THE NERVOUS SYSTEM OF *LOLIGO*
II. SUBOESOPHAGEAL CENTRES

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[Plates 1–10]

CONTENTS

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ABSTRACT

A well-marked hierarchy of centres can be recognized within the suboesophageal lobes and ganglia of the arms. The inputs and outputs of each lobe are described. There are sets of motoneurons and intermediate motor centres, which can be activated either from the periphery or from above. They mostly do not send fibres up to the optic or higher motor centres. However, there is a large set of fibres running from the magnocellular lobe to all the basal supraoesophageal lobes.

The centre for control of the four eye-muscle nerves in the anterior lateral pedal lobe receives many fibres direct from the statocyst and from the peduncle and basal lobes, but none direct from the optic lobe. The posterior lateral pedal is a backward continuation of the oculomotor centre, containing large cells that may be concerned in initiating attacks by the tentacles.

An intermediate motor centre in the posterior pedal lobe probably controls steering. It sends fibres to the funnel and head retractors, and by both direct and interrupted pathways to the fin lobe. It receives fibres from the crista nerve and basal lobes, but none direct from the optic lobe.

The jet control centre of the ventral magnocellular lobe receives fibres from the statocyst and skin and also from the optic and basal lobes. Some of these last also give extensive branches throughout the palliovisceral lobes.

The branching patterns of the dendritic collaterals differ in the various lobes. Some estimates are given of the numbers of synaptic points. The dendritic collaterals of the motoneurons spread through large volumes of neuropil and they overlap. The incoming fibres spread widely and each presumably activates many motoneurons either together or serially.

Many of the lobes contain numerous microneurons with short trunks restricted to the lobe, but there are none of these cells in the chromatophore lobes or fin lobes. The microneurons have only few dendritic collaterals, in contrast to the numerous ones on the nearby motoneurons.

1. INTRODUCTION

There is need for further studies of the organization of the more complicated invertebrate nervous systems. The very facts of their complication, and the elaborate behaviour that they mediate, makes them especially interesting, but methods for study of the connections and actions of such masses of nervous tissue are still little developed. The techniques for the investigation of single neurons and simple ganglia need to be supplemented by study of the connection patterns of complex brains, combined with studies of behaviour after removal of various parts. A further classical means for obtaining information about functions is to compare the organization of the brain in animals with differing habits. For this reason we have undertaken the present study of the brain of *Loligo*, to provide us with detailed knowledge of the anatomy of the brain of a decapod for comparison with *Octopus* (Boycott & Young 1950; Young 1971). The optic lobes have already been described (Young 1974) and comparative studies of *Sepia* and other squids are under way (Young 1976*a*).

Attempts to organize knowledge of the plan of a nervous system often make use of the concept of a hierarchy of higher and lower centres. This system of functional classification can indeed be usefully applied to the cephalopods and will be used here. It is broadly possible to recognize, in cephalopods, a series of systems for the control of increasingly larger segments of action (Boycott & Young 1950; Boycott 1961). Thus individual suckers of the arms of an octopus are operated by reflexes through a series of sucker ganglia (Graziadei 1971). The whole set of suckers in an isolated arm can make coordinated movements of acceptance or rejection by the actions of the nerve cord within it. Actions of all the arms together are controlled by centres in the brachial and pedal suboesophageal ganglia. Actions of the fins, mantle, eye muscles and other effectors of a cuttlefish are coordinated with those of the arms by the higher motor centres of the basal supraoesophageal lobes (Boycott 1961). These in turn are activated by the afferent inflow, especially through the optic lobes and regulated by the vertical lobe system.

In the present paper we consider the lower motor centres of the suboesophageal lobes of *Loligo*, but this is already a mixed category. The brachial and pedal lobes are in part centres controlling the actions of the complex ganglia of the arms and suckers. Other parts of them are however motor centres of the lowest level, containing, for example the motoneurons for the eye muscles and for the chromatophores of the head.

The presence of such a series of centres with distinct functions is one of the features that makes the study of cephalopod nervous systems especially rewarding. The lobes are largely anatomically distinct. We can contrast the types of large and small cells and of neuropil, dendrites and synapses that serve the different functions. Such a study obviously requires electronmicroscopy and physiological analysis. First, however, there is needed an account of the main features and fibre connections, which has been attempted here. In future papers of this series the organization of the higher motor centres of the supraoesophageal lobes will be compared with the lower ones here described. A final paper deals with the features found in the vertical lobe system (Young 1976*c*).

It is not easy to determine the exact relations of the various levels by either anatomical or physiological methods. Many afferent paths pass through the peripheral ganglia to the suboesophageal centres and from these to the supraoesophageal lobes. However, analysis of the connections suggests how each level acts to regulate movements of small or large segments of the motor system or of the whole animal. Comparisons with *Octopus* are especially interesting in view of the differing ways of life. Unfortunately there has yet been little experimental analysis of these centres in squids, but investigation of the details of their interconnections shows some of the principles upon which they are organized.

2. Organization of the suboesophageal lobes

The suboesophageal ganglia are conveniently divided anatomically into anterior, middle and posterior masses, often known as brachial, pedal and palliovisceral lobes (figures 1 and 2) (Young 1971). These latter names, however, are not wholly appropriate for various reasons (Young 1971). For example, by no means all of the fibres of the brachial nerves arise in the 'brachial' lobes, many pass directly from the pedal lobes to the arms. Moreover there are doubts as to whether the 'pedal' lobes are properly so named. The funnel is certainly a derivative of the foot (see *Nautilus*) but there are indications that the arms should more properly be considered as 'cephalic'. Again, the eye muscles, which are innervated from the 'pedal' lobes, can surely hardly be considered to be part of the foot. For such reasons we have preferred to use the more neutral terminology for the suboesophageal masses. The anterior and middle masses are very widely separated in *Loligo* and joined by long tracts of fibres. It is not clear what are the phylogenetic or functional implications of the separation. The middle and posterior masses are also sharply separated anatomically. The pedal arteries pass down between them (figure 33, p. 122). As in many cephalopods the arteries are unequal, the left larger than the right. At this level, too, the separation of the lobes is marked by the transverse septum. This is a sheet of fibrous tissue attached at the sides to the cranium and passing completely across the suboesophageal mass. The tracts of nerve fibres run through holes in the sheet.

The anterior suboesophageal mass contains neurons concerned with the movements of the arms and suckers. The middle mass is the main centre controlling movements of the whole animal. Many fibres reach from it direct to the arms. It probably includes the centres controlling operation of the tentacles and seizure of the prey following suitable signals from higher centres. Other cells here are final motoneurons for muscles of the head and eyes. Towards the hind end of the middle mass is a region controlling the direction of swimming, from which fibres run to the funnel and to the centres further back for the fins.

Around the hind end of the middle suboesophageal mass is the magnocellular lobe, containing the first order giant cells, the command pathway for swimming with the jet (Young 1939). Here also are other large cells with axons proceeding to the centres for the arms and fins,

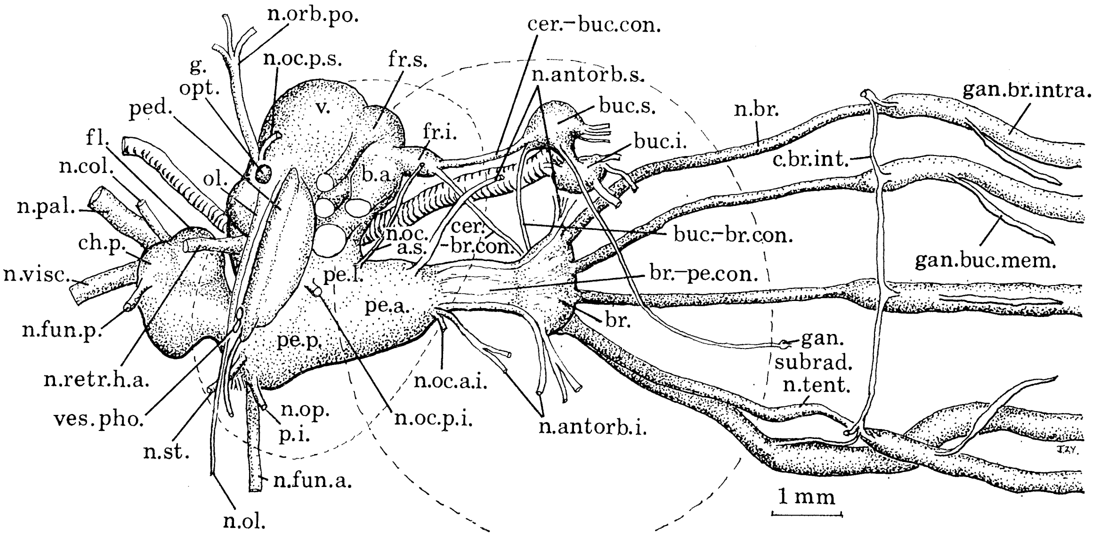

Figure 1

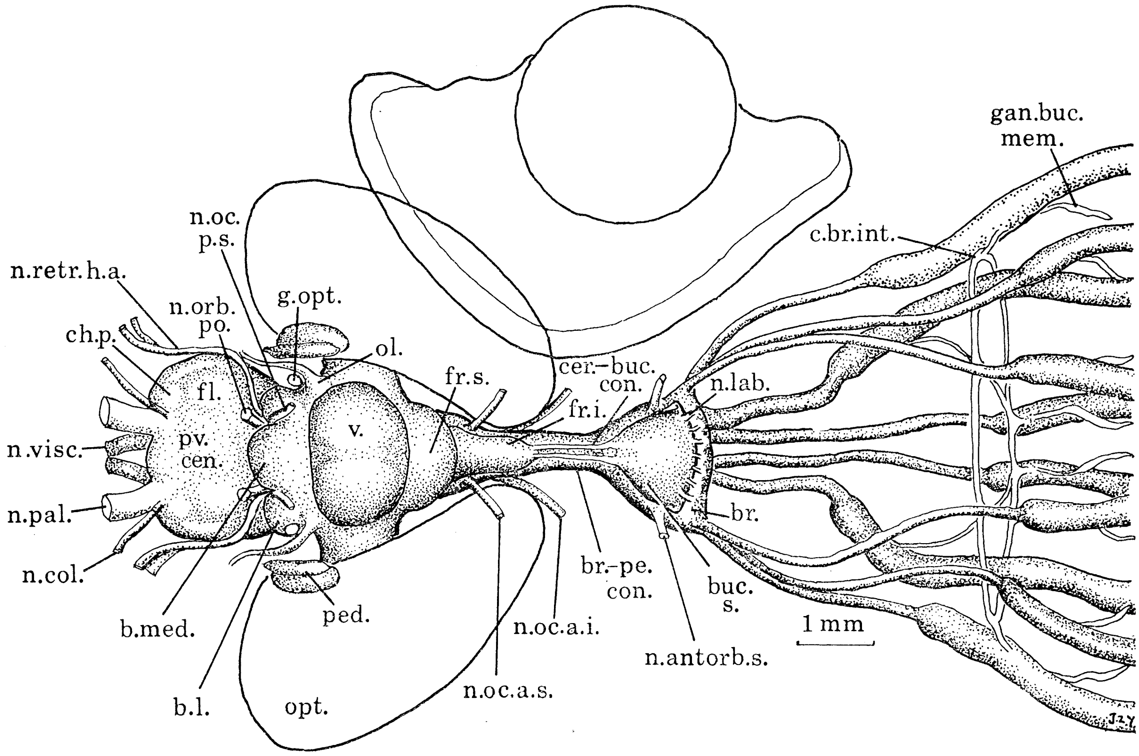

Figure 2

Figures 1 and 2. Reconstructions from tracings of transverse sections of the brain of a small *Loligo vulgaris* (5 cm mantle length). The outlines of the eye and optic lobe are dotted.

ensuring their appropriate actions during jet propulsion, perhaps particularly in taking evasive action.

The posterior suboesophageal mass contains the final motoneurons for the fins. Other cells here are involved in the jet propulsion movements of the mantle and retraction of the head, and yet others the movements of the respiratory muscles of the collar. The extreme hind end of the brain is concerned with control of the viscera and vascular system.

The muscles of the chromatophores and skin are controlled by final motoneurons in special lobes of the suboesophageal ganglia, the anterior chromatophore lobes in the middle and posterior chromatophore lobes in the hinder mass (Boycott, 1953). The operations of eating the food are motor actions not controlled from suboesophageal centres but by the superior and inferior buccal and subradular ganglia. It is convenient however to treat them here, with the other motor centres.

3. Materials and methods

The three species of *Loligo* and the methods used were as listed in the first paper of this series (Young 1974). Several series of sections of *Alloteuthis subulata* from Plymouth were also used. Unless otherwise mentioned all the measurements of sizes of cells and fibres were made on a series of transverse sections of *L. vulgaris* of 15 cm mantle length (series JA). It had been fixed in neutral formalin in sea water, stained with Cajal's stain and embedded and sectioned in celloidin (Stephens 1971).

Observations are recorded of the results of electrical stimulation of some of the lobes. These were mostly made to confirm that functions of the lobes are similar in *Loligo* to those more fully studied in *Sepia* and *Octopus* by Boycott (1961). The responses recorded were to threshold voltages delivered through a unipolar silver electrode applied to the brain shortly after bisecting it. Good responses can be obtained for a few minutes, especially in *Alloteuthis* or small *Loligo*.

4. The brachial nerves and intrabrachial ganglia: centres for arm and sucker reflexes

The naming of the nerves and ganglionated cords in the arms and tentacles gives rise to some difficulty (figures 1 and 2). The proximal portions, immediately anterior to the suboesophageal ganglia are without nerve cells and may be called the brachial (or tentacular) nerves in the strict sense. The ganglia within the arms will be called the intrabrachial ganglia or cords, to distinguish them from the brachial ganglia, which are part of the brain.

At the level at which the cells begin the brachial nerves are united by a circumbrachial commissure. This consists partly of fibres running between neighbouring arms, partly between those further apart (Graziadei 1971). The nerve to each arm beyond the level at which it becomes ganglionated contains a covering of cells of medium sizes (up to 20 μm diameter in the *L. vulgaris* of 5 cm mantle length). The larger cells lie towards the outside but there is not a very great gradation in size and no very small cells (figure 3, plate 1).

There are four main longitudinal bundles of fibres in each nerve. The largest group lies laterally (that is towards the outside) and this contains the largest fibres (up to 20 μm diameter in the same *L. vulgaris*, no doubt larger in an adult). There are about 40 of these large fibres in this bundle, arranged in two symmetrical groups. The bundle also contains many smaller fibres (figure 3). Of the bundles on the medial side the central one contains fibres with a range of diameters from 10 μm downwards. The other two bundles contain no fibres larger than 7 μm.

The nerves in the tentacles differ from those in the arms. The largest lateral fibres form a more compact and conspicuous group, possibly they operate the retractile mechanism, but they may be concerned with the 'club', either as efferents or afferents.

The ganglia in the 'pillars' of the buccal membrane (figures 1 and 2) are simple cylinders with cells of rather uniform small size (up to 10 μm diameter) and a central neuropil, but no large fibres.

5. THE ANTERIOR SUBOESOPHAGEAL MASS: INTERMEDIATE MOTOR CENTRES FOR ARM MOVEMENTS

This stands apart from the middle mass in *Loligo,* joined to it by thick bundles of fibres, the brachio-pedal connectives (figures 1 and 2). The mass is narrow behind, broader in front. Two distinct regions can be recognized, the pre-brachial and brachial lobes, as in *Octopus,* but the neuropils are continuous and it is not clear to what extent these are functionally distinct entities. Anatomically there is a distinction in the fact that the pre-brachial lobe is deeply divided at the centre by walls of cells, which separate the incoming brachial nerves (figures 4 and 5). The brachial lobe shows a single undivided outline, with cells all round (figure 7). The pre-brachial lobe differs markedly from that of *Octopus* in the absence of a suprabrachial commissure. This curious difference remains unexplained, but may be connected with the differences in use of the arms. The distinction between pre-brachial and brachial lobes is nevertheless marked clearly in *Loligo* by the presence of the walls of cells.

The place of these centres in the functional hierarchy is considered on p. 159. Electrical stimulation at the centre of the brachial lobe of *Sepia* produced movements of all the arms together, but not such as are normally shown in life (Boycott 1961).

Each brachial nerve has four distinct roots (figure 5, plate 1): (1) A dorsal or cerebral root, running to the supraoesophageal and buccal lobes. This contains mainly small fibres, probably afferents with a few up to 10 μm in diameter. (2) A medial root, consisting mainly of small fibres probably afferents. (3) A lateral root with large and small fibres up to 30 μm. The large fibres arise from the pre-brachial cells and are therefore efferents. (4) A pedal root running to the brachio-pedal connective and therefore making no connection with the anterior suboeso-

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DESCRIPTION OF PLATE 1

All figures are of *Loligo* or *Alloteuthis* and all stained with Cajal's silver method except where stated. A few have been retouched (see descriptions).

FIGURE 3. *Loligo vulgaris* (mantle length 5 cm). Tangential section showing the intrabrachial cord of the third arm.

FIGURE 4. Transverse section. Pre-brachial and buccal lobes of the same individual as in figure 3.

FIGURE 5. *L. vulgaris* (6 cm mantle length). Transverse section of the pre-brachial lobe.

FIGURE 6. *L. pealeii.* Transverse section of the brachial lobe.

FIGURE 7. *L. pealeii,* (juvenile). Sagittal section of the anterior suboesophageal mass showing descending fibres of the cerebro-brachial connective (*cer.-br.con.*).

