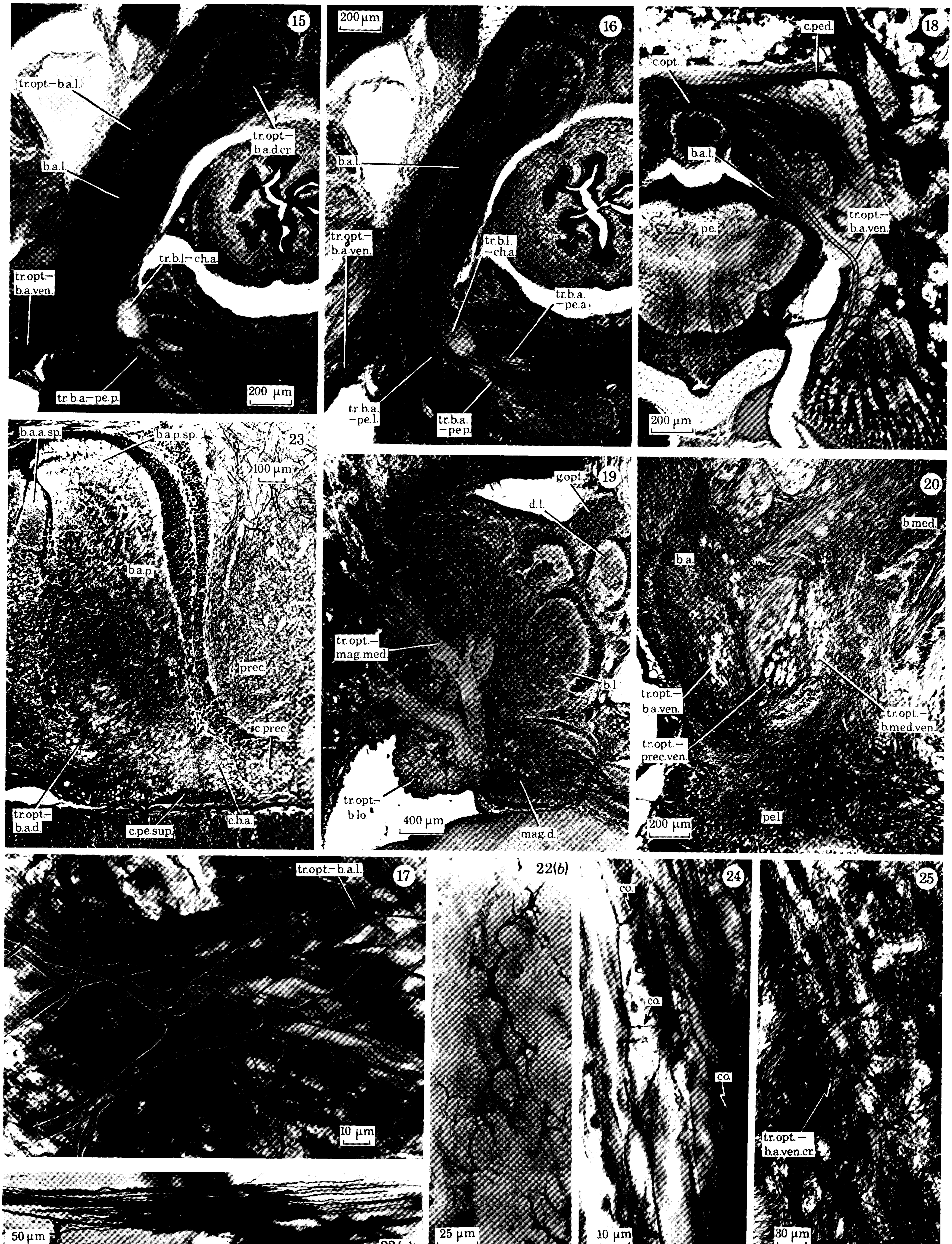
Figure 13. Horizontal section of a young animal to show the crossed bundles of the dorsal optic to anterior basal tract running to the lateral part of the lobe. Also fibres of the antero-median lobule running back towards the ipsilateral optic lobe. *L. pealeii.*

Figure 14. Oblique transverse section slightly in front of figure 11. Showing the complex interweaving of the bundles of the crossed dorsal optic to anterior basal tract and their unions with the bundles of the lateral optic to anterior basal tracts. *L. pealeii.*



FIGURES 2–14. For description see opposite.

(*Facing p.* 356)



FIGURES 15–25. For description see opposite.

has a 'spine' region of numerous very small cells with fine axons, many of which are elongated but do not leave the lobe, while others are very short amacrines.

Individual incoming visual and static fibres spread widely through the lobes, there is certainly not a sharp point-to-point localization. Nevertheless the visual fibres probably enter each lobe in a regular array, complicated by crossings, which maintain the topological relations that are conspicuous in the optic lobe (Young 1974). There are complex chiasmas on both the ipsilateral and crossed input pathways to the basal lobes, and probably also of the outputs to the optic lobes. These arrangements suggest that each lobe functions to control movements of the eyes or body by the regular progress of excitation along it. The functioning would thus depend upon the topology. Unfortunately it is not possible as yet to understand the details of these somatotopic arrangements. Indeed in the present state of knowledge it is difficult to give a fully coherent account of these lobes. There is very little in the previous literature to help. We shall try to present evidence that each of the parts named is a distinct unit and that all are organized on the same general plan. Not all the details of each feature appear equally clearly in every lobe.

3. The anterior basal lobe

3.1. *Position and relations*

This lobe lies behind the inferior frontal lobe and below the superior frontal and subvertical lobes, but it is not connected with these. Behind it lies the precommissural lobe and below it the perioesophageal sinus in the mid-line. It joins the middle suboesophageal mass at the sides. Laterally it receives very large tracts from the optic lobes and sends fibres back to them.

As already indicated, the lobe is considered to consist of two parts set at right angles to each other. They are separated by a narrow row of cells, which, however, is crossed by bundles of fibres running between them antero-posteriorly. The anterior and posterior parts of the lobe

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Description of plate 2

Figure 15. Oblique transverse section from another series of thick sections at a level further back than figure 11, showing the whole extent of the lateral anterior basal lobe and the dorsal and lateral sets of bundles of fibres joining it to the optic lobes. *L. peaeii.*

Figure 16. Same series as figure 15, but slightly further forwards, showing how bundles of fibres run from the lateral anterior basal to the lateral pedal lobe. *L. pealeii.*

Figure 17. Transverse section of the lateral optic to anterior basal tract, retouched to show that the large fibres cross each other and then divide within the lateral anterior basal lobe. *L. pealeii.*

Figure 18. Transverse section of young animal retouched to show the large fibres of the ventral part of the optic lobe running to the lateral anterior basal lobe. *L. pealeii.*

Figure 19. Sagittal section to show the bundle of large fibres of the optic to basal lobe tracts at the extreme ventral edge of the optic tract (tr.opt.–b.lo.). *L. vulgaris.*

Figure 20. Sagittal section medial to figure 19 showing the three separate bundles of large optic tract fibres. *L. vulgaris.*

Figure 22. (*a*) Fibrous glia cell from the fine parallel fibre region of the anterior anterior basal lobe. *Alloteuthis.* Golgi.

Figure 22. (*b*) Protoplasmic glia cell from the lateral anterior basal lobe. *L. vulgaris.* Golgi.

Figure 23. Sagittal section of the anterior basal lobe, showing the two regions of fine parallel fibres and the commissural bundles, especially those at the base with very large fibres. *L. vulgaris.*

Figures 24 and 25. Higher magnification of parts of the lateral anterior basal lobe seen in figure 5*a*, plate 1. Showing the large fibres coming from the opposite side and giving collateral branches (co.) and finally dividing (figure 25). These are probably the largest fibres from the opposite ventral optic to anterior basal lobe tract. *L. peaeii.*

join at the sides, where we may recognize a third division, the lateral anterior basal lobe at the sides of the oesophagus (figures 4 and 5*a*, plate 1). This constitutes part of the anterior anterior basal lobe and also carries the descending efferent tracts from both parts of the anterior basal lobe to the motor centres of the middle suboesophageal mass.

3.2. *Anterior anterior basal lobe*

This lies in an oblique vertical transverse plane, sloping backwards from above in front at about the same angle to the main axis of the animal as the optic and peduncle lobes. It extends far ventrally at the sides (figures 4 and 5*a*, plate 1). For description three parts may be recognized. (1) The lateral part contains large efferent cells, with axons passing to the oculomotor and other suboesophageal centres. (2) The antero-median lobule sends axons back to the optic lobes. (3) The parallel fibre region lies behind the other two and may influence the cells of both of them (figure 5*b*, and figure 49*a*, p. 370.)

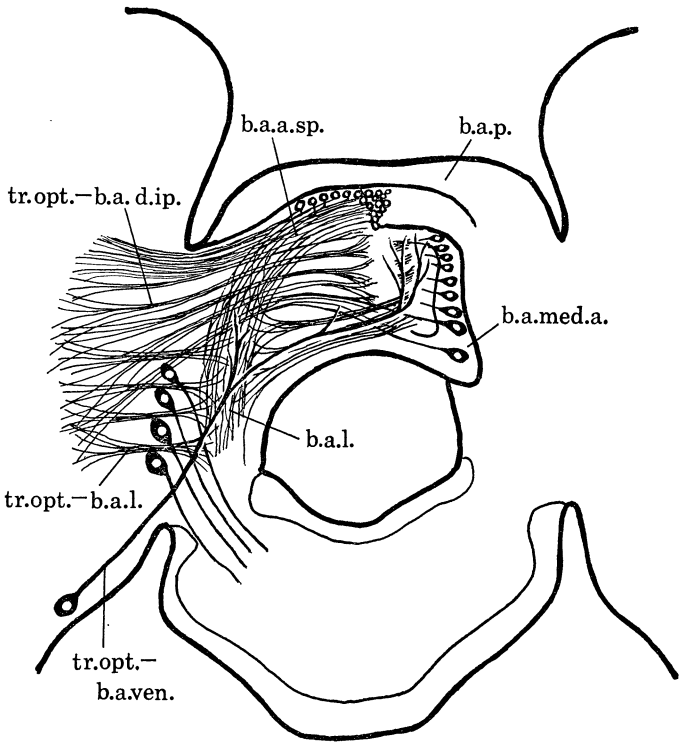


FIGURE 5 (*b*). Diagram of some of the connections of the anterior anterior basal lobe. The figure is of an oblique transverse section seen from the front. It is further forward on the left than the right.

The antero-median lobules lie in front dorsally. The parallel fibre zone has the form of a plate placed in the transverse vertical plane between the other two parts of the anterior anterior basal in front and the posterior anterior basal behind (figure 2, plate 1). Its fibres extend laterally down into the lateral anterior basal lobe (figure 14, plate 1), which joins the pedal lobe below.

3.3. *Efferent cells and output of the anterior basal lobe*

The lateral region can be considered first. It contains the main cells carrying impulses down to lower motor centres. These cells lie on its anterior and lateral faces. The wall here includes cells of various sizes from 30 μm diameter downwards (figure 5*a*, plate 1). The largest cells are the most ventral and the sizes decrease passing upwards. The cells send their axons down to the pedal lobe of the same side. Their main trunks are narrow close to the cell body and here stain darkly with silver. Further away they enlarge and proceed to the centres of the anterior and posterior pedal lobes. They have wide-spreading dendritic trees orientated in a general direction up and down the lobe (figure 6, below). The larger of the dendrites have main trunks from which spring secondary branches ending in tufts with numerous collaterals. Each of these cells must make many hundreds of terminal contacts, perhaps thousands. The rather smaller cells higher up the sides of the lobe have fewer main branches and numerous fine dendritic collaterals (figure 6). They have bushy terminals at various levels, presumably making contact with several of the ascending and descending bundles (p. 366). Many of their axons pass to the lateral pedal (oculomotor) lobe, others may pass to the optic lobe of the same side or backwards to the other basal lobes.

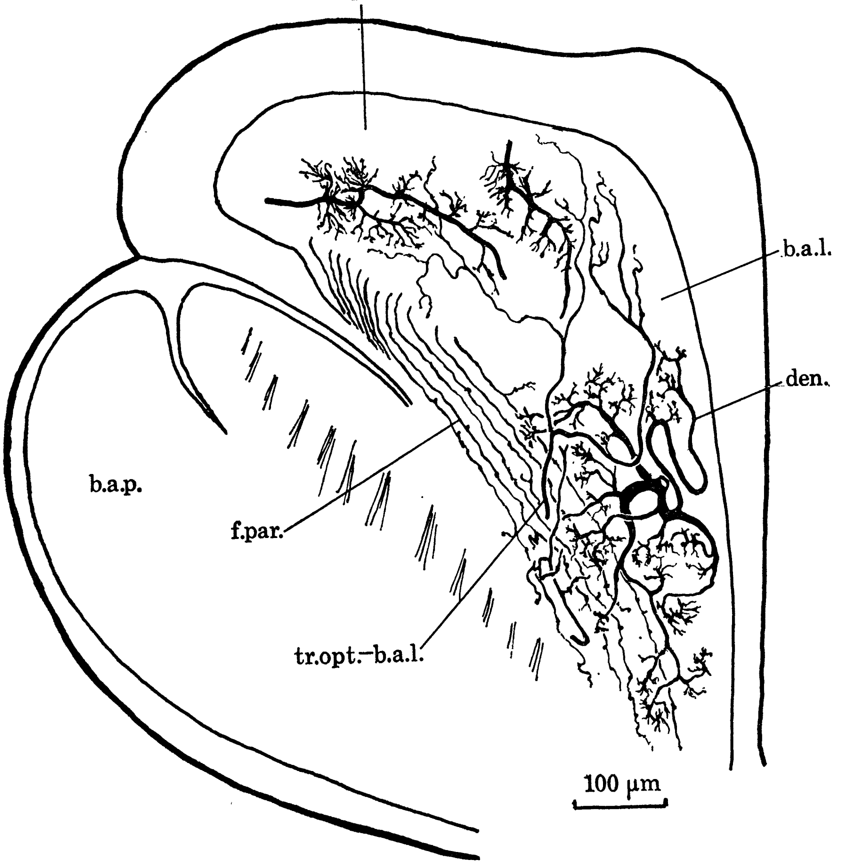


FIGURE 6. Drawing of a sagittal section of the lateral anterior basal lobe, to show parallel fibres, also the dendritic trees (den.) of a large efferent cell ventrally and smaller ones dorsally. Crossing these are the ascending branches of large fibres of the lateral optic to anterior basal tracts (tr.opt.–b.a.l.). *Alloteuthis*. Golgi.

In the more ventral parts of the lateral lobe none of the cells are very small amacrines, but passing dorsally small cells become more numerous and large cells fewer, until dorsally the lateral part of the lobe joins the parallel fibre ('spine') region, where the cells are all medium or small in size (figure 7, plate 1). There is here a rather thick anterior dorsal wall of uniformly small cells. This is continuous medially with the antero-median lobule, which is a conspicuous swelling with small cells dorsally, larger ones more ventrally (figure 8, plate 1). Its antero-ventral wall is comprised wholly of medium-sized cells, from 30 μm downwards, most, probably all, of which send axons to the opposite optic lobe (figures 9 and 10, pp. 360, 361, figure 49*a*, p. 370). The smaller cells more dorsally send their axons to the optic lobe of the same side, while some are microneurons restricted to the lobe (p. 368).

The larger cells sending axons back through the commissure to the opposite side have dendritic collaterals extending in all directions, mostly rather thin and simple and up to 20 μm long (figures 9 and 10, pp. 360, 361, figure 31, plate 3). Some of the dendrites, however, are short

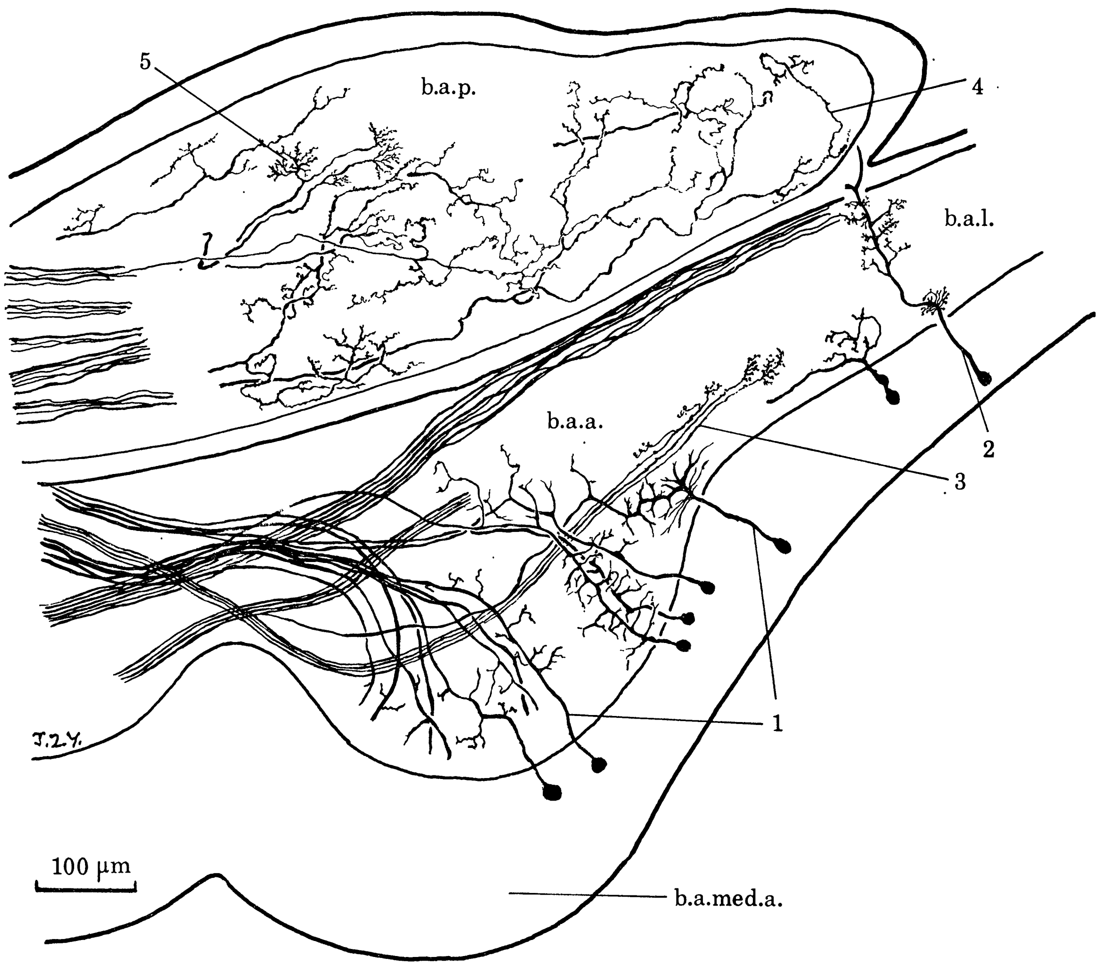


FIGURE 9. Drawing of a horizontal section of the anterior basal lobes, showing (1) cells of the median lobule with axons passing back to the opposite optic lobe, (2) cell of the lateral lobe with axon probably passing to other basal lobes, (3) endings of crossed fibres of the dorsal optic to anterior anterior basal tract, (4) crossed fibres of the dorsal optic to posterior anterior basal tract, (5) another type of ending in the posterior anterior basal lobe. *Alloteuthis*. Golgi.

and complex, especially those close to the cell layer. Each of these cells of the antero-median lobule thus samples a cylindrical field of neuropil in the path of incoming afferent fibres. The dendritic fields are regularly arranged but many neighbours overlap. Fields, like the axons, are largest ventrally and decrease progressively passing upwards.

The output of the anterior basal lobe thus passes to the following destinations: (1) the lateral pedal lobe (oculomotor centre); (2) the anterior pedal lobe (arm control centre); (3) the posterior pedal lobe (funnel control centre); (4) the palliovisceral lobe (fin control centre), this tract is described on page 384; (5) the other basal lobes; (6) the optic lobes of both sides.

3.4. *Input to the anterior anterior basal lobe*

3.4.1. *Introduction*

Afferents have been seen to come from (1) both optic lobes, (2) from the other basal lobes, (3) from the statocyst, (4) from the magnocellular lobe (figure 49*a*, p. 370). The connections of the lobe with the optic tracts are thus made by numerous bundles, containing fibres running in both directions. They form a complex system that is difficult to describe since the fibres passing in the two directions run in the same tracts. Some fibres cross while others remain on the same side. There are elaborate plexiform arrangements, especially in the dorso-ventral

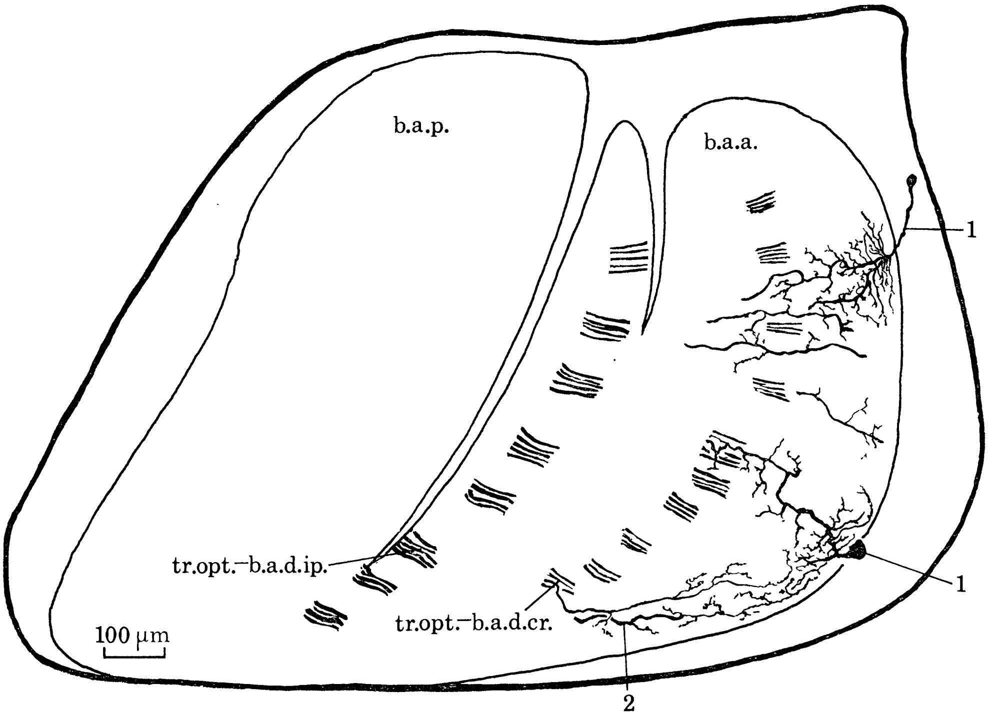


FIGURE 10. Drawing of a sagittal section of the antero–median lobule of the anterior basal lobe to show (1) cells with axons passing back to the opposite optic lobe, (2) afferent fibres from the crossed dorsal optic to anterior basal tract. *L. vulgaris*. Golgi.

plane and perhaps related to the chiasma of the optic nerves and the inversion of the retinal image (see Young 1974). The optic tract connections may perhaps include functionally distinct sets, some concerned with tracking of prey, others with the launching of an attack and still others with escape, shoaling or reproduction.

With all these complications these optic tracts seem to be divisible into three sets, the dorsal, lateral and ventral optic to anterior anterior basal lobe tracts (figure 5, p. 358, figure 49*a*, p. 370). The first set runs to the mid-line and forms an elaborate chiasm in the region between the antero-median lobules (figures 11 and 12, plate 1). The second consists of a set of bundles all down the sides of the lateral anterior basal lobes (figure 15, plate 2). Both sets probably contain fibres running in both directions. The third (ventral) set consists of very large fibres running to all the basal lobes (p. 362).

3.4.2. *Dorsal optic to anterior anterior basal tract*

These fibres arise in a very regular manner as seen in the transverse vertical plane from the optic lobe (figure 11, plate 1). As they approach the mid-line they become segregated into a series of bundles and these then form an elaborate system of crossings, perhaps producing a complete chiasma in which the dorso-ventral axis is reversed. Parts of this crossing system can be seen in figures 11 and 12, plate 1. After crossing some of the bundles turn forwards and their fibres end in the antero-median lobule (figures 12 and 13, plate 1). Each fibre makes fine terminal twigs occupying a considerable volume of the neuropil (figure 10, p. 361). Other bundles after crossing sweep laterally, some of the fibres reaching to the extreme lateral and ventral part of the anterior basal lobe (figure 14, plate 1), while others turn up or down and terminate earlier (figure 12, plate 1). At the sides of the antero-median lobes there is further interweaving of the bundles (figure 14, plate 1). They then proceed down the lateral part of the lobe. Here they not only interweave still further but also receive bundles from the incoming lateral optic to anterior basal tracts (figure 15, plate 2). This region thus contains a network of fine interweaving bundles running in a general downward direction along the lobe (figure 16, plate 2).

3.4.3. *Lateral optic to anterior anterior basal tract*

These bundles lie ventral to the last and enter the lateral part of the lobe all down its side (figures 14, plate 1 and 15, plate 2). They contain many fibres running from the optic to the anterior basal lobe and probably some passing in the opposite direction. The origins of the fibres in the optic lobes have not been fully traced. They enter the lateral anterior basal lobe as a series of bundles in which the fibres cross in a system that is probably regular and may serve to allow fibres from the more dorsal bundles to reach ventrally and vice versa. The bundles contain many large fibres, especially the more ventral ones. These fibres begin to divide as they enter the lobe and their branches proceed up and down within it (figure 17, plate 2).

3.4.4. *Ventral optic to basal lobes tract*

The most ventral of the optic to anterior basal fibres are the largest of all and are part of a special system of very large fibres leaving the ventral part of the optic lobe. They include the largest of all fibres in the optic tract and evidently serve a distinct function. Fibres of this system run not only to the anterior basal lobe but also to the precommissural, median basal, interbasal, magnocellular and (probably) peduncle lobes. Individual fibres send branches to more than one of these lobes, some perhaps to all of them (figure 26, p. 363). These large fibres enter the lateral anterior basal lobe at its extreme antero-ventral point, immediately above the lateral pedal lobe (figures 15 and 18, plate 2). They pass as a conspicuous bundle occupying the ventral edge of the optic tract, below the lateral optico-magnocellular tract (figure 19, plate 2). At the base of the optic lobe there is a group of especially large cells, occupying the medial ventral wall of the hilum (figure 18, plate 2). These cells have numerous dendritic collaterals in the neuropil of this ventral region of the lobe, which thus makes a special centre below and in front of the peduncle lobe. The large axons (up to 30 μm diameter) come together to make up the ventral optic to basal lobe tracts. The three bundles destined for these basal lobes separate where they enter the brain (figure 20, plate 2). One bundle runs to the anterior basal, the next to the precommissural, and the hind one to the median basal and interbasal lobes. A separate

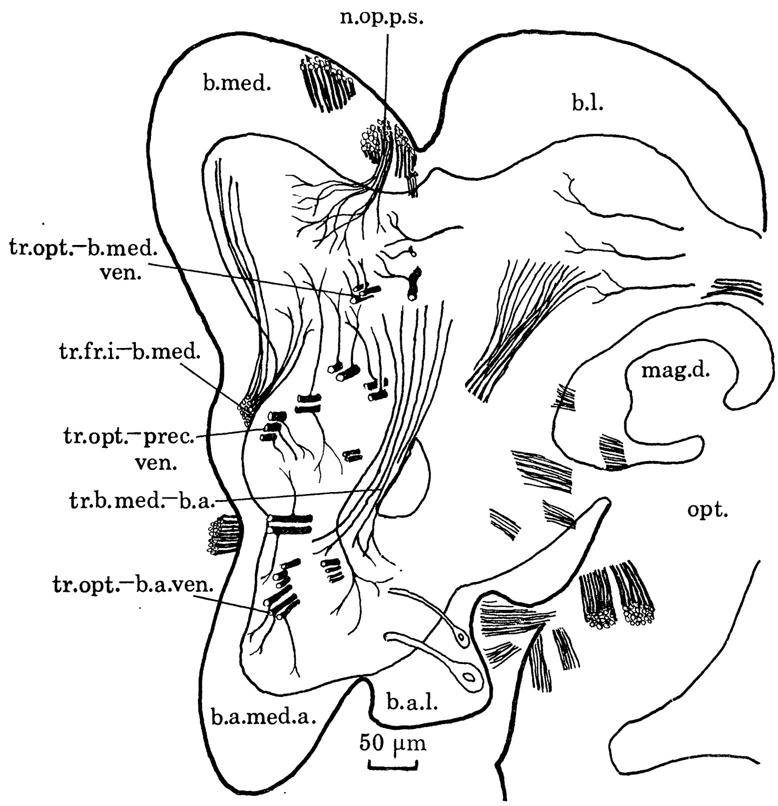


FIGURE 21. Drawing of a horizontal section of a young animal to show the branches of all the three bundles of large ventral optic to basal lobe fibres. *L. pealeii*. Cajal.

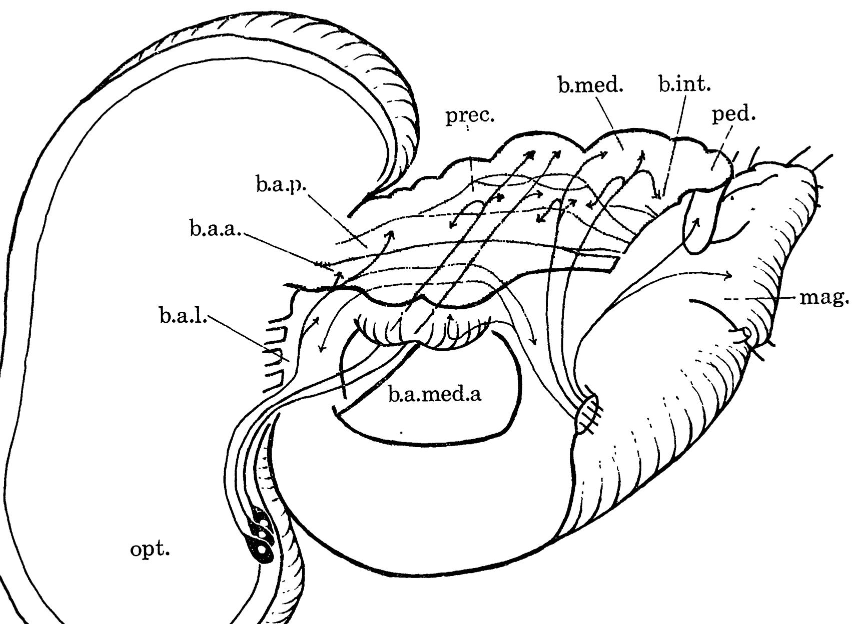


FIGURE 26. Diagram to show the courses of the fibres of the ventral optic to basal lobes tract. The shaded area is meant to show the upper surfaces of the basal lobes as revealed by a horizontal cut.

bundle runs to the magnocellular lobe and another has been traced towards the basal part of the peduncle lobe and it is assumed that it reaches to it (figure 26, p. 363).

The fibres in the bundles for the basal lobes divide as they pass upwards and each sends branches to one or more of the lobes of the same side (figures 21 and 26, p. 363, 34, plate 3). The main trunks then curve medially and cross in the commissural system at the base of the basal and precommissural lobes (figures 23, plate 2 and 28, plate 3), finally proceeding to distribution on the other side. They can be seen in figures 5*a*, plate 1 and 24, plate 2, descending after crossing and giving branches in the opposite lateral anterior basal lobe. They reach to its lowest part, where they end in a regular series of branches (figure 25, plate 2). It has not been possible to follow even the largest of these fibres individually for its full course, but it may be that single fibres send branches to all the basal lobes of both sides. Certainly some fibres send branches to several lobes on one side and then cross. The possible functions of this very wide-spreading system are discussed on page 394.

3.4.5. *Statocyst fibres to the anterior basal lobe*

The input from the same side consists of a compact bundle of small fibres passing forwards and upwards across the lateral basal to anterior chromatophore lobe tract (figure 27, plate 3), and reaching to both parts of the anterior basal lobe. The fibres probably include some from both the crista and the macula. Some of them may cross above the oesophagus in a suprapedal commissure (figure 23, plate 2) and spread out in the anterior basal lobe of the opposite side (Young 1976*a*). Within the anterior anterior basal lobe the static nerve fibres join the bundles of large optic tract fibres at the base of the antero-median lobule to form part of the system of fibres running upwards, but details of their endings are unknown.

There may also be branches of the large fibres of the crista nerve running to the anterior basal lobe. Large fibres pass from the middle pedal commissure to the lobe, but it has not been possible to distinguish between descending efferent fibres (p. 358) and possible afferents from the large crista nerve fibres.

Description of plate 3

Figure 27. Sagittal section to show the static nerve to anterior basal lobe tract. *L. pealeii.*

Figure 28. Horizontal section retouched to show the tracts running between the basal and precommisural lobes and the large fibres in the commissures. This is a thick section (100 μm) but the full courses of the branches of the very large fibres can only be followed approximately. They certainly spread very widely through the basal lobes. *L. pealeii.*

Figure 29. Thick horizontal section retouched to show the fibres running back from the anterior basal to the other basal lobes. Also the large lateral optic to anterior basal lobe fibres branching as they approach the commissure (c.b.a.). *L. pealeii.*

Figure 30. Transverse section to show the parallel fibres of the anterior anterior basal lobe passing down into the lateral anterior basal lobe. *L. pealeii.*

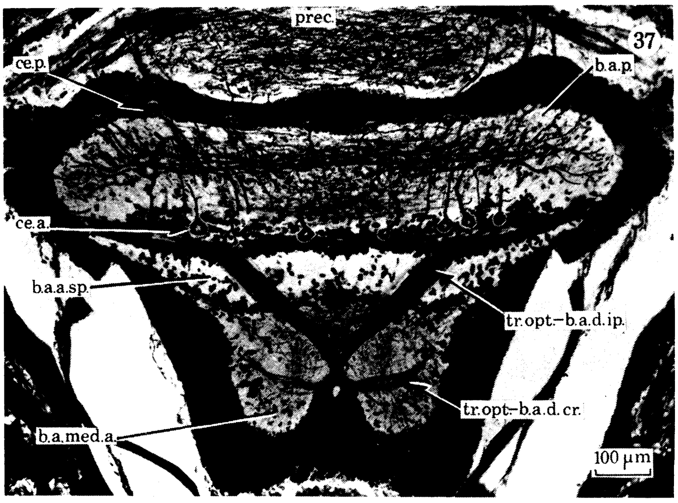
Figure 31. Horizontal section showing the trunks of the cells of the antero-median lobule giving collaterals and then passing through the commissure to the opposite optic lobe. *Alloteuthis.* Golgi.

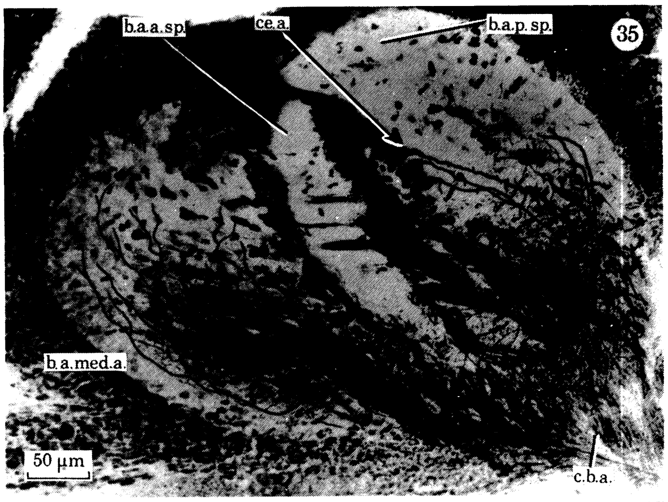
Figure 32. Transverse section of the front of the antero-median lobule of the anterior basal lobe, with the ascending branches of the fibres of the optic to anterior basal tract retouched. *L. pealeii.*

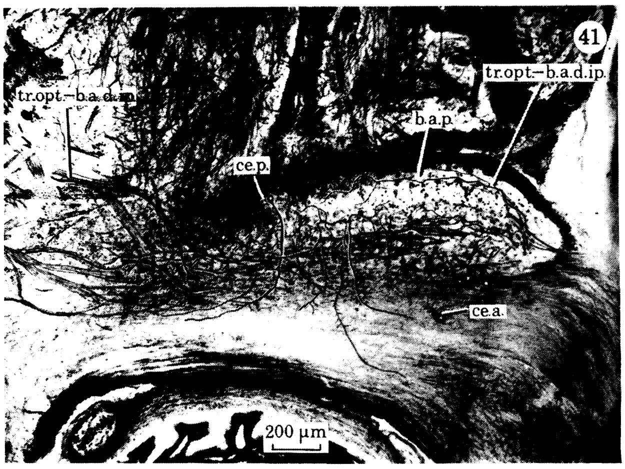
Figure 33. Sagittal section to show especially the transverse fibres of the posterior anterior basal lobe. The fibres are large ventrally, but smaller dorsally, where there are several rows of fine parallel fibres in the 'spine'. *L. pealeii.*

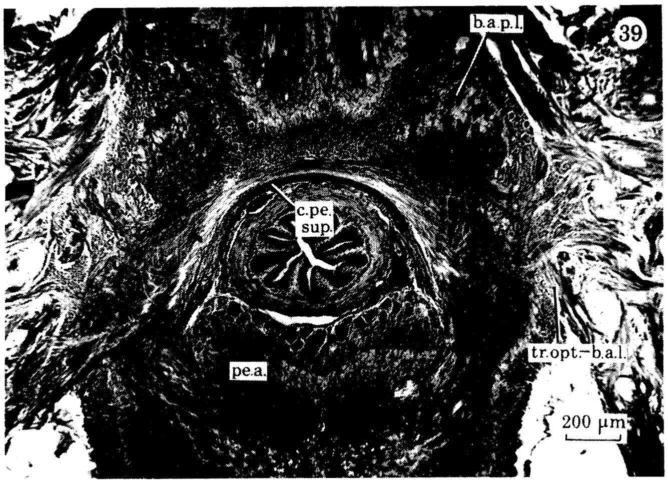
Figure 34. Sagittal section of a young animal retouched to show the large fibres of the ventral optic to anterior basal tract sending branches forward towards the precommissural lobe. *L. pealeii.*

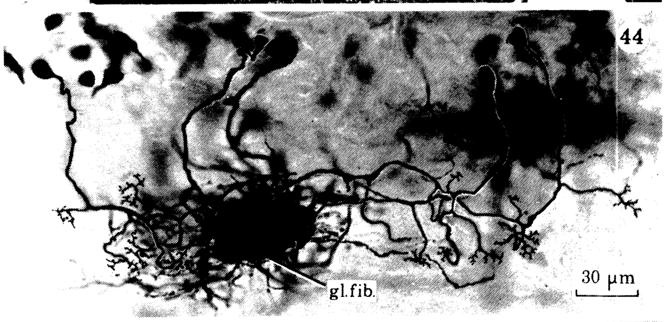
FIGURES 27–34. For description see opposite.

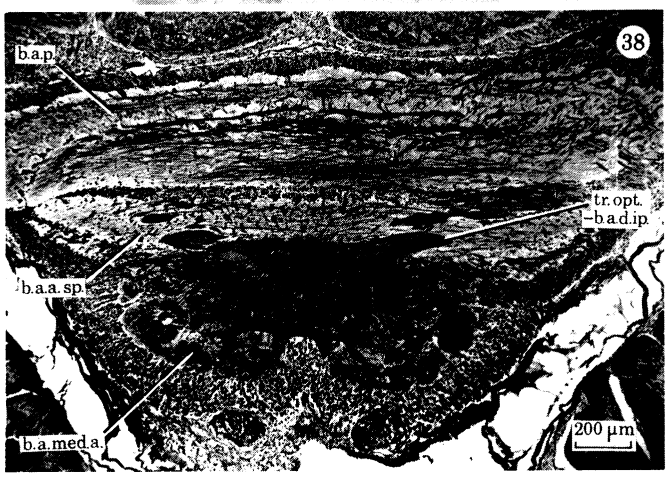












FIGURES 35–46. For description see opposite.

3.4.6. *Fibres running between the basal lobes*

An elaborate web of fibres runs forwards and backwards making connections in both directions between all three basal lobes and the precommissural lobe (figures 28, 29, plate 3, figure 56, plate 5). The fibres interlace in complicated patterns. Some of the smaller cells high up the sides of the lateral anterior basal lobe send their axons backwards to the other basal lobes (figure 29, plate 3). Fibres in the opposite direction join the bundles that run down the lateral anterior basal lobe.

3.4.7. *Magnocellular to anterior basal tract*

The large fibres that run up into the median basal lobe from the magnocellular lobe send collaterals forwards to the anterior basal lobe (p. 381). They run beneath the optic commissure and through the interbasal region. They turn up into both parts of the anterior basal lobes, but their detailed distribution has not been followed.

3.5. *Organization of the anterior anterior basal lobe*

3.5.1. *Organization of the lateral anterior basal lobe*

This neuropil is organized around the very numerous fibres that run along it in a vertical direction (figures 6, p. 359, 16 and 30, plates 2 and 3). These include fibres from several sources. The fine crossed axons of the dorsal optic to anterior basal tract make the descending bundles already described (p. 362). Fibres from the static nerves and from the other parts of the basal lobe complex also join these bundles. Among them pass the descending trunks of the larger cells of the lateral anterior basal lobe, proceeding to the lateral pedal and anterior and posterior pedal lobes. The fine parallel fibres form another component of these bundles. They descend from the spine region (figure 5*b*, p. 358, figure 14, plate 1) giving lateral branches as they pass (figure 6, p. 359). The fibres of the lateral and ventral inputs to the lateral anterior basal from the optic lobe enter and leave at the sides and below. Some of them form spreading trees across the descending bundles (figure 6).

DESCRIPTION OF PLATE 4

FIGURE 35. Sagittal section, of a young animal, medial to figure 34, plate 3, retouched to show the ascending fibres of the ventral optic to anterior basal lobe tracts and the descending fibres of the posterior anterior basal to pedal lobe tract (ce.a.). *L. pealeii.*

FIGURE 37. Horizontal section of a young animal, retouched to show the fibres and cells of the posterior anterior basal lobe. *L. pealeii.*

FIGURE 38. Horizontal section of the anterior basal lobe to show the orientation of fibres and cells. *L. forbesi.*

FIGURE 39. Transverse section of the extreme hind end of the anterior basal lobe. Note the large cells of the lateral lobules of the posterior anterior basal. Also the lateral optic to anterior basal tracts with large fibres, especially ventrally. *Alloteuthis.*

FIGURE 41. Transverse section of the posterior anterior basal lobe, retouched to show fibres entering from the optic lobes. Also shown are the trunks of cells of the back of the lobe (ce.p.) giving dendrites and then passing to the same or the opposite sides they cross bundles of fibres entering from the optic lobes. The section is oblique and further forward on the right, the large anterior cells of the lobe are seen (ce.a.) (see also figure 52, plate 5). *L. pealeii.*

FIGURE 44. Transverse section of the parallel fibres of the posterior anterior basal lobe, retouched to show the bushy dendrites at the origin of the trunks of the small cells. Note large fibrous glia cell. *Alloteuthis.* Golgi.

FIGURE 45. Transverse section of the parallel fibre region of the posterior anterior basal lobe showing collateral branches of an axon (n.f.) and a glia cell body and fibres (gl.fib.) *Alloteuthis.* Golgi.

FIGURE 46. Transverse section showing large cells of the postero-lateral region of the posterior anterior basal lobe; retouched. *L. pealeii.*

Presumably the arrangement of the fibres within the lateral anterior basal lobe is relevant for its functioning. The dorsal and ventral optic inputs pass through the lobe in opposite directions. This suggests systems for serial activation, perhaps modulated in some way by the fine fibres that descend from the parallel fibre region. The relation of all these sources of input to the cells of the lobe cannot unfortunately be determined at present.

Fibrous and protoplasmic type glia cells of the lateral anterior basal lobe are seen in figures 22*a*, *b*, plate 2. They are greatly elongated in a dorso-ventral direction (that of figure 22*a* is turned on the plate).

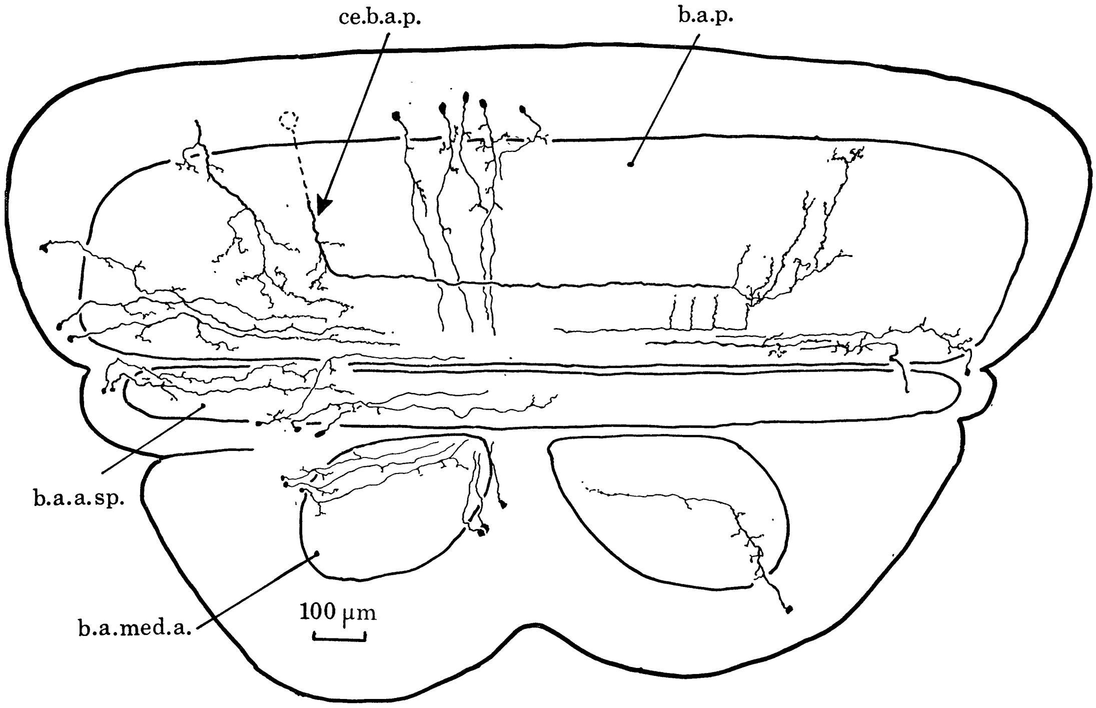


FIGURE 36. Drawing of a horizontal section showing the parallel fibre regions of both the anterior and posterior parts of the anterior basal lobe. Also the trunk of a cell whose axon runs from one side and terminates on the other (*ce.b.a.p.*). *Alloteuthis*. Golgi.

3.5.2. *Organization of the antero-medial lobule*

This lobule, as already indicated, consists largely or wholly of cells whose axons pass back to the opposite optic lobe (p. 360 and figures 9 and 10, pp. 360, 361). The input comes both from the dorsal and ventral optic to anterior basal lobe tracts. The former are from the opposite side, crossing in the manner described on page 361. The large ventral fibres probably come both from the same and the opposite sides (p. 362). They form conspicuous branching trees organized in a vertical plane (figures 32, plate 3 and 35, plate 4).

The trunks of the large and medium cells of the antero-median lobule have rather short dendritic collaterals orientated mainly laterally (figures 9, 10, pp. 360, 361 and 31, plate 3). They carry none of the bushy endings seen on the cells of the lateral anterior basal lobe. The fibres of the dorsal tract from the optic lobe are so distributed as to activate sets of these cells lying in horizontal planes. The large fibres of the ventral tract activate larger sets in the vertical plane, down the whole front of the lobe. These planes of distribution may prove to be significant.

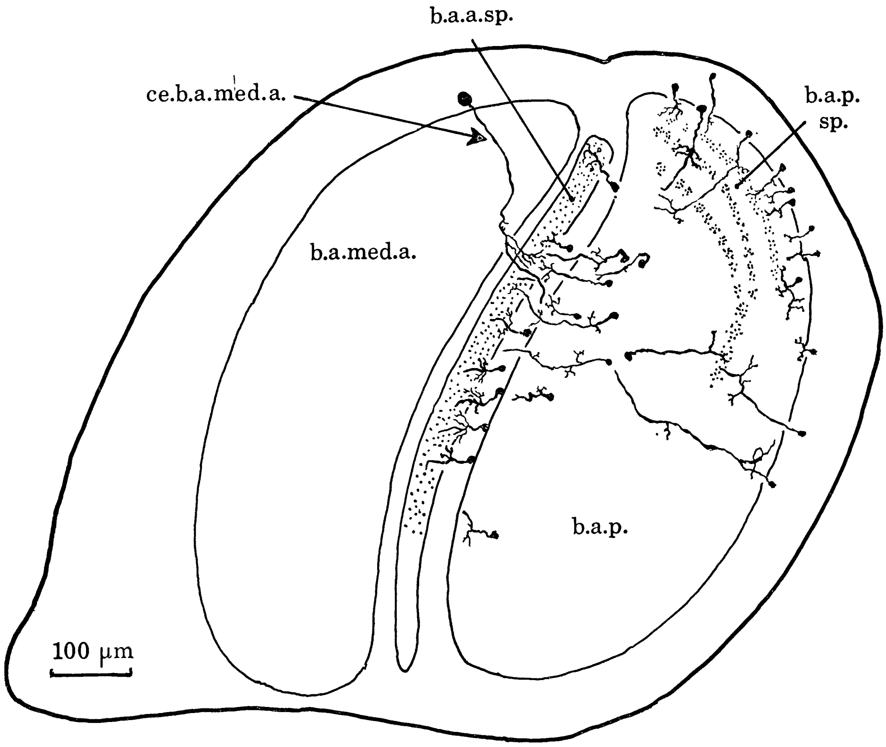


FIGURE 40. Drawing of a sagittal section to show cells of the two parallel fibre ('spine') regions of the anterior basal lobe. Both parts contain some amacrine cells with a few processes and others with longer trunks forming parallel fibres or running to the optic lobe. *L. vulgaris*. Golgi.

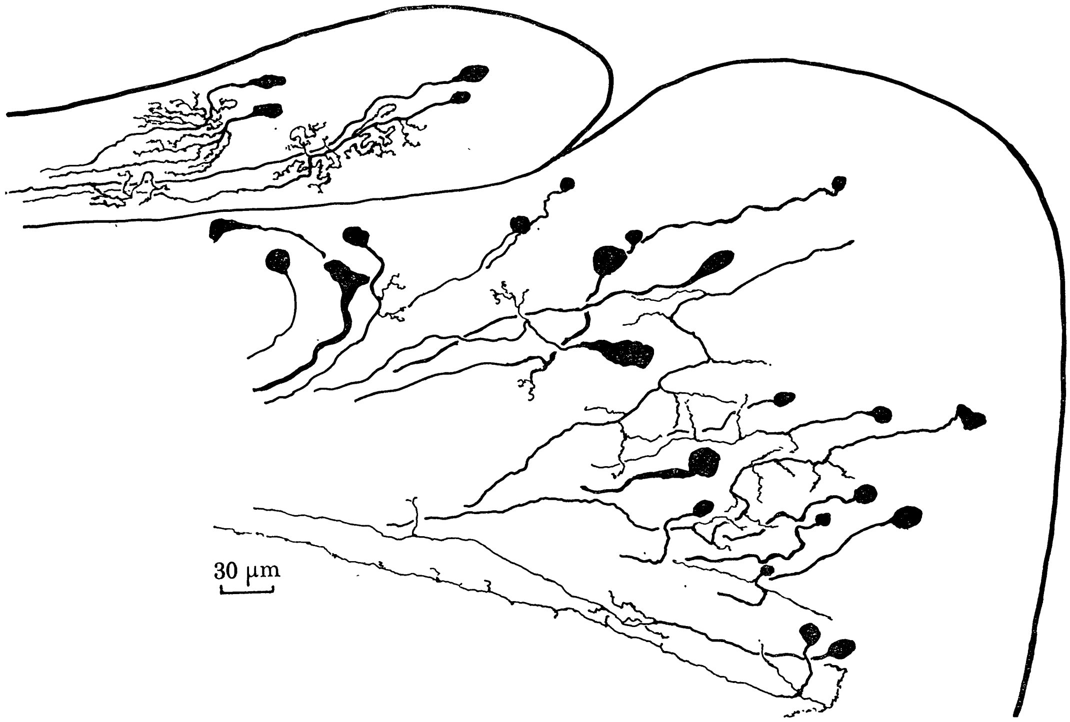


FIGURE 42. Drawing of two groups of small cells at side of the 'spine' of the anterior anterior basal lobe showing their collaterals. *Alloteuthis*. Golgi.

3.5.3. *Organization of the parallel fibre region of the anterior anterior basal lobe*

The region of parallel fibres of this lobe (comparable to the 'spine' of the peduncle lobe) has a rather complicated form difficult to describe. Its central part is a vertical plate running transversely behind the antero-median lobule and in front of the posterior anterior basal lobe (figures 36, p. 366, 40, p. 367, 33, plate 3, and 37, plate 4). It is thus at right angles to the spine

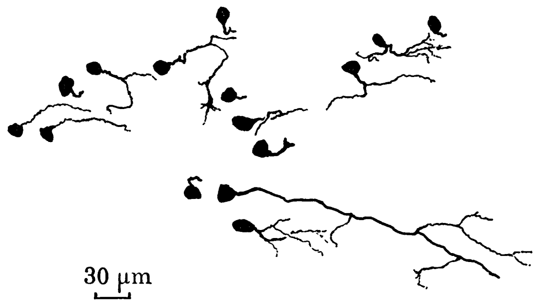


FIGURE 43. Drawing of cells of the 'spine' region of the anterior anterior basal lobe some of which are amacrines without any long axon. *Alloteuthis*. Golgi.

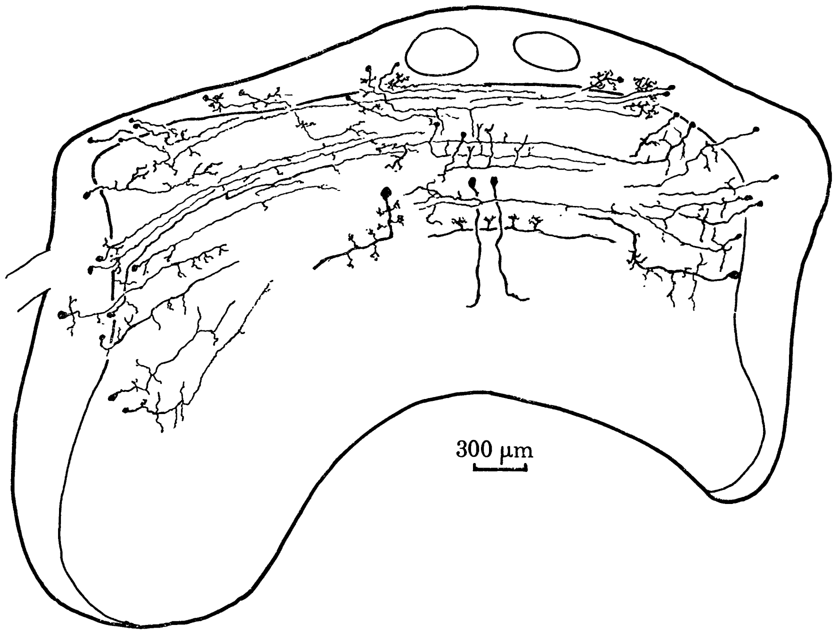


FIGURE 47. Drawing of a transverse section of the posterior anterior basal lobe, showing the fine parallel fibres and some larger cells and fibres. *Alloteuthis*. Golgi.

of the posterior anterior basal, which is a plate lying more nearly in the horizontal plane (figure 49*a*, p. 370). The parallel fibres run transversely across the mid-line but turn down into the lateral anterior basal lobe (figure 30, plate 3). Many of them arise from small cells at the sides, which have dendritic branches close to the cell body, and other short branches at intervals (figure 36, p. 366). Further small cells contribute to the parallel system along its length and have the same form as those at the sides. Many of them have a local mass of dendrites near to the cell body before turning laterally (figure 42, p. 367) and these proximal branches take various forms. It is not certain how far these fine fibres run. Probably some of them cross the mid-line and pass down into the opposite lateral anterior basal lobe, many others run down on the same side.

Several sources of input reach to the parallel fibres. Fibres from the optic lobes of the same and opposite sides certainly end here. Fibres of the ventral optic to anterior basal tract may also reach to this region. Fibres also enter it from behind from the other basal lobes.

The lobe contains numerous cells with very short processes ending in the neuropil close to the cell body (amacrine cells) (figures 40 and 43, pp. 367, 368). These very small cells are one of the striking features of all the small-cell parallel fibre regions. Their processes may be very short

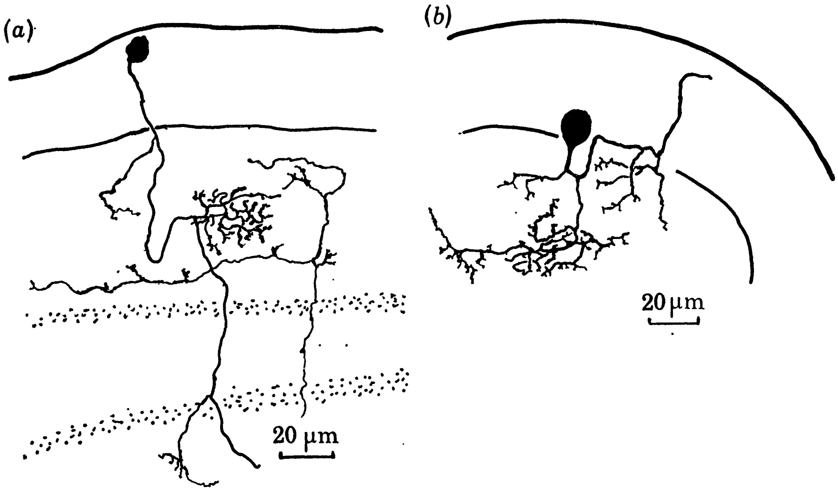


FIGURE 48. (*a*) Drawing of a sagittal section of the 'spine' region of the posterior anterior basal lobe showing a cell with characteristic tuft of dendrites, also an incoming afferent fibre. *L. vulgaris*. Golgi.

FIGURE 48. (*b*) Horizontal section of the spine of the peduncle lobe, showing a cell similar to that of 48*a*. *Alloteuthis*. Golgi.

and either stumpy or drawn out into a few fine tapering endings. It is of course impossible to prove that these cells are completely stained, but the branches of many of them have all the appearance of true termination. They can be distinguished from the trunks of slightly longer cells that are cut off short where they leave the section. These too, however, may end within the lobe, though at a greater distance. The presence of these amacrine cells, together with the parallel fibres, may provide major clues to the function of these lobes. Similar small cells also form a considerable proportion of the cells down the sides of the antero-median lobule, as well as in the parallel fibre region itself.

It is not clear how the fine parallel-fibre region exerts its influence. Many of the fibres probably make contact with the cells of the lateral anterior basal lobe, others turn laterally and perhaps pass to the optic lobe. The trunks of the larger fibres of the antero-median lobule pass through the parallel fibre region and give off dendrites there (figures 9, 10, pp. 360, 361 and 40, p. 367). They then pass on either side to the optic lobe or backwards to the other basal lobes. The parallel fibres thus seem to be so placed as to influence both the output fibres to the oculomotor and other centres and the reafferent fibres that pass back to the optic lobes.

4. The posterior anterior basal lobe

4.1. *Organization of the lobe*

This is a more compact lobe than the anterior part and it is organized around rows of cells and fibres lying in the transverse plane (figures 23, plate 2, 37 and 38, plate 4). The plane is actually inclined so as to follow that of the optic lobe, with the dorsal side more anterior. This lobe is not divided into parts so distinctly as the anterior anterior basal, but yet has similar three components (figures 49*a*, *b*, pp. 370, 371). The main central part, lying transversely, is

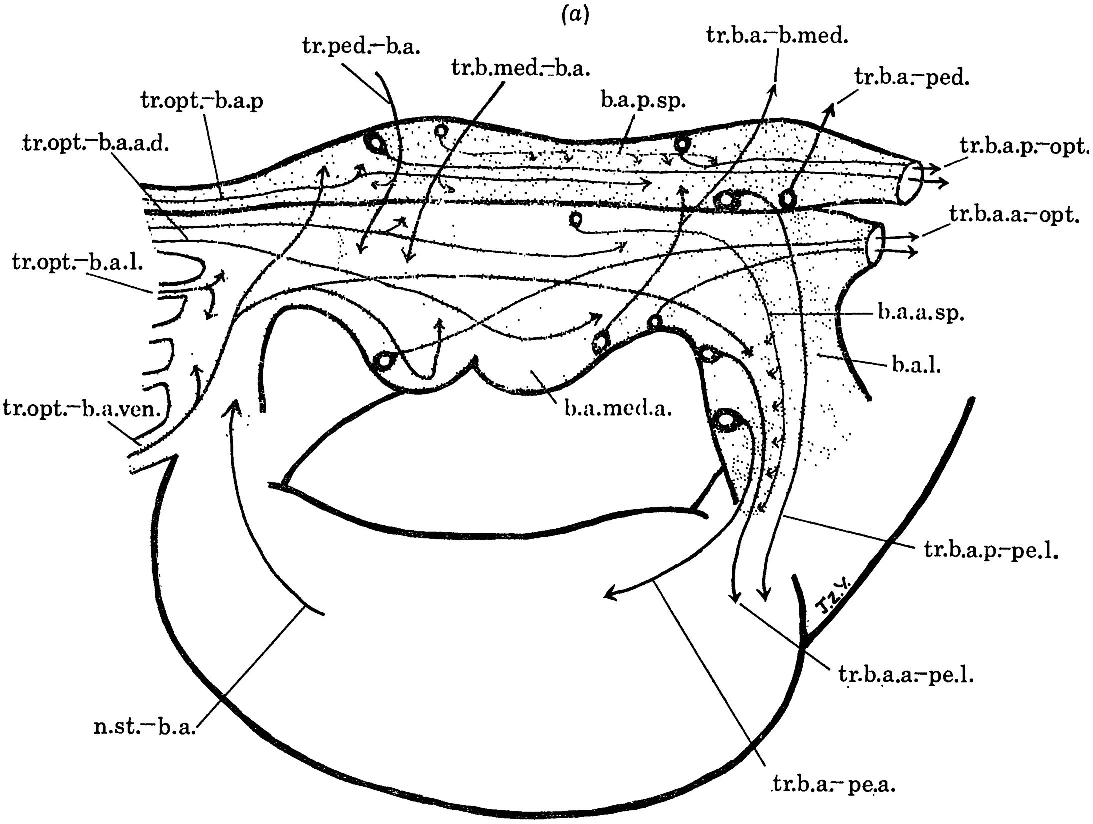


Figure 49. (*a*) Diagram to show the main connections of the two parts of the anterior basal lobe. Inputs are shown on the left, outputs on the right.

comparable with the lateral anterior basal lobe. It has cells of various sizes, some sending axons down to suboesophageal centres, others to the other basal lobes and some to the optic lobes. At the sides posteriorly are lateral lobules, perhaps corresponding to the antero-median lobules of the anterior part of the lobe, but less conspicuous (figure 39, plate 4). Finally, dorsally lie numerous very small cells and fine fibres clearly constituting a region of fine parallel fibres corresponding to the peduncle lobe 'spine' (figure 40, p. 367).

There is a well differentiated set of fibres of various sizes, running transversely (figure 33, plate 3). Ventrally there are very large ones and proceeding dorsally they become progressively smaller. In the dorsal spine region there are two rows of medium-small fibres, followed by a set of exceedingly small ones (< 1 μm).

4.2. *Efferent cells and output of the posterior anterior basal lobe*

The output fibres of the posterior anterior basal lobe probably proceed to the same six destinations as those of the anterior part of the lobe (p. 360). The fibres that have been followed in detail are those that run down to the pedal lobe and laterally to the optic lobes. Many of the cells of the lobe lie on its posterior face and send their trunks forwards and downwards across the transverse bundles of the lobe (figures 37 and 41, plate 4, figure 49*a*, p. 370). The largest cells ventrally and laterally (up to 40 μm diameter) send their axons down to the sub-oesophageal lobes of the same or opposite sides (figure 52, plate 5). They form a regular series

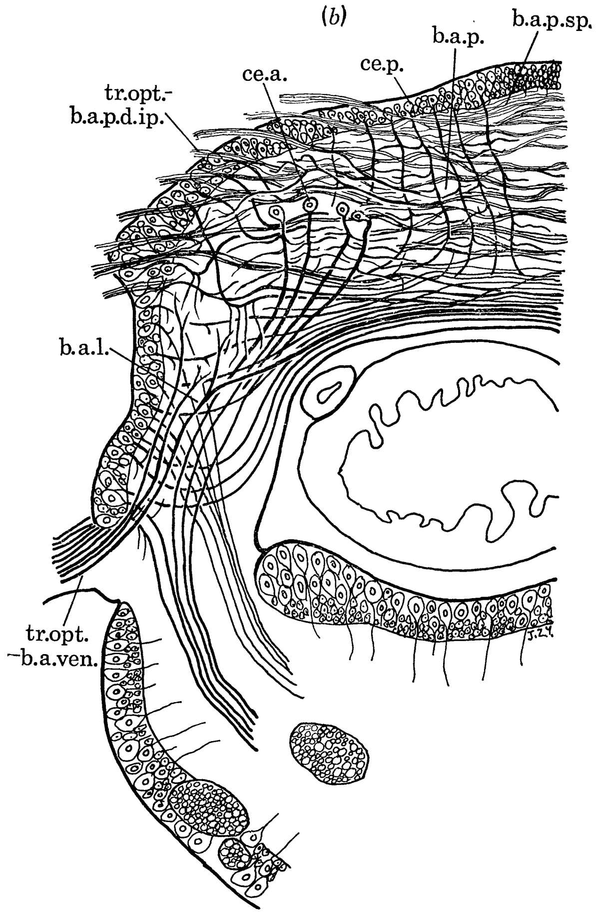


FIGURE 49. (*b*) Diagram of some of the connections of the posterior anterior basal lobe. The figure is of a transverse section, further forward on the left than on the right.

along the back of the lobe, with dendritic collaterals spreading laterally, so that each cell samples a relatively small volume of neuropil (figure 46, plate 4).

There is also a row of very large cells along the front face of the lobe, sending their axons downwards mainly on the same side, perhaps some crossed (figures 34, plate 3 and 35, plate 4). These cells have very abundant short dendrites along their length (figure 50, plate 5). The descending fibres of the lobe pass like those of the anterior anterior basal either to the oculomotor centre (lateral pedal lobe) or to other parts of the pedal lobe. In small animals single axons can be followed all the way from the cell body to the oculomotor centre (figure 7, plate 1), The second main destination of the axons of the lobe is to the optic lobe. Some of the medium-sized cells in the lateral lobules send their axons transversely and they probably reach to the optic lobe of the opposite side. They thus correspond to the cells of the antero-median lobule of the anterior anterior basal, which are also of medium size and send axons to the opposite optic lobe. There are also numerous rows of smaller cells along the back of the lobe whose axons run transversely and proceed towards the optic lobe of the same or the opposite side (figure 49*a*, p. 370). Passing from ventral to dorsal the cells become progressively smaller and there is no sharp distinction between the main part of the lobe and its parallel fibre (spine) region (figure 33, plate 3).

4.3. *Cells and fibres intrinsic to the posterior anterior basal lobe*

The fibre marked ce.b.a.p. in figure 36 (p.366) is one of a set whose cells have dendrites close to the cell body on one side and then send an axon to ramify in a corresponding position on the other side. Several axon terminals of this sort are shown in the figure. The fibre ce.b.a.p. does not give any other collateral branches along its course but others may do so.

Passing further dorsally the cells become smaller, merging into those of the 'spine' region of fine parallel fibres (figures 40, p. 367, 47, p. 368, and 48*a*, p. 369). These are similar to those in the other 'spine' regions. Figure 48*b* shows a similar cell from the peduncle lobe spine. Their trunks close to the cell carry several short collaterals ending in bushy terminals (figures 44, plate 4, 51, p. 373). They turn laterally and run for varying distances, giving collateral branches. On some of them the branches are mostly close to the cell body and at the end, others show collateral branches all along their length (figure 45, plate 4). Many of these collaterals end in complex terminal formations of swellings and spines (figure 54, plate 5). These fibres presumably serve to carry signals for shorter or longer distances across the lobe. Some taper away to a simple ending after only a short distance, others proceed across the entire lobe, either giving axonic collaterals at intervals or dividing up in a limited region on the opposite side. The whole set forms a remarkable system of parallel fibres, some making a series of connections along their length. Among them are numerous fine elongated glial fibres, proceeding from relatively large central cell bodies (figure 44, plate 4). Very many of the small cells have only extremely short trunks and are presumably to be classed as amacrines.

4.4. *Input to the posterior anterior basal lobe*

The incoming fibres run in a series of bundles interweaving in the transverse vertical plane, with larger fibres ventrally, smaller ones dorsally. As in the other basal lobes they come from at least four sources: (1) the optic lobes; (2) the statocyst; (3) the other basal and peduncle lobes; and (4) the magnocellular lobe. Some of the fibres end on the same side, others are crossed.