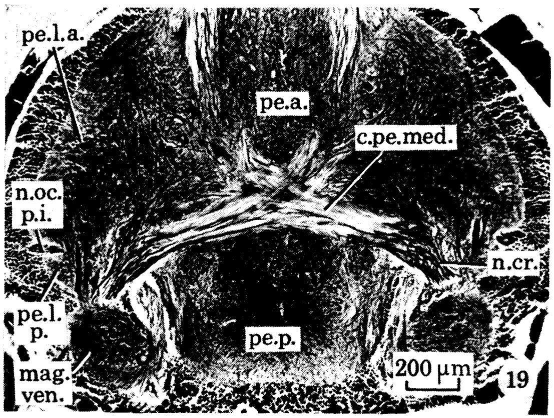
FIGURE 8. *A. subulata.* Horizontal section of the anterior suboesophageal mass.

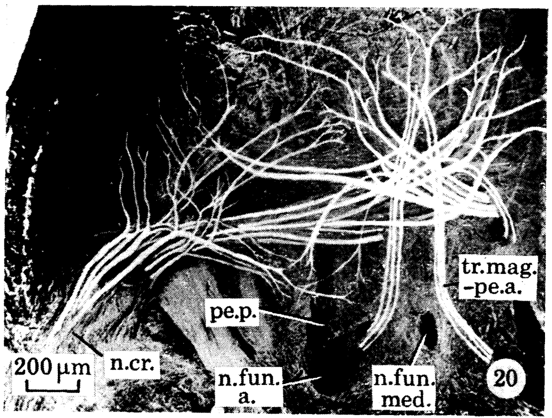
FIGURE 9. *A. subulata.* Horizontal section to show divisions of the middle suboesophageal mass.

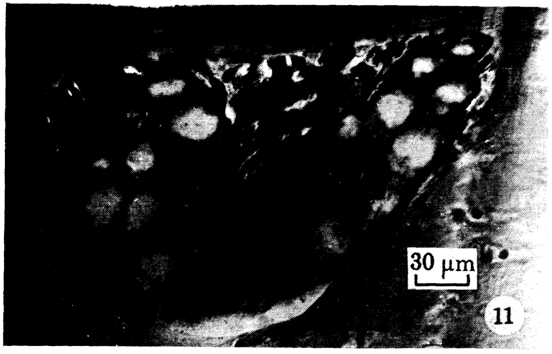
FIGURE 10. *L. vulgaris* (adult). Horizontal section to show nerves of statocyst.

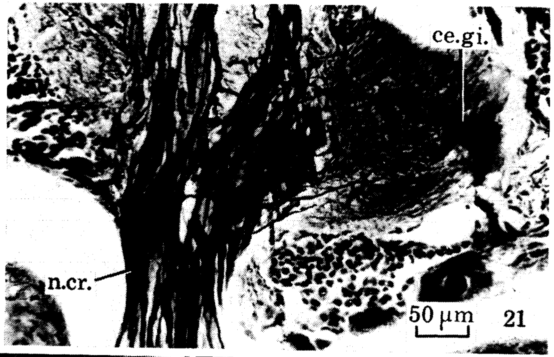
FIGURE 11. *L. pealeii* (adult). Horizontal section of dorsal crista nerve. (*n.cr.d.*)

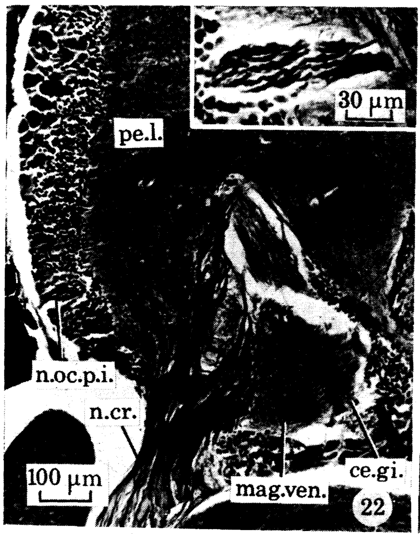
FIGURES 3–10 AND 18. For description see opposite.

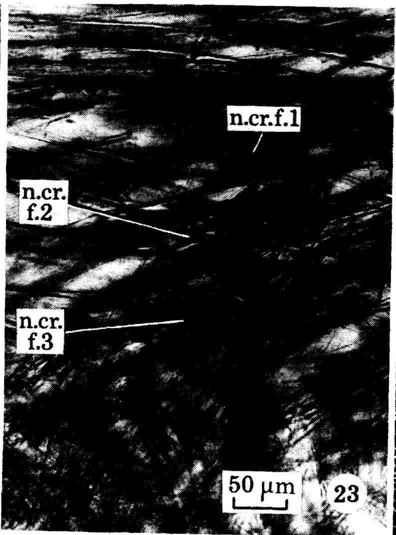


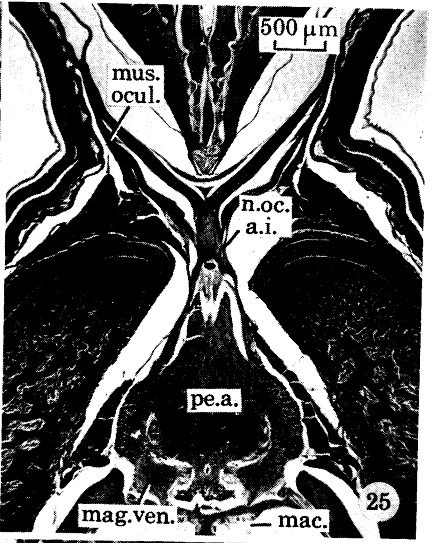


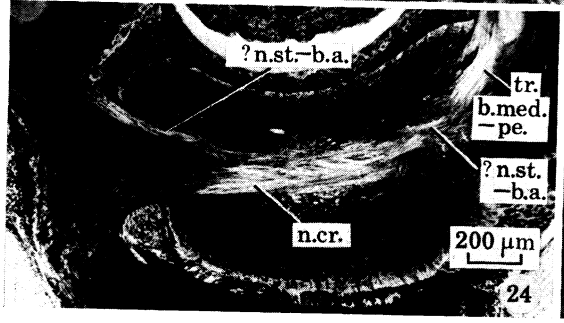


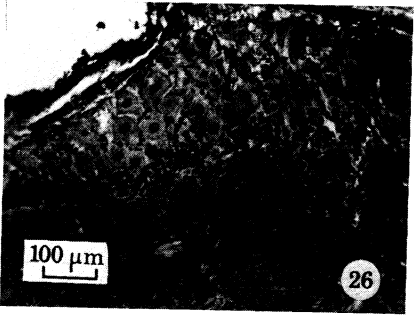












FIGURES 11 AND 19–26. For description see opposite.

phageal mass (figure 8, plate 1). It contains large and small fibres, the largest are up to 50 μm. These last are probably the fibres that make up the lateral bundle of large fibres in each brachial nerve (p. 107), but it has not been possible to show this conclusively.

From each brachial nerve, as it enters, there first separates the cerebral root, and the five of these on each side form conspicuous bundles in the dorsal part of the lobe (figure 4, plate 1). They run to the hind end of the mass and make part of the cerebro-brachial and bucco-brachial connectives. As they pass backwards these bundles show a considerable amount of interweaving. At the hind end of the mass they aggregate to form the connectives on each side (figure 6, plate 1 and figure 32, p. 121). It seems likely that the interweaving bundles contain afferent fibres carrying information directly from the arms to higher centres. It is interesting that strict topographic arrangement is not preserved, at least there is much interchange between the bundles from the different arms. The cerebro-brachial connectives also carry large descending fibres from the posterior buccal (inferior frontal) lobe, spreading out in the brachial lobe (figures 6 and 7).

The bucco-brachial connectives lie lateral to the cerebro-brachial connectives (figure 6). Their fibres come from the more lateral parts of the brachial lobes, partly from the same interweaving bundles as the cerebro-brachial connectives. They probably include afferents from the arms perhaps also efferents passing downwards, but the fibres are all rather small and have not been seen to branch in the brachial lobes.

The small fibres of the medial roots of the brachial nerves spread out in the neuropil of the pre-brachial lobe. They enter in small bundles, each presumably related to some feature of the arm (? a sucker). Each individual fibre divides into a medial and a lateral branch, which run across the trunks of the large cells of the lobe. These trunks form the transverse bundles that are characteristic of the lobe. They run round, with much interweaving, and cross the mid-line ventrally. The fibres then leave as the large axons of the roots of the brachial nerves. This is obviously a system for interchange of information between the arms. It is not clear what further actions are involved in the pre-brachial lobe, but it contains numerous small cells of diameter

Description of plate 2

Figure 18. *A. subulata*. Horizontal section of the anterior chromatophore lobes. (*ch.a.*)

Figure 19. *L. vulgaris* (5 cm mantle length). Horizontal section to show the course of the crista nerves. Holmes' stain. Some branches of two uncrossed and one crossed fibres have been retouched.

Figure 20. *L. pealeii* (adult). Horizontal section of fibres of the *n. crista statica* and magnocellular to anterior pedal tract. The fibres have been retouched with white. Branches of the crista fibres reach to the anterior pedal, lateral pedal and posterior pedal lobes of the same and the opposite sides.

Figure 21. *L. vulgaris*. Fibres of the *n. crista statica* showing collateral branches reaching the ventral magnocellular lobe among the dendrites of the first order giant cell. Holmes' stain. Retouched.

Figure 22. *L. vulgaris*; same specimen as figure 21 showing small fibres of the *n. crista statica*, running to the lateral pedal lobe. Also collaterals entering the ventral magnocellular lobe. Inset figure 22*a*. Fibres of the posterior inferior oculomotor nerve at higher magnification.

Figure 23. Same preparation as figure 20 showing the three main branches of a fibre of the crista nerve immediately after crossing. b1 goes to the posterior pedal, b2 to the lateral pedal and b3 to the anterior pedal lobe. Branching of smaller fibres is also shown.

Figure 24. *L. pealeii*. Transverse section of the middle pedal commissure. Large fibres run between this region and the median basal lobe, but their direction is uncertain (see text).

Figure 25. *L. vulgaris*. Horizontal section to show course of anterior inferior oculomotor nerve.

Figure 26. *L. vulgaris*. Cells and neuropil of the lateral pedal lobe.

less than 6 μm, mainly occpied by the nucleus. A few of the larger cells reach 50 μm in transverse diameter, these lying at the outside of the cell layers. In the regions where there are numerous small cells (mainly dorsally) there is an outer layer of fine-fibre neuropil, showing pale yellow with silver stain.

The brachial lobe proper is a rather short region at the back of the anterior suboesophageal mass, where there is no division down the middle and few or no transversely running bundles (figure 6). The cell walls are uniform all round with a composition essentially the same as that of the pre-brachial lobe.

The neuropils of both brachial and pre-brachial lobes receive the three brachio-pedal connectives, paired lateral bundles and a median one (figure 8). The fibres of all three bundles run to both brachial and pre-brachial lobes. Some of them are quite large, and these probably run forwards and divide within the brachial lobes. Other smaller fibres also spread throughout the lobes (figure 6) these may include fibres running backwards as well as forwards.

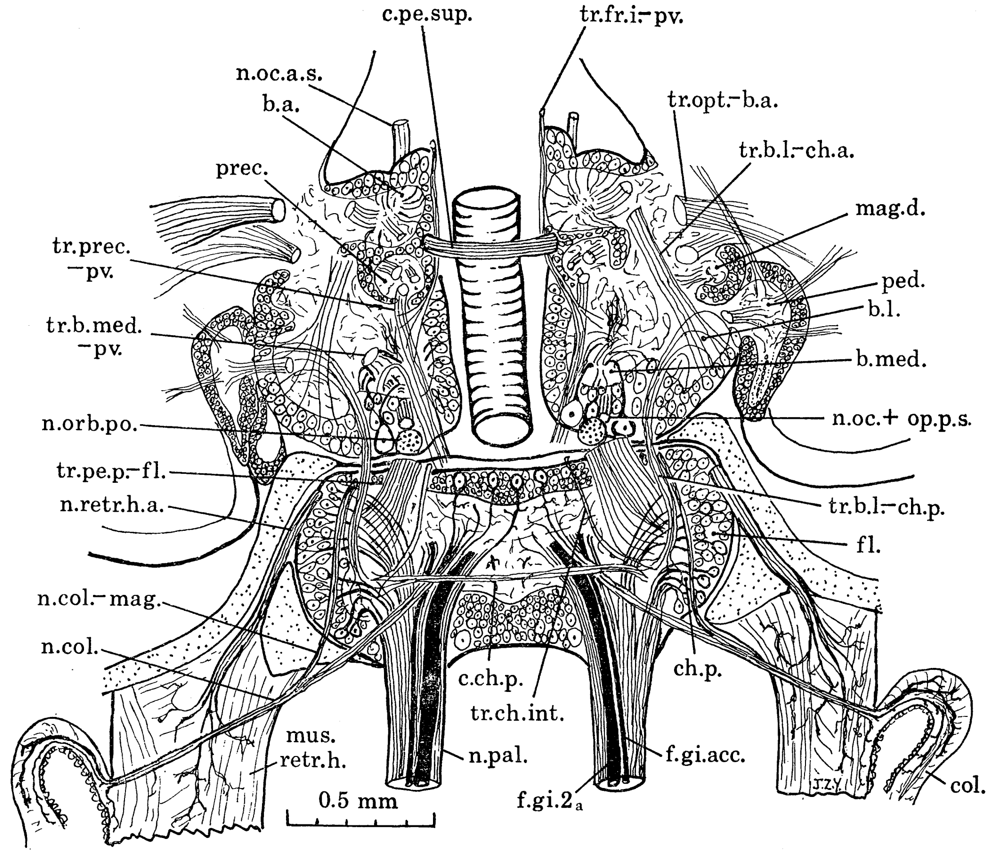


FIGURE 12. For description see p. 115.

6. THE BRACHIO-PEDAL CONNECTIVES

The wide separation of the anterior and middle suboesophageal masses is a characteristic feature of many decapod brains and the name brachio-pedal connective will be used for the complicated bundles of fibres connecting the two (figures 13, 15 and 32 and figure 8, plate 1). There are obvious difficulties in terminology because of the various parts referred to as 'brachial'. The brachio-pedal connective should more strictly be called the 'anterior to middle suboesophageal mass connective', since it contains elements that do not run between the brachial and pedal lobes. Its components are (1) The anterior oculomotor nerves (2) The superior antorbital nerves (3) The inferior antorbital nerves (4) The brachio-palliovisceral tracts (5) The brachio-magnocellular tracts (6) The brachio-pedal tracts. The first three are peripheral nerves arising in the middle suboesophageal mass and running forward to their destinations by way of the brachio-pedal connectives. The next three are complex bundles formed from fibres running partly from and to the brachial nerves and partly from and to the brachial and prebrachial lobes. Their fibres are therefore involved in a complicated pattern of re-assortment at

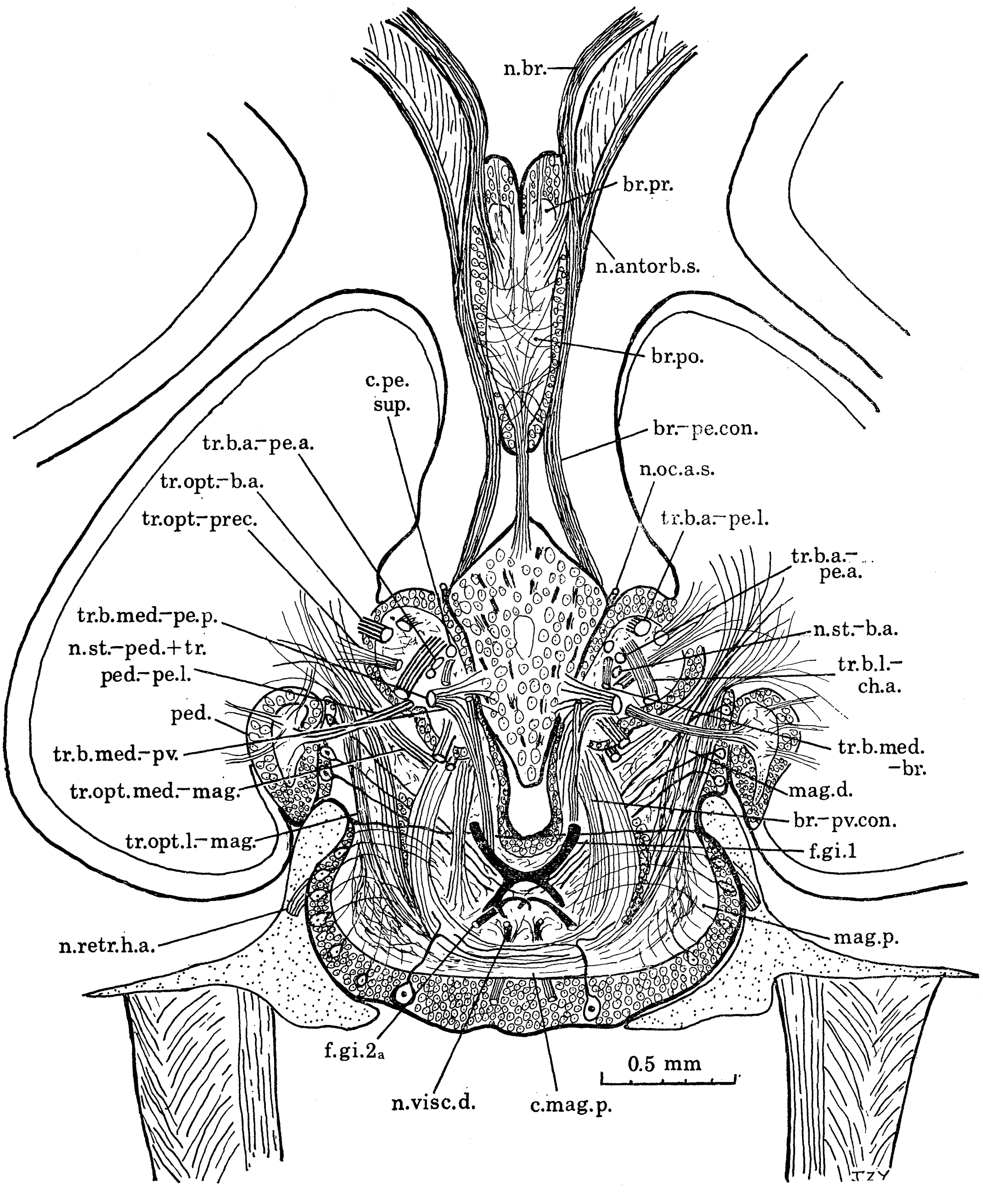


FIGURE 13. For description see p. 115.

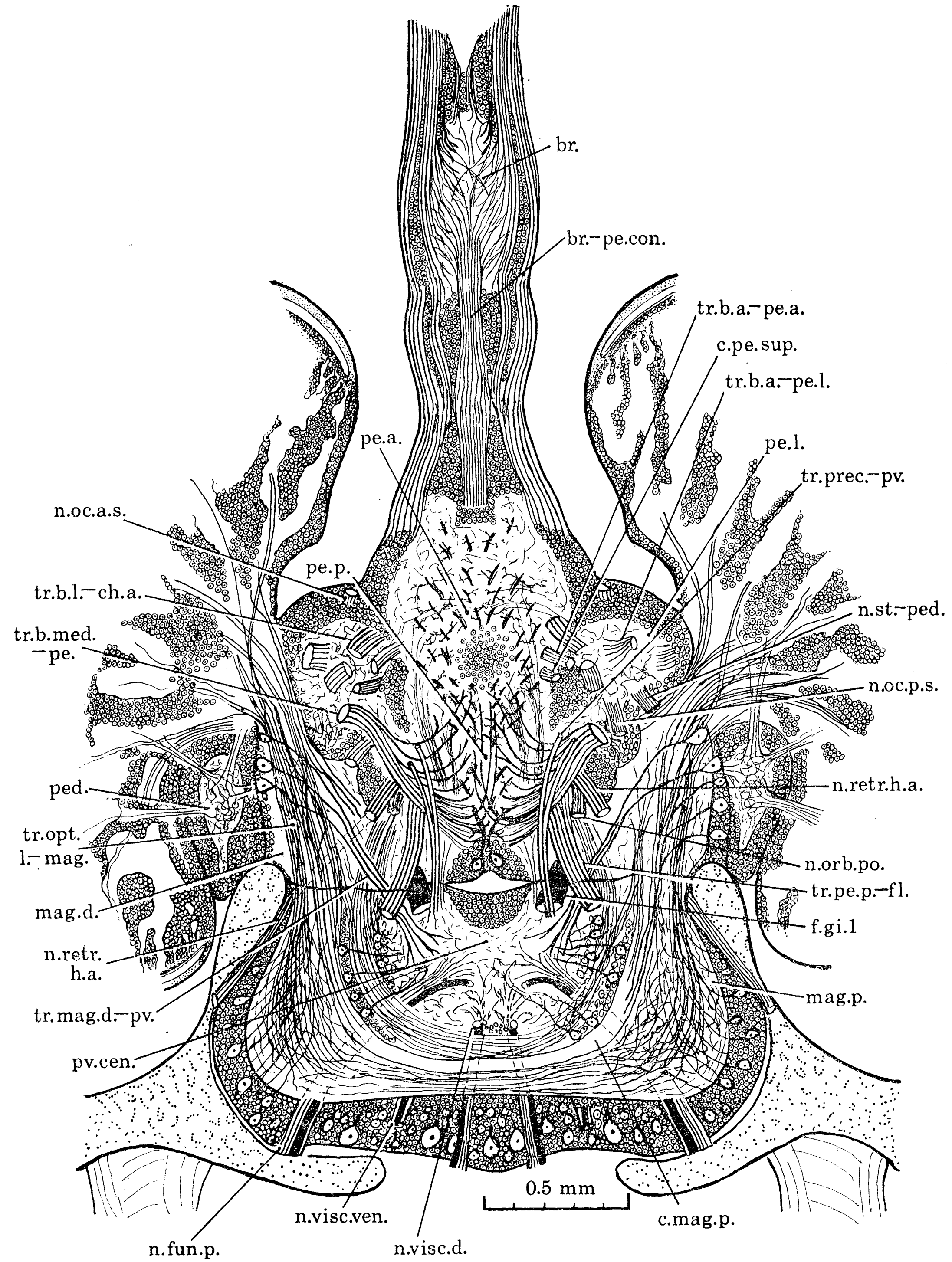


FIGURE 14. For description see p. 115.

the hind end of the anterior suboesophageal mass (figure 8). It is very difficult to follow individual large fibres or bundles through their whole course, but it is certain that many fibres run direct between the arm nerves and the pedal lobes, also to the brachio-palliovisceral tract. A name is needed for these direct bundles containing fibres running in both directions between the arms and the pedal lobe. They will be called intrabrachio-pedal connectives, a name that is exact if not elegant (figure 15).

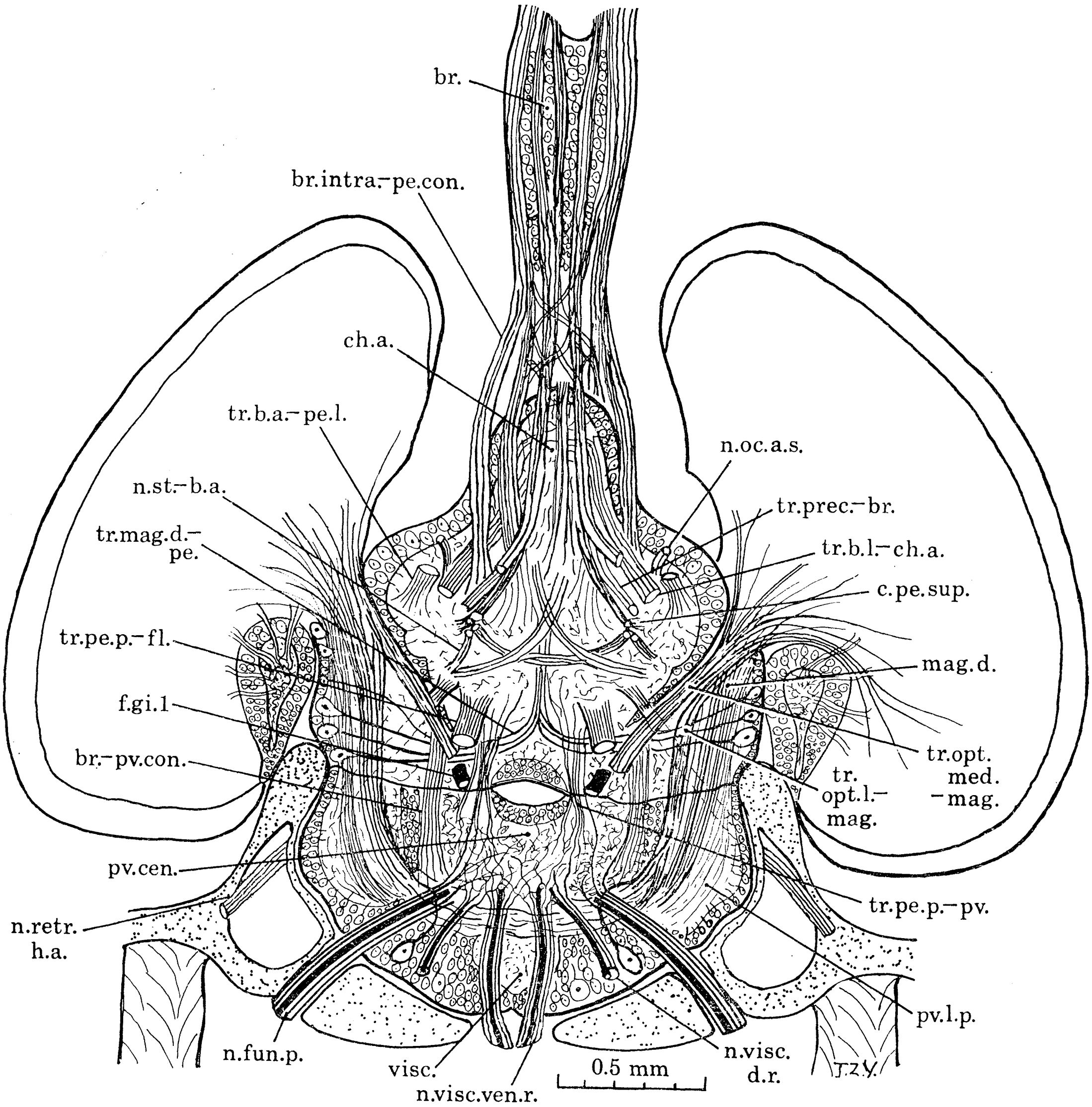


FIGURE 15. For description see p. 115.

7. MIDDLE SUBOESOPHAGEAL MASS

7.1. *Position and relations*

This region includes five subdivisions, broadly connected together, anterior pedal, lateral pedal (anterior and posterior) and posterior pedal lobes and the anterior chromatophore lobes (figure 9, plate 1 and figures 14 and 15). These are the centres that control many of the animal's movements, under the higher control of the basal centres of the supraoesophageal lobes. Movements of the arms and anterior head muscles are controlled by the anterior pedal lobes, movements of the eyes by the anterior lateral pedal lobes. The direction of movement by means of the funnel and fins is controlled from the posterior pedal lobe. The magnocellular lobe, lying at the sides and below the rest, initiates the jet propulsion movements of the mantle and also perhaps with the posterior lateral pedal lobe the use of the tentacles for the seizure of prey. Much can be discovered from the connections of these various parts about the way in which integrated action of the whole animal is achieved.

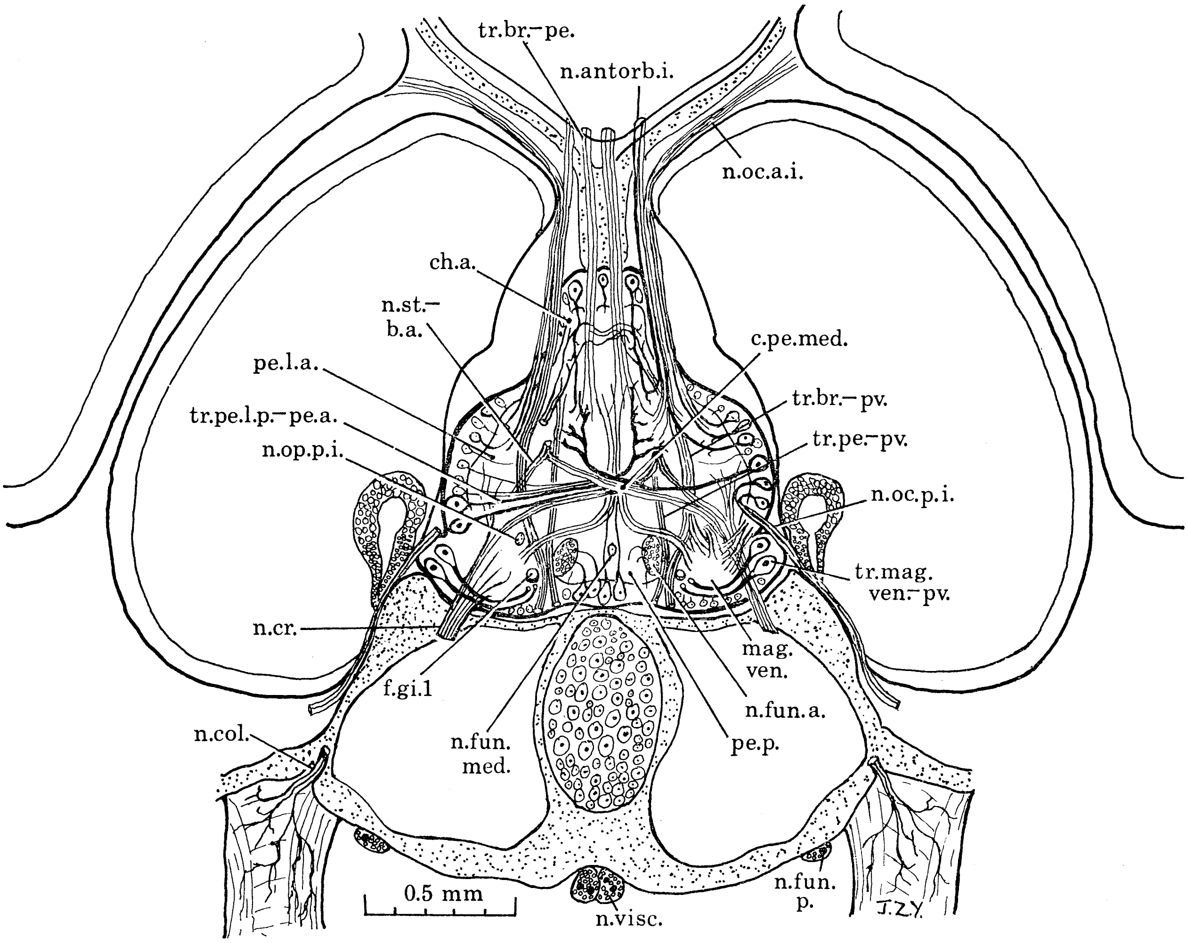


FIGURE 16. For description see p. 115.

The middle suboesophageal mass is narrow transversely in front and broadens behind. The anterior pedal lobe and anterior chromatophore lobes occupy the front half, the lateral pedal lobes the swellings at the sides. The middle pedal commissure is a conspicuous landmark, containing static and other fibres. It can serve to mark the boundary between the anterior and posterior pedal divisions but they are continuous above and below it. There is also a conspicuous posterior pedal commissure (figure 39, plate 3). There are many crossings elsewhere, particularly between the anterior chromatophore lobes (figures 9 and 12). There is also a suprapedal commissure, crossing above the oesophagus (figures 12, 14 and 15). It probably includes fibres crossing between the lateral pedal lobes, but may perhaps also carry them from other parts of the pedal lobes and from the statocyst.

7.2. *Anterior chromatophore lobes: control of skin of the arms and head*

These lobes occupy the front face of the middle suboesophageal mass. They are not clearly marked externally, but have characteristic structure and connections (figure 18, plate 1). The cell wall here, both dorsally and ventrally consists of cells graded in size from very large (100 μm transverse diameter) to moderate (20 μm), but with no inner layer of very small cells.

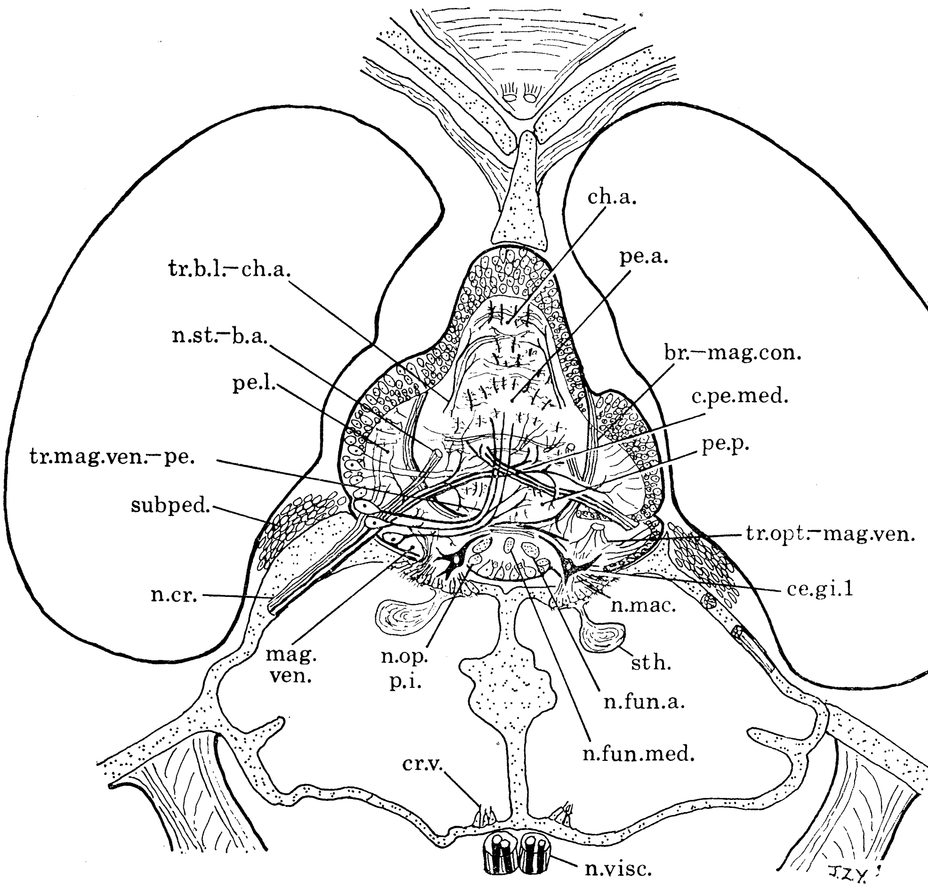


FIGURE 17

FIGURES 12–17. Are from consecutive horizontal sections of a newly hatched *Loligo pealeii*, each 50 μm thick stained with Cajal's method. Proceeding from dorsal to ventral, figure 12 is from seven sections (350 μm), 13 from two, 14 from one, 15 from three, 16 and 17 from five. Each figure is seen from above.

There is also no layer of fine fibre neuropil next to the cell layer. The neuropil contains a web of darkly staining fibres coming from the lateral basal to anterior chromatophore lobe tract (figures 15 and 17). These divide, giving one branch on the same side and another crossing, as in the commissure of the posterior chromatophore lobes (p. 147). Some of these fibres cross above and some below the numerous bundles of the brachio-pedal connectives. The neuropil of the lobes is directly continuous with that of the anterior pedal lobes and they probably exchange fibres. There are also sets of fibres joining this lobe with the posterior chromatophore lobes (p. 147). There may also be fibres reaching the anterior chromatophore lobes from the arms.