4.4.1. *The optic to posterior anterior basal tracts*

We shall distinguish two main sets of optic fibres, ventral ones, entering through the lateral anterior basal lobe and dorsal ones entering directly at the sides. The ventral fibres belong to the set of very large fibres that leave the ventral part of the optic lobe (figure 26, p. 363). They run up to the base of the posterior anterior basal, where they send branches to it on that side. They then curve medially, cross the midline and proceed up through the lobe on the opposite side. Here they divide into numerous branches, displayed mainly in the transverse plane. They form a regular series, with characteristic wide loops, and probably terminating in an orderly manner, from the mid-line laterally (figure 55, plate 5). It has not been possible, however, to distinguish clearly between the endings of these and other fibres reaching the lobes. The whole neuropil is filled with large incoming axons branching to give finer and finer fibres lying among the dendrites of the outgoing cells of the lobe.

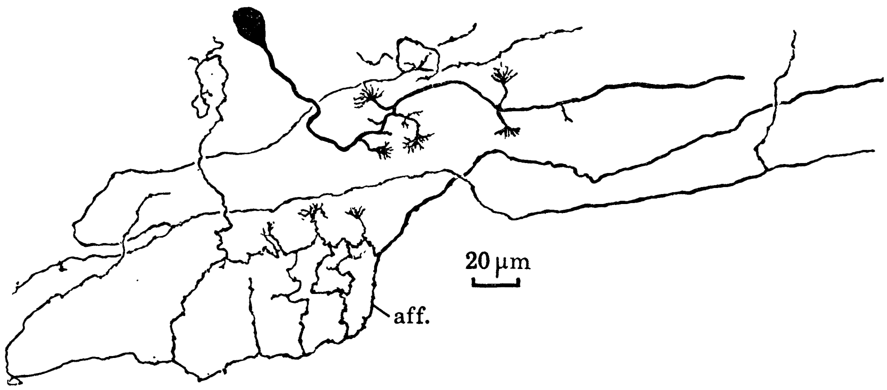


FIGURE 51. Drawing of a transverse section from the parallel fibre region of the back of the posterior anterior basal lobe. *Alloteuthis*. Golgi.

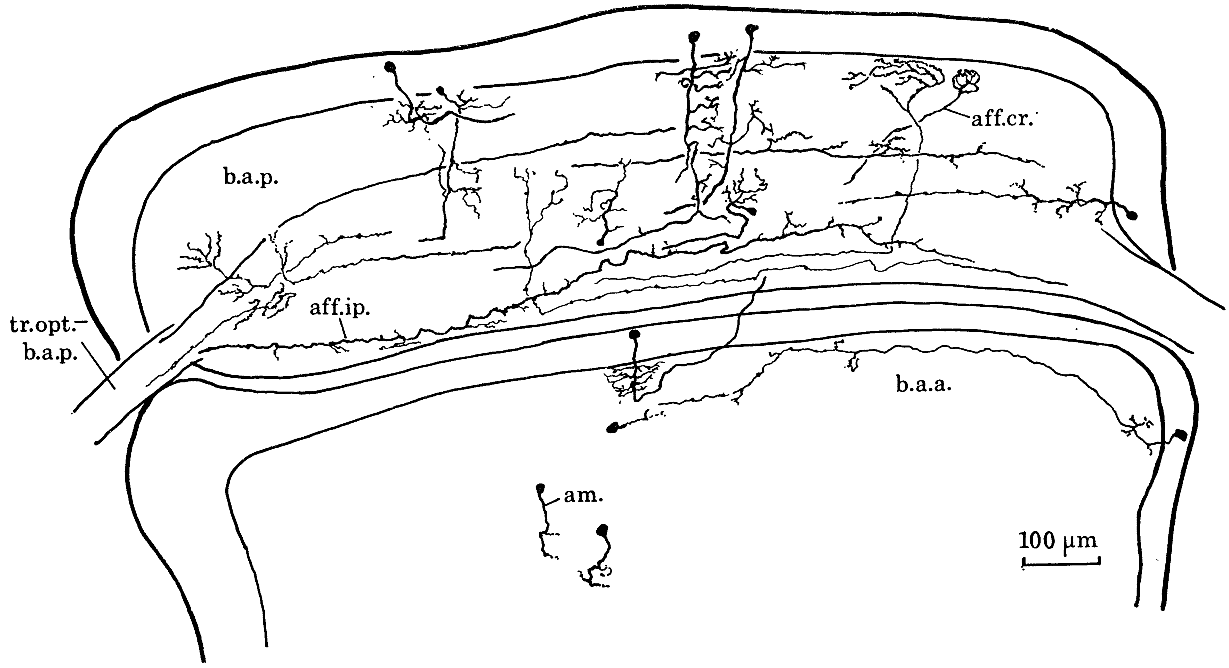


FIGURE 53. Drawing of an oblique section of the anterior basal lobe, showing cells of both parts. *Alloteuthis*. Golgi.

The fibres of the dorsal optic to posterior anterior basal tract collect in the optic lobe in a regular dorso-ventral pattern (figure 57, plate 5). Within the lobe the fibres pass through a system of repeated crossings, having the effect of bringing the ventral fibres dorsally and vice versa (figure 52, plate 5). This system of weaving continues throughout the bundles of the lobe (figure 41, plate 4). Some of the optic nerve fibres terminate on the same side, but many cross. Both sorts divide to make fine axon terminals apparently occupying large volumes of neuropil (figure 9, p. 360). They seem to be of two types. One forms much-branched fibres carrying swellings with minute collaterals, presumably synaptic (figure 58, below). These make systems of rather irregular nets lying across the transverse fibre bundles (figure 51, p. 373). The other type of ending consists of sprays of terminals, finer than the first type and provided with minute swellings. In the most dorsal part of the parallel fibre region some very complex endings were seen (figure 53, p. 373 aff.cr.).

The posterior anterior basal lobe thus shows a differing neuropil structure passing from ventral to dorsal. There seem to be three zones, partly distinct, with thicker fibres ventrally, smaller in the middle zone and finest dorsally. In all parts each incoming optic nerve fibre spreads very

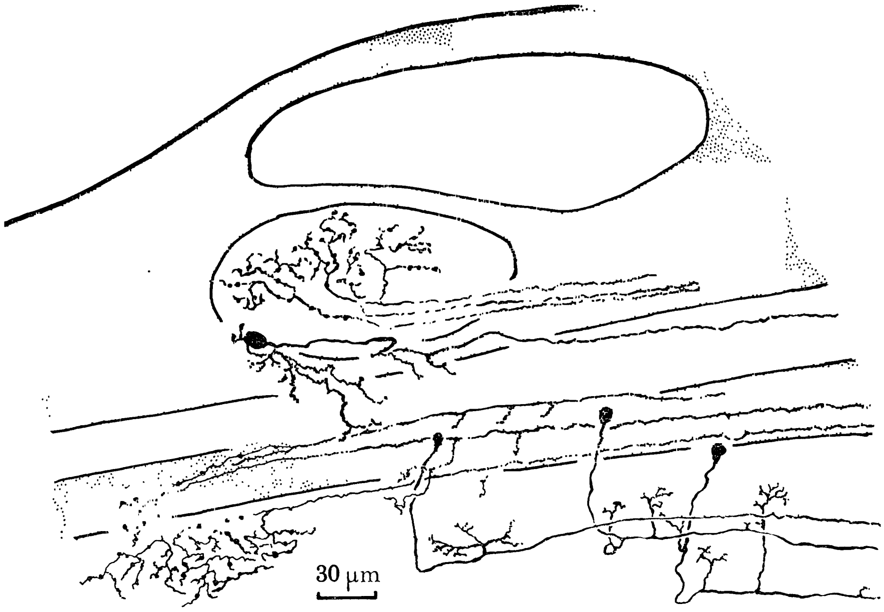


FIGURE 58. Drawing of a section of the posterior anterior basal lobe showing afferents from the optic lobe spreading in the transverse plane and cells with trunks proceeding transversely. *L. forbesi*. Golgi.

DESCRIPTION OF PLATE 5

FIGURE 50. Transverse section of the posterior and lateral anterior basal lobes retouched to show trunks of the cells at the front (ce.a.) and back (ce.p.) and also fibres of the optic to anterior basal lobe tracts. *L. pealeii.*

FIGURE 52. Oblique transverse section of the posterior anterior basal lobe, showing the large cells of the front wall on the right (ce.a.) and of the hind wall on the left (ce.p.). Large ascending and descending fibres are seen in the lateral anterior basal on the left. This is the section behind figure 41, plate 4. *L. pealeii* (retouched).

FIGURE 54. Terminations of the dendrites on a small cell from the 'spine' of the posterior anterior basal lobe. *Alloteuthis*. Golgi.

FIGURE 55. Transverse section of the posterior anterior basal lobe, showing afferents from the optic lobe running transversely with characteristic loops (aff.) across the trunks of the outgoing cells (ce.p.). *L. pealeii* (retouched).

FIGURE 56. Horizontal section retouched to show the tracts between the median basal and the more anterior lobes. *L. pealeii.*

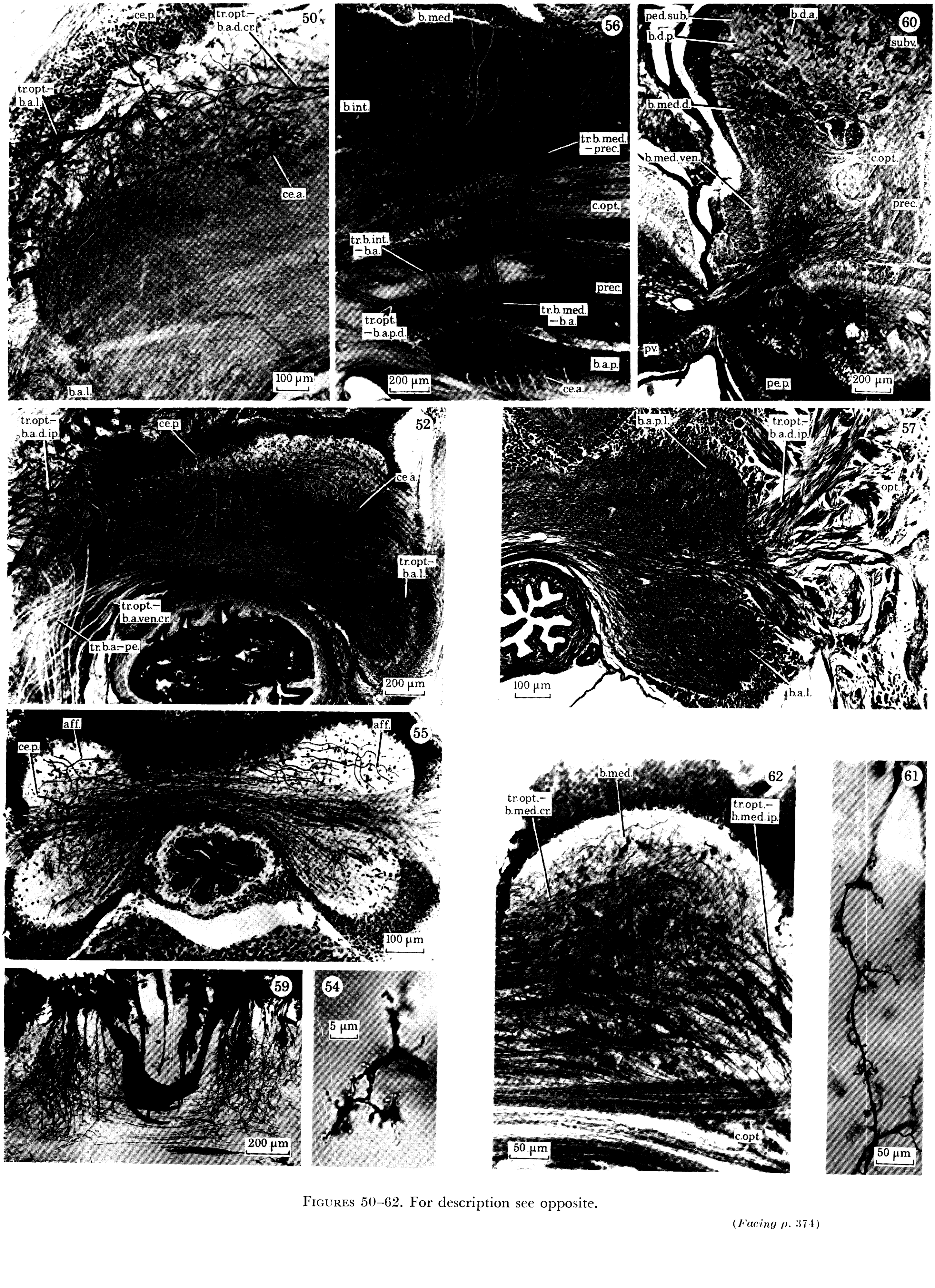
FIGURE 57. Transverse section of the posterior anterior basal lobe, showing the bundles of fibres of the dorsal optic to posterior anterior basal lobe tracts. *Alloteuthis.*

FIGURE 59. Horizontal section showing numerous trunks of cells of the median basal lobe, reaching forwards across the bundles of the optic tract fibres. *Alloteuthis.* Golgi.

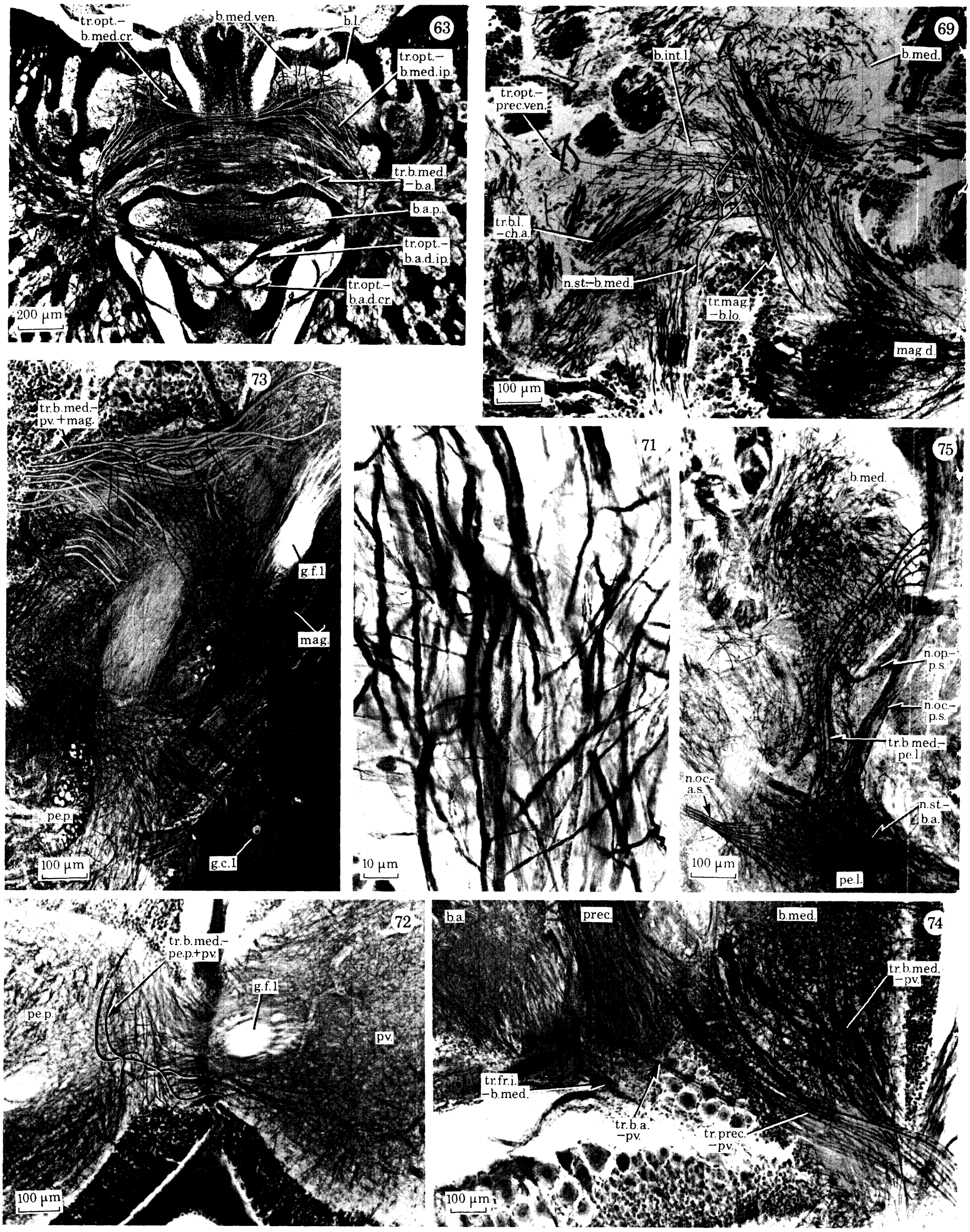
FIGURE 60. Sagittal section to show the dorsal and ventral parts of the median basal lobe. *Alloteuthis.*

FIGURE 61. Single median basal cell seen in horizontal section, showing the dendritic collaterals. *Alloteuthis* Golgi.

FIGURE 62. Horizontal section of the median basal lobe, showing the optic to median basal lobe tracts, the ipsilateral enters from the right, the contralateral from the left. *L. pealeii.*



FIGURES 50–62. For description see opposite.



FIGURES 63–75. For description see opposite.

widely, ending in fine varicose terminals. The branching systems of the incoming fibres probably lie mostly in the transverse vertical plane. In the more ventral parts a close network of bundles of fibres is formed. In the middle zone the meshwork is more open and in the dorsal region the single varicose fibres form the networks, accompanying the trunks of the parallel fibres arising from the cells there. The processes of other cells of the lobe pass down across the transverse bundles and turn laterally to return to the optic lobes (figure 58, p. 374).

4.4.2. *The median basal to posterior anterior basal tracts*

Numerous fibres pass in both directions between these lobes (figures 28, plate 3 and 63, plate 6). The bundles run over the main ventral optic commissure. They interweave in a complicated manner, whose details have not been unravelled. Many of the fibres are small, but there are also some larger ones. Within the posterior anterior basal lobe the fibres of these tracts turn to run both medially and laterally. They make an important contribution to the bundles running transversely across the lobe. Some of these bundles interweave with those coming from the region of the optic tract either from the optic lobe itself or from the interbasal region (figure 56, plate 5).

4.4.3. *Static nerves to the posterior anterior basal lobe*

These fibres presumably also run in the transverse bundles, but no preparations that show their course have been found.

4.4.4. *Magnocellular to posterior anterior basal lobe tract*

Numerous collaterals of the fibres entering the median basal from the magnocellular lobes pass forwards to this lobe (p. 382.)

5. Posterior basal region

5.1. *General plan and divisions*

The region at the back of the supraoesophageal lobes is complex and difficult to describe. It is often called the posterior basal lobe, but as it is not a single homogeneous entity the name

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Description of plate 6

Figure 63. Horizontal section of a young animal, retouched to show the optic to median basal tracts (ipsilateral and crossed) and tracts between median basal and anterior basal lobes. *L. pealeii.*

Figure 69. Sagittal section of a young animal, retouched to show the magnocellular to basal lobes tract, with the branches of its fibres spreading upwards and also forwards to the interbasal region. A branch from the ventral optic to precommissural tract is also seen, reaching back to the interbasal region. Note also fibres of the static to median basal tract. *L. pealeii.*

Figure 71. Detail of an area at the centre of figure 69 to show the branches of the fibres of the magnocellular to basal lobes tract passing, some forwards and some backwards (to the right).

Figure 72. Sagittal section showing fibres branching to form the median basal to posterior pedal and anterior palliovisceral tract. *L. pealeii* (retouched).

Figure 73. Sagittal section to show the median basal to palliovisceral tract, with its fibres sending collaterals to the magnocellular lobe. *L. pealeii* (retouched).

Figure 74. Sagittal section to show the tracts from the anterior basal, precommissural and median basal lobes to the palliovisceral lobe. Note a fibre from the precommissural lobe giving a collateral towards the magnocellular lobe. *L. pealeii* (retouched).

Figure 75. Sagittal section of a young animal, retouched to show the median basal to lateral pedal tract. *L. pealeii.*

posterior basal region will be used only to describe the whole complex, as it was used also in *Octopus* (Young 1971). Although the posterior basal lobe is not homogeneous the functions of its various parts are nevertheless related and many of them refer at least in part to movement of the whole animal. No doubt there is a functional significance in the close anatomical relations of these parts. Thus the centres concerned with the control of reproduction, through the optic gland, may also be related to the production of actions of the animal in mating and egg-laying. A large part of the posterior basal region is a steering centre based on a plan somewhat similar to the anterior basal and peduncle lobes. Its ventral part will be called the median basal lobe. The more dorsal regions, known as the anterior and posterior dorsal basal lobes, contain many very small cells and they may represent the fine parallel-fibre or 'spine' region of the complex. Across the back of the brain dorsally lie the subpedunculate lobes, whose connections though little understood are possibly related to control of neurosecretory tissue in the orbit (Froesch 1975). However, these subpedunculate lobes are themselves diverse and contain what appear to be neurosecretory systems, with functions as yet unknown. At the sides dorsally the median basal lobes carry a pair of dorso-lateral lobules connecting with the olfactory lobes and giving rise to the nerves to the optic glands, which control development of the reproductive system in *Octopus* (see Wells & Wells 1977). Below this lie the lateral basal lobes, concerned with control of the colour patterns of the animal in *Octopus*, *Sepia* and *Sepioteuthis* (see Boycott, 1953, 1961 and 1965). Finally, at the base of the median basal is a region receiving bundles of fibres from many peripheral nerves, which may be the centre for control of capture of the prey by the tentacles. This region will be called the interbasal lobe. It is not clearly marked off anatomically but the name expresses its position and agrees at least approximately with the regions named 'interbasal lobe' by Boycott (1961) in *Sepia* and Young (1971) in *Octopus*.

The parts of the posterior basal region can therefore be listed with their probable functions as:

(1) median basal lobe	steering and jet control centres
(2) dorsal basal lobes (anterior and posterior)	(steering and jet control centres)
(3) interbasal lobe	tentacle control centre (?)
(4) dorso-lateral lobe	reproduction control centre
(5) subpedunculate lobe	ocular pressure control centre (?)
(6) lateral basal lobe	chromatophore control centre

5.2. *Median basal lobe*

5.2.1. *Introduction*

This lobe is larger than either of the parts of the anterior basal lobe or the peduncle lobe, and it is internally more diverse. Nevertheless it is organized on a plan that is somewhat similar to these. The lobe is more extended antero-posteriorly than the others (figures 2 and 3, plate 1). The small-celled region of the dorsal basal lobes lying above and in front of the median basal seems to correspond to the small parallel fibre regions of the anterior basal and peduncle lobes. The median basal lobe is certainly part of the oculomotor control system and also probably operates in the control of motion forwards and backwards and for turning laterally in the yawing plane, movements that are operated by the funnel and fins.

Although the median basal lobe shows the same general plan as the other basal lobes, it also shows differences, perhaps due to the fact that it is related to lobes concerned with other functions besides steering. Its large connection with the magnocellular lobe gives it an important function in escape reactions and indeed in all propulsion with the jet. Its connections with the palliovisceral lobe probably include some that influence the respiratory movements and perhaps other visceral functions. The median basal also probably collaborates with the neighbouring lateral basal lobe in the control of colour change. Through its connections with the dorsolateral lobule this region may influence the behaviour leading to copulation and egg-laying.

5.2.2. *Position and relations of the median basal lobe*

As in the other basal lobes we can recognize two parts here, ventral and dorsal. The ventral is the large-celled output region. The dorsal contains medium-sized cells, some with descending axons, others leading back to the optic lobes and to the other basal lobes. The region of fine parallel fibres or 'spine' is perhaps represented by the dorsal basal lobes, which will be considered separately.

The ventral regions are paired swellings on either side of the oesophagus (figures 29, plate 3, 60, plate 5, 63, plate 6) and they join the back of the middle suboesophageal mass. Their relations are with the lateral basal lobes laterally, the perioesophageal sinus medially, the optic commissure in front and the postorbital nerve behind, which runs in a groove between the median and lateral basal lobes (figure 29, plate 3). This ventral part of the median basal lobe has nerve cells mainly on its medial and posterior walls and many of them are large. The interbasal region lies immediately below these large cells and they may be related to it (p. 385).

The more dorsal part of the median basal lobe is directly continuous with the ventral part and occupies the back of the supraoesophageal mass (figure 60, plate 5). Here it is related posteriorly to the perioesophageal sinus and postorbital nerve and laterally to the olfactory and peduncle lobes. It has relatively thick walls laterally, but thin in the mid-line. It is not sharply marked off from the posterior dorsal basal lobe lying above it, but the two are distinct in their neuropil and partly in their connections, though they may well be part of a single functional complex.

5.2.3. *Cells of the median basal lobe*

The ventral portions of the lobe contain large cells of up to 40 μm diameter (figure 104, plate 9). The largest lie at the extreme hind end of the brain at the level of the oesophagus. Other large ones are somewhat higher up the back of the lobe. They send their trunks a long way forwards and then downwards. Some of the largest reach forwards over the interbasal region before turning down as very large fibres into the suboesophageal lobes. They have dendrites spreading in all directions and running among the incoming optic nerve fibres (figures 64, 65, p. 378). The individual dendritic trunks vary. Some are not greatly branched, others are quite short with numerous collateral twigs (figure 66, p. 379). Each of these cells thus has dendrites occupying a cylinder of neuropil with a radius of up to about 100 μm. The trunks run approximately parallel to each other, but may cross, or take irregular courses (figures 59, plate 5, 104, plate 9). The dendrites of any one cell certainly overlap with those of others. This does not mean that there is no regularity in the arrangement. The cell bodies form rows across the back of the lobe and it may be that they are excited in a regular order. Their axons proceed to various destinations listed later.

Accompanying the large cells are some smaller ones, in this lower part of the median basal lobe. They are associated with a system of fine fibres running downwards and have bushy terminals (figure 67, p. 379). It is probable that these trunks do not leave the lobe. They have some similarity to the fibres of the parallel fibre regions but their significance in this situation is not clear.

The region of very large cells is marked off by a constriction from the medial region above it, where the cells are smaller (figure 60, plate 5). The axons of the cells of this upper region proceed partly ventrally, partly forwards to the dorsal basal, precommissural and anterior basal lobes (figure 68, p. 380), partly to the optic lobes. These cells mostly carry rather few and short collateral dendrites (figure 61, plate 5; figure 66, p. 379), and therefore sample a rather narrow cylinder of neuropil.

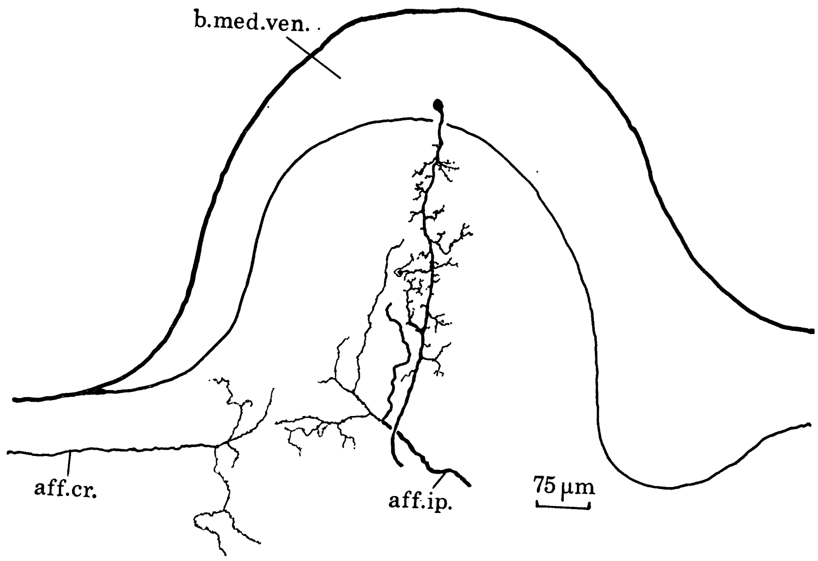


FIGURE 64. Drawing of a part of the same preparation as figure 59 to show dendritic branches of a single cell of the median basal lobe and one fibre each of the ipsilateral and crossed optic to median basal tracts. *Alloteuthis*. Golgi.

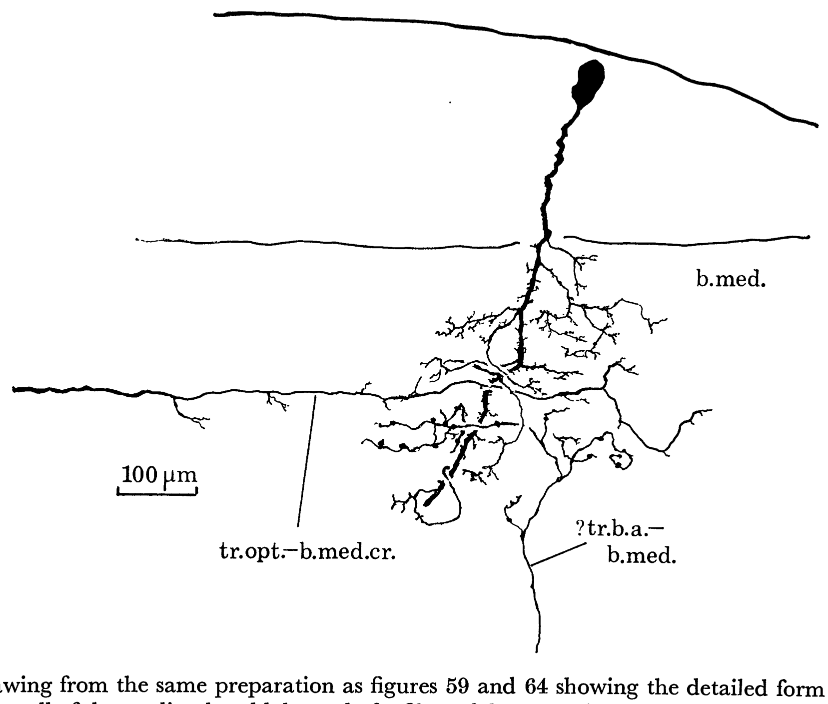


FIGURE 65. Drawing from the same preparation as figures 59 and 64 showing the detailed form of the dendritic endings of a cell of the median basal lobe and of a fibre of the crossed optic to median basal tract. *Alloteuthis*. Golgi.

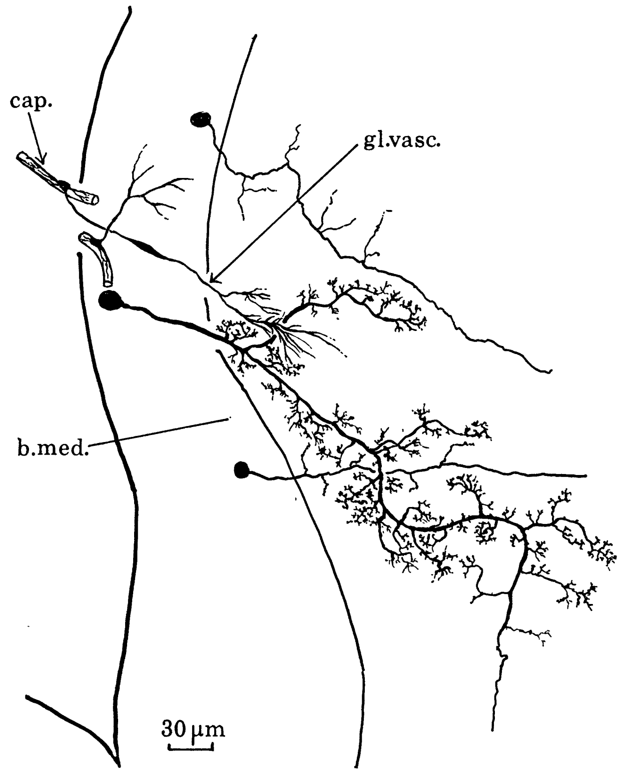


FIGURE 66. Drawing of a sagittal section of the median basal lobe, to show the extent of the dendritic collaterals of a single cell. Terminal branches of two gliovascular cells are also seen. *Alloteuthis*. Golgi.

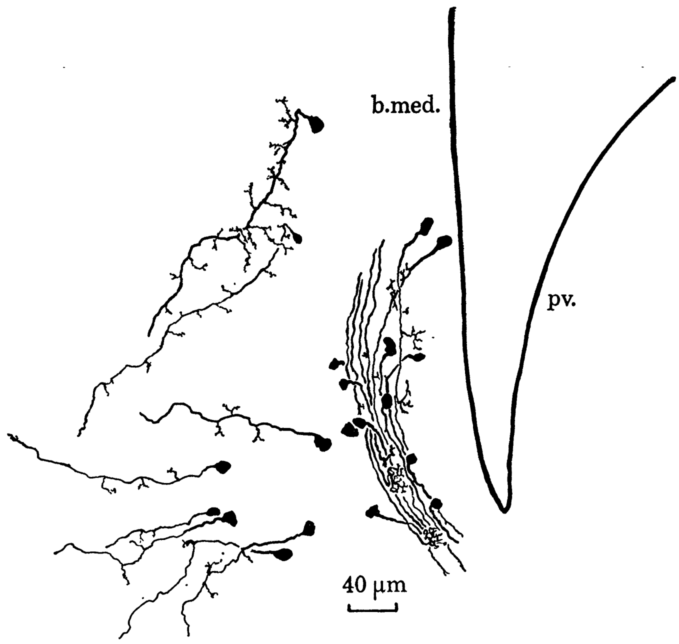


FIGURE 67. Drawing from a sagittal section of cells at the back of the median basal lobe. Besides small cells with descending axons there is a region of very small cells with parallel fibres. *Alloteuthis*. Golgi.

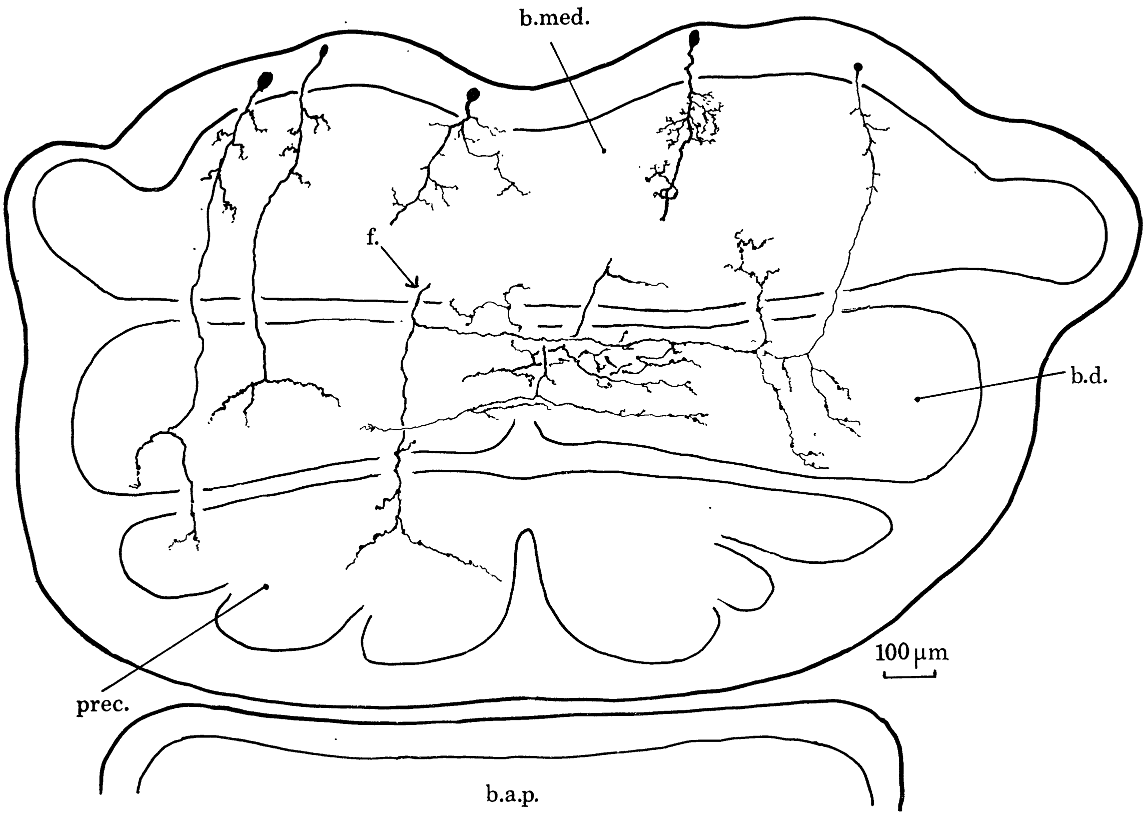


FIGURE 68. Drawing of a hoiizontal section through the upper part of the median basal and the dorsal basal and precommissural lobes. Fibres run forwards from the median basal to the other lobes. One of them (f.) has branches on both sides. *Alloteuthis*. Golgi.

5.2.4. *Input to the median basal lobe* (figure 84, p. 382).

5.2.4.1, 2. *Optic to median basal lobe tracts*. There are ventral and dorsal optic inputs, as there are to each of the two parts of the anterior basal lobe (p. 361). The ventral input comes from the large fibres entering from in front and below. Some of those that send branches to the precommissural lobes and perhaps anterior basal also send them back to the median basal lobe (figures 21, p. 363 and 26, p. 363). In addition there is an independent group of large fibres running from the anterior ventral region of the optic lobe to the median basal lobe. These fibres enter the ventral region of the lobe, close to the large cells, and to the interbasal region. They divide into branches spreading both vertically and horizontally, together with the branches of the more dorsal tracts. Some of the largest of the ventral fibres cross in the commissural bundles at the base of the median basal lobe, but it is not known whether any one fibre contributes to both sides.

The very numerous dorsal optic to median basal input of fibres arises somewhat in front of the lobe as a series of bundles collected from all parts of the optic lobe. As they pass back the bundles interweave (figure 62, plate 5), forming a complex system of transverse fibres, of larger diameter ventrally than dorsally. The fibres spread out backwards and upwards and end partly on the same side, partly after crossing to the other. They are darkly staining with silver and form characteristic sinuous curves.

Some of the fibres run transversely and branch across the trunks of the outgoing cells, especially in the more ventral region (figures 64, 65, p. 378). Others pass up the lobe, crossing the various rows of cells. The finer branches form curling varicose endings among the dendritic collaterals of the trunks of the cells. These carry swellings with fine twigs, presumably synaptic. Some of them reach up into the dorsal basal lobes.

5.2.4.3. *Inferior frontal to median basal lobe tract.* The ventral median basal lobe receives a small bundle from in front, the inferior frontal to median basal lobe tract (figures 21, p. 363, 29, plate 3). The fibres branch and spread out in the ventral part (figure 104, plate 9).

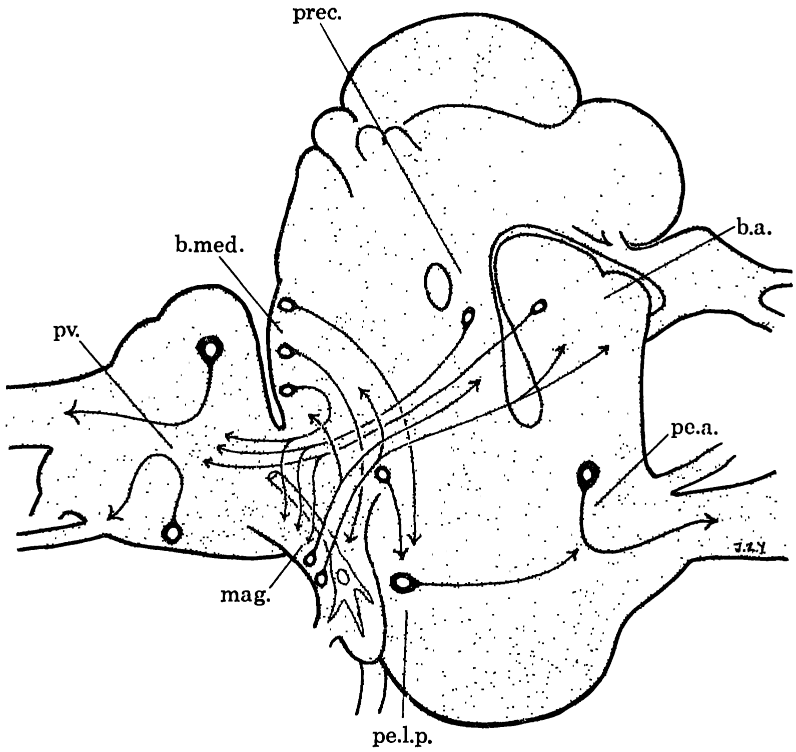


FIGURE 70. Diagram of the ascending and descending pathways between the magnocellular and basal lobes.

5.2.4.4. *Pallioviscera1 to median basal lobe tract.* This forward-running bundle brings fibres from the pallioviscera1 to the median basal lobe. They may include afferents from peripheral nerves. Some of these fibres pass on forwards to the inferior frontal lobe.

5.2.4.5. *Interbasal to median basal lobe tract.* Fibres from the various bundles reaching to the interbasal region probably also reach to the median basal lobe (p. 385).

5.2.4.6. *Peduncle lobe to median basal lobe tract.* Bundles of fibres enter the median basal lobe coming from both the peduncle spine and basal regions.

5.2.4.7. *Statocyst to median basal lobe tract.* Fibres run directly upwards from the static nerves of the same side and break up in the region of the interbasal and median basal lobes (figure 69, plate 6). These probably include fibres from both macula and crista nerves. Fibres from the opposite side probably also reach the lobe after crossing in the middle pedal commissure. The details of the terminals of the statocyst fibres have not been seen, but the individual fibres branch widely.

5.2.4.8. *Magnocellular to basal lobes tract.* These lobes have a reciprocal relationship mediated by separate lateral and medial magnocellular-median basal tracts (figure 70, above). The lateral tract contains fibres running upwards, with a remarkably wide distribution throughout the supraoesophageal lobes. This bundle includes many large fibres giving off slender long branches in various directions (figures 69 and 71, plate 6). Some pass upwards into the median basal lobe, others forwards through the interbasal region. These forward branches make a conspicuous set passing below the optic commissure and reaching to both parts of the anterior basal lobe and perhaps also to the precommissural lobe. These large fibres arise from the large cells of the lateral and ventral walls of the magnocellular lobes (figure 85, plate 8). They lie close to the first order giant cell and must share much of its input. They are presumably involved in the initiation of jet propulsion, both for attack and retreat. It is not clear what special

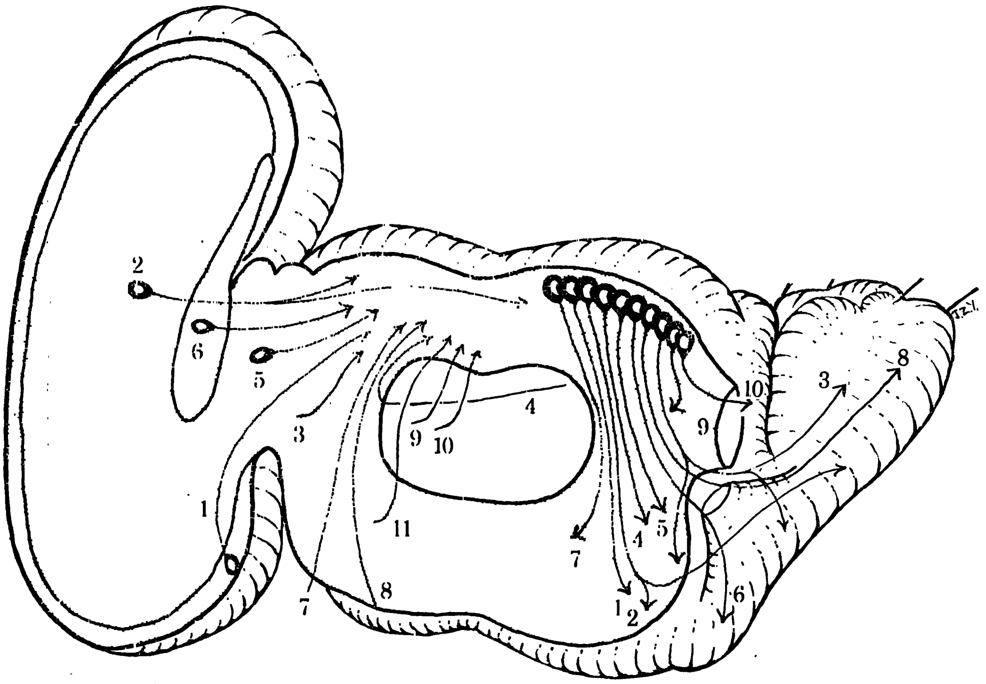


FIGURE 84. Diagram of the connections of the median basal lobe. The numbers are listed in the text. Note that the order of the tracts as shown from medial to lateral is not that actually present.

DESCRIPTION OF PLATE 7

FIGURE 76. Sagittal section of a young animal, showing fibres of the median basal to posterior pedal tract. Also of the posterior pedal to anterior palliovisceral and fin lobe tracts. The fin lobe lies lateral to this section but a few of its cells are shown with fibres proceeding to the fin nerve. *L. pealeii* (retouched).

FIGURE 77. Horizontal section to show the interbasal region and the tract to it from the peduncle lobe. *Alloteuthis.*

FIGURE 78. Sagittal section of the medial interbasal region to show the interchange of fibres coming from the various peripheral nerves. *L. pealeii.*

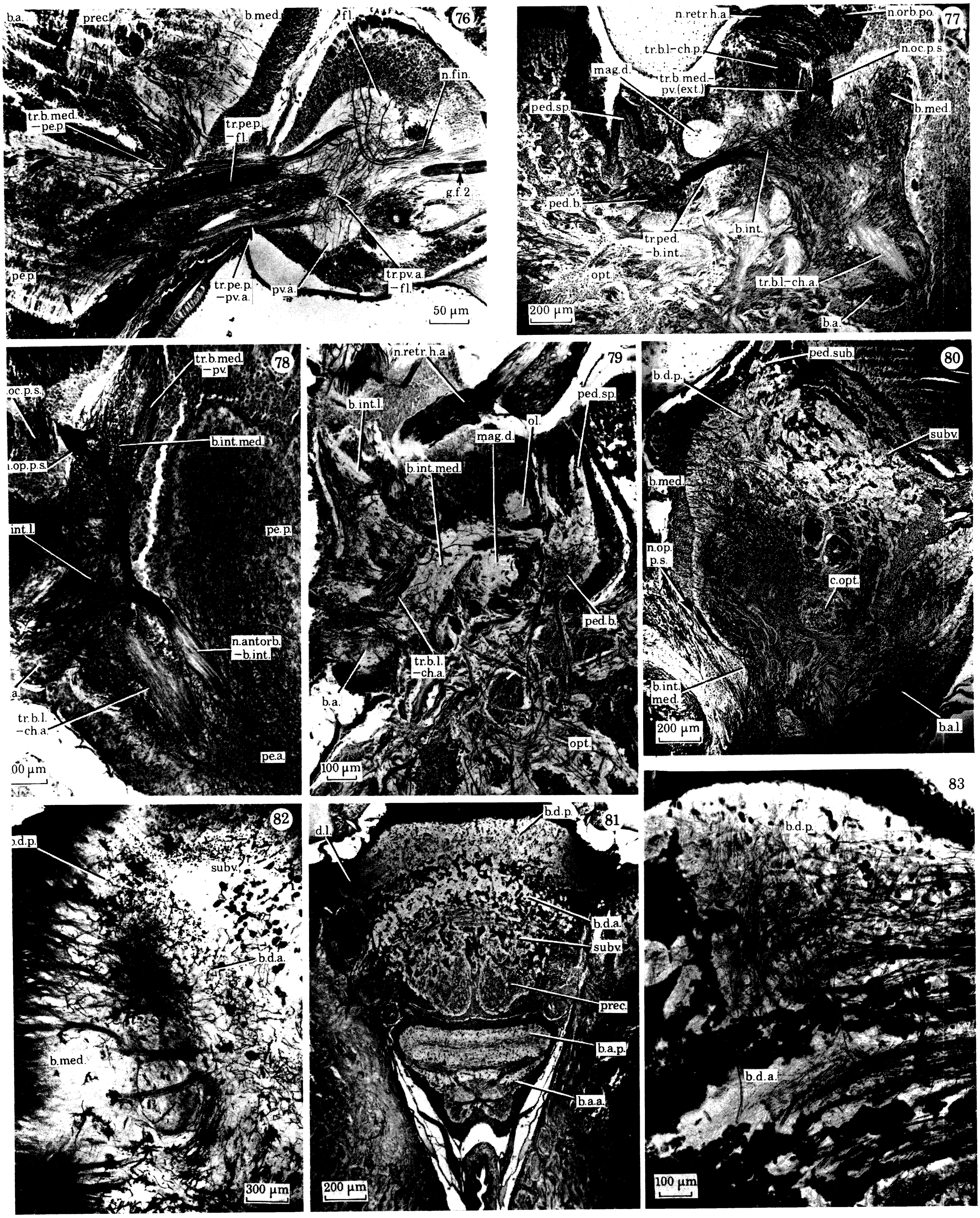
FIGURE 79. Horizontal section showing the relations of the interbasal region. *Alloteuthis.*

FIGURE 80. Sagittal section to show the relations of the interbasal, median basal and dorsal basal lobes. *Alloteuthis.*

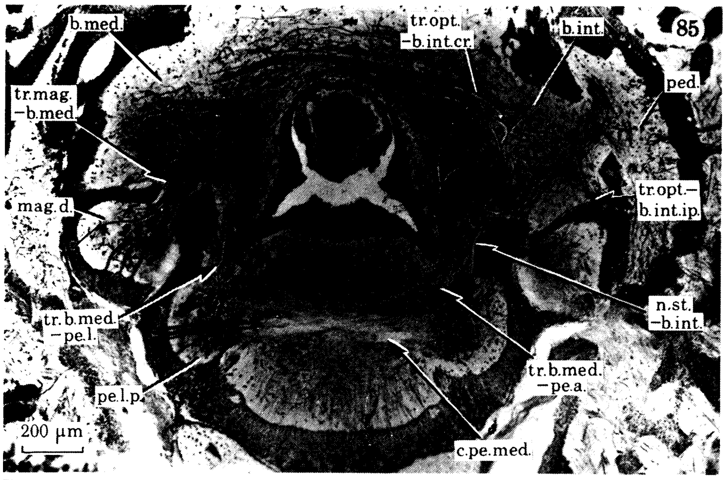
FIGURE 81. Horizontal section showing the neuropil and cells of the two parts of the dorsal basal lobes and their relations to the subvertical lobes. *L. vulgaris.*

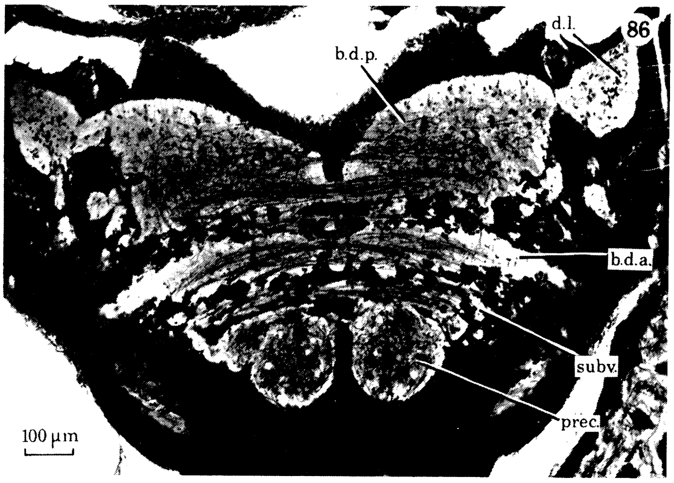
FIGURE 82. Sagittal section showing how the fibres of the posterior dorsal basal interweave on their way to the anterior dorsal basal and to the optic tract. *L. vulgaris.* Golgi.

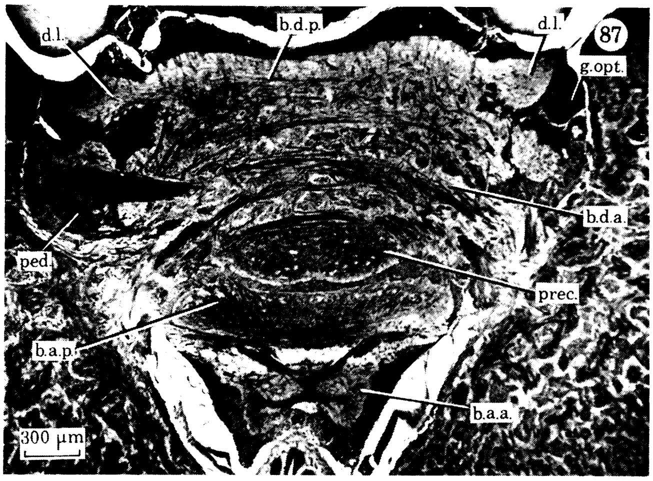
FIGURE 83. Horizontal section of the dorsal basal lobes of a small animal, showing fibres entering the two parts and others running between them. *L. pealeii.*

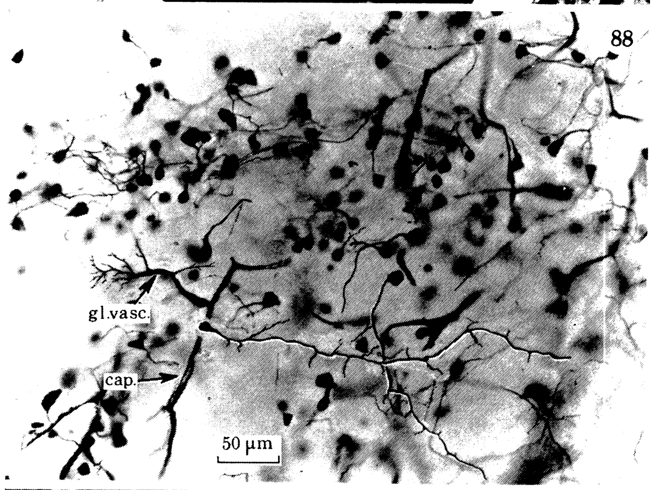


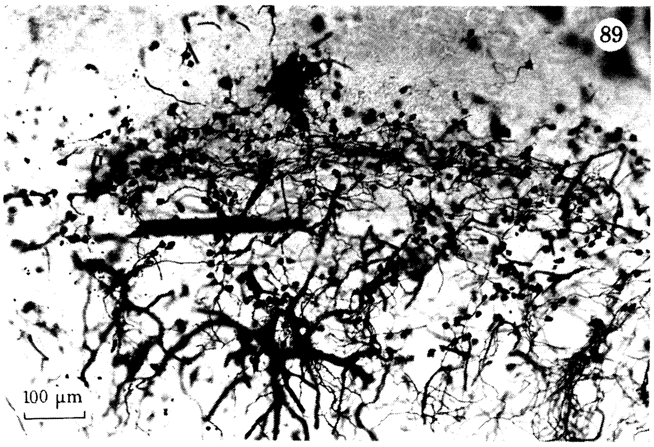
FIGURES 76–83. For description see opposite.

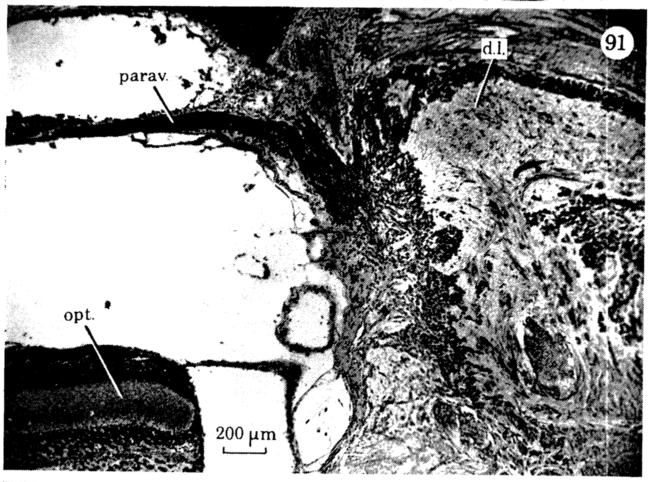


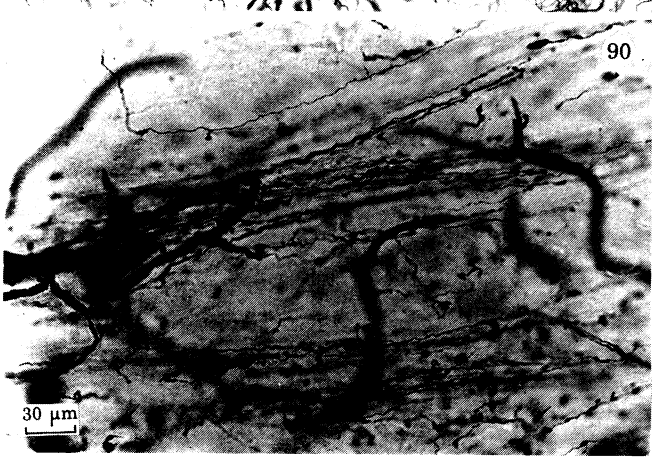












Figures 85–92. For description see opposite.

function the tract ascending to the basal lobes serves. There are many large terminal knobs in the neuropil around the origin of these fibres in the magnocellular lobe.

5.2.4.9. *Precommissural to median basal lobe tract.* Large fibres turn back from the base of the precommissural lobe and divide within the lower part of the median basal lobe. They are not very numerous but may provide an important pathway by which the vertical lobe system influences behaviour.

5.2.4.10. *Anterior basal to median basal lobe tracts.* The abundant fibres running between these lobes almost certainly include some running backwards (p. 365). Fibres coming from in front branch each within a restricted volume of the base of the lobe (figure 56, plate 5).

5.2.4.11. *Brachial to median basal lobe tract.* The bundles running from the roots of the antorbital and brachial nerves to the interbasal region almost certainly contain fibres that also reach to the median basal lobe (p. 385).

5.2.5. *Output of the median basal lobe* (figure 84, p. 382).

The large cells of the back of the lobe send their trunks forwards and downwards to reach to ten distinct destinations. These may be listed from the most medial, passing laterally.

5.2.5.1. *Median basal to posterior pedal lobe tract (funnel control fibres).* Large fibres pass down into the posterior pedal lobe and some pass to its centre and round ventrally, crossing the trunks of the fibres that give rise to the median funnel adductor nerve (see Young 1976*a*). These may therefore control the direction of swimming, forwards or backwards.

Somewhat more laterally are fibres crossing the trunks of the fibres of the paired anterior funnel nerves, which serve to turn it to right or left. Many of these fibres are large (about 10 μm) (figure 76, plate 7). Some end on the opposite side after an elaborate and regular system of crossings. This is obviously an important part of the steering system.

5.2.5.2. *Median basal to posterior pedal and anterior palliovisceral lobe tracts (fin and head retractor control pathway).* More laterally fibres pass directly downwards to near the base of the posterior pedal lobe (figure 72, plate 6). Here they divide and one branch runs forward across the trunks of the cells of the anterior swimming centre of the posterior pedal lobe, including presumably those that give rise to the anterior head retractor nerve and posterior pedal to fin lobe tract

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Description of plate 8

Figure 85. Transverse section of a small animal to show the magnocellular to median basal tract. Also the median basal to posterior lateral pedal tract. The lateral interbasal region receives ipsilateral and crossed optic fibres and fibres from the static nerve. The tract marked tr.b.med.–pe.a. also contains ascending fibres from the statocyst. *L. pealeii* (retouched).

Figure 86. Horizontal section of a small animal, showing the relations of the median basal and dorsal basal lobes and the fine transverse fibres. *L. pealeii.*

Figure 87. Horizontal section of the posterior dorsal basal lobe. *Alloteuthis.*

Figure 88. Transverse section of the dorsal basal lobes, showing neurons with trunks running in various directions. A gliovascular cell is shown attached to a capillary, its trunk ends in fine branched terminals (*gl. vasc.*). *Alloteuthis* (retouched). Golgi.

Figure 89. Transverse section of the anterior dorsal basal lobe to show the irregular arrangement of cells and fibres. *Alloteuthis.* Golgi.

Figure 90. Transverse section of the anterior dorsal basal lobe showing transversely running fibres, probably afferents from the optic lobe and glial fibres. *L. vulgaris.* Golgi.

Figure 91. Sagittal section of the dorso-lateral lobule, showing the relation of its cells to those of the strand of paravertical tissue proceeding to the orbit. *L. vulgaris.*

Figure 92. Transverse section of the posterior end of the brain to show the hindmost set of subpedunculate lobes. *L. vulgaris.*

(Young 1976*a*). The posterior branch runs back into the anterior pallioviscerał lobe to the region of the posterior swimming centre. These fibres thus end in two regions that also send large tracts to the fin lobe and head retractor, concerned with fin action, perhaps steering.

5.2.5.3. *Median basal to pedal, magnocellular and pallioviscerał tract* (*jet and retractor control pathway*) This is a remarkable set, including the largest fibres leaving the supraoesophageal lobes (up to 15 μm diameter) (figure 70, p. 381). As they run backwards each sends a branch ventrally to the posterior pedal or magnocellular lobe (figure 73, plate 6). These collaterals have a striking appearance as seen in sagittal section; some of them reach to the region of the first order giant cells. Each main fibre then proceeds on to the centre of the pallioviscerał lobe and there branches widely, probably reaching to the posterior swimming centre and to the neurons activating the jet system. It may be that these fibres are concerned in producing attacks by jet propulsion. This tract is joined by large bundles of fibres from the precommissural and small bundles from each part of the anterior basal lobes (figure 74, plate 6).

5.2.5.4. *Median basal and interbasal to posterior lateral pedal lobe tract* (*tentacle control pathway*). These fibres may be functionally related to the last if the large cells of the lateral pedal lobe are concerned with control of the tentacles (see Young 1976*a*). Fibres run down from the median basal lobe through the interbasal region, which also contributes fibres to the tract (figure 85, plate 8). They end close to the trunks of the large cells of the posterior lateral pedal lobe as these proceed to the middle pedal commissure and then forward to the anterior pedal lobe. Other fibres that may belong to the same set run lateral to the posterior pedal to fin lobe tract and then rather close to the cell layer of the floor of the pedal lobe.

5.2.5.5. *Median basal to anterior lateral pedal lobe tract* (*oculomotor control pathway*). This large tract is part of the system for control of the extrinsic eye muscles. Fibres arising from cells of the posterior face of the median basal lobe run forwards and down to spread out across the outgoing fibres of the four oculomotor nerves (figures 27, plate 3, 75, plate 6).

5.2.5.6. *Median basal to ventral magnocellular lobe tract* (*jet control pathway*). Besides the collaterals of the median basal to pallioviscerał tract already mentioned there is also a direct set of fibres passing to the region of the giant cell. This includes some large fibres dividing in the region of the lateral dendrites of the first order giant cell, and in the region behind it.

5.2.5.7. *Median basal to anterior pedal lobe tract* (*arm control pathway*). A descending bundle, including large fibres, curves medially and divides in front of the middle pedal commissure (figure 85, plate 8). This may be the pathway for control of the arms, whereas the tentacles are operated by other fibres, perhaps by way of the interbasal lobe (p. 385).

5.2.5.8. *Median basal to visceral lobe tract* (*visceral control pathway*). This arises together with the median basal to pallioviscerał and magnocellular lobe tract (figure 74, plate 6). It runs back lateral to the posterior superior oculomotor nerve and medial to the anterior head retractor nerve, turning ventrally and medially across the dorsal side of the magnocellular lobe and below the posterior pedal to fin centre tract. So it passes in to the centre of the pallioviscerał lobe and back below the 2nd order giant fibre to divide up in the visceral lobe among the posterior roots of the visceral nerves (see Figures 68 and 71 of Young 1976*a*). The tract contains some large fibres.

5.2.5.9. *Median basal to precommissural and anterior basal lobe tract*. Numerous fibres of moderate size arising from cells at the back of the lobe run forwards as discrete bundles to end in the precommissural lobe and posterior area of the anterior basal lobe (see p. 375). These bundles arise at all dorso-ventral levels but probably none come from cells of the dorsal basal lobes.

5.2.5.10. *Median basal to optic lobe tract* (*efference copy pathway*). It is not known for certain how many of the cells belonging to the median basal lobe in the narrow sense send axons back to the optic lobes, but it is assumed that many do so. A main pathway in this direction is however from the dorsal basal system (see below).

5.3. *Interbasal region*

At the base of the median basal lobe is a region with some very distinctive features that is yet hard to describe. It occupies a position on each side lateral to all the other basal lobes and between them and the optic lobe (figures 77 and 78, plate 7). It consists of rather distinct lateral and medial parts, separated by the lateral basal to anterior chromatophore lobe tract. The medial part lies below the median basal lobe, lateral to the median basal to palliovisceral lobe tracts (figure 79, plate 7). Here it is therefore dorsal to the posterior lateral pedal lobe (figure 85, plate 8) and anterior to the postorbital and posterior superior oculomotor nerves (figure 80, plate 7). The lateral part of the interbasal region lies medial to the dorsal magnocellular lobe (figure 79, plate 7) and the dorsal magnocellular to median basal lobe tract runs above it. The peduncle to median basal lobe tract enters between the two parts. The dorsal, medial and anterior extents of the interbasal region are very hard to define since it merges with the median basal and anterior basal lobes (figure 79, plate 7). The interbasal region could thus be considered to include the whole neuropil behind the anterior basal lobe. The two parts are rather widely separated and it is not clear that they form a single functional system. The lateral part does not participate in the interchange of fibres described below.

The most obvious feature of the region is this interchange in the medial part, made by an elaborate set of interweaving fibres coming from various peripheral nerves (figure 78, plate 7, see also Figure 34 of Young 1976*a*). The effect of this very complicated junction seems to be to distribute fibres from the various sources to many of the supraoesophageal lobes, perhaps to all of them. Bundles have been traced to this region from the following sources:

(1) Posterior superior ophthalmic nerve. These fibres enter the region from directly behind and spread out upwards and downwards (figures 75, plate 6, 80, plate 7).

(2, 3). A large bundle enters posteriorly from below(figure 75, plate 6). This comes partly from the anterior funnel nerve, partly from the inferior posterior ophthalmic nerve.

(4) A smaller bundle enters from the front and below, perhaps from the inferior antorbital nerve.

(5, 6). A larger tract enters from in front dorsally (figure 78, plate 7). This comes from the anterior pedal lobe and from there can be traced to the bundles forming the brachio-pedal connectives. It probably includes fibres from the antorbital and brachial nerves.

(7) Fibres enter this region from the magnocellular lobe, perhaps originally from the pallial nerve.

(8) A bundle of large fibres enters from the optic lobe. They come from below, medial to the peduncle lobe (figure 85, plate 8). These fibres are part of the set of large ventral optic to basal lobe fibres that arise from the median ventral part of the optic lobe (figure 26, p. 363). Many of them divide up in the interbasal lobe of the same side and some cross (figure 85, plate 8).

(9) Fibres from the peduncle lobe almost certainly end in the interbasal region.

The fibres from all these various sources may either terminate here or pass on through the interchange system to various destinations. Many of them run upwards into the median basal, precommissural and perhaps anterior basal lobes, but others turn down and may reach any of the suboesophageal lobes.

So many fibres pass through this region that it is not possible to analyse its connections into input and output. Few nerve cells can be specifically assigned to the region, but many send dendritic processes to it. These come particularly from the trunks of the large neurons of the median basal lobes, on their way to the posterior pedal and palliovisceral centres. Fibres from the cells of the dorsal magnocellular lobe proceeding to the posterior pedal or palliovisceral lobe, also send dendritic branches (see Young 1976*a*).

One interpretation for this region is that it is a centre for distribution of fibres from the surface of the body including those signalling trauma. These would need to reach to various efferent centres, for example, to those for avoidance reactions and for defensive responses to attack on any part of the body. They would also need to reach to higher centres concerned with learning. It is not easy to see how these activities may be related to the results obtained by stimulation of this region in *Sepia*, namely movement of the tentacles (Boycott 1961). However, the large fibres from the optic lobes may be involved in that action, perhaps through the posterior lateral pedal centre, which is close.

The interbasal lobe of *Octopus* is in approximately the position described here but lies relatively more anteriorly and laterally (Young 1971). Moreover, it has a rather more definite structure, with its own specific cells. It also differs from that of the squid in not receiving the fibres of many afferent nerves and not showing the conspicuous interchange system. However a region nearby in *Octopus*, at the base of the median basal lobe does receive fibres from the posterior superior ophthalmic nerve and from the superior antorbital nerve. A further complication is that it has been suggested that this region at the base of the median basal lobe of *Octopus* represents the centre responsible for innervation of the pre- and post-ocular tentacles of *Nautilus* (Young 1971, p. 40). The further work on this topic mentioned there has unfortunately not been completed and the suggestion remains speculative. More important is the new fact that in *Loligo* afferent fibres from many sources converge here and are distributed to many destinations, but our lack of understanding of this region is very unsatisfactory.

5.4. *Dorsal basal lobes*

These consist of two partly separate regions, anterior and posterior dorsal basal, divided by an irregular wall of cells pierced by many fibre bundles (figures 81, plate 7, 86, plate 8). The lobes occupy the dorsal part of the brain posteriorly, above the median basal lobe. More anteriorly they lie below the subpedunculate and subvertical lobes and in front of the median basal. Laterally the posterior dorsal basal lobe is related to the dorso-lateral lobule and the anterior dorsal basal lobe to the optic tract and optic tract lobes. The anterior dorsal basal lobe is related ventrally to the optic commissure.

The cell wall of the back of the posterior dorsal basal lobe has outer layers of rather large cells (25 μm diameter, nucleus 10 μm) with clear cytoplasm. The inner layers contain smaller cells, but no very small ones. There is no sharp break in the composition of the cell wall either between the median basal below and the dorsal basal or between the latter and the subpedunculate lobe above. Nevertheless, the posterior wall of the dorsal basal is marked off as a distinct swelling laterally.