The cells of the ventral part of the lobes are larger than those of the dorsal, perhaps they innervate large areas of the undersides of the head and arms where the colour patterns are rather simple. The cells of the lobe send axons direct to the brachial nerves (figures 16 and 32), probably reaching the muscles of the chromatophores without further synapse. It is possible that some of the fibres of cells of these lobes run backwards as interchromatophore lobe tracts (p. 147).

7.3. *Static nerves*

The nerves from the statocyst enter all the remaining parts of the middle suboesophageal mass and it is convenient to describe them here (see figure 109, p. 156). Two nerves reach the brain from the crista on each side. A smaller more dorsal branch comes from the anterior (transverse) arm of the crista and a more ventral branch from the other divisions (Stephens & Young 1976). The dorsal branch contains about 20 large fibres, the largest 40 μm in diameter. The ventral branch has about 60 large fibres. Both have numerous smaller fibres (figures 10 and 11, plates 1, 2).

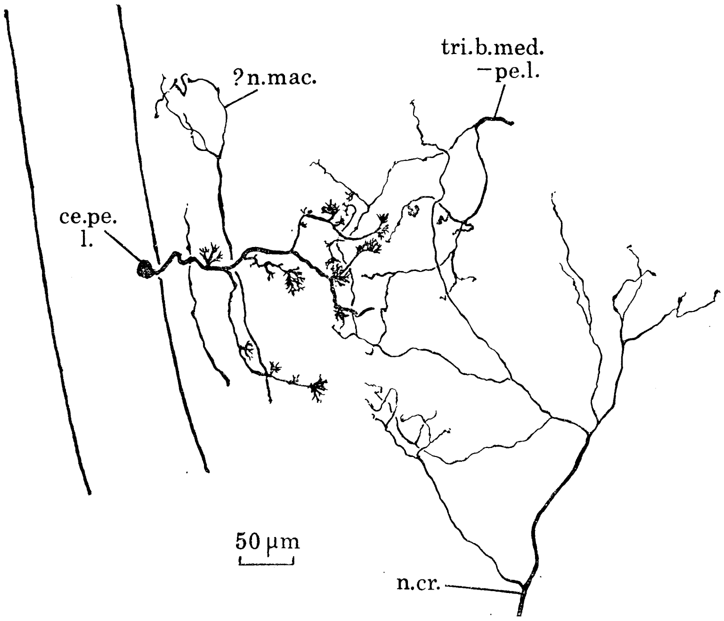


FIGURE 27. *Alloteuthis subulata*. H.S. lateral pedal lobe, showing an oculomotor neuron and its dendrites and input fibres from the static nerve and median basal lobe. Golgi.

The crista nerves enter between the posterior lateral pedal and ventral magnocellular lobe, marking the boundary between them (figure 19, plate 2). They then proceed medially across the magnocellular lobe, defining the limit between its dorsal and ventral divisions. The large fibres divide at entry giving their first branch to the ventral magnocellular lobe (figure 21), while the main trunk continues upwards and forwards. Many of the small fibres of the crista nerve also enter the ventral magnocellular lobe. The nerve then bends medially and gives many fibres to the lateral pedal lobe. These first run across the trunks of the large cells of the posterior lateral pedal lobe. They then pass on forwards across the trunks of the cells that give rise to the oculomotor nerve fibres. The small fibres of the crista nerve cross these trunks close to the cell layer (figure 22, plate 2). The branches of the larger fibres contact the oculomotor fibres more distally. Some of the smaller crista nerve fibres turn towards the cell layer as if to arise from the cells of the lateral pedal lobe and they may be efferents that run to the crista (Stephens & Young 1976). There is, however, no sure evidence for the origin of these efferent fibres

The further course of the large crista nerve fibres will be described assuming that each fibre gives branches on either the same or opposite side, but not both. No crossing fibre has been seen to give branches on its own side but it has not been possible to follow any one fibre through its entire course so the question remains uncertain.

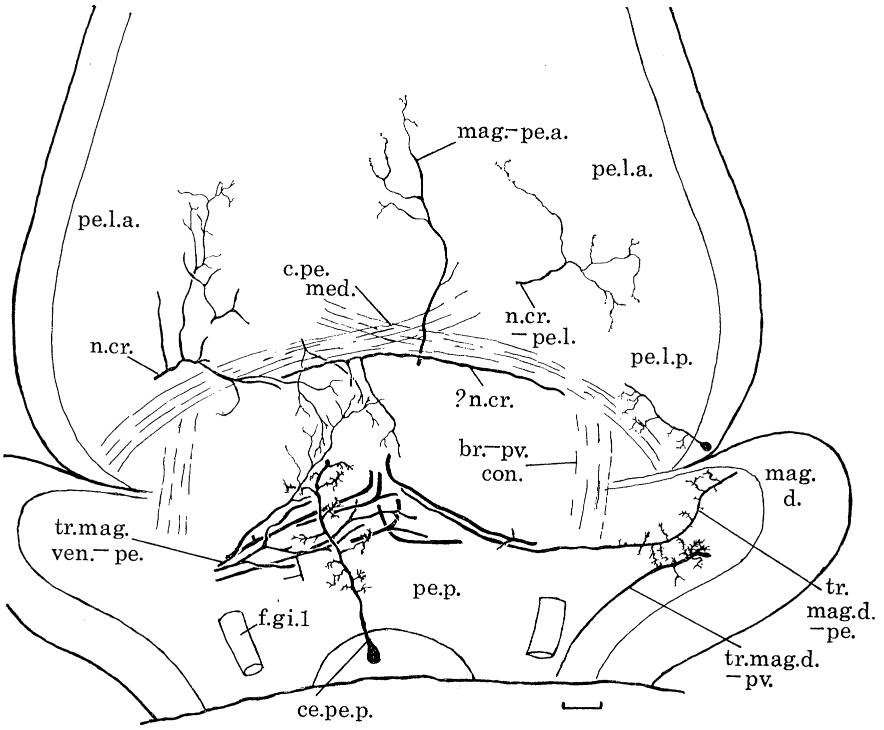


FIGURE 28. *Alloteuthis subulata*. H.S. showing crista nerve fibres, a cell of the posterior pedal lobe and fibres of the magnocellular to posterior pedal and palliovisceral lobes. Golgi.

Each of the large fibres reaches to at least three further destinations (figure 20, plate 2). On entering the pedal lobe of its own side each fibre divides into a backward branch to the posterior pedal lobe, a lateral branch to the lateral pedal lobe and an anterior branch to the anterior pedal lobe. Each of these branches then divides again many times in its territory.

The crossing fibres divide immediately after the chiasma. One branch runs back to the posterior pedal, one laterally to the lateral pedal and one turning sharply forwards to the anterior pedal lobe (figures 20 and 23, plate 2). Each then divides again many times (figures 27 and 28). The branches are often of very unequal size. A few fibres have been followed all the way to their endings. The finest branches are spread widely so that each large crista nerve fibre sends branches to a large part of the lateral pedal lobe (see p. 126). The terminations are in the form of fine varicose fibres, running mainly forwards across the trunks of the cells of the lobes, but often making irregular loops (figures 27 and 28).

The large crossing fibres of the crista nerve may perhaps also send branches through the upper part of the back of the pedal lobe to the median basal lobe (figure 24, plate 2), it is difficult to distinguish these from descending fibres of the median basal to posterior pedal tract.

The nerves from the macula contain no very large fibres such as are found in the crista nerves. The largest are about 10 μm in diameter. There are 100 or more of approximately this size and numerous smaller ones. They arise as two roots, dorsal and ventral, innervating two distinct parts of the macula princeps upon which the statolith hangs (figures 31 and 32). There are also small branches to the maculae neglectae (Stephens & Young 1976). The fibres of the macula nerve spread out in the ventral magnocellular lobe among the dendrites of the first order giant cell (figures 47, 57, plates 5, 6). From here they pass up to other parts of the magnocellular lobe and to the lateral pedal lobe.

Fibres from the static nerves also run to various destinations in the supraoesophageal and peduncle lobes, but it is not certain whether they come from the crista or macula. A large bundle of small fibres runs to both parts of the anterior basal lobe of the same side (figures 13–15 and 30). These probably also include fibres that have crossed in the middle pedal commissure as shown in the text-figures. A large bundle runs from the static nerves to the median basal lobe.

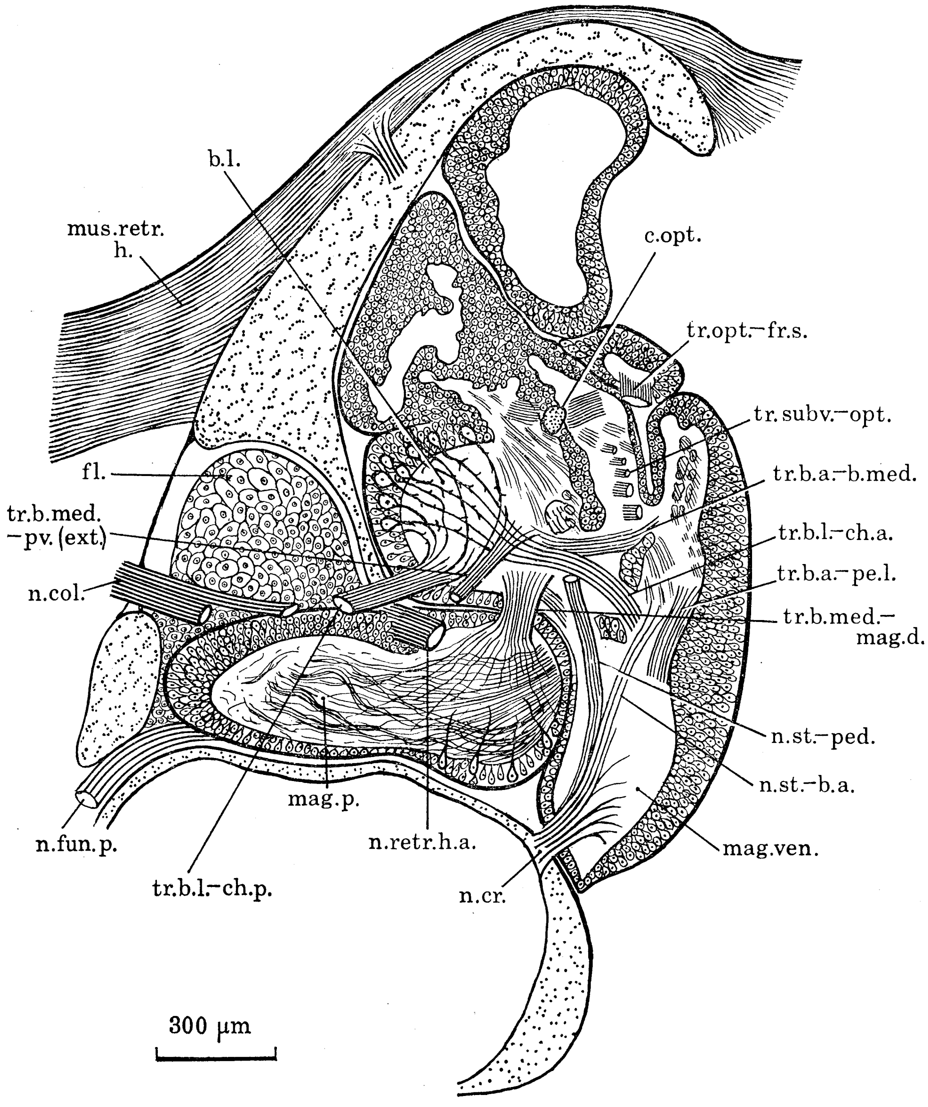


FIGURE 29. For description see p. 122.

The fibres from the static nerves to the peduncle lobe have been very hard to follow. They run with the peduncle to lateral pedal tract, in front of the dorsal magnocellular lobe (figure 37, plate 3 and figure 29). They include some large fibres, which can be clearly seen dividing within the peduncle lobe (Hobbs & Young 1973). It has not been possible to decide whether they come wholly from the same or the opposite side, or whether from the crista or macula or both.

Fibres of the static nerves probably cross above the oesophagus in the suprapedal commissure (p. 114), as they have been proved to do in *Octopus* (Young 1971).

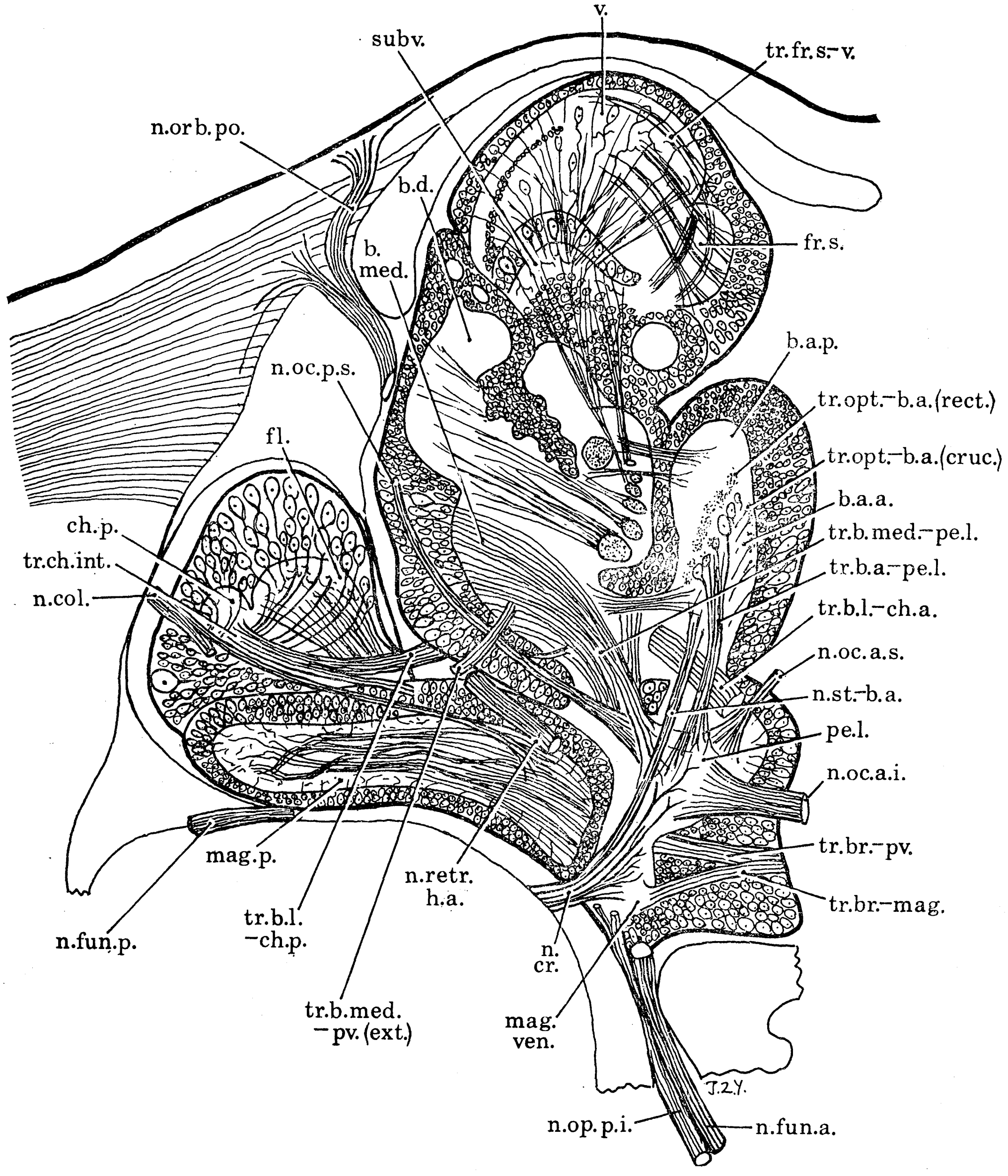


FIGURE 30. For description see p. 122.

7.4. *The oculomotor and ophthalmic nerves*

7.4.1. *Introduction*

There is much confusion in the literature over the innervation of the eyes of decapods (see Richter (1913) for *Stenoteuthis*, Schkaff (1914) for *Loligo* and *Sepiola*, Hillig (1912) and Tompsett (1939) for *Sepia*). The confusion is partly due to the differing degrees of development of the eyelids, also to uncertainty about the composition and destinations of the nerves. It is useful to distinguish between oculomotor nerves, with large fibres running to the extra-ocular muscles and ophthalmic nerves running to the skin around the eyes. The latter seem to consist of bundles of small fibres and they sometimes run with the oculomotor nerves. Further work is needed to verify the functions of these nerves.