The trunks of the cells of the posterior walls of the posterior dorsal basal run forwards and downwards in characteristic interweaving bundles (figure 82, plate 7). Many run to the optic tract, but others pass down into the median basal lobe, still others forwards to the precommissural and anterior basal lobes. There are also a few much larger cells in the layer in front that separates the anterior and posterior dorsal basal regions. Their trunks proceed downwards across the bundles of axons of the smaller cells that proceed forwards. Each of these larger cells carries a series of lateral dendrites extending for a short distance (up to 200 μm), with spines. These cells would therefore be influenced by, or together with, a series of the smaller cells. They perhaps send axons to suboesophageal destinations.

The anterior dorsal basal region is an oblique vertical plate of neuropil with irregular cell layers in front and behind. It thus has a general similarity to the small-celled regions of the other basal lobes (figures 83, plate 7, 87, plate 8). Its numerous small cells form a series of irregular islands and lobules not sharply marked off from the similar lobules of the subpedunculate and subvertical lobes (figure 80, plate 7). They include some medium and many very small cells. The smaller cells take various forms, some resembling the cells of the fine parallel fibre regions of other lobes. Their trunks turn laterally and carry a few dendritic collaterals and then other branches some distance away (figure 88, plate 8). They differ from the cells of the other regions of fine fibres in that the fibres do not run regularly parallel for long distances from side to side, but form a mesh-work (figure 89, plate 8). Some rather larger cells send their trunks ventrally and laterally across the mesh-work, presumably to reach the optic lobe or the other supraoesophageal centres.

Both parts of the dorsal basal region contain many very small amacrine cells, carrying only a few branches terminating in their immediate neighbourhood (figure 94, plate 9). There may be only one single trunk or several short ones, running in various directions and carrying a few knobs and short spines. There are also very simple bipolar cells. It is never easy to be sure that such cells are completely stained, but it seems likely that these are very short amacrine cells, such as are abundant in the small-celled regions of the other basal lobes.

The input to the dorsal basal lobes comes from bundles similar to those entering the median basal lobe, largely of optic fibres. They distribute to either the same or the opposite side. Some leave the bundles in the anterior dorsal basal and run back to the posterior dorsal basal (figure 83, plate 7). Conversely, some of the axons arising on the posterior wall of the posterior dorsal basal are distributed to the optic lobe of the same or opposite side with the bundles joining the anterior dorsal basal lobe. Evidently the two parts are similar and work together.

The incoming optic bundles form a series of fine fibres running transversely (figure 90, plate 8). The fibres turn out of the bundles and make a mesh of varicose fibres somewhat similar to that seen in the spine regions of the other basal lobes. At intervals they give collaterals ending in swellings with fine terminals (figure 93, plate 9).

The dorsal basal lobes also receive fibres from the median basal lobe (figure 68, p. 380). These fibres may branch very widely on both sides with branches also extending to the precommissural lobes.

5.5. *Dorso-lateral lobes*

These are a pair of small lobules at the back of the supraoesophageal mass, important as the source of the fibres of the optic gland nerve, which probably influences reproduction in the squid as in *Octopus*. Each lobule lies in relation to the posterior dorsal basal lobe medially and to the lateral basal below. The peduncle and olfactory lobes are in front of it (figures 86, 87, plate 8). The optic gland lies on its lateral surface and in front of this a mass of small cells of the subpedunculate and paravertical tissues (figure 91, plate 8). The postorbital nerve lies between this lobule and the dorsal basal lobe.

The walls of the dorso-lateral lobes contain no large cells, but not all are the same size. The larger ones reach a diameter of 12 μm, with nucleus 6 μm (adult *Loligo*) and there are numerous smaller ones (figure 95, plate 9). The form of the cells and destination of their axons have not been closely studied. The fibres of the optic gland nerve certainly arise here (figure 95). The input to the lobe can best be summarized by the connections of its neuropil. It opens widely laterally to the olactory lobe (figure 102, plate 9), and receives many fibres from it. A tract runs to it from the peduncle lobe, through the base of the olfactory lobe. It is broadly continuous with the dorsal basal lobe, from which many fibres reach to it (figure 87, plate 8). Many optic tract fibres reach the lobule by this route and this is a major source of input.

5.6. *Subpedunculate lobes*

Across the back of the brain above the median basal lobe are three layers of lobules, which will be called, from back to front, subpedunculate lobes 1, 2 and 3 (figures 92, plate 8, 97, 98, plate 9). They correspond only partly to the lobes that were given this name in *Octopus* because in that animal but not in *Loligo* the axons form a separate subpedunculate nerve, running below the optic tract ('peduncle') (Thöre 1939). In *Loligo* subpedunculate 1 is a distinct lobe with relatively large cells resembling the larger cells of the posterior dorsal basal lobe (figure 96, plate 9). The largest reach 12 μm diameter, with nuclei 8 μm. The trunks of these cells form compact bundles of axons, which run towards the optic tract (figure 97, plate 9). They are clearly distinct from the bundles arising in the dorsal basal lobes and do not show the interweaving characteristic of the latter. These tracts of nerve fibres thus have some similarity to the subpedunculate nerves of octopods, but they have not been followed to distinct nerves leaving the brain. They seem to join the optic tracts and may perhaps thus reach the blood vessels of

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DESCRIPTION OF PLATE 9

FIGURE 93. Transverse section of the anterior dorsal basal lobe, showing endings presumed to be of a fibre of the optic tract. *L. vulgaris*. Golgi.

FIGURE 94. Cells of the dorsal basal lobe. *Alloteuthis*. Golgi.

FIGURE 95. Sagittal section of the optic gland and its nerve. *L. vulgaris*, 15 cm mantle length.

FIGURE 96. Sagittal section showing the fibres from the hinder subpedunculate lobe forming tracts that may correspond to the subpedunculate nerves of *Octopus*. *L. vulgaris*.

FIGURE 97. Sagittal section of the three sets of subpedunculate lobes and the subpedunculate nerve. *Alloteuthis*.

FIGURE 98. Horizontal section to show the subpedunculate lobes. *Alloteuthis*.

FIGURE 100. Transverse section of the subpedunculate lobes, showing the tangles of afferent fibres entering, presumably from optic tract fibres. *L. vulgaris*. Golgi.

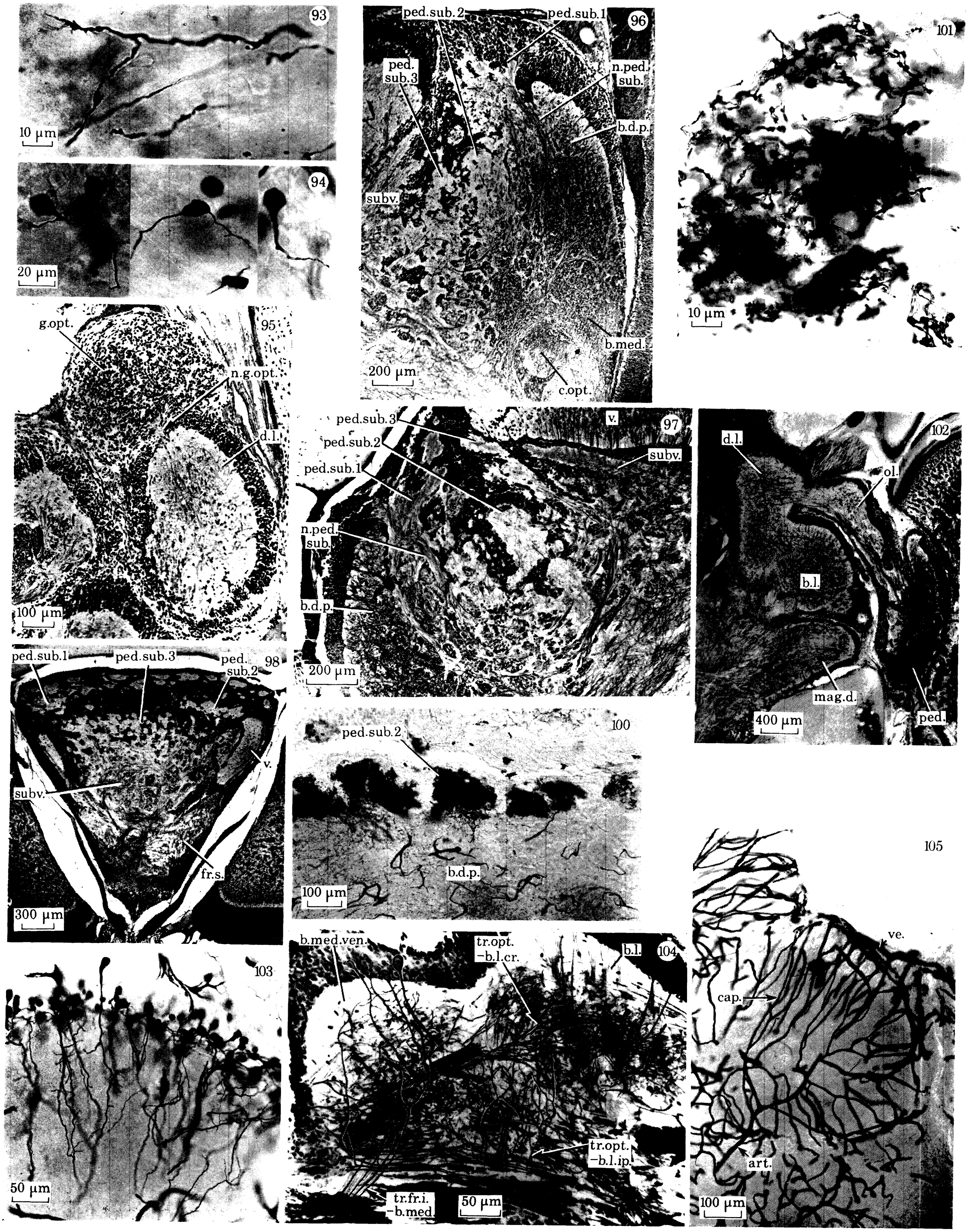
FIGURE 101. Details of one of the tangles of fibres in the subpedunculate lobes, and their endings. *L. vulgaris*. Golgi.

FIGURE 102. Transverse section to show the relation of the dorso-lateral lobule to the olfactory and peduncle lobes. *L. pealeii*.

FIGURE 103. Transverse section of the lateral basal lobe. *Alloteuthis*. Golgi.

FIGURE 104. Horizontal section of the median basal and lateral basal lobes of a young animal retouched to show the ipsilateral and crossed optic to lateral basal tracts. The inferior frontal to median basal tract is also shown. *L. pealeii*.

FIGURE 105. Transverse section of the lateral basal lobe, showing the artery at the centre with a radial array of capillary branches that join the vein at the outer margin. *Alloteuthis*. Golgi.



FIGURES 93–105. For description see opposite.

(Facing p. 388)

the orbit, whose neurovenous tissues are innervated by these nerves in *Octopus* (Young 1971; Froesch 1975).

Subpedunculate lobes 2 and 3 form two rows of more irregular lobules composed of mainly much smaller cells (figures 97, 98, plate 9). Among these small cells are a few that are larger, but always much smaller than those of subpedunculate 1. The axons of these cells probably form bundles reaching to the optic tracts, but they are very fine and have not been seen clearly. The cells of the lobe have characteristic dendritic systems. From a short trunk there spring numerous branches, running round the lobule and ending in rather simple sprays of tapering twigs, with some varicosities (figure 99, below). It is not known whether these cells

FIGURE 99. Drawing of a transverse section of cells of the sub-peduncuIate lobe. *Alloteuthis*. Golgi.

carry axons. Presumably they are related to the incoming afferents (see below). The lower set of lobules (subpedunculate 2) is in relation to the upper part of the anterior dorsal basal lobes and could be regarded as related to that region as the lobules of subpedunculate 1 are to the posterior dorsal basal. The upper set of lobes, subpedunculate 3, are related to the posterior part of the subvertical lobes, from which they receive fibres.

The main input to the whole subpedunculate system is from optic nerve fibres. These come from the web of bundles in the dorsal basal lobes (figure 92, plate 8). The centre of each lobule of the two upper subpedunculate lobes is occupied by a dense tangle of these incoming fibres (figures 100, 101, plate 9). They branch repeatedly and show many swellings. They terminate in fine twigs, often less stained by the Golgi method than the main parent branch. The whole network gives the impression of a powerful secreting apparatus. The swellings and terminations are similar to those of the optic fibres in the nearby dorsal basal lobe, but are more abundant. They have presumably become developed for some special function, whose nature remains unknown. The second input that has been detected consists of fine fibres from the subvertical lobes, but their endings have not been seen. There may be yet other inputs.

The afferent fibres to the larger-celled subpedunculate lobe 1 have not been stained well by the Golgi method and it is not clear that the arrangement of this part is really similar to those of the other two sets. Unlike those lobes its cells clearly have axons.

5.7. *Lateral basal lobes*

These are functionally one of the most clearly distinct parts of the brain, probably concerned wholly in *Loligo* as in *Sepia* and *Octopus* with the muscles of the chromatophores and other muscles of the skin (Boycott 1953, 1961). The lobes are anatomically distinct, although broadly continuous with others. They lie at the back and sides of the supraoesophageal lobes in relation to the magnocellular lobes below, the olfactory and peduncle lobes laterally, median basal medially and dorso-lateral lobule dorsally (figure 102, plate 9).

The cells are all on the posterior wall. The largest are up to 30 μm in diameter, with nucleus 10 μm, and there are numerous smaller ones and some very small (figure 103, plate 9). All the large and medium cells send axons to the output tracts leading to the anterior and posterior chromatophore lobes. They have characteristic short and simple collateral dendrites, with few branches and many small swellings. The dendrites occur throughout the lobe from the periphery to the centre (figure 103, plate 9). The smallest cells are microneurons with simple trunks restricted to the lobe and often ending only in the outer layers of the neuropil.

The input to the lateral basal lobe is mainly optic. The fibres run backwards from the optic tract with the bundles running to the median basal and dorsal lobes (figure 104, plate 9). Some end on the same side and others cross. The fibres run circumferentially round the lobe across the trunks of the cells. They branch on entry to the lobe and then many times later, so that each sends its influence to a large part of the lobe. A single fibre probably sometimes sends branches to both sides. A small number of large fibres entering from below can be traced to the middle pedal commissure and almost certainly come from the statocyst. They branch throughout the lobe. Fibres also enter from the nearby peduncle lobe.

6. Blood vessels and glia of the basal lobes

The blood supply of the lateral basal lobe is shown in figure 105, plate 9. This will serve as an example of the pattern found in all the lobes. Arteries enter from the centre and give off branches at right angles. These then divide further at more acute angles and finally join to form veins at the surface. There are thus no very fine capillaries. Interchange with the tissues is produced through the system of gliovascular channels (see Stephens & Young 1969; Young 1971).

The forms of the glia cells previously described in the suboesophageal lobes have also been seen in the basal supraoesophageal lobes. Gliovascular channels leading from the capillaries are shown in figures 66, p. 379 and 88, plate 8). They consist of a broad foot attached to the vessel and carrying the nucleus. From this foot a trunk proceeds outwards and forms exceedingly fine branches among the tissues. These can easily be mistaken for neuronal branches, a similarity no doubt due to the fact that the two sets are interdigitated. It is not known how materials are carried by these cells, which appear to end blindly.

The fibrous glia cells have very long processes, many stretching along the tracts of nerve fibres (figure 22*a*, plate 2). They may however have processes running in all directions around the central cell body (figure 44, plate 4). The fibres often run for very long distances without branching and are easily confused with nerve fibres. The protoplasmic glia is a more enigmatic category. Sometimes distinct branching or net-like structures are seen (figure 22*b*, plate 2). In other situations material of the same sort seems to be combined with the central part of a fibrous glia cell (figure 22*a*). Probably the tissues are everywhere penetrated by webs of glial material, whose characteristics have never been fully described.

7. Discussion

7.1. *Comparison with* Octopus

It has now been possible to make a much fuller analysis of the basal lobes than was achieved in *Octopus* (Young 1971). The two parts of the anterior basal lobe were recognized in that account, but the fact that the two contain comparable components, including fine parallel fibres, was not realized. With the knowledge we now have it is clear that in all the coleoid cephalopods so far examined the basal lobes have this same arrangement, similar to that of the peduncle lobes, forming together a system that has certain resemblances to a cerebellum. The data from *Octopus* included degeneration and regeneration studies, which confirm some of the most important features of the present analysis of the organization, including the presence of a reverse projection from the basal lobes to the optic lobes, the crossed pathway from optic lobe to antero-median lobule and the efferent pathways from all the basal lobes to the suboesophageal motor centres.

The connections between the peduncle lobe and anterior basal lobes have been confirmed in *Octopus* with the Nauta technique by Woodhams (1975). Following lesions in the peduncle lobe he showed massive degeneration across the parallel fibre region of the anterior basal lobe. He has also shown that the appearance in the electron microscope of the fine parallel fibres of the anterior basal lobe of *Octopus vulgaris* in cross sections is so like that of the 'spine' of the peduncle lobe 'that one would be very hard put to it indeed to distinguish between the two'. Fluorescence microscopy, again in *O. vulgaris*, has also shown the similarity of the parallel fibre regions of the anterior basal and peduncle lobes. In both there is a bright yellow fluorescence, probably due to 5-hydroxytryptamine (Matus 1973). This fluorescence is apparently in fibres and cells *within* the lobes, rather than in the optic nerve fibres that enter them. Some sign of this fluorescence was seen also in the dorsal basal region, but less marked than in the anterior basal region. Thus as in *Loligo* there is very strong reason to consider that the peduncle and anterior basal 'spines' are similar but that the dorsal basal region is somewhat different.

The close relations between the dorsal basal and median basal lobes were seen in *Octopus* as in *Loligo*, indeed the general arrangement of the parts of the 'posterior' basal regions are strikingly similar. One big difference is the presence of a distinct subpedunculate nerve in *Octopus*. However, the present work shows that somewhat similar bundles of fibres are present in *Loligo*. It remains to be discovered whether they reach to neurosecretory tissue in the orbit as they do in *Octopus* (Froesch 1975).

7.2. *Structural organization of the basal lobes*

It may be that the particular anatomical arrangement of these lobes is the result of their origin from a series of circum-oesophageal commissures in an ancestral mollusc (see Young 1971). The two parts of the anterior basal lobe might represent one such ring (or possibly two), and the median basal another. Appearances such as figure 5*a*, plate 1, certainly emphasize that these lobes lie *around* the oesophagus, rather than only above it. Possibly several further rings should be included. Thus the vertical and precommissural lobes make such a ring, perhaps including also the interbasal lobe. Another suggestion (made to me by Professor B. B. Boycott, F.R.S.) is that the peduncle lobes with the median basal constitute one of these rings and the dorsal basal and olfactory lobes another one. Figure 102 (plate 9) shows this condition and fibres run down from the olfactory to the magnocellular lobe (Young 1976*a*). Although these are speculative suggestions they may help towards an understanding of the arrangement of these lobes. In particular, as Professor Boycott has suggested to me, the presence of layers of cells *within* the main bodies of the ganglia, which is unusual in an invertebrate, may be explained by their origin from distinct commissural bands.

7.3. *Functional organization of the basal lobes*

These lobes are evidently concerned with the control of movement, particularly in relation to visual and static inputs. The only direct connection of the optic lobes with suboesophageal centres is through the magnocellular lobes, probably an avoidance pathway (p. 394). All the more subtle responses to visual stimuli such as tracking prey, are mediated through the peduncle lobes and basal lobes, The system consists of four distinct lobes on each side. This separation allows for different orientations of their neuropils and the somatotopic organization of these may be the basis of the system for steering the squid towards or away from its targets. The anterior anterior basal lobe is extended largely dorso-ventrally, though its fibres cross in the mid-line. The posterior anterior basal lies transversely. It may be that these two regions are responsible for control of movement in the dipping and rolling planes respectively. The median basal lobe is extended antero-posteriorly and may be responsible, among other things, for steering to right and left, in the yawing plane. Its connections with the swimming and funnel centres of the posterior pedal and palliovisceral lobes support this suggestion.

There is some experimental evidence to help with these problems. Boycott (1961) showed that in *Sepia* electrical stimulation of the median basal lobe can produce either gentle respiratory movements or violent mantle contractions, with ejection of ink. Wave movements of the fins were produced by stimulation of either anterior or median basal lobes. Stimulation of the anterior basal lobe produced movement of the eyes, with or without turning of the head, arms and funnel. There was also reflexion of the arms over the head as when preparing to eject the tentacles at the prey (Messenger 1968). Movements of the tentacles themselves were obtained by stimulation in the interbasal region (p. 385). Boycott's results suggest that steering is mainly an activity of the anterior basal lobe, while the median basal lobe produces the jet (and of course has other actions).

Some experiments involving removals have also been made in *Sepia* (Boycott & Young 1950). After unilateral removal of the anterior basal lobe on one side the fins worked to produce a continuous spinning so that the intact side was at the periphery. This was attributed to a removal of inhibition because after bilateral removal of the supraoesophageal lobes a cuttlefish moves continually forward. Unilateral removal of the anterior basal lobe from an octopus also produces rotation in the same sense as in *Sepia* (unpublished data).

These experiments thus confirm that these basal lobes are concerned with the initiation of movement, with its direction, and with its termination. They do not help us greatly in the interpretation of the significance of the detailed organization of the lobes. Nor do they carry us far towards understanding the significance of the presence of three divisions of the basal lobes and the similar peduncle lobes. The work of Boycott (1961), on *Sepia*, and Messenger (1967), on *Octopus*, shows that this latter lobe also influences many movements.

Consideration of the functions of all the lobes may be helped by examining species with various habitats, and such a comparative study, which should clarify many of these problems, is now under way. The basal and peduncle lobes are present in all cephalopods so far examined. They have approximately the same structure and orientation, with the curious exception that the peduncle lobes of *Octopus* and *Sepia* lie horizontally.

7.4. *The basal lobes as visuostatic centres*

All of these lobes receive their inputs mainly from the optic lobes and static nerves. The hint that they lie in different planes suggests that they may perform some kind of mapping operations. It has already been noted that in the organization of the optic lobes of cephalopods there is a retention of the topological representation on the retina (see Young 1971, 1976*b*). It is probable that at least some features of this topology are retained in the projections from the optic lobes to the basal lobes. The technical difficulties have prevented definite conclusions about the details of these tracts. There is certainly a regularity in the input from the optic lobe to the anterior basal lobe (figure 11, plate 1). There is also very elaborate interweaving of bundles, on the ipsilateral side and as they cross the mid-line. Furthermore, towards the ends of the optic to basal lobe tracts the fibres again show signs of regular order (e.g. figures 32, plate 3 and 55, plate 5). The projection of the optic lobe to the peduncle lobe spine has been shown by Nauta degeneration in *Octopus* to retain the order of the optic lobe (Woodhams 1975).

The problem is complicated by the fact that each optic fibre spreads through a considerable volume of neuropil, and they overlap. Each must influence many cells of the basal lobe. Conversely each efferent cell has dendrites that are influenced by a rather long cylinder of neuropil and these again overlap. It seems likely that we have to consider an organization that comprises whole sets of incoming and outgoing fibres, rather than, or as well as, detailed specific interneuronal connections. Furthermore, we do not know how the axons of the efferent cells of the basal lobes themselves are distributed, either in the oculomotor and other suboesophageal centres or on the reverse pathways to the optic lobes. We also have no detailed knowledge of how the fibres of the static nerves contribute to the pattern. These are all matters that should repay further research.

7.5. *The parallel fibres and cerebellum-like plan*

Although we are ignorant of so much there is a further set of facts to suggest how these lobes act. Each of them contains a system of parallel fibres of various diameters, carrying serial collaterals. This is most clearly shown in the region where the fibres are very fine, which is precisely comparable to the 'spine' of the peduncle lobes (Messenger 1967, 1971). These systems are unlike those known in any other invertebrate, but have a strong resemblance to the parallel fibres of the vertebrate cerebellum, which is also a visuostatic centre. It is impossible to carry this suggestion much further until more details of the connections are available. In the peduncle lobe of *Octopus* the parallel fibres make synapses with each other along their length (Woodhams 1975). Some of them turn down into the basal zone and this may be the efferent pathway via the larger cells. Some of the outgoing axons of the cells of the lobes run across the parallel fibres and could thus be influenced by them in the manner of Purkinje cells. The presence of a series of fibres of various diameters, including very fine ones, suggests that conduction velocities are an important feature of the system. In each of these lobes there are larger cells and fibres ventrally and a series of smaller and smaller ones passing dorsally. There are some signs that the series is not continuous but divided into several sets, for example among the parallel fibres of the posterior anterior basal lobe (p. 370). Whether or not this division is significant there is certainly some reason for the differences in diameter of the fibres. A simple suggestion is that each of the basal lobes serves to regulate the timing of movement in a particular direction. This may include both acceleration and deceleration of ballistic actions as suggested by Breitenberg (1967). The large re-afferent pathways to the optic lobes must play an important part in this control mechanism. A 'corollary discharge' or 'efference copy' is clearly required for tracking behaviour (Sperry 1950; v. Holst 1973 but see also MacKay 1973). The very large connections across the mid-line and between the various basal lobes are also obviously significant elements in the organization.

7.6. *The large ventral optic tract fibres: the attack pathway?*

This is the first account of an extensive system of very large fibres leaving the lower part of the optic lobe (p. 362). They arise in a special sub-division of that lobe, which had not previously been described (figure 26, p. 363). The cell bodies of the fibres form a row along the median surface of the optic lobe. Their axons are the lowest in the optic tract, and proceed upwards to distribute to all the basal lobes and to the magnocellular and (probably) peduncle lobes. They divide extensively and individual fibres send branches to several of the basal lobes (perhaps sometimes to all of them) and to both sides. They cross in commissures at the base of the anterior basal and precommissural lobes, where they are the largest fibres in the whole supraoesophageal system (figure 5, p. 358).

These fibres are evidently a set with a single function, probably overriding all other activities of the system. Obviously suggestions for this function are for attack or retreat. Attack is likely to be the termination of a regulated process of tracking, which may end with the image of the prey object acting upon particular regions of the retinae and optic lobes of both sides (figure 70, p. 381).

7.7. *Reciprocal median basal and magnocellular tracts: the avoidance pathway?*

Avoidance is perhaps achieved by the median basal to magnocellular tracts, together with the direct optic to magnocellular tracts. Both of these include fibres running direct to the first order giant cell in the ventral magnocellular lobe and also a remarkable set of collaterals of the median basal to palliovisceral and magnocellular tract (figure 73, plate 6). These pathways could therefore produce rapid escape reactions, including ejection of ink.

There is a conspicuous reverse pathway from the dorsal magnocellular lobe to median basal lobe (figure 69, plate 6 and figure 70, p. 381). Collaterals of these fibres also reach to all the other basal lobes. These fibres are of medium size and it is possible that they are concerned with stopping (or preventing) action, rather than initiating it. The basal lobes thus receive ventrally two sets of widely spreading fibres – from the optic lobes in front and from the magnocellular lobes behind. In addition they receive detailed projections from the more dorsal parts of the optic tracts. The hypothesis now suggested is that the dorsal tracts are concerned with tracking operations, which are terminated by the coming into action of one or other of the large fibre systems, the optic ones for attack and the magnocellular ones for retreat.

7.8. *Microneurons and amacrine cells*

The basal lobes contain very numerous cells whose trunks are restricted to the lobe and may thus be defined as microneurons. Two sorts can be distinguished (1) those that have a relatively long process, which is probably an axon ending within the lobe and perhaps carrying action potentials and (2) very short amacrines. The former include many short-axon cells of the anterior basal, median basal and lateral basal lobes. They are intermingled with larger fibres and may perhaps produce lateral inhibition. Another class of microneurons are the parallel fibres, especially the fine ones of the 'spine' regions, many of which have been shown to end within the lobes (p. 393).

The regions occupied by the trunks of the microneurons stain very poorly with Cajal's stain, presumably because the fibres contain few neurofibrils (see Guillery 1970). Such areas are especially conspicuous in the more dorsal parts of the basal lobes and at the margins of those lobes that contain microneurons as well as larger cells. Thus in the suboesophageal lobes such areas are conspicuous in the anterior pedal and palliovisceral lobes but not in the chromatophore lobes and fin lobes, which lack microneurons (Young 1976*a*). It is possible that the small cells in these lobes are concerned with reciprocal reflex inhibition. It is less easy to guess at their function in the basal lobes. Where they can be stained by the Golgi method, as in the subpedunculate lobes, the fibres have very extensive branches in a small volume, suggesting a secretory function.

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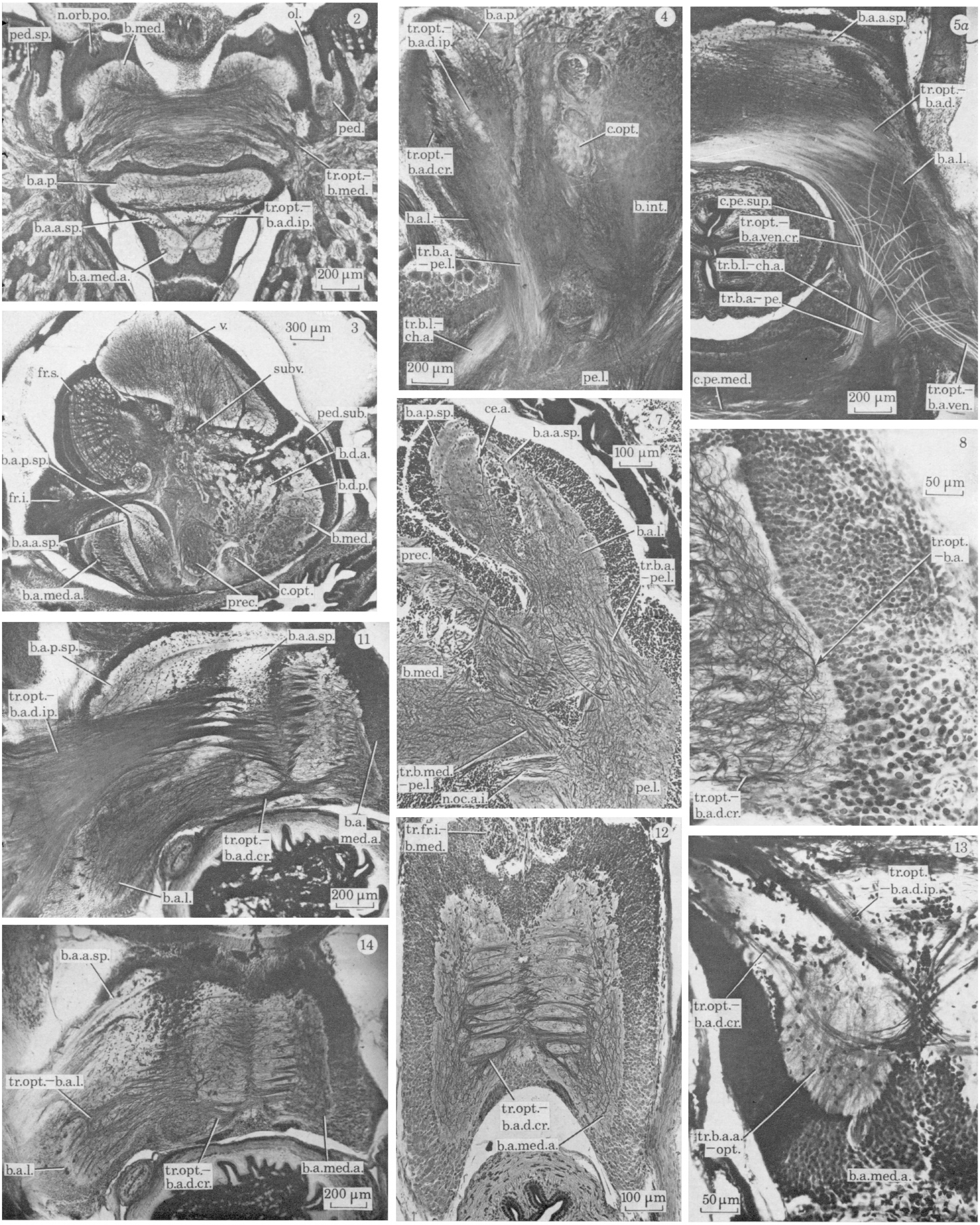
Abbreviations used on line figures and plates

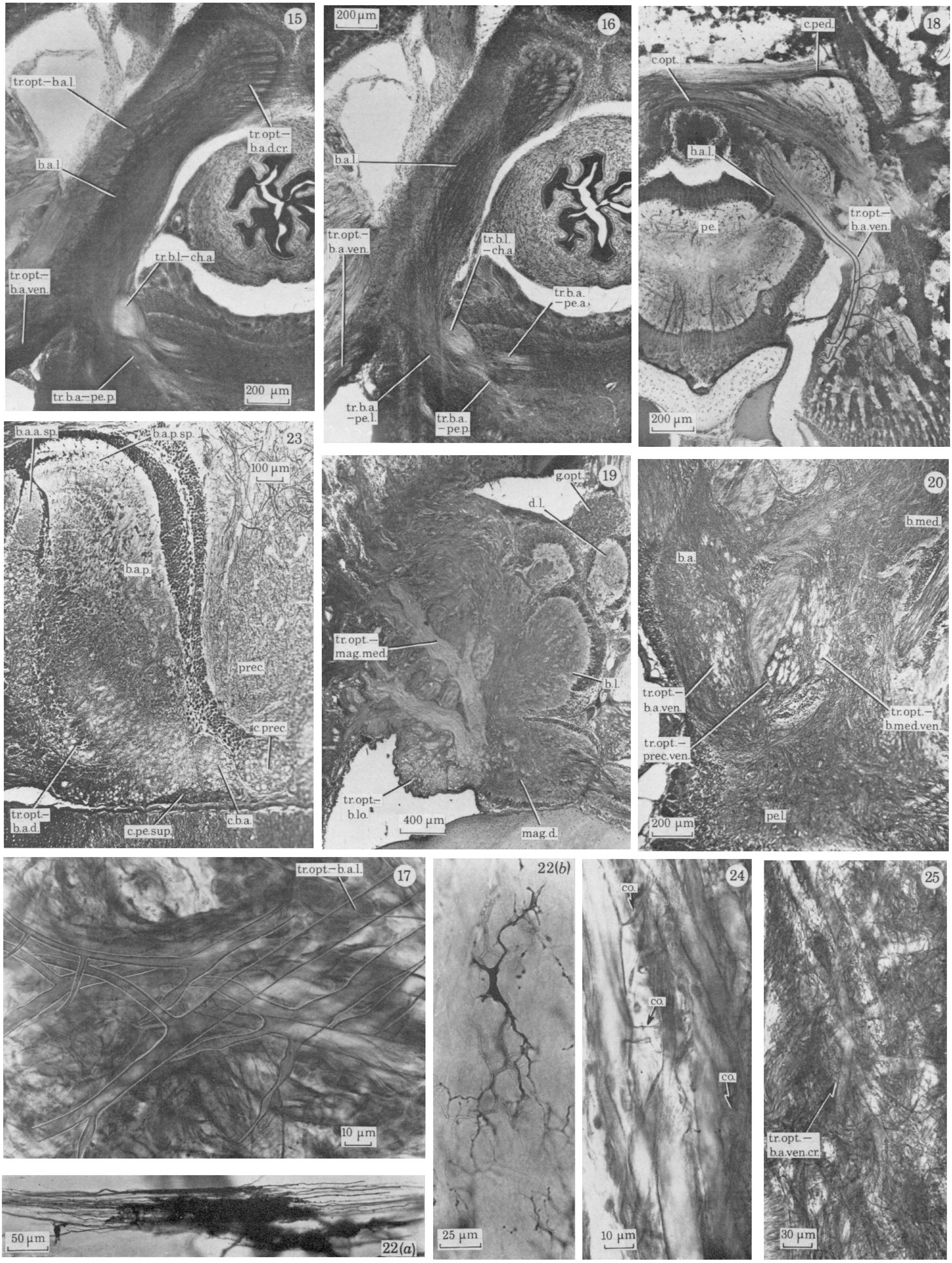
aff.	afferent fibre
aff.cr.	crossed afferent
aff.ip.	ipsilateral afferent
am.	amacrine
art.	artery
b.a.	anterior basal lobe
b.a.a.	anterior anterior basal lobe
b.a.l.	lateral anterior basal lobe
b.a.med.a.	antero-medial anterior basal lobe
b.a.a.sp.	spine of anterior anterior basal lobe
b.a.p.	posterior anterior basal lobe
b.a.p.l.	lateral lobe of posterior anterior basal lobe
b.a.p.sp.	spine of posterior anterior basal lobe
b.d.	dorsal basal lobe
b.d.a.	anterior dorsal basal lobe
b.d.p.	posterior dorsal basal lobe
b.int.	interbasal lobe
b.int.l.	lateral interbasal lobe
b.int.med.	medial interbasal lobe
b.l.	lateral basal lobe
b.med.	median basal lobe
b.med.d.	dorsal median basal lobe
b.med.ven.	ventral median basal lobe
br.	brachial lobe
c.b.a.	commissure of anterior basal lobe
c.opt.	optic commissure
c.pe.med.	middle pedal commissure
c.pe.sup.	suprapedal commissure
c.ped.	commissure of peduncle lobe
c.prec.	commissure of precommissural lobe
cap.	capillary
ce.a.	anterior cell
ce.b.a.med.a.	cell of antero-medial anterior basal lobule
ce.b.a.p.	cell of posterior anterior basal lobe
ce.p.	posterior cell
co.	collateral branches
cr.	crista
d.l.	dorso-lateral lobe
den.	dendrites
f.par.	parallel fibres
fl.	fin lobe
fr.i.	inferior frontal lobe
fr.s.	superior frontal lobe
g.c.1	first order giant cell
g.f.1	first order giant fibre
g.f.2	second order giant fibre
g.opt.	optic gland
gl.fib.	glial fibre
gl.vasc.	gliovascular cell
mac.	macula
mag.	magnocellular lobe
mag.d.	dorsal magnocellular lobe
n.antorb.–b.int.	antorbital nerve to interbasal tract
n.cr.–b.a.	crista nerve to anterior basal lobe

n.f.	nerve fibre
n.fin	fin nerve
n.g.opt.	optic gland nerve
n.oc.a.i.	inferior anterior oculomotor nerve
n.oc.a.s.	superior anterior oculomotor nerve
n.oc.p.i.	inferior posterior oculomotor nerve
n.oc.p.s.	superior posterior oculomotor nerve
n.op.p.s.	superior posterior ophthalamic nerve
n.orb.po.	postorbital nerve
n.pal.	pallial nerve
n.ped.sub.	subpedunculate nerve
n.st.	static nerves
n.st.–b.a.	static nerve to anterior basal tract
n.st.–b.int.	static nerve to interbasal tract
n.st.–b.med.	static nerve to median basal tract
n.retr.h.a.	anterior head retractor nerve
n.visc.	visceral nerve
ol.	olfactory lobe
opt.	optic lobe
parav.	paravertical tissue
pe.	pedal lobe
pe.a.	anterior pedal lobe
pe.l.	lateral pedal lobe
pe.l.p.	posterior lateral pedal lobe
pe.p.	posterior pedal lobe
ped.	peduncle lobe
ped.b.	basal peduncle lobe
ped.sp.	spine of peduncle lobe
ped.sub.	subpedunculate lobe
ped.sub.1–3	subpedunculate lobes 1–3
prec.	precommissural lobe
pv.	palliovisceral lobe
pv.a.	anterior palliovisceral lobe
subv.	subvertical lobe
tr.b.a.–b.med.	anterior basal to median basal tract
tr.b.a.–opt.	anterior basal to optic tract
tr.b.a.–pe.	anterior basal to pedal tract
tr.b.a.–pe.a.	anterior basal to anterior pedal tract
tr.b.a.–ped	anterior basal to peduncle tract
tr.b.a.–pe.l.	anterior basal to lateral pedal tract
tr.b.a.–pe.p.	anterior basal to posterior pedal tract
tr.b.a.–prec.	anterior basal to precommissural tract
tr.b.a.–pv.	anterior basal to palliovisceral tract
tr.b.a.a.–opt.	anterior anterior basal to optic tract
tr.b.a.a.–pe.l.	anterior anterior basal to lateral pedal tract
tr.b.a.p.–opt.	posterior anterior basal to optic tract
tr.b.a.p.–pe.l.	posterior anterior basal to lateral pedal tract
tr.b.int.–b.a.	interbasal to anterior basal tract
tr.b.l.–ch.a.	lateral basal to anterior chromatophore tract
tr.b.l.–ch.p.	lateral basal to posterior chromatophore tract
tr.b.med.–b.a.	median basal to anterior basal tract
tr.b.med.–pe.a.	median basal to anterior pedal tract
tr.b.med.–pe.p.	median basal to posterior pedal tract
tr.b.med.–pe.l.	median basal to lateral pedal tract
tr.b.med.–pe.p. + pv.	median basal to posterior pedal and palliovisceral tract
tr.b.med.–prec.	median basal to precommissural tract
tr.b.med.–pv.	median basal to palliovisceral tract
tr.b.med.–pv.(ext.)	external median basal to palliovisceral tract
tr.b.med.–pv. + mag.	median basal to palliovisceral and magnocellular tract
tr.fr.i.–b.med.	inferior frontal to median basal tract
tr.mag.–b.lo.	magnocellular to basal lobes tract
tr.mag.–b.med.	magnocellular to median basal tract

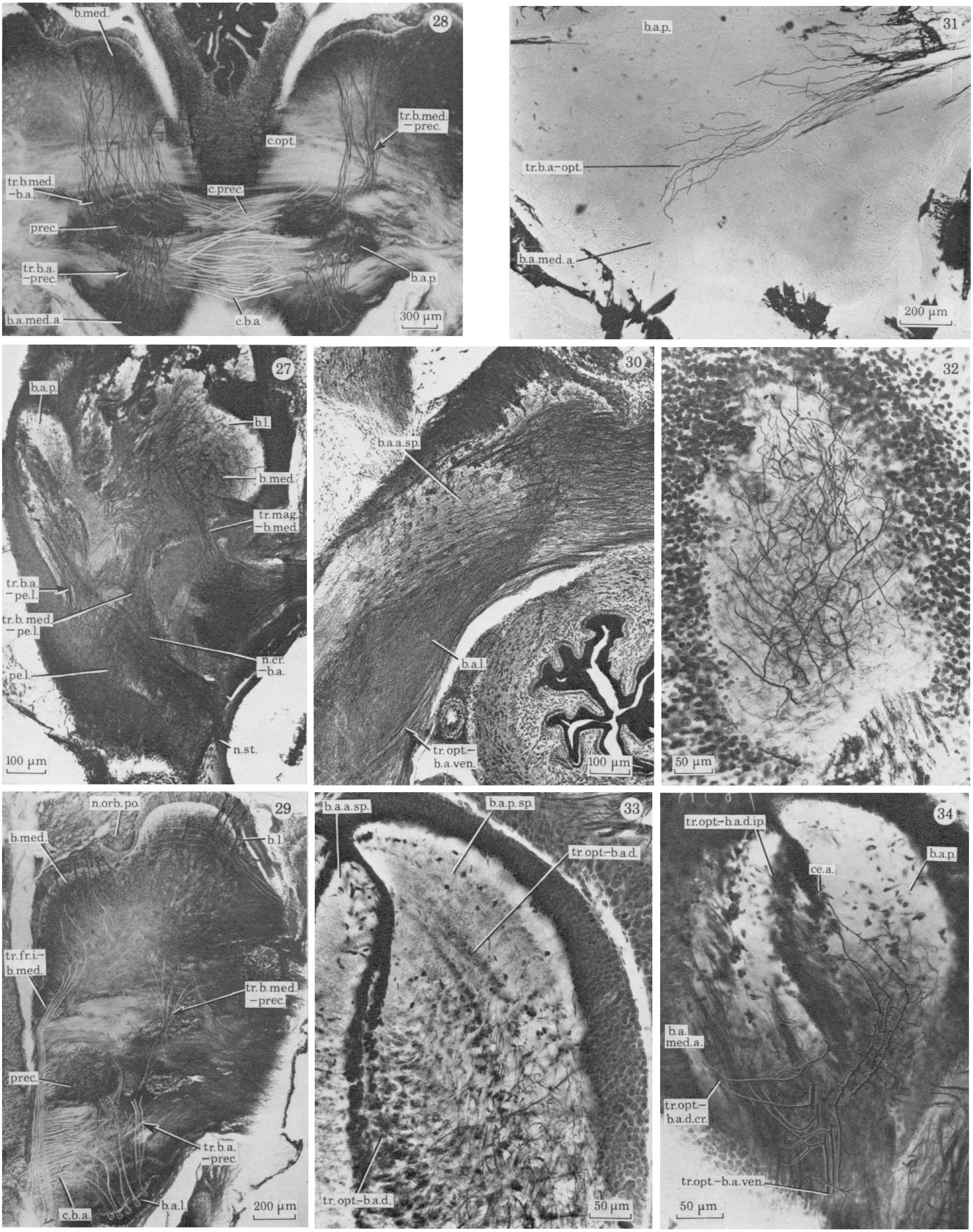
tr.opt.–b.a.	optic to anterior basal tract
tr.opt.–b.a.a.d.	dorsal optic to anterior anterior basal tract
tr.opt.–b.a.d.	dorsal optic to anterior basal tract
tr.opt.–b.a.d.cr.	crossed dorsal optic to anterior basal tract
tr.opt.–b.a.d.ip.	ipsilateral dorsal optic to anterior basal tract
tr.opt.–b.a.l.	lateral optic to anterior basal tract
tr.opt.–b.a.p.	optic to posterior anterior basal tract
tr.opt.–b.a.p.d.	dorsal optic to posterior anterior basal tract
tr.opt.–b.a.p.d.ip.	ipsilateral dorsal optic to posterior anterior basal tract
tr.opt.–b.a.ven.	ventral optic to anterior basal tract
tr.opt.–b.a.ven.cr.	crossed ventral optic to anterior basal tract
tr.opt.–b.int.cr.	crossed optic to interbasal tract
tr.opt.–b.int.ip.	ipsilateral optic to interbasal tract
tr.opt.–b.l.cr.	crossed optic to lateral basal tract
tr.opt.–b.l.ip.	ipsilateral optic to lateral basal tract
tr.opt.–b.lo.	optic to basal lobes tract
tr.opt.–b.med.	optic to median basal tract
tr.opt.–b.med.cr.	crossed optic to median basal tract
tr.opt.–b.med.ip.	ipsilateral optic to median basal tract
tr.opt.–b.med.ven	ventral optic to median basal tract
tr.opt.–mag.med.	median optic to magnocellular tract
tr.opt.–prec.ven.	ventral optic to precommissural tract
tr.pe.p.–fl.	posterior pedal to fin lobe tract
tr.pe.p.–pv.a.	posterior pedal to anterior palliovisceral tract
tr.ped.–b.a.	peduncle to anterior basal tract
tr.ped.–b.int.	peduncle to interbasal tract
tr.prec.–pv.	precommissural to palliovisceral tract
tr.pv.a.–fl.	anterior palliovisceral to fin lobe tract
v.	vertical lobe
ve.	vein



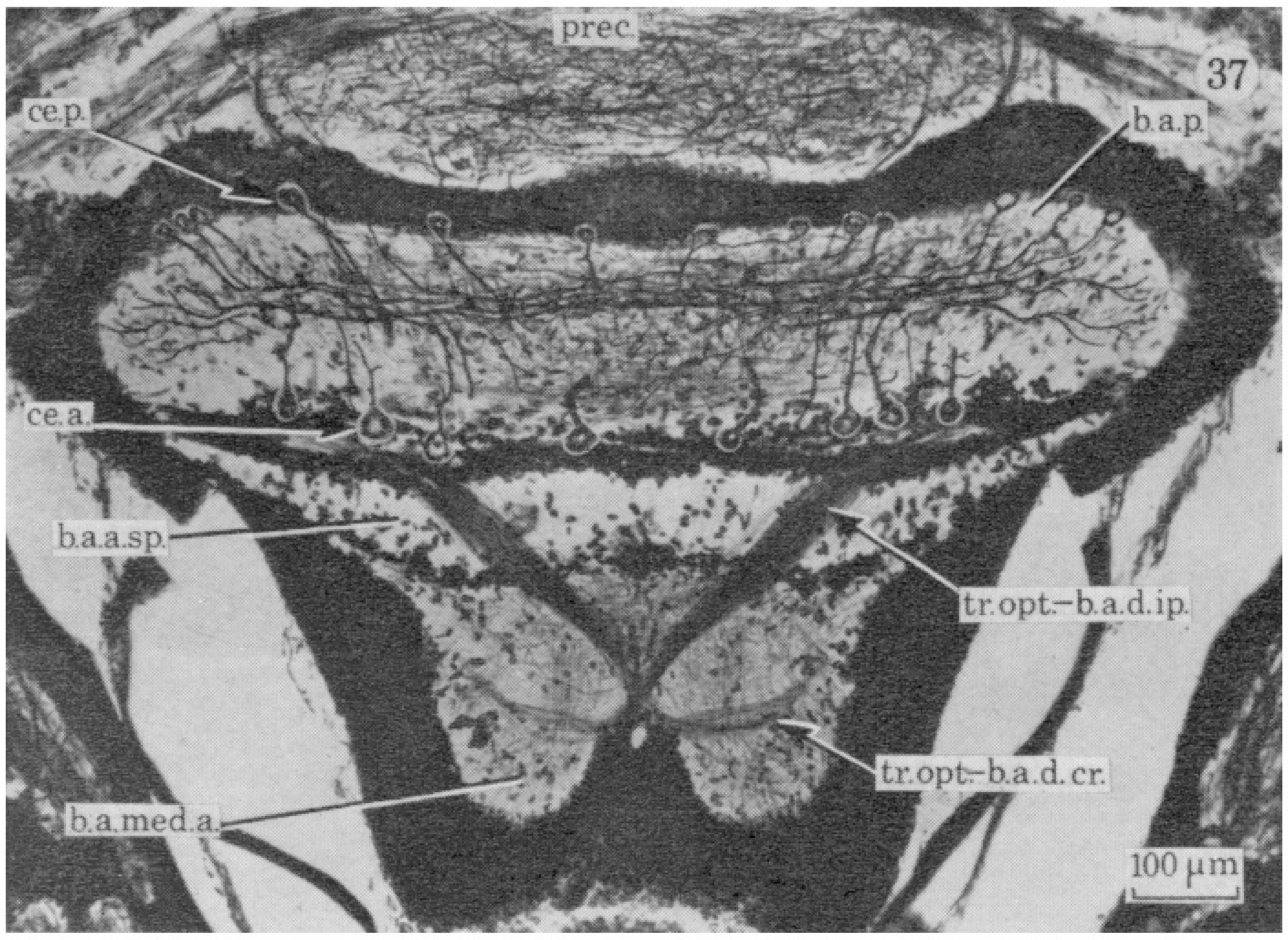
FIGURES 2–14. For description see opposite.

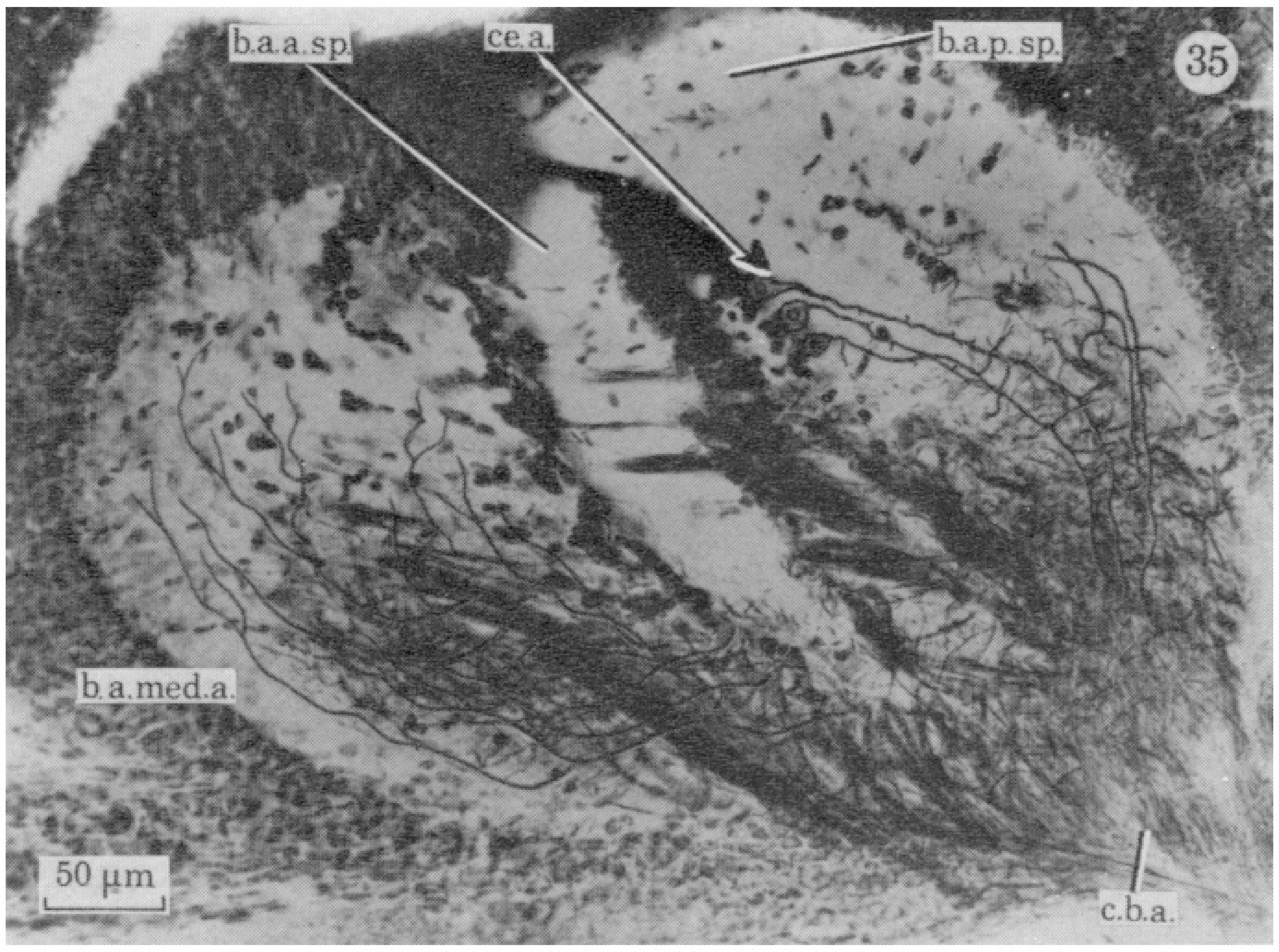


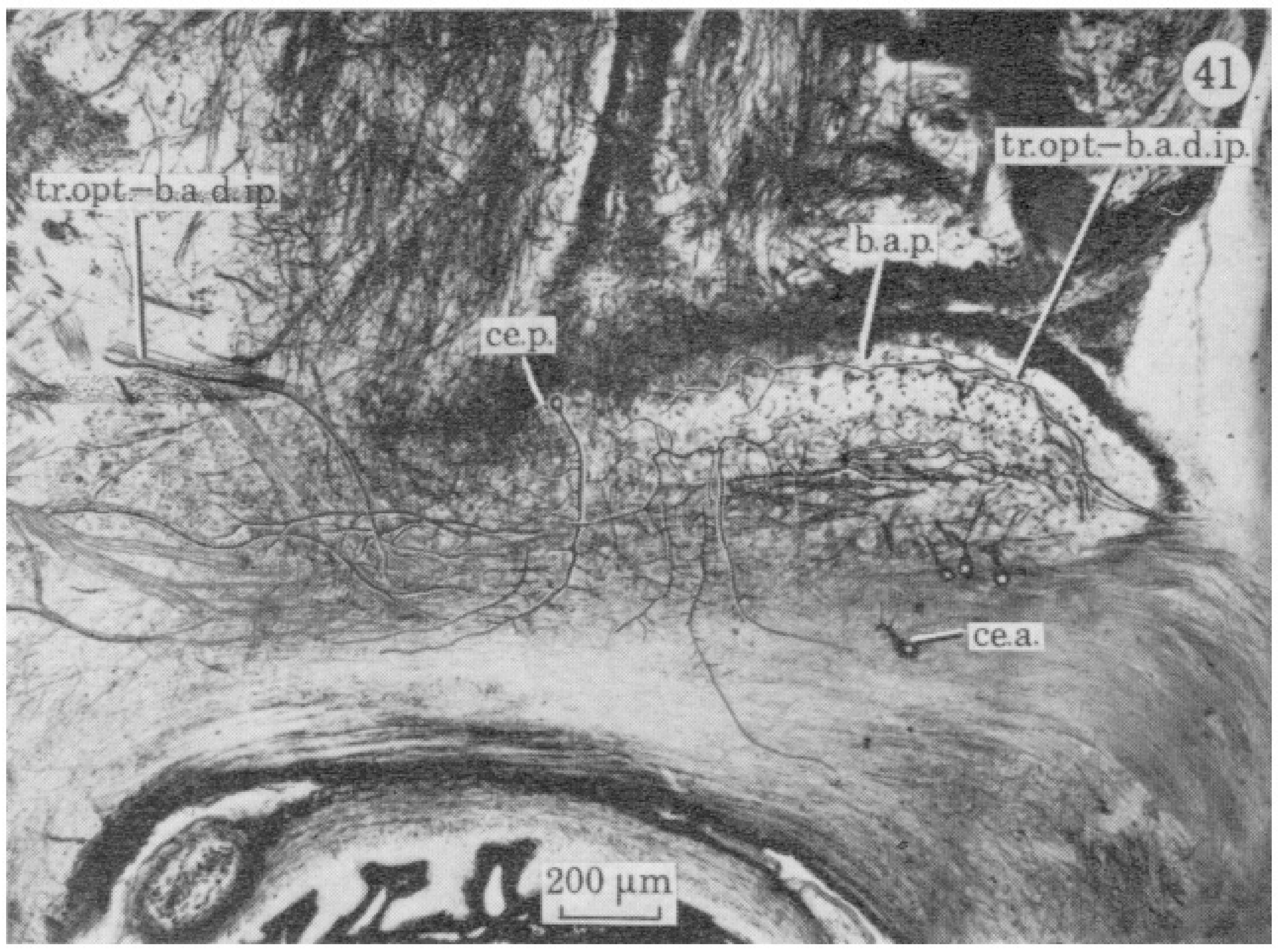
FIGURES 15–25. For description see opposite.

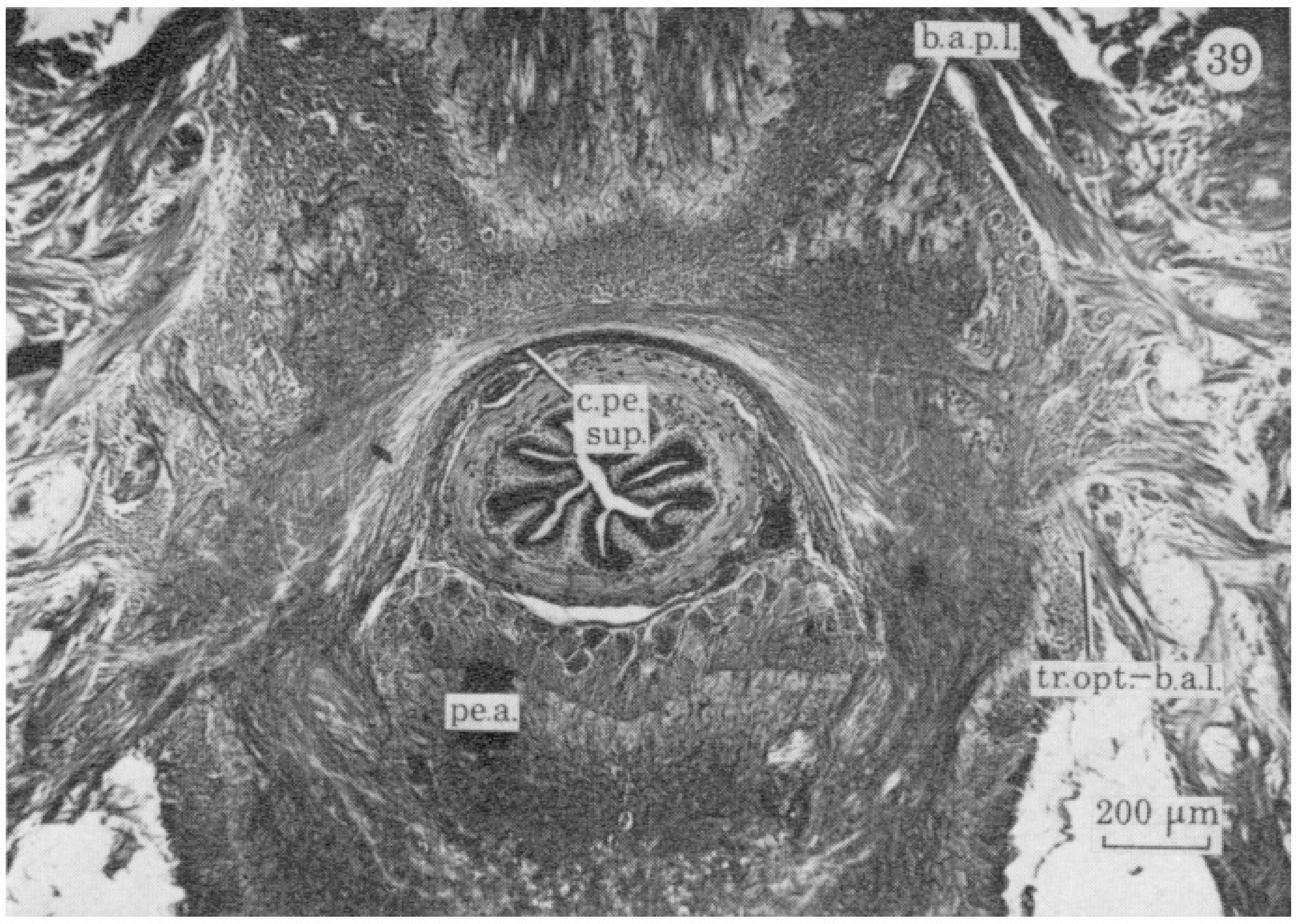


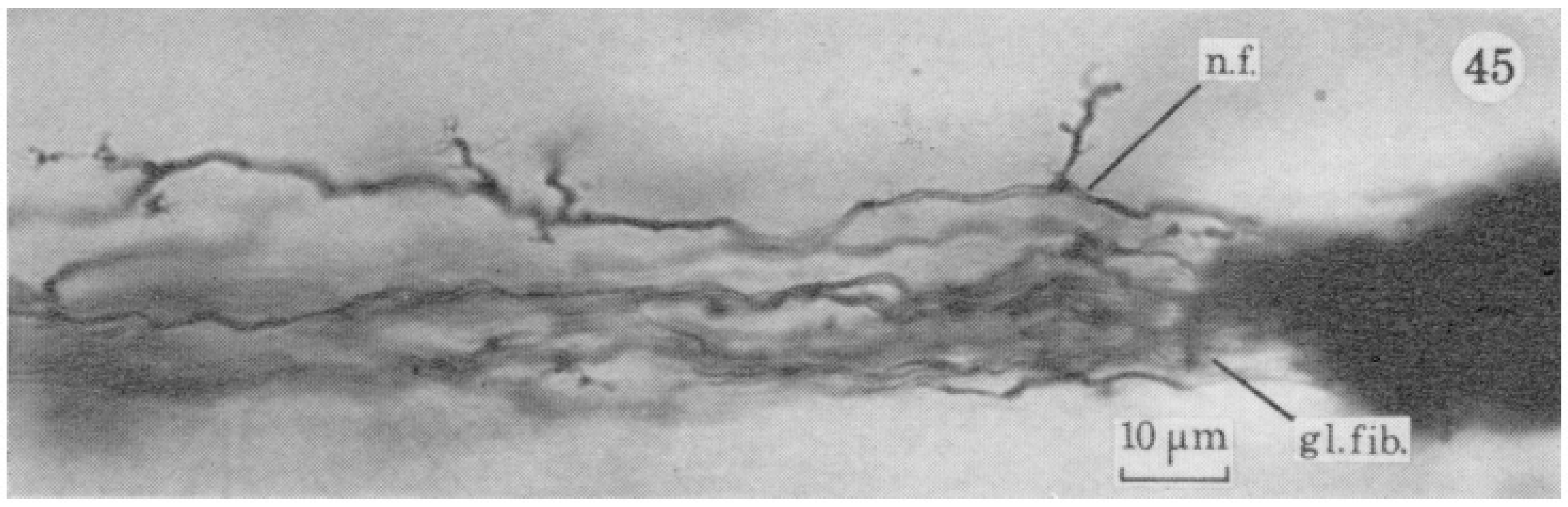
FIGURES 27–34. For description see opposite.