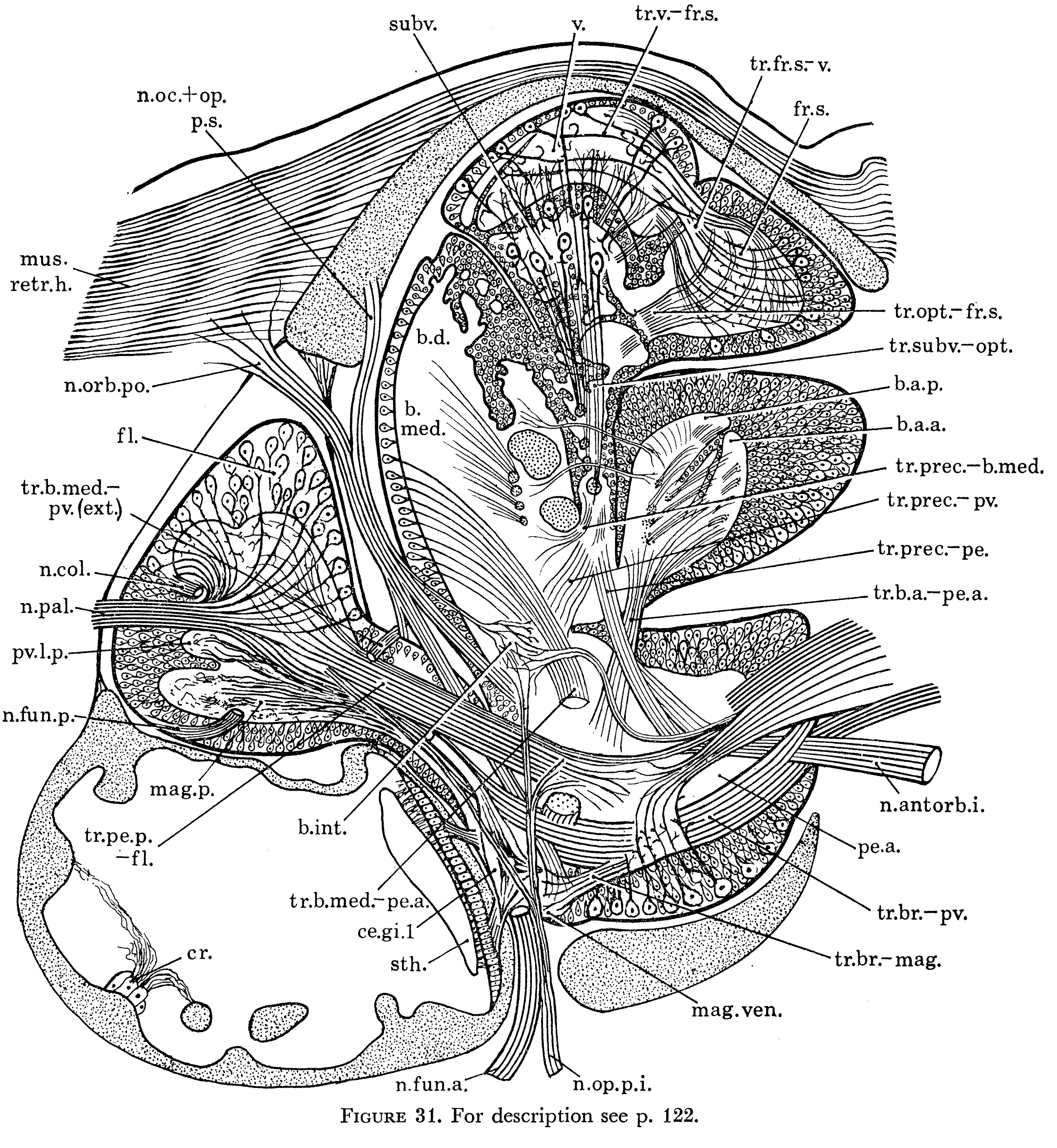


FIGURE 31. For description see p. 122.

In *Loligo* four nerves on each side carry fibres to the extrinsic eye muscles. Each nerve contains a relatively small number of very large fibres (30 μm) and some of them also contain some much smaller ones (< 3 μm). These latter occur in small groups in the nerves at the entry to the muscles (figure 41, plate 3). They do not appear to be branches of the large fibres and are considered to be a distinct class, perhaps of afferents. The posterior inferior oculomotor nerve probably consists only of large fibres (figure 22*a*, plate 2).

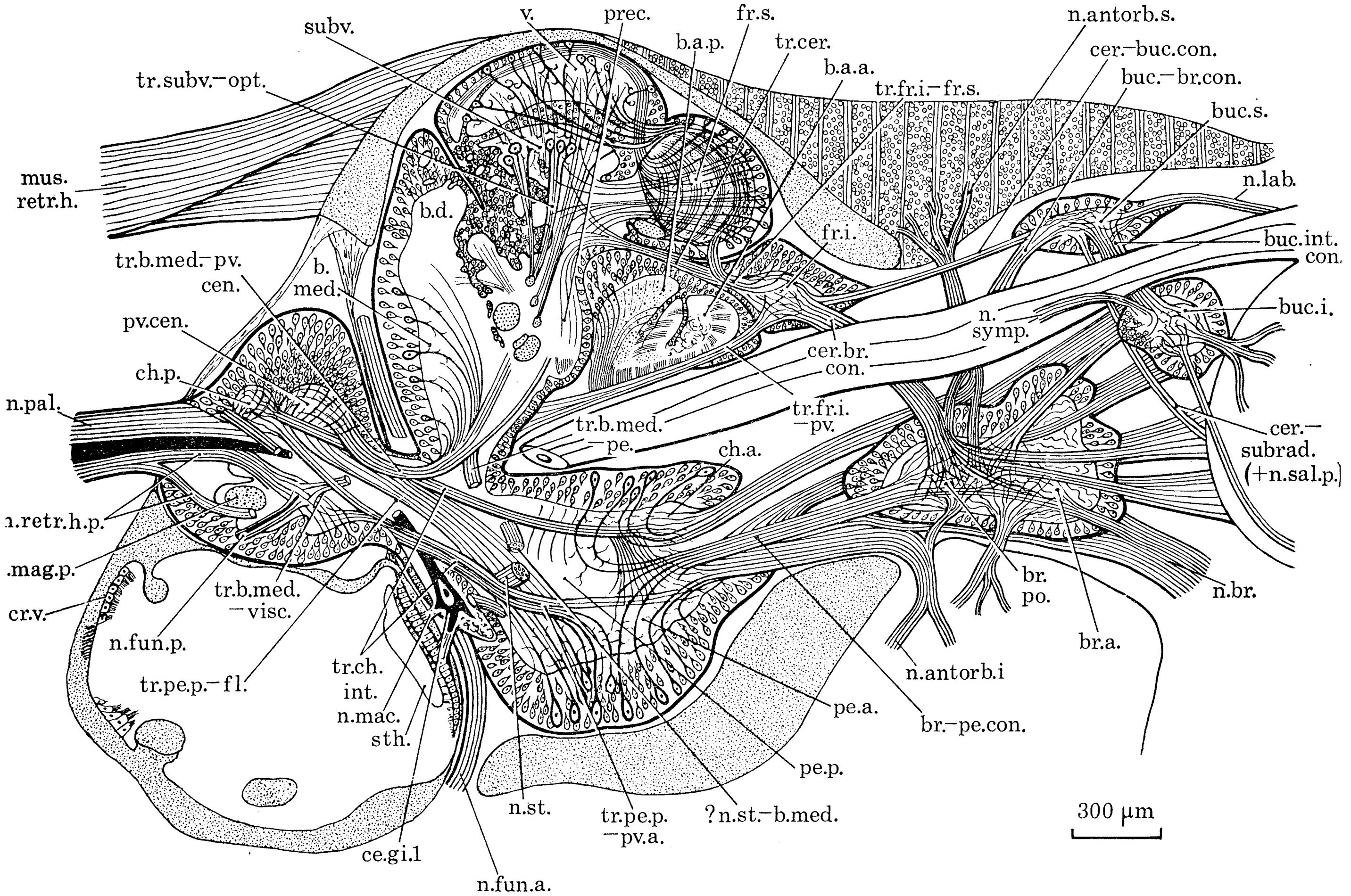


FIGURE 32. For description see p. 122.

The posterior superior oculomotor is also associated with a large distinct bundle of fine fibres that do not enter the eye muscles but run to the surface of the eye, probably to the cornea (figure 41). The oculomotor fibres of this nerve arise like the others from the lateral pedal lobe but these 'ophthalmic' fibres pass to the interbasal region above and behind this, between it and the median basal lobe (figures 31, 34, plate 3). This region is conspicuous in silver preparations since it receives bundles of fibres from various directions. Its significance will be considered in connection with the median basal lobe (Young 1976*b*).

Another bundle from this interbasal region proceeds ventrally to join with other fibres to form an inferior ophthalmic nerve supplying the lower surface of the back of the eye (see below). This nerve contains only a very few large fibres and does not supply extrinsic eye muscles, it is therefore a pure ophthalmic nerve. Probably the small fibres accompanying both the superior oculomotor and inferior ophthalmic nerves include nocifensor fibres from the eyes and perhaps chromatophore fibres.

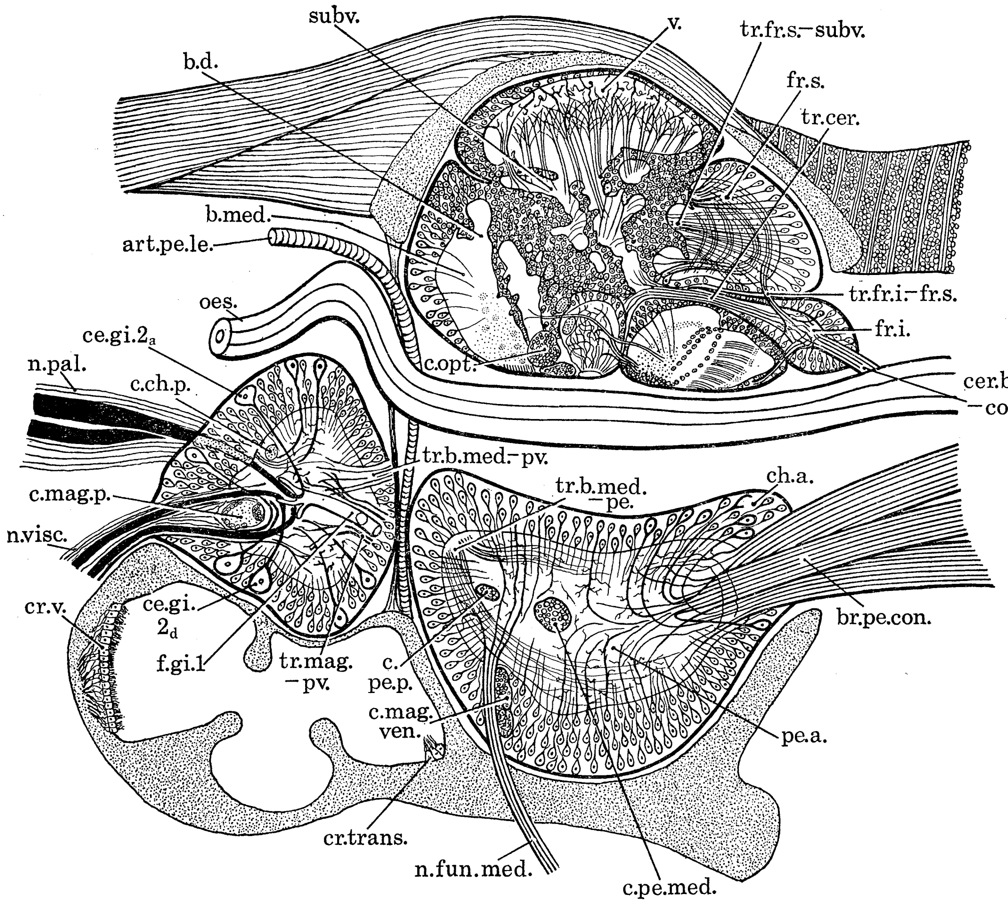


Figure 33

Figures 29–33. Are consecutive sagittal sections, each 50 μm thick, from a specimen of the same brood as figures 12–17. Proceeding from lateral to medial, figure 29 is from two sections, 30 from one, 31, 32 and 33 from two each. Some features are included from neighbouring sections to give more complete views, especially in figure 32. Each drawing shows the tracts as if seen from the medial surface of the section.

7.4.2. *Courses of the oculomotor and ophthalmic nerves*

We recognize, therefore, four oculomotor nerves and two opthalmic nerves, but there are almost certainly 'ophthalmic' fibres in other nerves, in particular in the superior and inferior antorbital nerves.

oculomotor nerves
  anterior superior oculomotor
  anterior inferior oculomotor
  posterior superior oculomotor
  posterior inferior oculomotor

ophthalmic nerves
  superior ophthalmic (runs with posterior superior oculomotor and is often called posterior superior ophthalmic)
  inferior ophthalmic (often called posterior inferior ophthalmic).

It is interesting that no ganglia such as are found in the orbit of octopods have been found along these nerves.

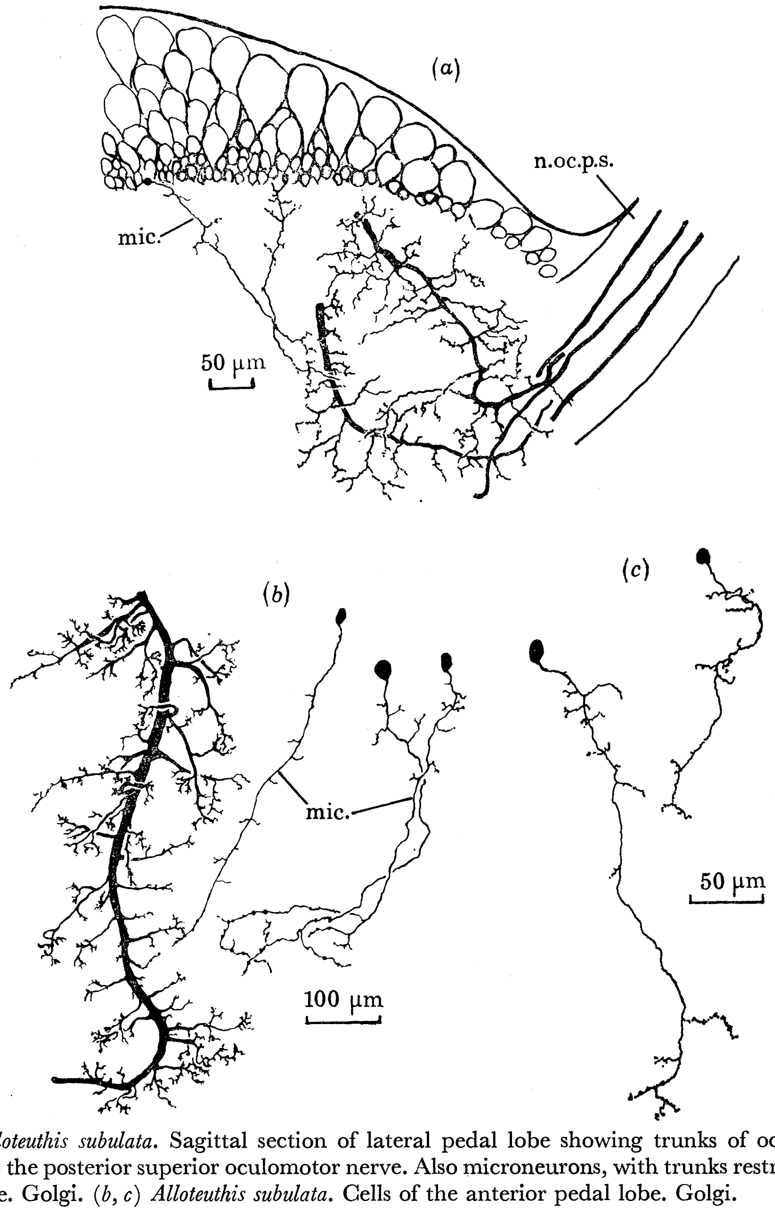


FIGURE 33 (*a*). *Alloteuthis subulata.* Sagittal section of lateral pedal lobe showing trunks of oculomotor neurons proceeding to the posterior superior oculomotor nerve. Also microneurons, with trunks restricted to the neuropil of the lobe. Golgi. (*b, c*) *Alloteuthis subulata.* Cells of the anterior pedal lobe. Golgi.

The anterior superior oculomotor nerve is not recorded by the authors mentioned. It leaves the front of the lateral pedal lobe and passes upwards and forwards (figure 34, plate 3, figures 15 and 30). It runs close to the oesophagus until it turns laterally to enter the orbit and innervates some of the eye muscles at the front of the eye (see Tompsett 1939).

The anterior inferior oculomotor nerve passes downwards and forwards from the lateral pedal lobe to accompany the brachio-pedal connective to the front of the middle suboesophageal mass (figure 34, plate 3). Here it turns laterally and immediately enters one of the eye muscles (figure 25, plate 2). Its large fibres divide up at once and make very numerous endings. Where the muscle is attached to the cranium the nerve fibres appear to be degenerating, and this was seen in several animals. The significance of this degeneration is not known.

The posterior superior oculomotor nerve leaves the upper posterior corner of the lateral pedal lobe and runs with the posterior superior ophthalmic behind and over the side of the supraoesophageal lobe (figure 34, plate 3, figure 30, p. 119). It turns laterally into the orbit and runs to some of the superior oculomotor muscles.

The posterior inferior oculomotor nerve contains only large fibres and leaves the lateral pedal lobe laterally just in front of the magnocellular lobe (figure 22, plate 2 and 35, plate 3). It turns down with the optic vein and olfactory nerve and then laterally into the orbit to the postero-ventral eye muscles. Figure 16, p. 114 shows its course, although it is not fully included in the sections drawn.

The only fully independent ophthalmic nerve is the posterior inferior ophthalmic (figure 34, plate 3 and figure 31, p. 120). It runs lateral to the anterior funnel nerve for a considerable distance passing ventrally, and this makes it hard to trace the sources of the fibres of both nerves. It contains some medium small and small fibres and possibly innervates the chromatophores, skin and some muscles at the back of the eye. Centrally its root passes medial and behind the first order giant cell (figure 46, plate 4) and then medial to the brachio-palliovisceral tract, with which part of it runs back into the posterior suboesophageal mass. Some of these fibres probably arise in the posterior chromatophore lobe (p. 147). Other fibres of the nerve run up to the interbasal lobe. Still others turn medially and arise either in the posterior pedal or lateral pedal lobes or from both.

The ophthalmic nerve fibres are among the hardest in the whole body to identify and trace. According to Richter (1913) there are anastomoses (in *Stenoteuthis*) between branches of the superior antorbital and posterior superior ophthalmic and post-orbital nerves. He does not mention any similar anastomoses ventrally, but shows branches of the inferior antorbital and posterior inferior ophthalmic near together. Possibly there is a ring of nerves joining each other all round the cornea of decapods.