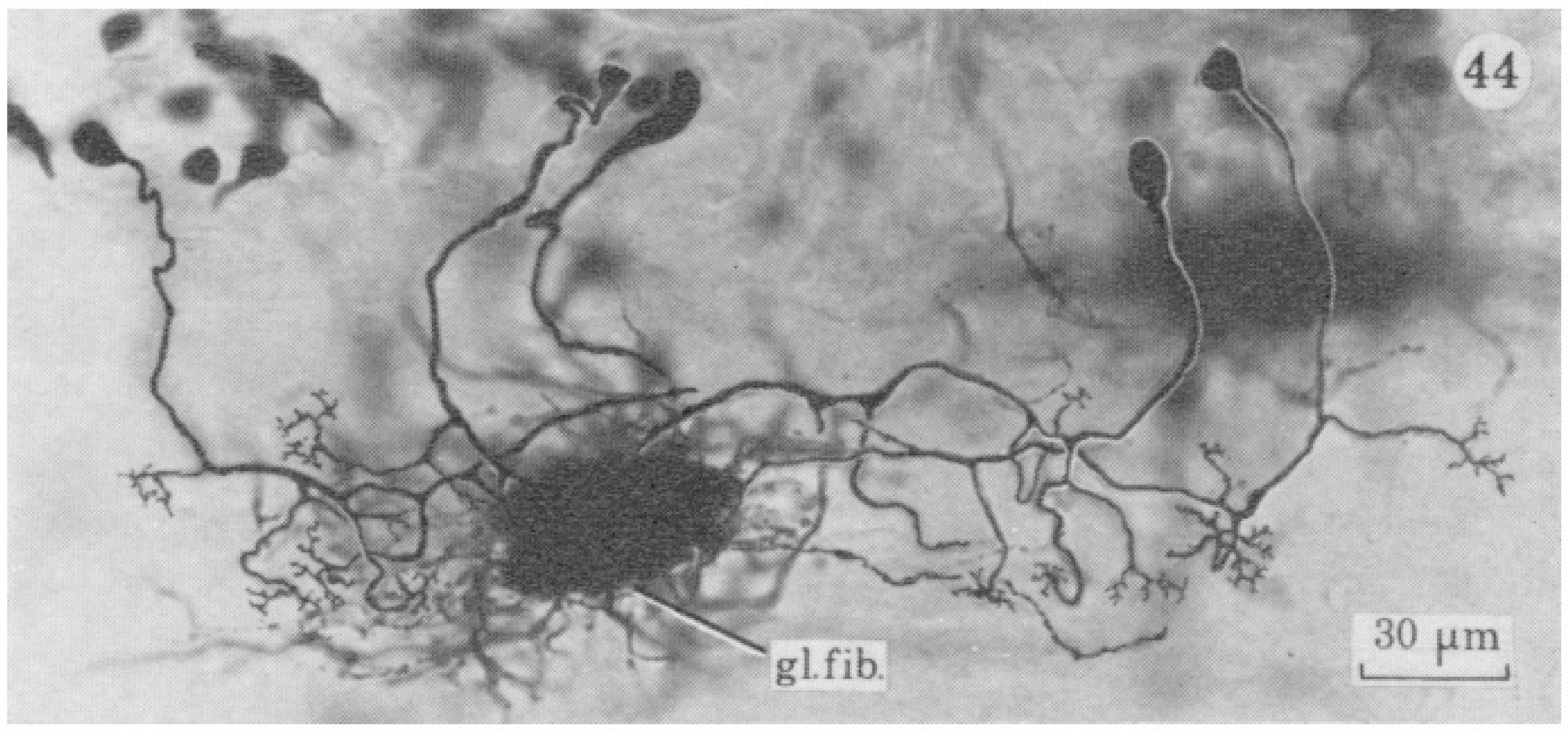


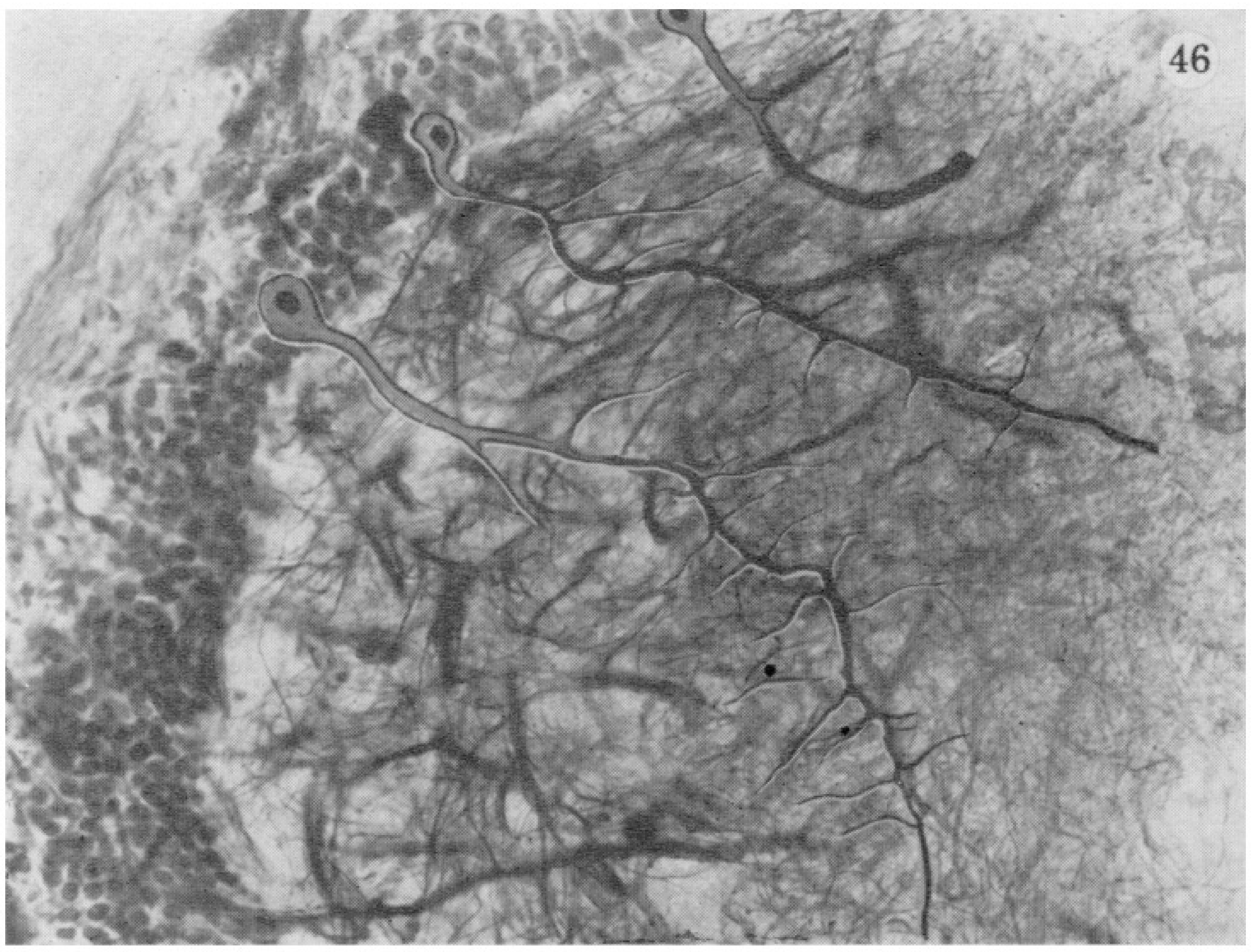


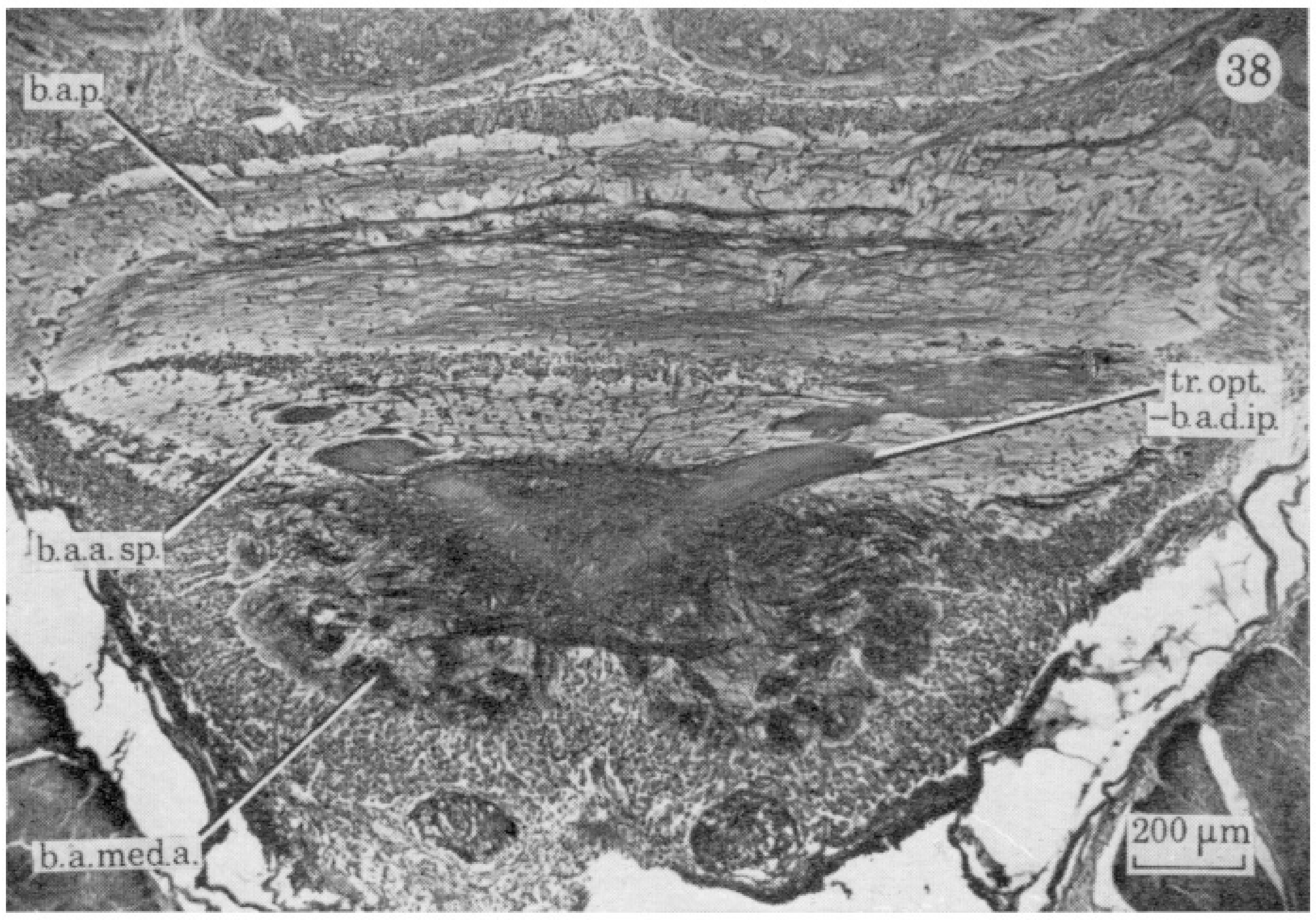




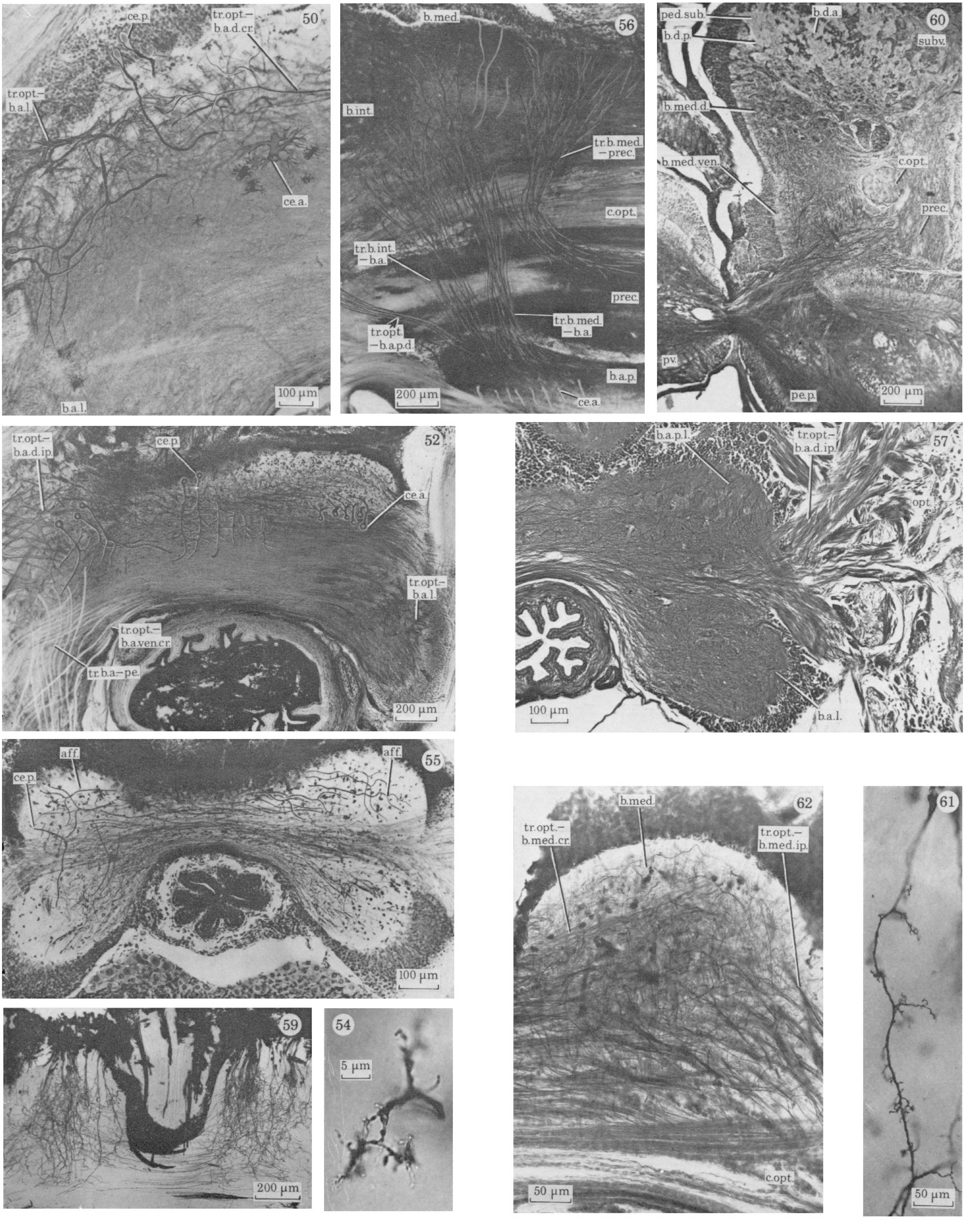




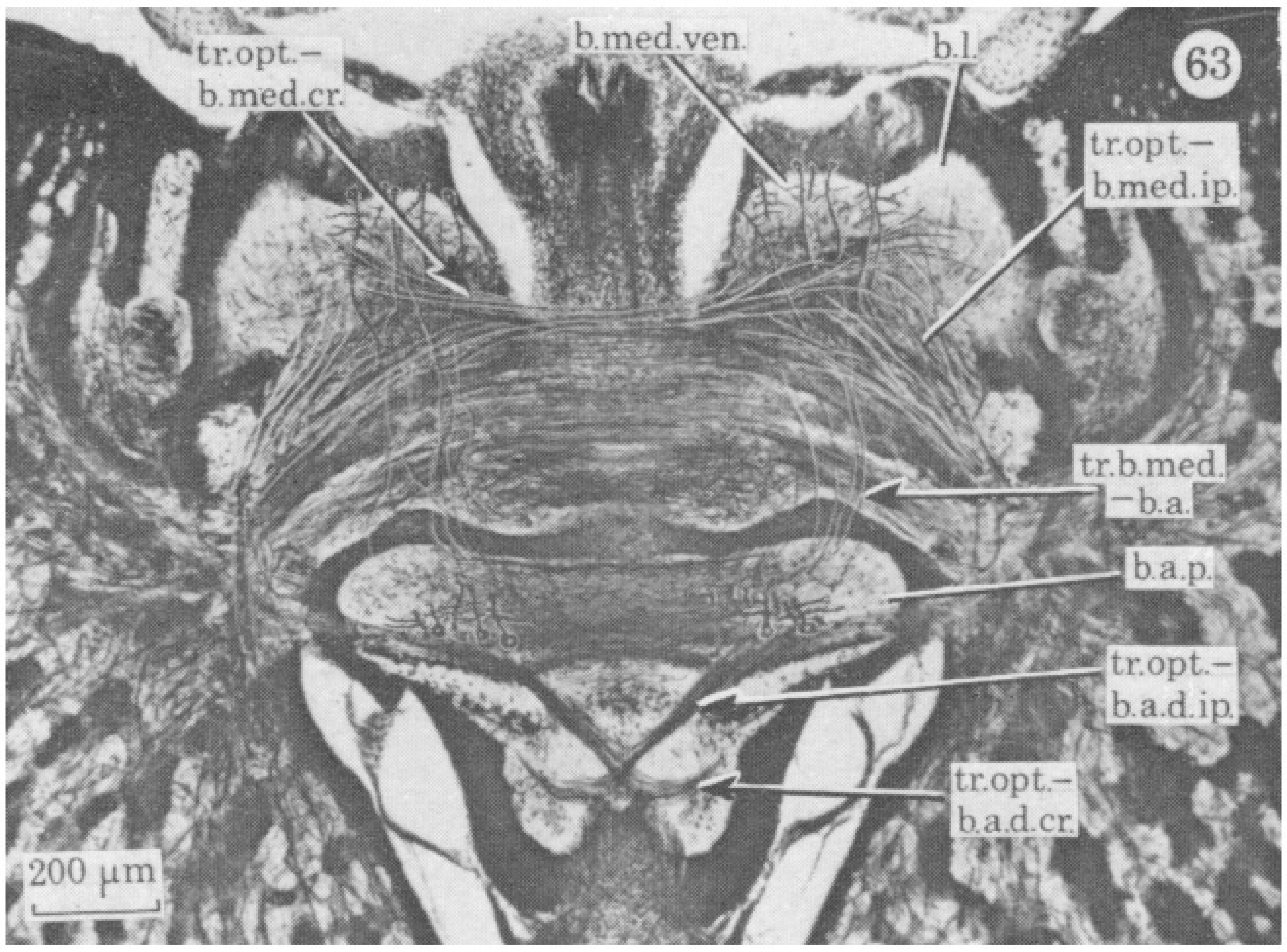


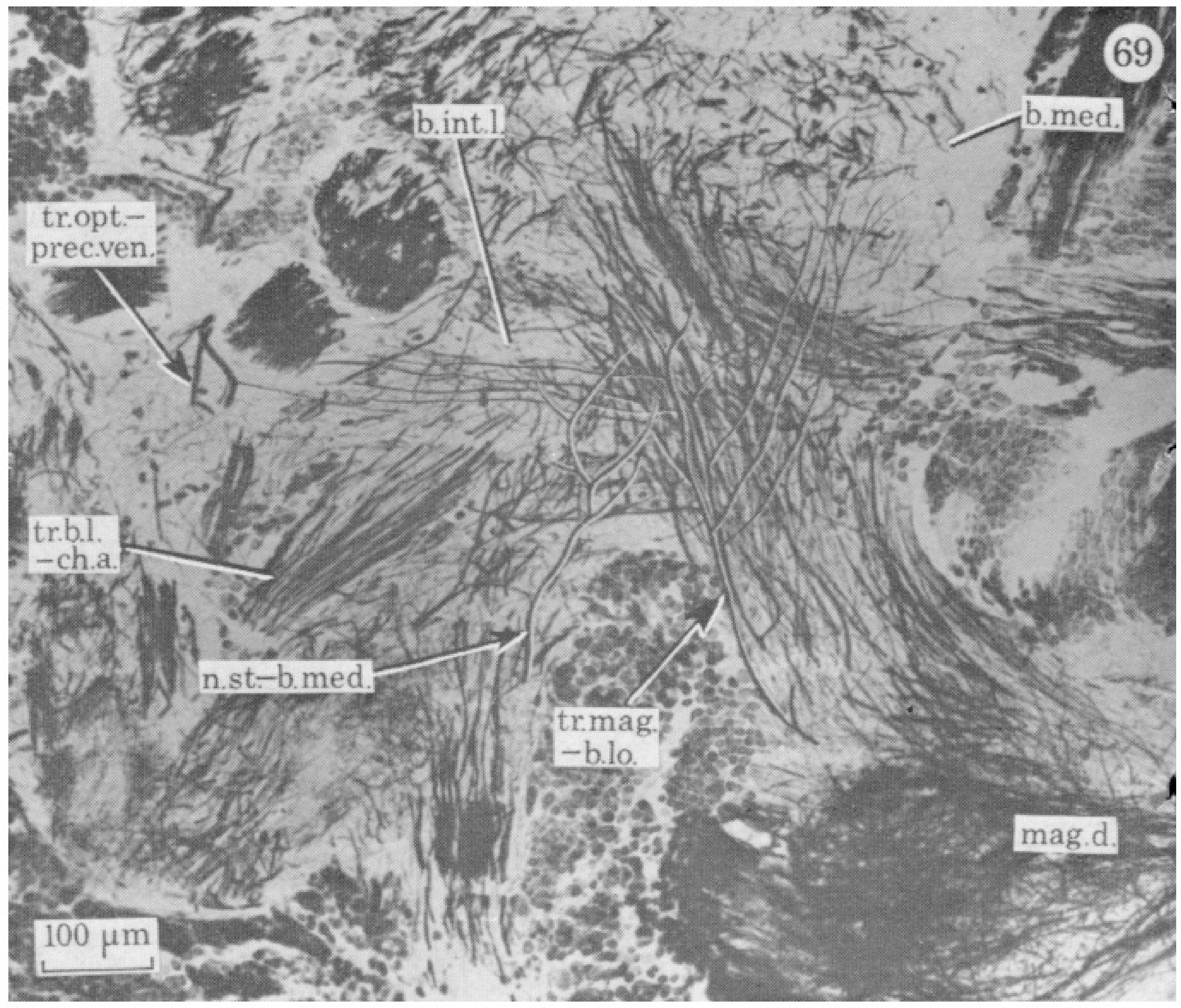


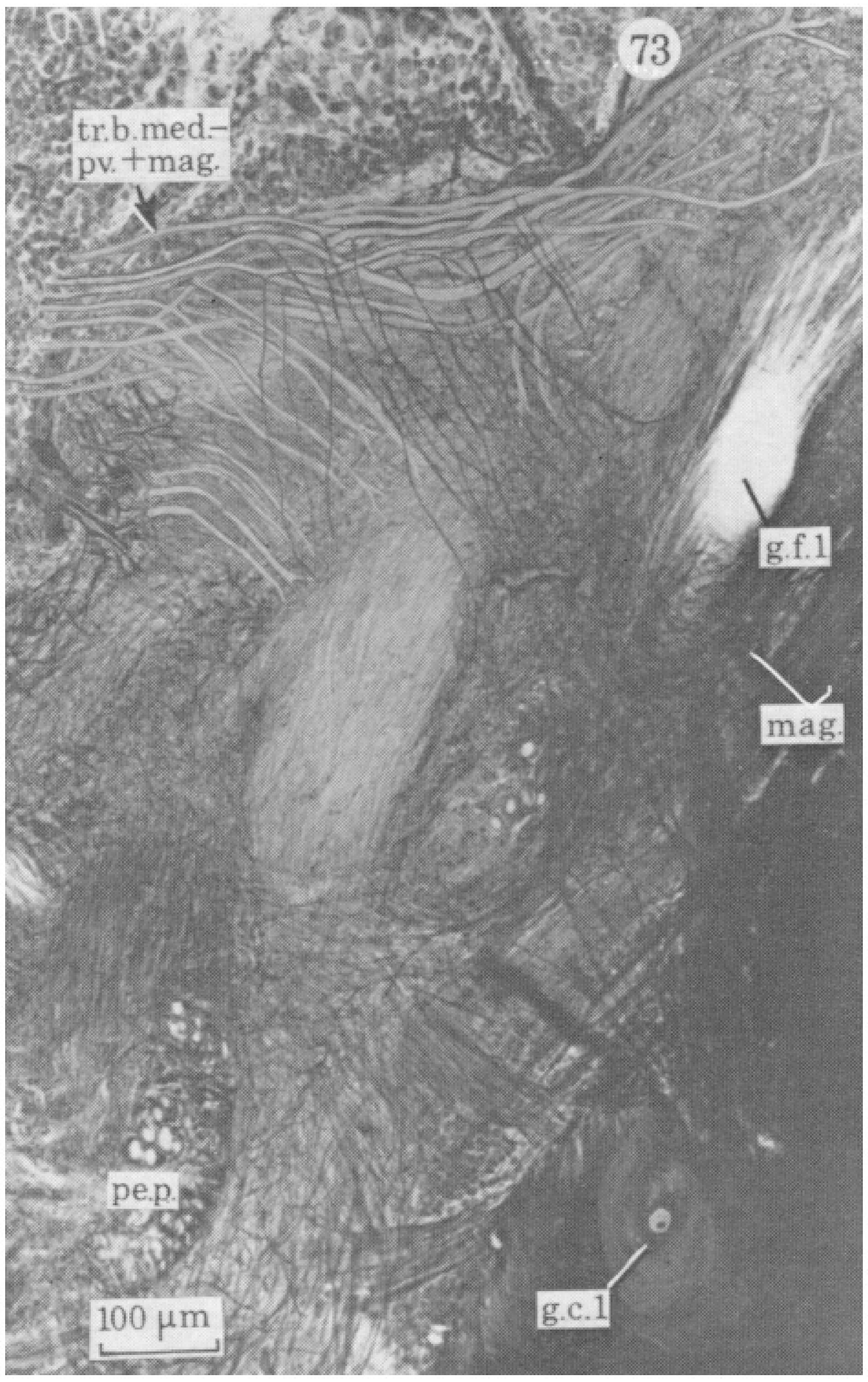
Figures 35–46. For description see opposite.

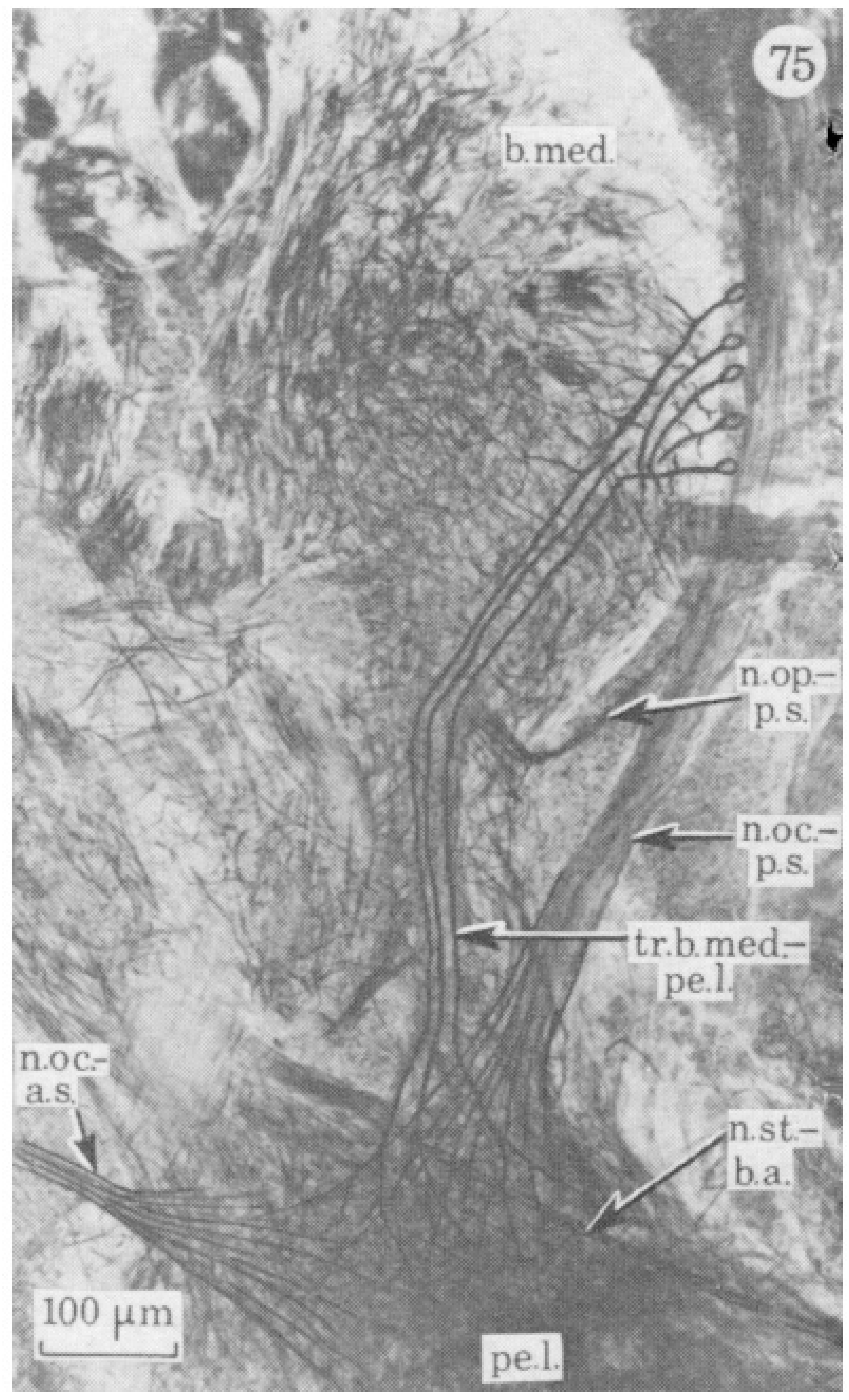


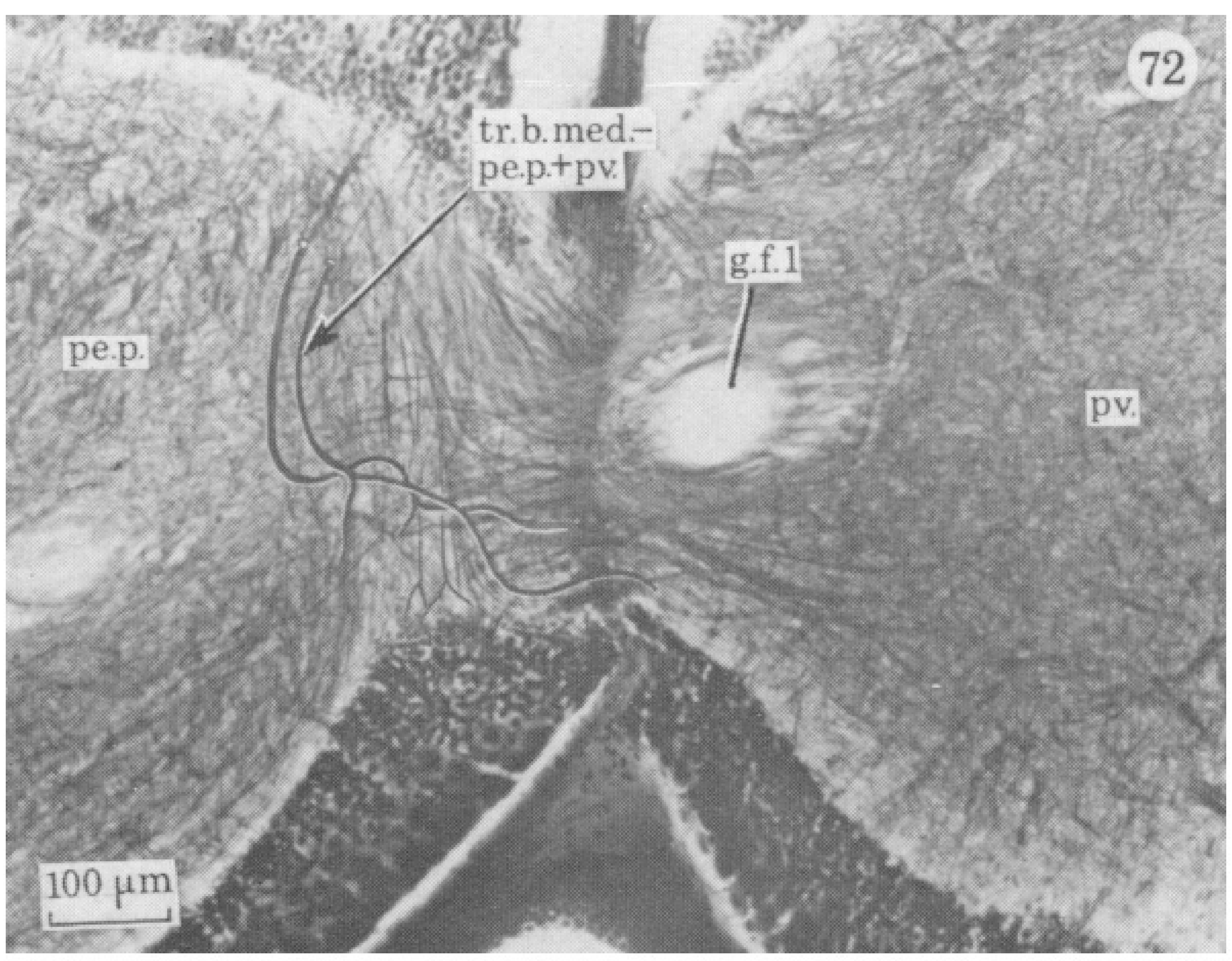
FIGURES 50–62. For description see opposite.