DESCRIPTION OF PLATE 3

FIGURE 34. *L. pealeii* (juvenile). Sagittal section of lateral pedal lobe to show roots of the oculomotor nerves.

FIGURE 35. *L. pealeii* (adult). Transverse section to show root of posterior inferior oculomotor nerve.

FIGURE 36. *L. pealeii* (adult). Transverse section to show the anterior basal to lateral pedal lobe tract.

FIGURE 37. *L. pealeii* (juvenile). Transverse section to show peduncle lobe to lateral pedal lobe tract.

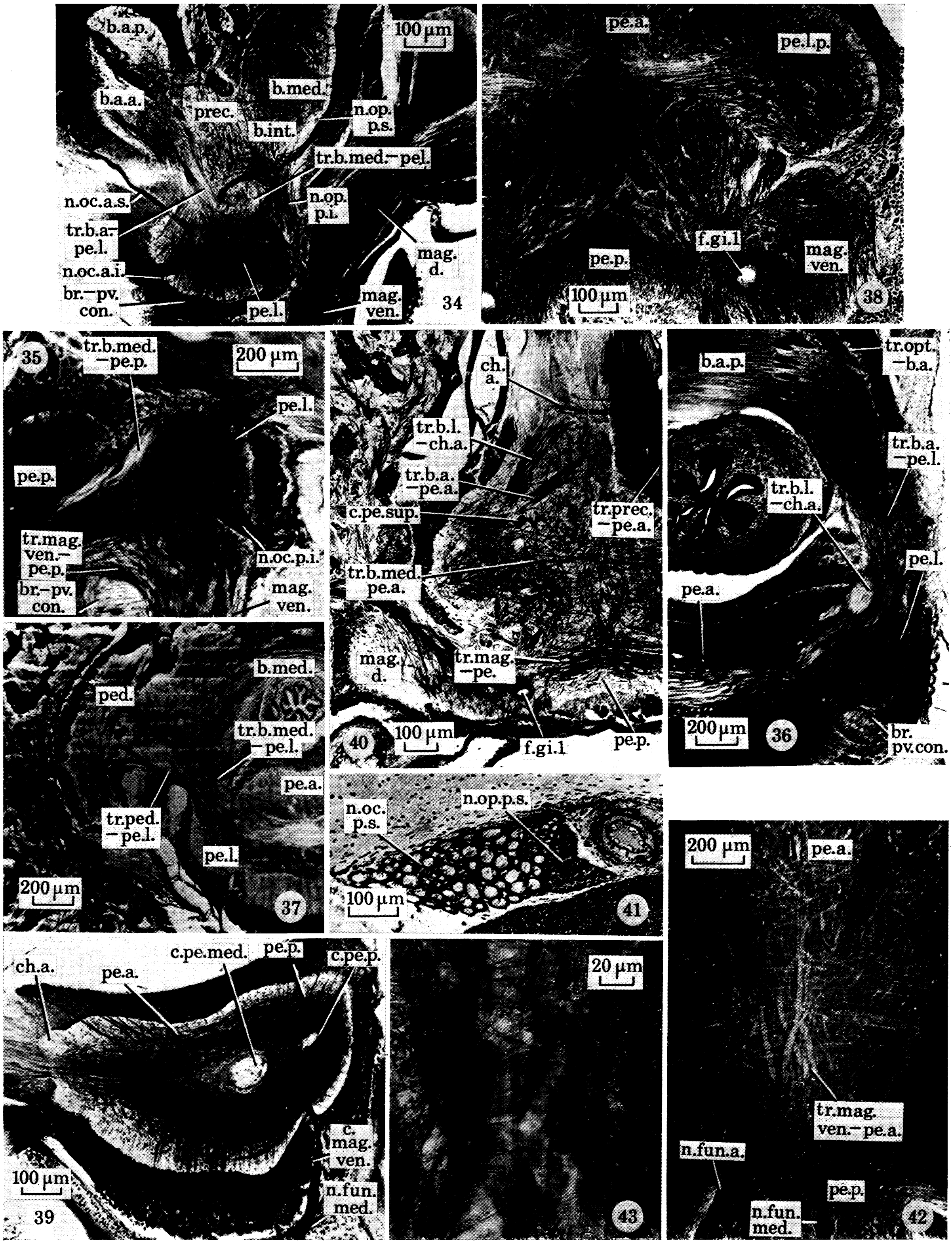
FIGURE 38. *A. subulata*. Horizontal section of the posterior lateral pedal and ventral magnocellular lobes showing large cells and fibres running to the anterior and posterior pedal lobes.

FIGURE 39. *L. pealeii* (juvenile). Sagittal section of middle suboesophageal mass.

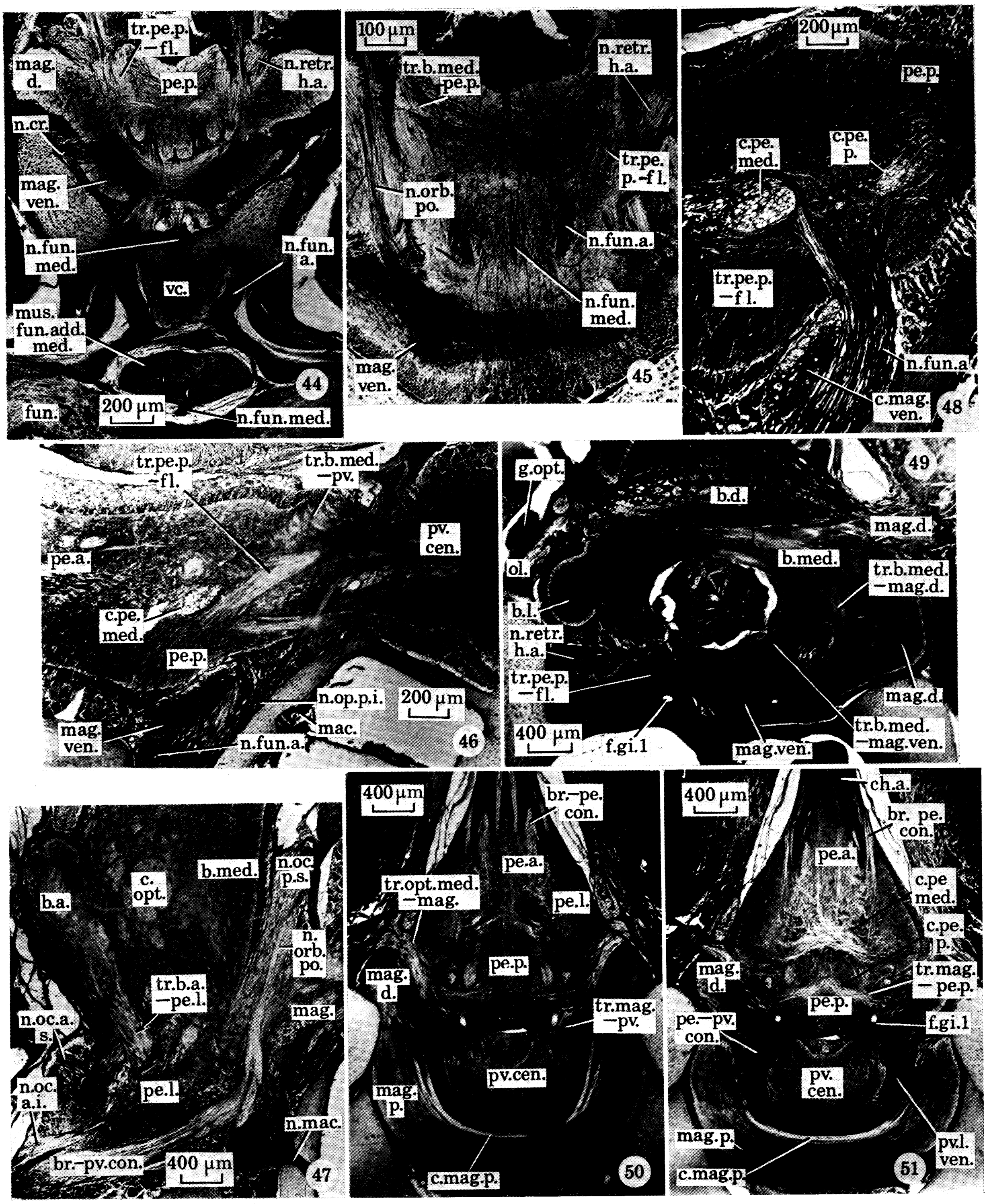
FIGURE 40. *L. pealeii* (juvenile). Horizontal section to show connections of the anterior pedal lobe.

FIGURE 41. *L. vulgaris*. Transverse section of the posterior superior oculomotor and ophthalmic nerves. The former contains large and small fibres, the latter only small ones.

FIGURES 42 AND 43. *L. pealeii*. Horizontal section of the anterior pedal lobe showing large fibres of the ventral magnocellular to anterior pedal lobe tract. As seen in figure 43 the fibre on the left divides around the fibre on the right.



Figures 34–43. For description see opposite.



FIGURES 44–51. For description see opposite.

7.5. *The oculomotor centre: lateral pedal lobe*

7.5.1. *Position and relations*

This lobe occupies the lateral upper parts of the middle suboesophageal mass, behind the anterior chromatophore lobes (figure 17). It is marked off below by the brachio-palliovisceral connective (figure 34, plate 3). At the sides it is in contact with the optic lobe, but receives no fibres directly from it. Above, the lateral pedal lobe is continuous with the anterior and median basal lobes and medially with the anterior pedal lobe. The lobe consists of a large anterior and smaller posterior lateral pedal, only the former being strictly an oculomotor centre. The posterior lateral pedal is continuous with the magnocellular lobe, and will be considered separately.

The lateral pedal lobes of the two sides are connected by a suprapedal commissure (figures 12–14). This may also include fibres running between the anterior pedal lobes of the two sides. The course of this commissure suggests that the lateral pedal and perhaps anterior pedal lobes are not truly suboesophageal centres at all. There are suggestions that large parts of the suboesophageal mass should be morphologically assigned to the cerebral region (Young 1971). It seems especially likely that the oculomotor centre is of cerebral origin since it can hardly be that the eye muscles are part of the foot. It may be that the only strictly 'pedal' part of the brain is the posterior pedal lobe, innervating the funnel.

7.5.2. *Cells of the oculomotor centre: the anterior lateral pedal lobe*

The cells of the anterior lateral pedal lobe are large at the outside, but somewhat smaller than the largest of the anterior pedal lobe, presumably because their fibres are shorter (figure 26, plate 2). There are numerous small cells in the inner layers (figures 26 and 33*a*, *b* and *c*, p. 123). The trunks of the large cells carry numerous fine branches immediately they enter the neuropil and along their length (figures 27, p. 116 and 33*a*). These all come off at right angles to the main shaft, which is slightly expanded where each arises. They reach a maximum of 10 μm diameter and range from a few micrometres to 100 μm long. Some are unbranched, others divide a few times dichotomously. The larger ones taper from 2–3 μm to < 0.5 μm at the tip. Each branch carries swellings along its length, but seldom at the tip, which is the smallest part. There are collateral spines at rather rare intervals, each having a swollen base, staining brown with Golgi, and a fine little-stained tip.

There were 35 main collaterals on one neuron studied, each showing about five small spines. Together with about 20 spines on the otherwise smooth main trunk there must be a total of about 200 on the whole neuron. This gives a minimal estimate for the number of synaptic

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DESCRIPTION OF PLATE 4

FIGURE 44. *L. pealeii* (juvenile). Transverse section of the posterior pedal lobe and anterior funnel nerves.

FIGURE 45. *L. pealeii* (juvenile). Transverse section of the posterior pedal lobe slightly behind figure 44.

FIGURE 46. *L. vulgaris* (adult). Sagittal section of posterior pedal lobe.

FIGURE 47. *L. vulgaris*. Sagittal section showing postorbital and oculomotor nerves.

FIGURE 48. *L. vulgaris*. Sagittal section of roots of anterior funnel nerve.

FIGURE 49. *L. pealeii*. Oblique transverse section to show the dorsal and ventral magnocellular lobes.

FIGURE 50. *Alloteuthis*. Horizontal section of the pedal, magnocellular and palliovisceral lobes.

FIGURE 51. Horizontal section below that in figure 50.

contacts. It excludes however the possibility that many of the swellings along the branches represent contacts. Indeed the distinction between a swelling and a spine is hard to draw. Probably a better estimate including terminal branches would be 500–1000 synaptic contact points, but there may be even more.

Some axonal endings of input fibres are seen in the preparations (figures 27 and 28). They lie on fibres carrying conspicuous beads, up to 4 μm long and ending with one or two terminal branches with swellings.

The main trunk of each oculomotor cell narrows down gradually to 3–5 μm but the fibres become larger again more peripherally as they proceed to the roots of the four oculomotor nerves. The trunks of the larger cells of the lobe enter the neuropil in bundles (figure 34). They then spread out and it may be that fibres from each bundle reach to all of the four oculomotor nerves. Conversely the roots of the fibres of each nerve spread out as if to arise from various parts of the wall of the lobe (figure 35, plate 3).

7.5.3. *Input to the oculomotor centre*

The control of the eye muscles is by the static nerves direct and indirectly by the optic lobes, through the anterior basal and median basal and the peduncle lobes. A direct connection between optic and lateral pedal lobes has been mentioned in *Sepia* by Boycott (1961, p. 506). Figure 4.10 of Young (1971) also shows an 'optic to lateral pedal tract' in *Octopus*, but the text describes the actual situation. The tract in question is the ventral optic to anterior basal lobe tract (Young 1976*b*). As the anterior basal lobe is directly continuous with the lateral pedal lobe, the question might seem to be one of definition of boundary. But the tract may be very important as carrying the fibres that produce seizure by the tentacles. It enters just above the posterior lateral pedal lobe, which may serve this action (pp. 127 and 159). The question will be further considered in the next paper of this series.

The inputs to the anterior lateral pedal lobe may therefore be listed as: (1) The crista nerve, which sends both small and large fibres to the lateral pedal lobe (p. 116). The former run across the cells of the lobe close to their cell bodies (figure 22, plate 2). The large fibres of the same side are the second branches of the large crista nerve fibres and cross the oculomotor axons further from their cell bodies (figure 20, plate 2 and 27, 28, pp. 116, 117). Each of the larger fibres sends branches to a very large region, but it is not clear how they are arranged. The contralateral fibres of the crista nerve distribute in a similar way throughout the opposite

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DESCRIPTION OF PLATE 5

FIGURE 52. *L. pealeii*. Sagittal section to show medial optic to magnocellular tract.

FIGURE 53. *A. subulata*. Transverse section of the pedal and magnocellular lobes.

FIGURE 54. *L. vulgaris*. Oblique horizontal section of the ventral magnocellular lobe and giant cells.

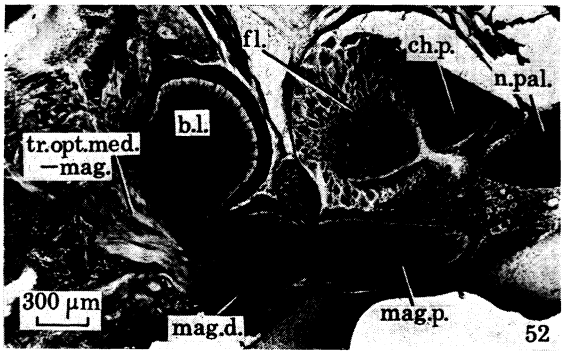
FIGURE 55. *L. vulgaris*. Horizontal section of the ventral magnocellular lobe to show first order giant and other large cells.

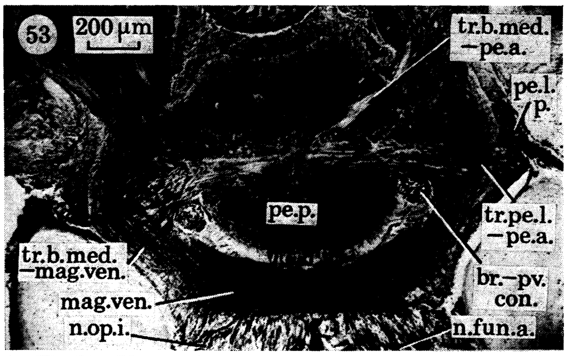
FIGURE 56. *L. pealeii*. Horizontal section. Re-touched to show courses of axons of large cells of the magnocellular lobe.

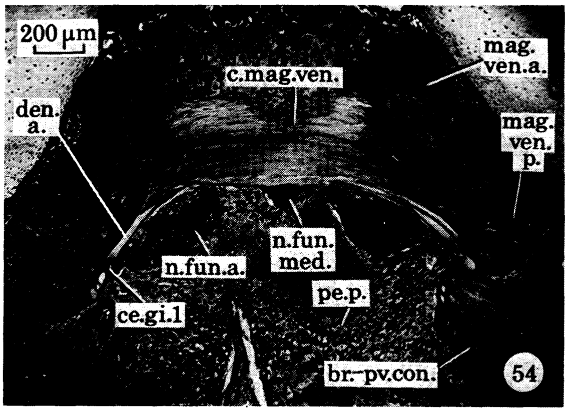
FIGURE 58. *L. vulgaris*. Cell and neuropil of anterior part of ventral magnocellular lobe.

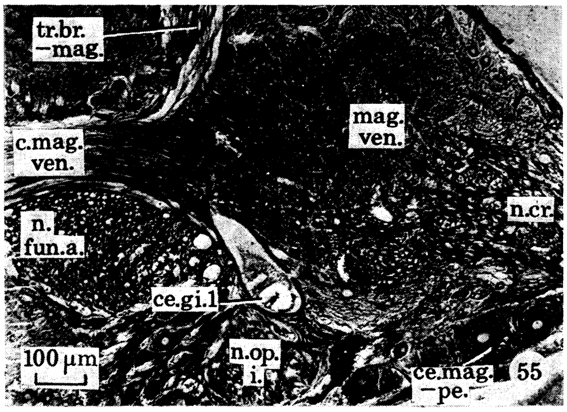
FIGURE 59. *A. subulata*. Horizontal section of the anterior ventral magnocellular lobe to show neuropil, small cells and fibres from anterior funnel nerve.