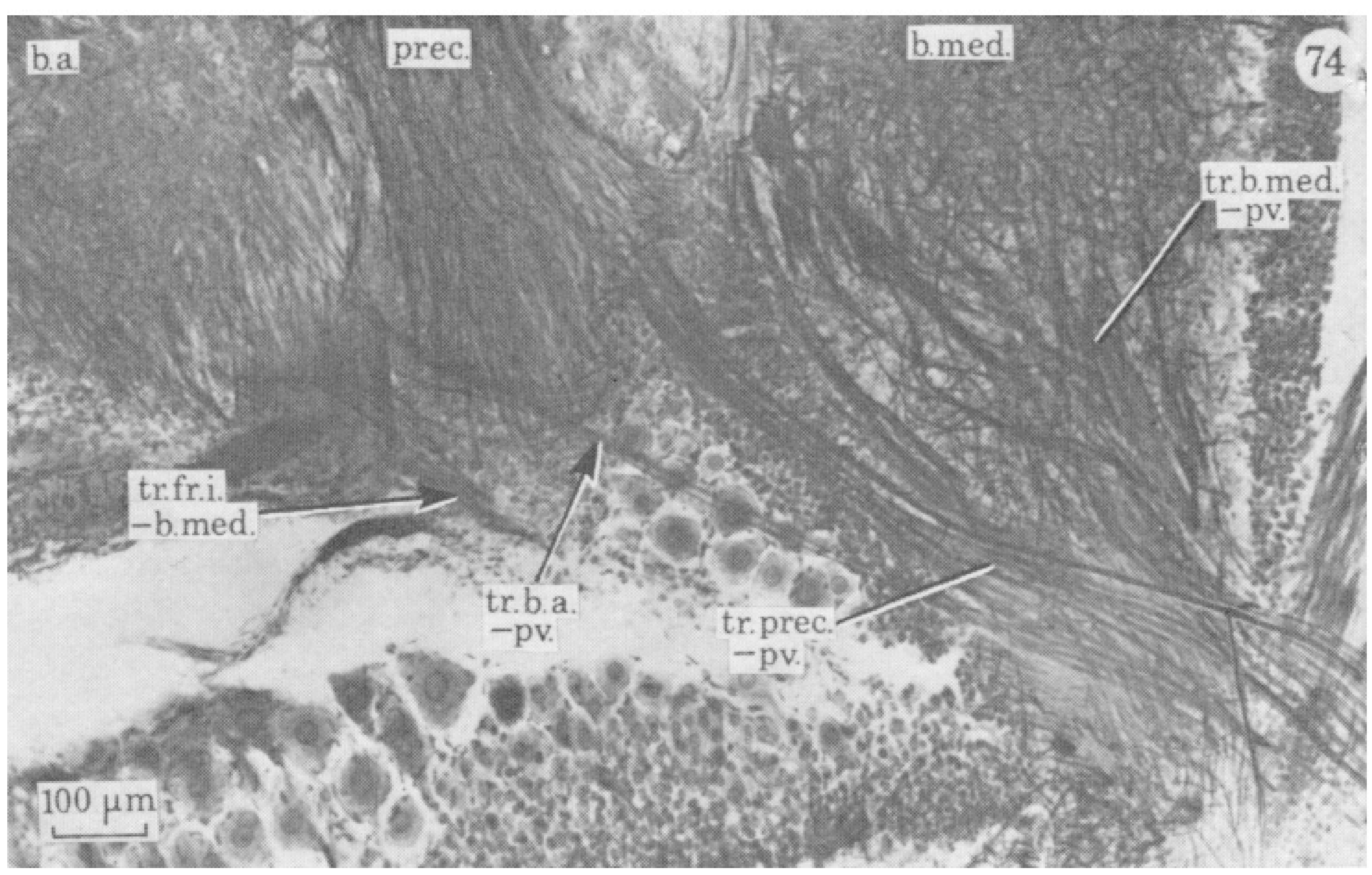




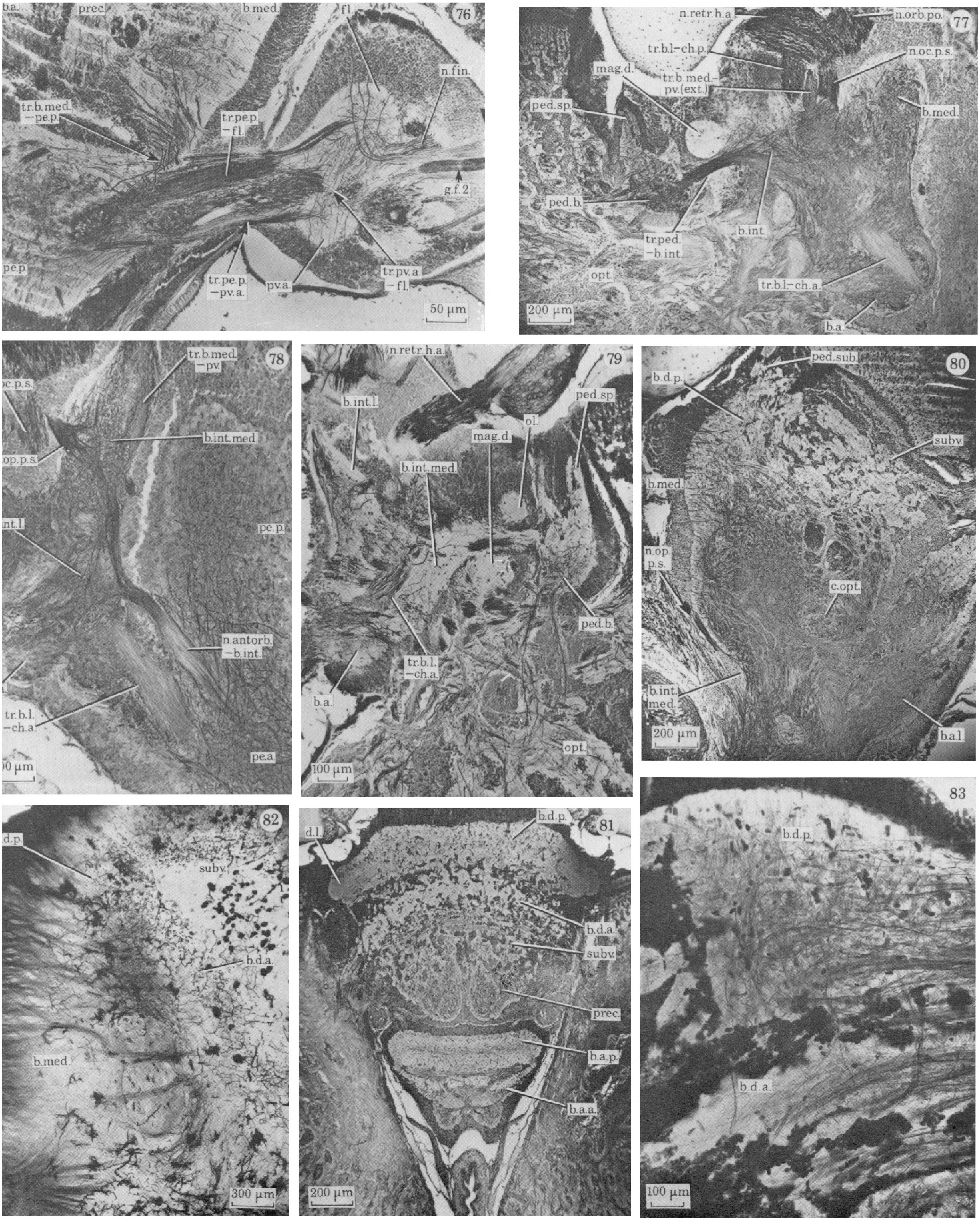




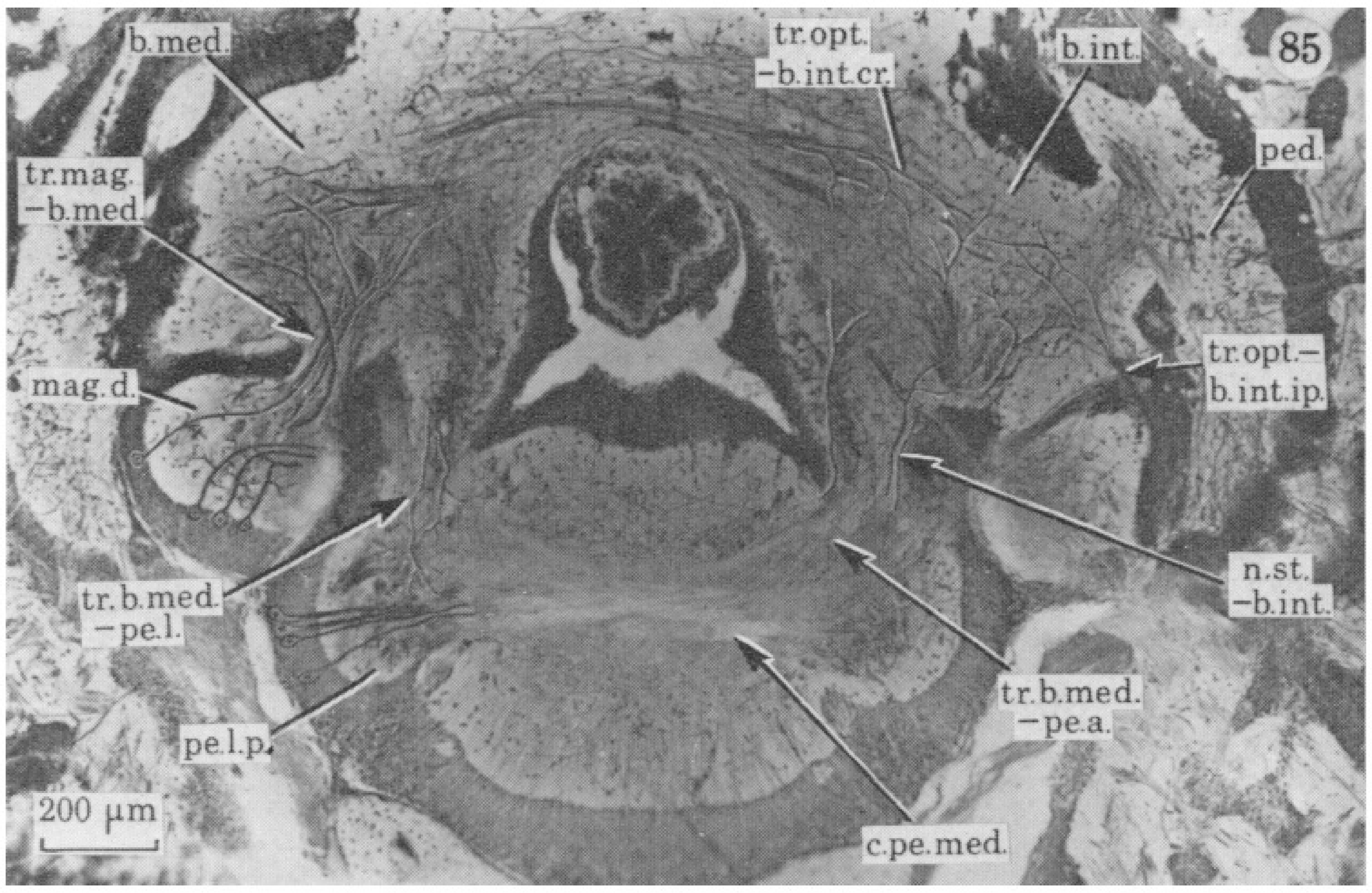


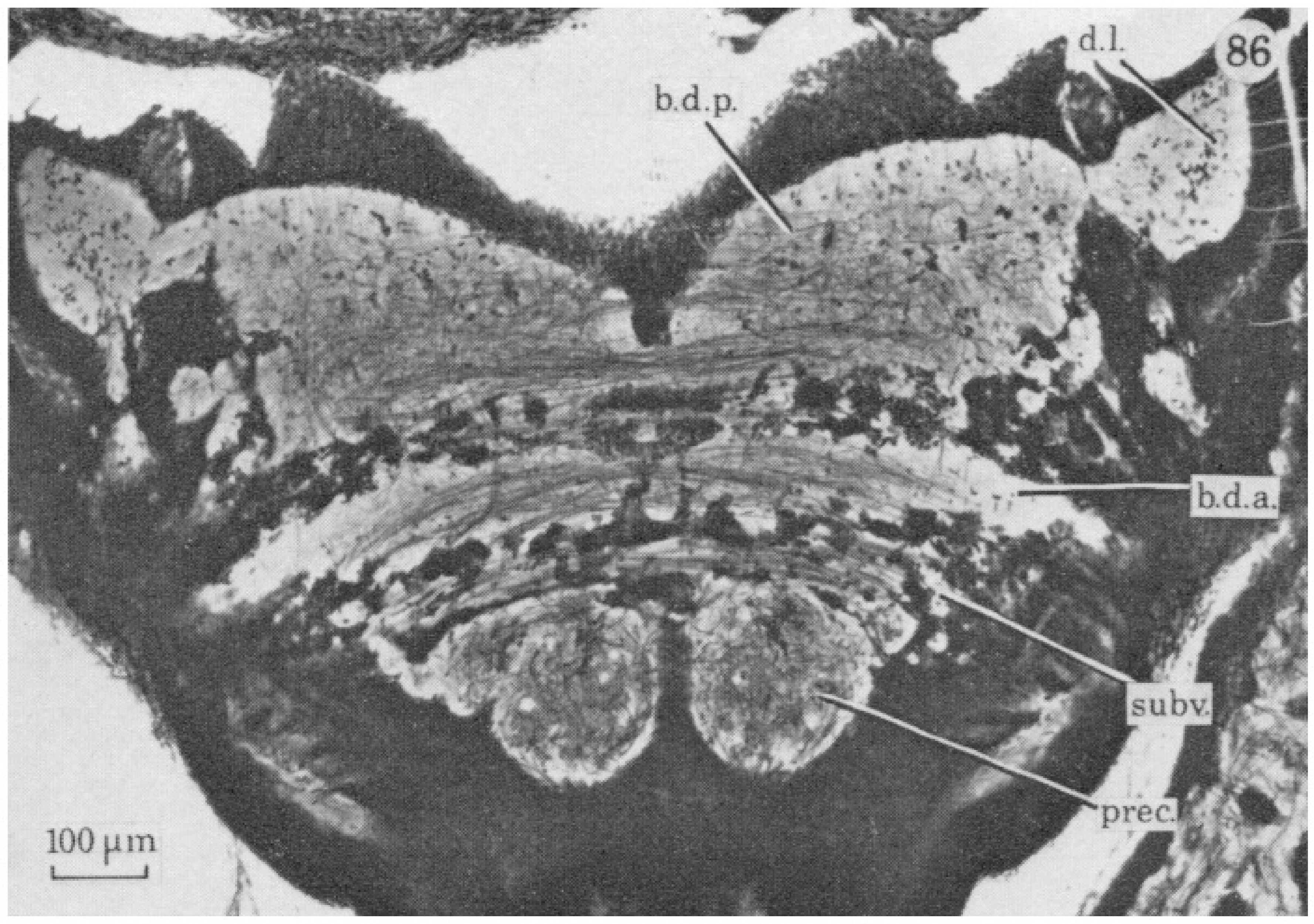


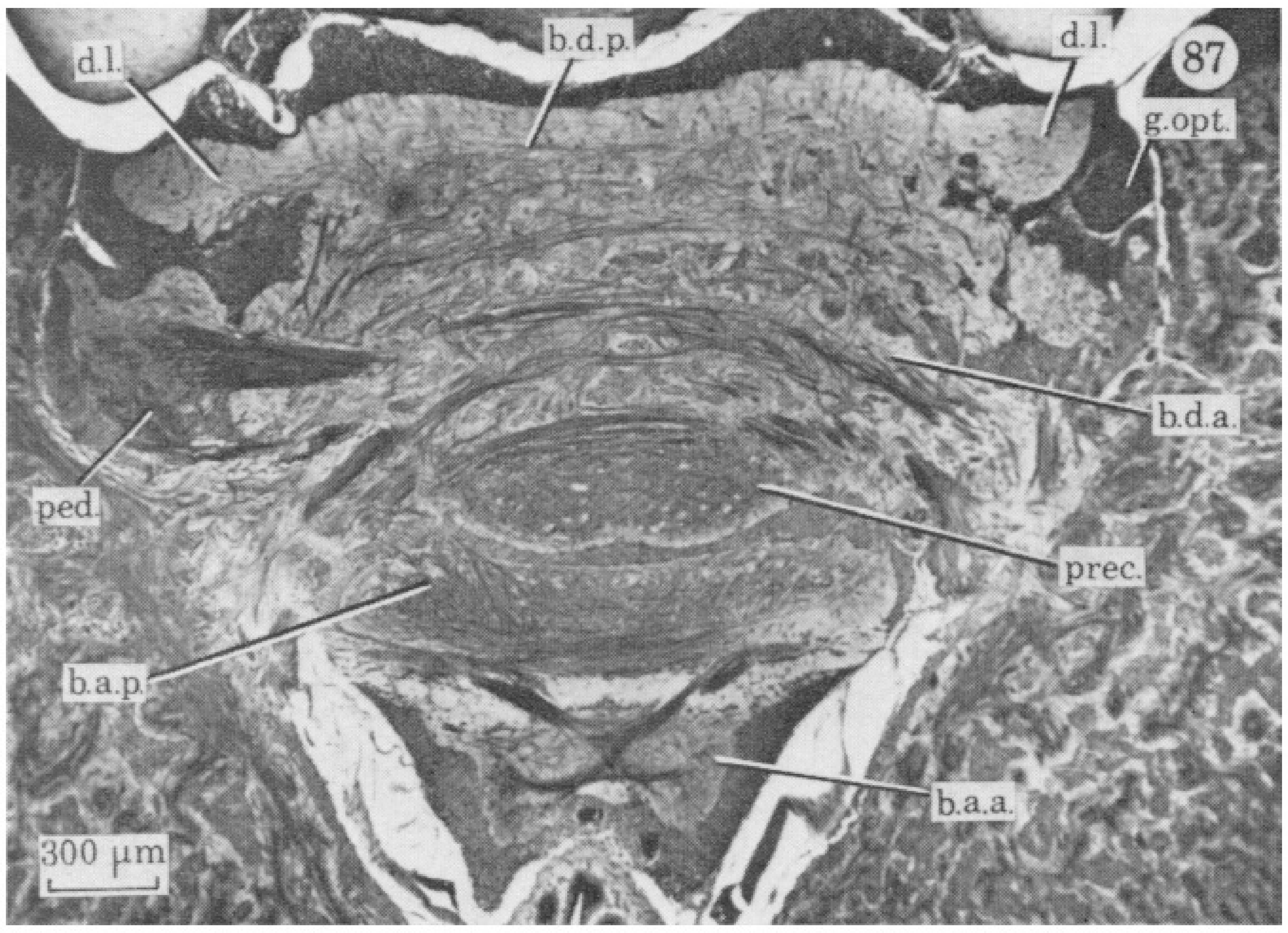
FIGURES 63–75. For description see opposite.

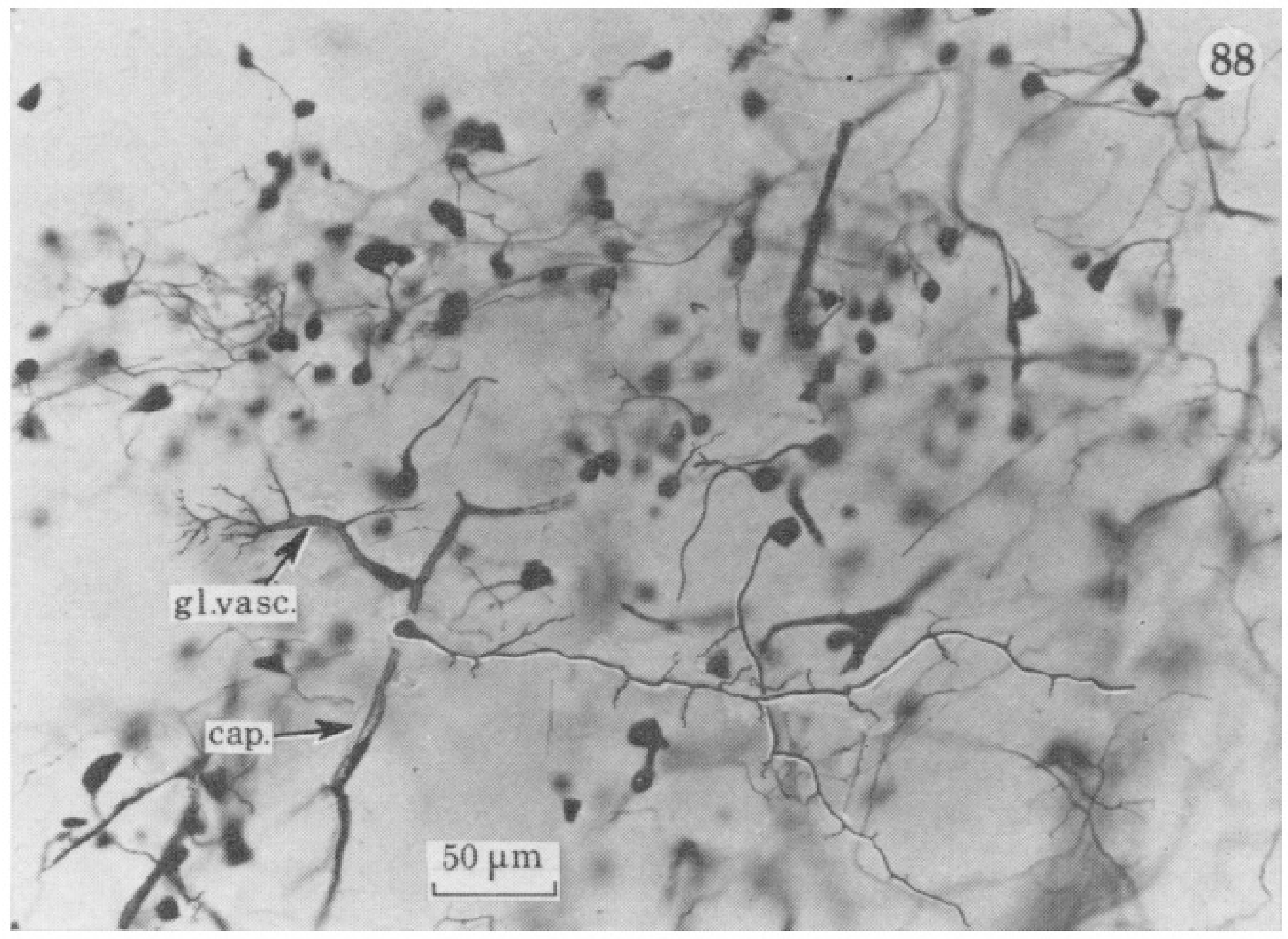


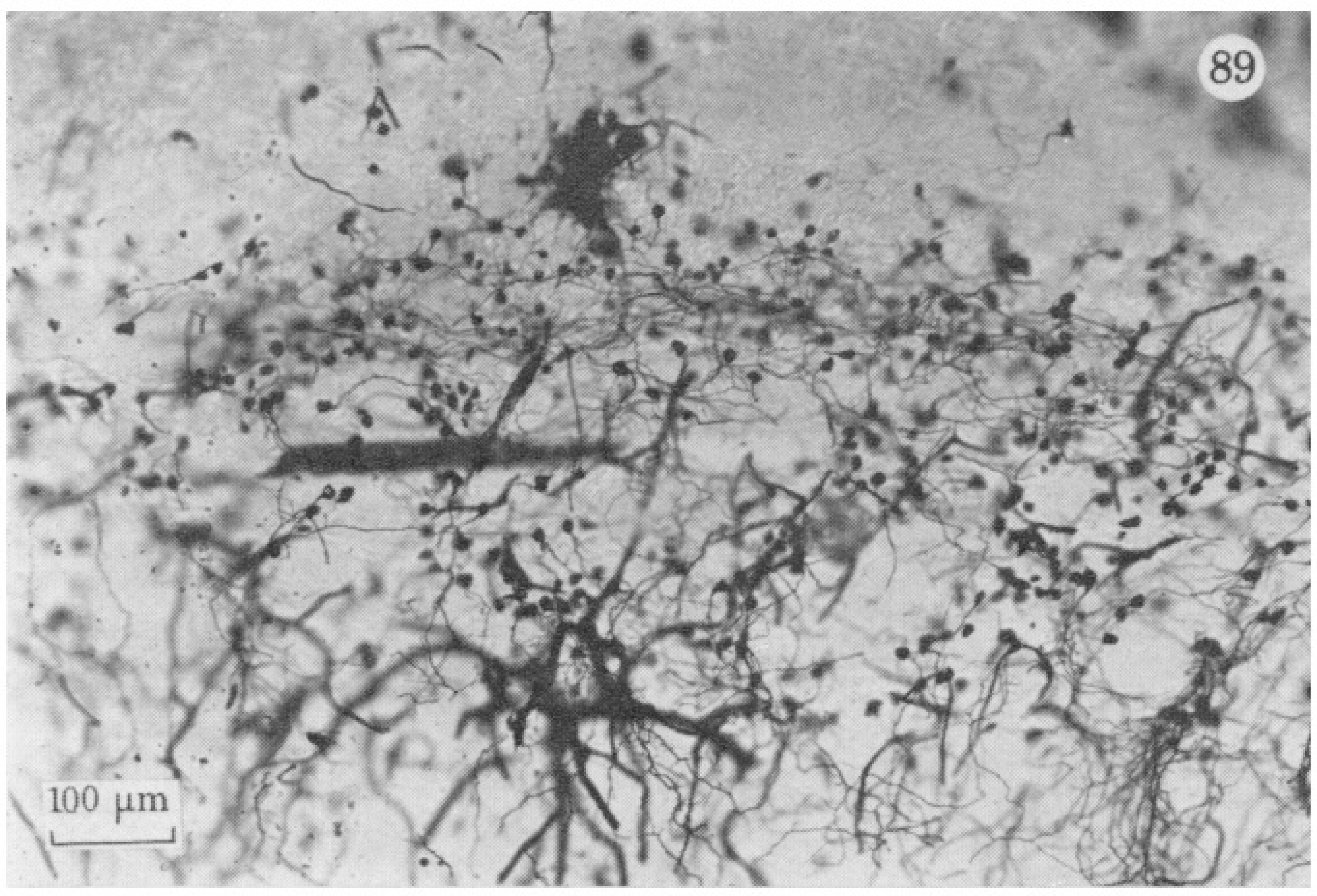
FIGURES 76–83. For description see opposite.

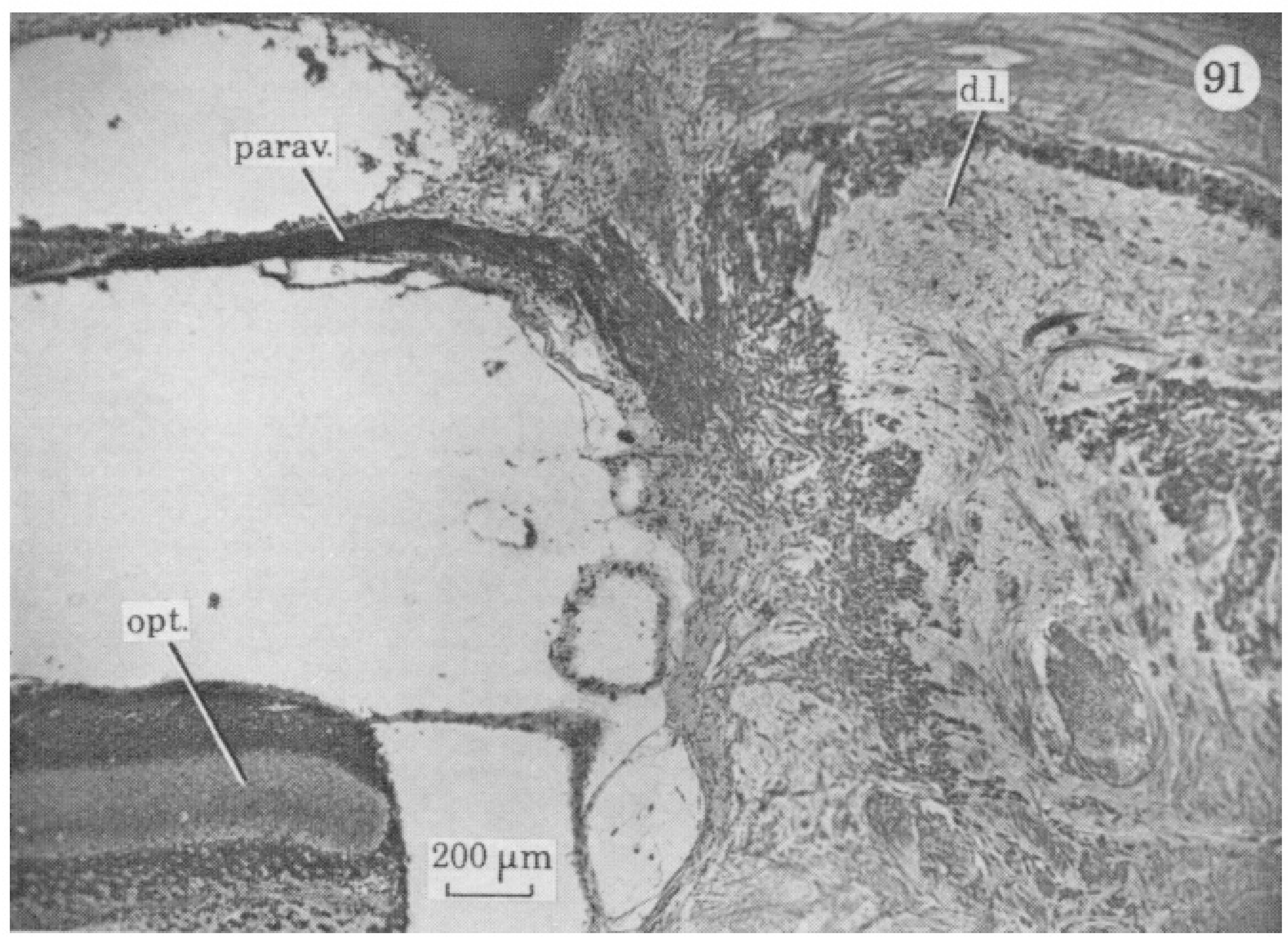


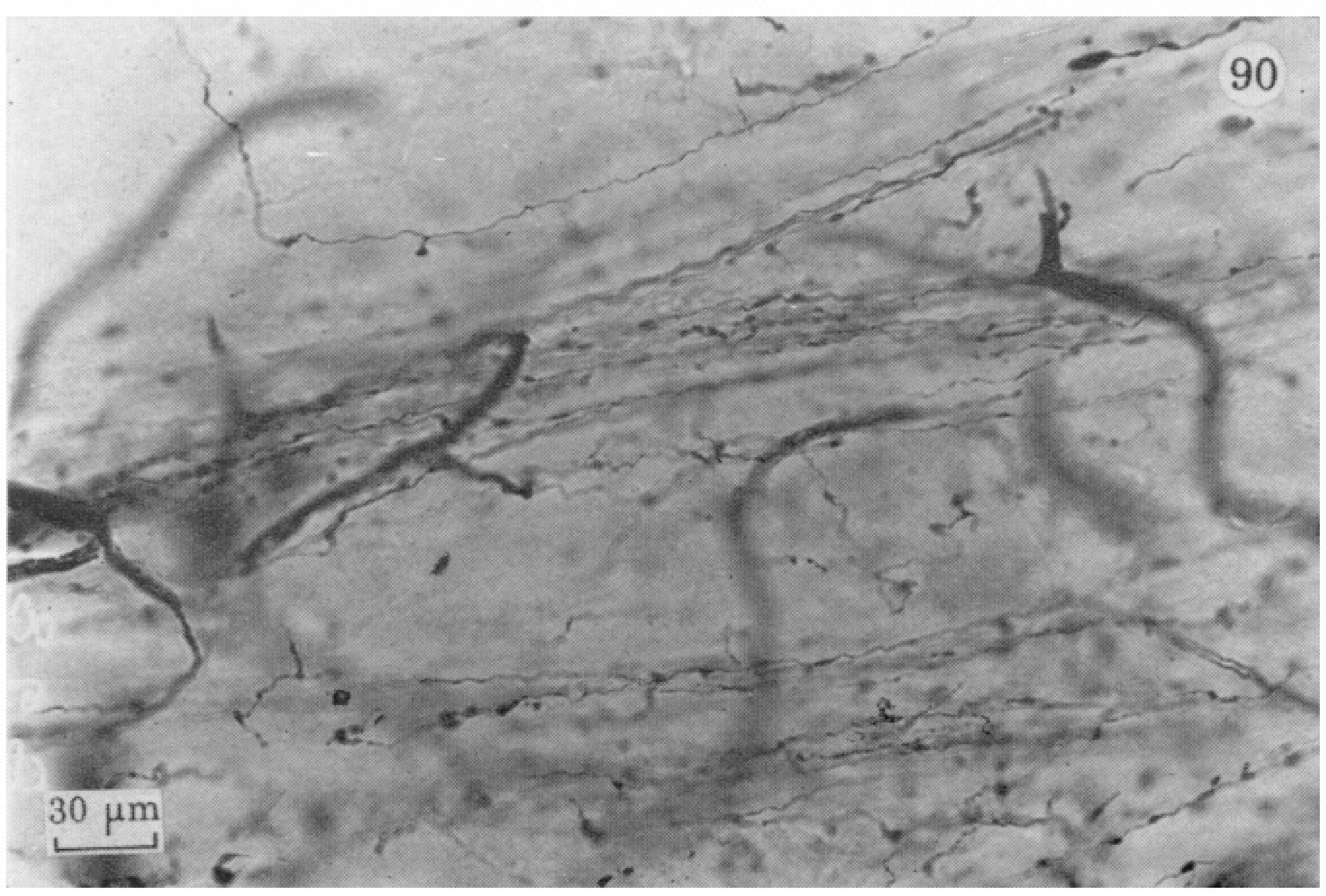


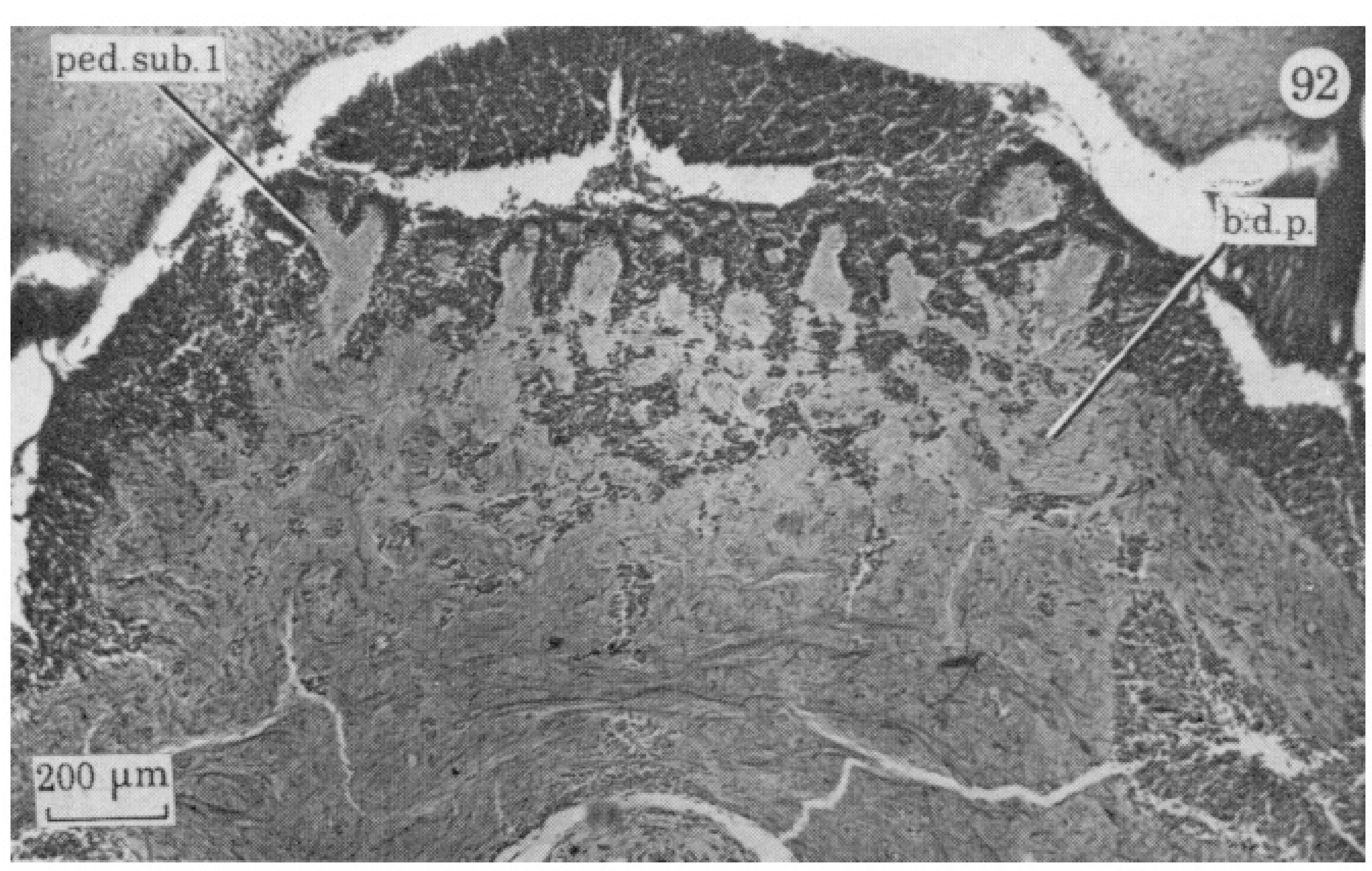




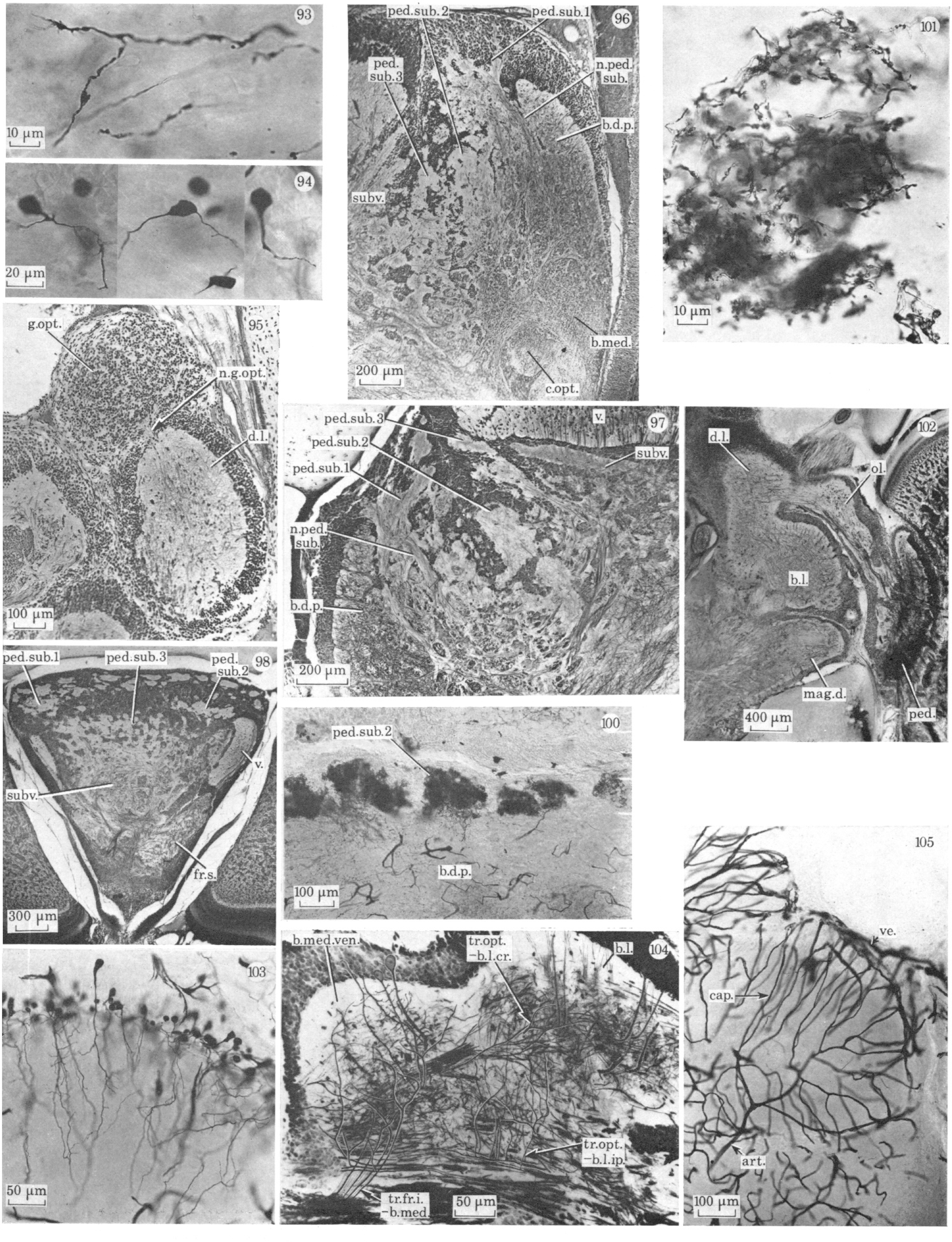








FIGURES 85–92. For description see opposite.



FIGURES 93–105. For description see opposite.