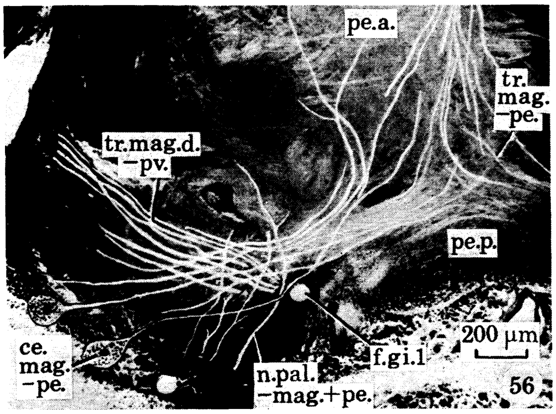
FIGURE 60. *L. pealeii* (juvenile). Sagittal section to show fibres of postorbital nerve to magnocellular lobes.

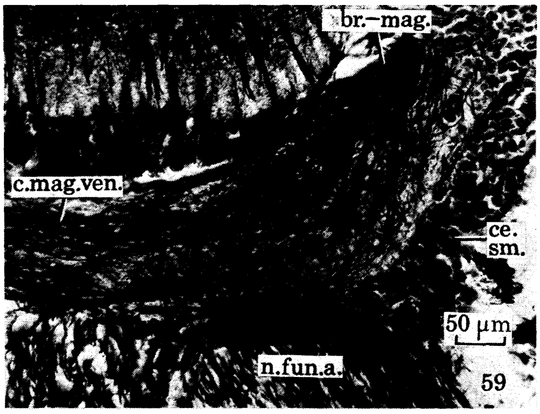


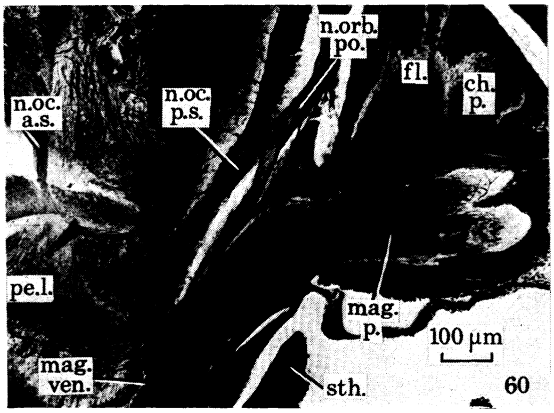


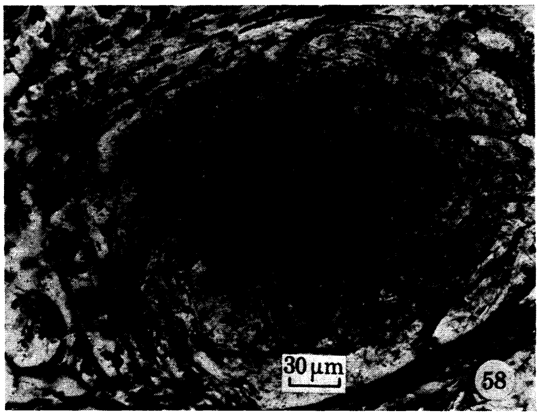




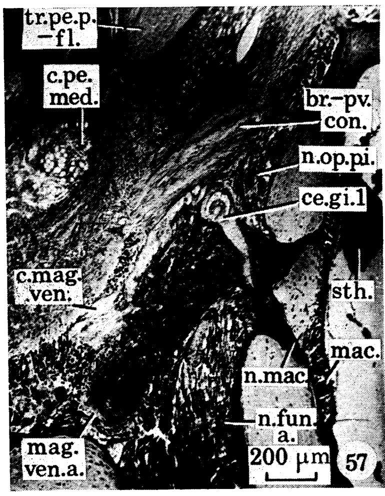


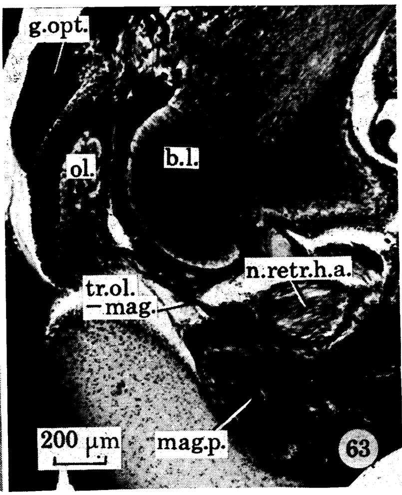


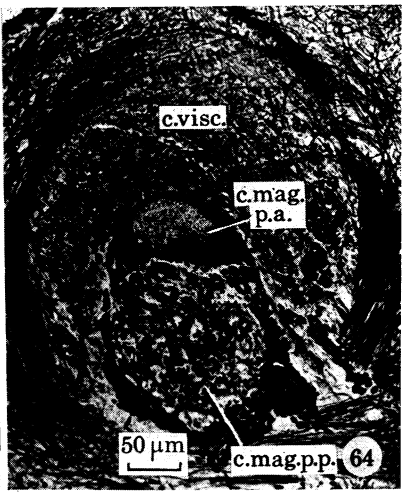


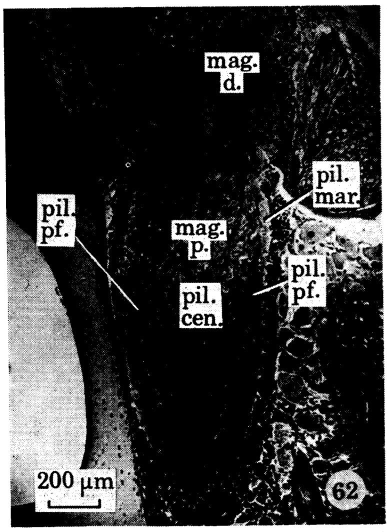


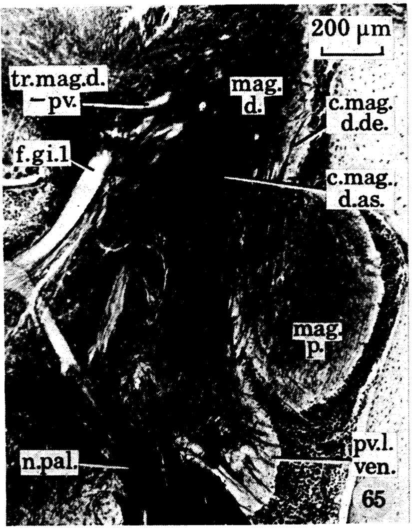
FIGURES 52–56 AND 58–60. For description see opposite.

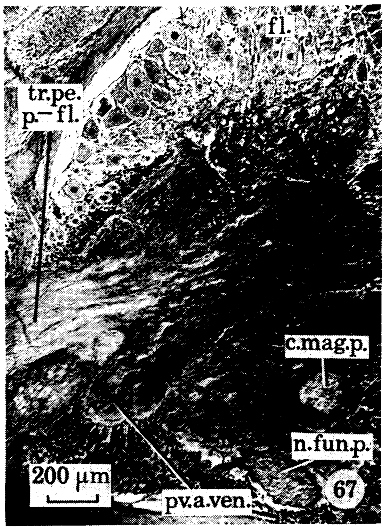


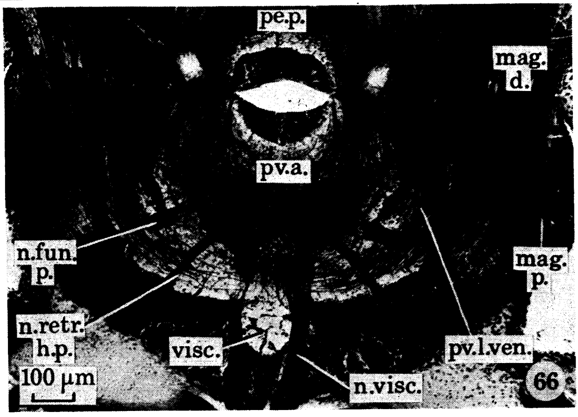


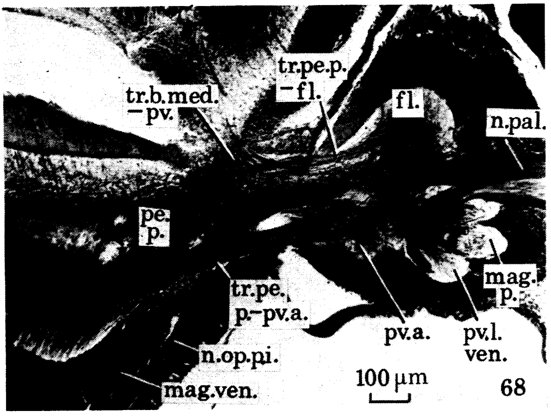












Figures 57 and 62–68. For description see opposite.

lateral pedal lobe (figure 28). (2) Fibres of the macula nerve pass into the lateral pedal lobe through the magnocellular lobe. (3), (4) Large fibres from each of the two parts of the anterior basal lobe pass to the lateral pedal lobe (figure 30, p. 119). Those from the anterior anterior basal lobe certainly include many from the same side, but both parts probably also send numerous crossed fibres through the anterior basal commissure. The numerous fibres of these tracts arise in a complicated series of bundles in the lateral anterior basal lobe (figure 34). Some of them probably arise in the upper parts of both the anterior and posterior parts of the anterior basal lobe. The tracts from the two parts cross and fibres of both spread out to all parts of the lateral pedal lobe. The tract from the posterior anterior basal contains some especially large fibres. (5) The median basal sends a large bundle of large fibres in to the back of the lateral pedal lobe and these spread to all parts (figure 30). (6) There is a bundle of large fibres from the peduncle lobe (figure 37, plate 3).

All of the tracts from the basal lobes contain fibres that preserve some degree of parallel arrangement until they reach the lateral pedal lobe. They then proceed to spread out in a regular manner and reach to all parts of the lobe. The effect of this spread and of the method of formation of the oculomotor nerves is to produce a criss-cross arrangement with a high degree of order, partly shown in figure 34, plate 3. Each basal lobe fibre branches to supply a large region (figure 27). The terminal branches are fine varicose fibres, similar to those of the static nerve fibres.

It is probable that there are no feed-back fibres from the eye muscles to the lobe, since the nerves that run only to the eye muscles contain only large fibres, p. 121, as in *Octopus* (Young 1971). Nor is there evidence of fibres from the lateral pedal to the basal lobes. The latter have abundant reciprocal relations with the optic lobes (see p. 157). It may be noticed also that there are no fibres from the precommissural lobe or other route from the vertical lobe system to the oculomotor centre.

7.6. *The posterior lateral pedal lobe: ? centre for tentacle control*

The posterior lateral pedal lobe is a direct backward continuation of the anterior lateral pedal and itself continues back into the magnocellular lobe (figures 9, 19, plates 1, 2, figure 16, p. 114). The boundary with the magnocellular lobe may be taken at the entry of the crista nerve. There is no sharp anatomical division between the anterior and posterior lateral pedal lobes but the important difference is that whereas the anterior part gives rise to oculomotor

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DESCRIPTION OF PLATE 6

FIGURE 57. *L. vulgaris*. Transverse section of the first order giant cell and macular nerve.

FIGURE 62. *L. vulgaris*. Sagittal section of posterior magnocellular lobe and its three sorts of neuropil.

FIGURE 63. *L. pealeii*. Transverse section showing fibres running from the olfactory lobe to the posterior magnocellular lobe.

FIGURE 64. *L. pealeii*. Sagittal section to show the posterior magnocellular and visceral commissures.

FIGURE 65. *A. subulata*. Horizontal section to show the lateral (descending) and medial (ascending) bundles that form the posterior magnocellular commissure.

FIGURE 66. *L. pealeii* (juvenile). Horizontal section of ventral part of posterior suboesophageal mass.

FIGURE 67. *L. vulgaris*. Oblique sagittal section showing small cells of antero-ventral pallioviscera lobule.

FIGURE 68. *L. pealeii* (juvenile). Sagittal section to show anterior and posterior retractor centres and their interconnection.

fibres the posterior has quite a different output by a set of large fibres, the lateral pedal to anterior pedal tract (figure 38, plate 3, figure 53, plate 5, figure 16, p. 114). Their trunks run across to join the fibres of the static nerves and form some of the largest members of the middle pedal commissure. Some turn forwards immediately after crossing and break up in the centre of the anterior pedal lobe, others probably pass back to the posterior pedal lobe. Presumably this pathway ensures coordinated action of arms and tentacles and eyes. It has not been possible to decide whether the posterior lateral pedal lobe receives input fibres from the same sources as the oculomotor centre (see p. 126). It may be that these cells are concerned with producing the action of the tentacles to seize their prey, by coming into action when the image falls on the back parts of both retinas (p. 159).

7.7. *Anterior pedal lobe: control of arm movements*

7.7.1. *Position and relations*

This is a very large and important region, but only some of the details of its construction are understood. It certainly sends many fibres direct to the arms and probably to the tentacles, and others to the anterior suboesophageal mass, but because of the wide separation of the lobes it is hard to identify which are which. The anterior pedal lobe also supplies motor fibres to the retractor muscles of the front of the head, in the superior and inferior antorbital nerves.

The lobe receives the brachio-pedal connectives in front and three connectives from above, from the anterior basal, precommissural and median basal lobes. In the mid-line it is related dorsally to the perioesophageal sinus and ventrally makes the floor of the brain, except at the extreme hind end where the magnocellular lobe lies beneath it. Posteriorly its boundary with the posterior pedal lobe is marked by the middle pedal commissure and here there is an important division of functions, control of arms in front and swimming from behind the commissure (figure 39, plate 3). However, above and below it the neuropils are continuous. The oculomotor centres of the lateral pedal lobe lies at the sides, and again their neuropils are continuous with that of the anterior pedal lobe.

7.7.2. *Cells and synapses of the anterior pedal lobe*

The cells of the lobe include typical large motoneurons both dorsally and ventrally. Cell bodies range up to 150 μm in diameter with nuclei of 20 μm. There are also numerous smaller cells in the inner layers. Their trunks proceed alongside those of the large motoneurons giving a few short collateral branches (figures 33*b*, *c*). Many of them end within 100–200 μm of the cell body without any distinct axon, Others have fine axon-like fibres dividing into terminal branches at a distance of a few hundred micrometres. Their possible significance is discussed on p. 155.

The trunks of the large cells are over 25 μm in diameter in the neuropil and form even larger fibres in the connectives running to the arms (up to 80 μm). The cells send their trunks into the neuropil, giving off numerous collaterals immediately and then at all levels of the neuropil from periphery to centre. The dendritic collaterals characteristically run straight and tangentially. They are short and show few major branches, but carry numerous lateral and terminal spines. These are perhaps more numerous than on the cells of the lateral pedal lobe. On one large cell, 40 major collaterals were counted, each with at least 50 spines. There are, therefore, at least 2000 contact points on this cell. There is a narrow zone of small-fibre neuropil at the periphery. Within this are conspicuous bundles of fibres running round from back to front from the precommisural and median basal to anterior pedal tracts (figure 33, p. 122). At the centre of the lobe the collaterals of the large cells meet the fibres of the anterior basal to anterior pedal tract. The fibres arising in the lobe then turn forwards, some to run in the direct pedo-intrabrachial connectives to the arm nerves and others in the pedo-brachial connectives to the anterior suboesophageal mass (figure 39, plate 3). Superior and inferior antorbital nerves also arise in this region and run forwards with the brachio-pedal connective before turning up or down to innervate large muscle masses responsible for attachment of the arms and tentacles (figure 32). They contain large fibres. The cell layers of the anterior pedal lobe are similar throughout and no distinct regions have been recognized.

7.7.3. *Inputs to the anterior pedal lobe*

The anterior pedal lobe is therefore a region of homogeneous function in the sense that it controls the arms and tentacles, but the actions of these are obviously very diverse and enter into many activities of the animal. Correspondingly the region is influenced from several sources (1) Afferents presumably reach this region from the arms direct and from the anterior suboesophageal mass. (2) The anterior basal to anterior pedal tract enters from above. It contains large fibres (up to 15 μm), probably arising from both parts of the anterior basal lobe although the bundle arises at its hind end. The fibres spread out across the trunks of the cells at the centre of the anterior pedal lobe in front of the middle pedal commissure, some reaching forward to the midline bundles of the brachio-pedal connectives (figure 40, plate 3). (3) Precommissural to anterior pedal and (4) median basal to anterior pedal tracts run round the lobe at a level behind the fibres of the anterior basal to anterior pedal tract (figure 14, p. 112). The median basal fibres are the axons of large cells at the back of that lobe, including two or three exceptionally large ones (figure 12, p. 110). Their axons divide immediately in front of the centre of the middle pedal commissure. Some of the branches pass forwards into the anterior pedal, others backwards into the posterior pedal lobe. This is a large tract, presumably of command fibres controlling movements of large parts of the animal (figure 14, p. 112). (5) The posterior lateral pedal lobe sends very large fibres across the mid-line in the middle pedal commissure and forwards to break up at the centre of the anterior pedal lobe (p. 127). (6) Magnocellular to anterior pedal tract. Large cells send fibres medially in to the back of the posterior pedal lobe, where they cross in the posterior pedal commissure and turn forwards to the centre of the anterior pedal lobe (figures 16 and 17, figure 20, plate 2). These fibres are a complex set (see p. 136). Some of them arise from the large cells lying laterally in the ventral magnocellular lobe (figure 38, plate 3 and figure 56, plate 5), but others arise further dorsally in the dorsal magnocellular lobe (figures 15 and 28). A few exceptionally large fibres on each side run directly forwards in the mid-line. The two largest come together so that one lies on top of the others at the centre of the anterior pedal lobe (figures 42 and 43, plate 3). They then divide up into branches which make contact with the trunks of cells of the lobe, whose axons turn forwards to the arms. This whole complex of fibres has been especially well seen in the small active deep sea squid *Pterygioteuthis* (Young 1976*a*). Here the large fibres with axons in the mid-line can be traced to cells of the magnocellular lobe. The whole set of fibres from both parts of the magnocellular lobes may be concerned with initiating movements of attack with the tentacles, in cooperation with the fibres of the posterior lateral pedal lobes (p. 159). (7) Fibres of the nerve from the crista statica spread out forwards into the anterior pedal lobe. (figure 20 plate 2). There may also be fibres from the macula. (8) Fibres running forwards from the palliovisceral lobe, perhaps from the pallial nerve may reach to the anterior pedal lobe.

7.8. *The posterior pedal lobe: the anterior swimming centre*

7.8.1. *Introduction: position and relations*

This is a motor centre probably controlling the direction of swimming by regulating the position of the funnel and the action of the fins. It sends fibres directly to the muscles of the funnel and to the head retractors. It also sends fibres forwards to the arm centres of the anterior pedal lobe and backwards to the centres that control jet propulsion from the palliovisceral lobe and fin movements from the fin lobe. This complex set of connections illustrates the difficulties of a Jacksonian terminology. The cells that innervate the funnel and retractors are final motor neurons whereas the pathways for the fins pass through one, and for the mantle muscles two further synapses. The posterior pedal is thus both a 'lower' and an 'intermediate' motor centre. The fact that these groups of cells lie together suggests that this centre is concerned with steering. This always involves the funnel, retractors, arms, fins and mantle, but the last two *also* require independent control, presumably provided at the further synapses.

This important centre occupies the back of the middle suboesophageal lobe (figure 39, plate 3). It is broadly continuous with the anterior pedal lobe in front and shares many connections with it, but the middle pedal commissure makes an arbitrary dividing line. Laterally it joins the lateral pedal and magnocellular lobes (figure 16, p. 114, figure 44, plate 4). Dorsally it is continuous with the median basal at the sides, but is in relation to the perioesophageal sinus in the mid-line. Behind, it joins the posterior suboesophageal mass at the sides but is separated from it by the pedal arteries in the mid-line. Ventrally it occupies the floor of the brain, but lies above the ventral magnocellular commissure (figures 39 and 44). There is a conspicuous posterior pedal commissure (figure 48, plate 4), containing large fibres, mainly originating in the magnocellular lobes. The fibres originating in the posterior pedal lobe keep largely to their own side (or the mid-line, see below).

7.8.2. *Cells and output of the posterior pedal lobe* (figure 111, p. 158)

The cell layers all contain some large cells, but they are not all alike. Six sets of neurons can be recognized. (1) The cell layers ventrally include outer cells up to 60 μm diameter and very numerous small ones near the neuropil. The trunks of the larger cells turn backwards to make the numerous fibres of the posterior pedal to fin lobe tract (figure 46, plate 4). (2) Other cells of the ventral region send fibres back to the antero-ventral palliovisceral lobule, which is a region that contains the cells of origin of the posterior head retractor nerve and some that reach up to the fin lobe (p. 140). (3), (4) The dorsal and posterior walls contain rather large cells up to 80 μm diameter and few small ones. The large trunks pass down to make up the anterior infundibular nerves, which turn the funnel to right or left, and the nerve to the median funnel adductor muscle, which turns the funnel backwards and thus determines the direction of swimming with the jet. The trunks pass straight downwards to the nerves, giving off rather short collateral dendrites (figures 28, p. 117 and 45, plate 4). (5), (6) Other cells of the walls of this lobe provide the motoneurons for the postorbital and anterior head retractor nerves, which innervate the muscles attached to the back of the cranium (pp. 131, 132).

7.8.3. *Input to the posterior pedal lobe*

The control of the direction of swimming is mainly by optic influences, with some from the statocyst. (1) The optic control comes largely through the median basal lobe and the fibres of the median basal to posterior pedal tract form two sets (figure 14, p. 112). Some turn dorsally and divide across the trunks of the cells of the anterior funnel nerve (figure 45, plate 4) and are restricted to more lateral parts of the lobe, perhaps related to the fibres of the paired anterior funnel nerves. Others, mostly more posterior, run into the middle line and may be concerned with turning the funnel to point forwards or backwards. Still other fibres of this tract run round the ventral part of the lobe and are presumably concerned with the fibres of the posterior pedal to fin lobe tract (figure 33). All of these bundles include large fibres, they are the axons of large cells with trunks reaching forwards across the median basal lobe and well placed to receive directional inputs from optic tract fibres. These bundles from the median basal lobe may also include fibres from other sources, for instance the peduncle lobes. (2) Fibres of the crista nerve send branches backwards to the posterior pedal lobe (p. 116) (figure 20, plate 2 and figure 28, p. 117). (3) Large cells of the dorsal and ventral magnocellular lobes send fibres to the posterior pedal (p. 129). Some of these end or give branches on the same side before passing forwards to the anterior pedal lobe others cross in the posterior pedal commissure. (4) Fibres proceed from the posterior lateral pedal to the posterior pedal lobe either on the same side or after crossing (p. 128). (5) Numerous fibres enter the posterior pedal lobe from behind in the pedal-pallio-visceral connective. These probably include afferents from the pallial nerve. (6) It is presumed that fibres enter from the front, including some from the arms.

No direct pathways from the anterior basal lobe or precommissural lobes to the anterior swimming centre have been seen, but they may exist.

7.9. *Nerves of the posterior pedal lobe*

Four important nerves arise from the anterior swimming centre, the paired postorbital anterior head retractor, and anterior funnel nerves and the nerve to the median funnel adductor

7.9.1. *The postorbital nerve* (*n. postorbitalis*)

This is a large nerve arising by four roots at the back of the posterior pedal lobe (figure 31 p. 120 and figure 47, plate 4). It runs directly upwards close to the posterior superior oculomotor and ophthalmic nerves to innervate the muscles at the back of the head, branches also passing through the muscles to the skin. It was called the nuchal nerve by Schkaff (1914) (a name used wrongly in Young 1939).

(1) Only one of the four roots arises from the posterior pedal lobe, this is the part containing the fibres for the muscles at the back of the head and may be called the dorsal head retractor nerve.

(2) A second large root is presumably sensory and runs straight down to the ventral magnocellular lobe bringing afferents from the skin of the top of the head. Electrical stimulation of the surface of the back of the head produces giant fibre contractions at a very low threshold (*Alloteuthis*, personal observation.)

(3) A third root diverges forwards from the second and joins the brachio-palliovisceral connective (figure 47). These are presumably afferent fibres that operate the characteristic response in which a squid or cuttlefish turns the arms back over the surface of the head and back if the animal is seized.

(4) A fourth root enters the posterior magnocellular lobe and probably also carries afferent fibres (figure 47).

7.9.2. *The anterior head retractor nerve* (*n. retractor capitis anterior*)

This large nerve also arises from the posterior pedal lobe, probably from cells in the floor in front of those that give rise to the posterior pedal to fin lobe tract. This region is close to that giving rise to the antorbital nerves, innervating the retractor muscles at the front of the head (figures 15, 44 and 45, plate 4). The nerve runs lateral to the magnocellular lobe and to the postorbital nerve and back alongside the fin lobe. Here it divides into dorsal and ventral branches running through the cartilage to the anterior part of the retractor muscles of the head. Its fibres are large, but do not include any of those of the giant fibre system. It is presumed to contain no afferents.

7.9.3. *The anterior funnel nerves* (*n. infundibuli anterior*)

These are a pair of mixed nerves. The motor fibres arise from cells of the dorsal wall of the posterior pedal lobe (figure 45). A bundle of fibres turns forwards and divides around the middle pedal commissure (figure 48). These may include afferents, reaching to the anterior pedal lobe (but some are large). A bundle of small fibres, joins the ventral magnocellular lobe (figures 44 and 46, plate 4). Some fibres of the nerve probably reach back as a bundle behind the giant cell to the palliovisceral lobe. These are perhaps afferents from the inside of the funnel, mediating escape reactions.

The trunk of each nerve passes down immediately behind the ventral magnocellular commissure and leaves the brain medial to the *n. macula statica*. It passes directly downwards to the funnel and then laterally over its surface thus innervating the muscles that control the direction of the jet whether to right or left. The nerve contains large fibres (up to 30 μm) but no giant fibres. There are also many small fibres, presumably afferents.

7.9.4. *The nerve of the median funnel adductor* (*n. adductor infundibuli medianus*)

This arises between the roots of the two anterior funnel nerves, and is a strictly mid-line nerve (figures 44 and 45, plate 4). It runs down between the two paired funnel nerves to innervate the large muscle attached to the roof of the funnel. The nerve contains a few very large fibres but none of the giant fibre system. The median funnel adductor muscle consists largely of longitudinal fibres responsible for raising the tip of the funnel in the mid-line (figure 44). The fibres diverge posteriorly but are joined to make a single muscle bundle in front. The nerve enters in the mid-line where the two parts diverge. Its large fibres send branches laterally into the muscle. A small bundle passes through the muscle and on to join the roof of the funnel. Here it turns forwards and innervates the transverse muscle fibres that raise the lateral tips of the lip of the funnel. This mid-line nerve is probably responsible for the direction of swimming whether forwards or backwards.

8. THE MAGNOCELLULAR LOBE: THE CENTRE CONTROLLING JET PROPULSION

8.1. *Introduction*

The region around the sides and back of the brain was called the magnocellular lobe because of its most obvious component (Young 1939). It is indeed concerned with jet propulsion but it is much more than a single centre of convergence on the first order giant cells. Moreover, it is not a homogeneous entity but contains several parts functioning at different levels in the interlocking set of centres for the control of movement.

Its organization and functions are still far from understood but three main parts can be recognized (figures 12–17).

(1) The dorsal magnocellular lobe contains large cells whose axons reach to centres influencing the arms, funnel and fins as well as the mantle and are under optic and supraoesophageal influence.

(2) The ventral magnocellular lobes contain the two first order giant cells, which are the main command units for production of the jet. They receive a very wide range of inputs from many parts of the body and brain.

(3) The posterior magnocellular lobe is the least understood. It is partly a commissural pathway between the dorsal lobes, but contains many cells, which are perhaps concerned with escape reactions. Boycott (see Young 1971) showed that in *Octopus*, stimulation of the optico-magnocellular tract produces the dymantic response and of the posterior magnocellular lobe inspiration (which is part of the dymantic response). There is no evidence of a dymantic response in *Loligo* (though there is in *Sepioteuthis*, Boycott 1965). All parts of the lobe contain many small as well as large cells.

8.2. *The dorsal magnocellular lobe*

8.2.1. *Position and relations*

This is a cylinder passing round on each side of the brain from the dorsal border of the optic tract to the statocyst (figure 49, plate 4). Dorsally anteriorly and medially it is related to the subvertical and median basal lobes, dorso-laterally to the peduncle and optic lobes (figure 13, p. 111). More ventrally it forms the floor of the brain laterally, medially it merges directly with the ventral magnocellular lobe. The division between the two is taken to be the level of the crista nerve anteriorly. The boundary is less clear behind, but the region in front of the transverse septum will be considered to belong to the dorsal magnocellular division. The cylinder continues backwards as the posterior magnocellular lobe along the sides of the palliovisceral lobe to the large posterior magnocellular commissure (figures 50 and 51, plate 4).

8.2.2. *Cells of the dorsal magnocellular lobe*

The walls in the extreme dorsal region consist of 10–20 closely packed layers of medium-small cells of transverse diameter 10 μm and nuclei 7 μm, some smaller. There are occasional larger cells, some far dorsally in the hilum of the optic lobe. Passing ventrally the large ones become more frequent and many have diameters of 30 μm and nuclei of 10 μm. These large cells have coarse dendritic collaterals, ending in numerous fine twigs. These collaterals may come off throughout a considerable length of the lobe (figure 28, p. 117). The trunks of the cells then curve downwards and form bundles of large axons. Many pass with the first order giant axon to the centre of the palliovisceral lobe (figures 13, 14 and figure 50, plate 4). Others turn forward to the posterior pedal lobe (figures 15 and 51). Here they either divide immediately on entering the lobe or pass on to give branches to various parts of it as far forward as the middle pedal commissure (figure 28, p. 117). Some probably proceed even further forwards into the anterior pedal lobe and thus influence the arms. The large fibres are accompanied by numerous very fine ones, which probably also end in the posterior pedal lobe (figure 28).

Other cells of the dorsal magnocellular lobe send axons back into the posterior magnocellular lobe, probably crossing in the posterior magnocellular commissure and then running forwards to end in the dorsal lobe of the opposite side. Still other cells send their axons upwards into the median basal lobe (p. 135). It may be that some of the axons give branches to several of these various destinations. For instance it was suspected that some of those sending fibres to the palliovisceral lobe also send collaterals to the median basal lobe. The extent of such branching is not known, but in any case the output of the lobe passes both downwards and upwards (p. 135).

8.2.3. *Inputs to the dorsal magnocellular lobe*

The lobe is under strong optic influence, but is connected by tracts with several other parts, perhaps carrying fibres in both directions.

(1) The most dorsal connection is with the subvertical and the dorsal basal lobes (figure 49, plate 4). This is a large set of bundles of mainly fine fibres. Their direction cannot be determined, they may be efferents or perhaps afferents ascending from the pallial and other nerves through the posterior magnocellular lobe to the vertical lobe system.

(2), (3) The lobe opens broadly at the side to the optic lobe, from which it receives the large lateral and medial optico-magnocellular tracts (figure 15). The former consists of small darkly-staining fibres, the latter of large pale ones, coming from all parts of the optic lobes (figure 52, plate 5). The medial tract forms a compact bundle at the front of the lobe, running down to be distributed to the ventral magnocellular lobe. It is hard to exclude that some of its fibres turn into the posterior pedal lobe or the palliovisceral lobe because it is difficult to distinguish them from large fibres arising in the magnocellular lobe itself (figure 50). Probably the optic fibres all end in the magnocellular lobe.

The fine fibres of the lateral optico-magnocellular tract form a complicated set of interweaving bundles (figure 15). Many fibres leave the bundles and presumably make connection with the cells of the lobe.

(4) The dorsal magnocellular lobe is joined by a large tract from the median basal lobe (figures 29 and 49, plate 4). This tract carries ascending fibres, described below. There is also a remarkable set of large descending fibres in it. They arise from all the basal lobes and from the precommissural lobe. Each fibre gives a series of branches to the magnocellular and palliovisceral lobes. This must be an important command pathway and will be fully described later (Young 1976*b*).

(5) The dorsal magnocellular lobe probably receives fibres from the small-celled anterior region of the ventral magnocellular lobe of the same and opposite sides (p. 135).

(6) There are also many bundles of fine fibres running forward from the posterior magnocellular lobe. Many of these come from cells of that lobe, others may be fibres from the optic lobe that have crossed in the posterior magnocellular commissure. This set may therefore be largely concerned with coordination of actions of the two sides.

8.2.4. *Neuropil of the dorsal magnocellular lobe*

This contains the large trunks of the cells running to the posterior pedal and palliovisceral lobes (figure 28, p. 117). They cross the bundles of optico-magnocellular fibres and also the trunks of the numerous fine fibres running forwards from the posterior magnocellular lobe. These latter mostly end in a lateral region of characteristic neuropil, staining light yellow with silver and presumably composed of very fine fibres. This is a massive input and presumably has some important influence on the dendrites of the large fibres.

8.2.5. *Output of the dorsal magnocellular lobe*

The output fibres of the lobe proceed (1) medially to the posterior pedal lobe (p. 131) and (2) to the anterior pedal lobe and (3) backwards to the palliovisceral lobe. (4) There is also a large set of fibres passing upwards to the median basal lobe. These also send branches to other basal lobes and are thus a very interesting return path from suboesophageal to supraoesophageal centres (Young 1976*b*). No clear separation of the cells of origin of these sets has been seen and it is possible that they are activated together by visual and/or median basal input. The lobe evidently plays some important part in the system of motor control. It clearly cooperates with the jet actions produced by the ventral lobe and is indeed directly influenced from that lobe.

8.3. *Ventral magnocellular lobe: the giant cells*

8.3.1. *Position and relations*

This is a transverse band of tissue occupying the floor of the brain at the hind end of the middle suboesophageal mass (figures 17, 31, 32 and figures 53 and 54, plate 5). It is therefore in contact below with the cartilage and the roof of the statocyst. In front, dorsally and medially it is continuous with the posterior pedal lobe and with the lateral pedal lobe (figure 25, plate 2). The brachio-palliovisceral tract runs along its medial border. Above this the lobe is continuous with the dorsal magnocellular lobe. The lobes of the two sides are joined by the ventral magnocellular commissure, containing fibres and neuropil.

The anterior funnel nerve and median funnel adductor nerve run immediately behind the lobe and the crista nerve above it on each side. The macula nerves enter it from below. The posterior inferior ophthalmic nerve runs up behind it (p. 124).

8.3.2. *Divisions of the ventral magnocellular lobe*

The lobe has two rather distinct parts, broadly continuous but distinguished by different cells and neuropil. The anterior part, where the two sides are joined by the commissure, has numerous small cells and receives the input from the brachio-magnocellular tracts (figure 55). The cells of this anterior part probably send axons to other parts of the magnocellular system and to the lateral pedal lobe (p. 127). In the posterior part, which is paired, the wall of the lobe is very thin but contains the largest cells in the body some of whose axons proceed forward and others backwards.

8.3.3. *Neuropil of the lobe*

The neuropil of the ventral magnocellular lobe is also differentiated into two sorts (figures 54, plate 5, 57, plate 6). Posteriorly, where the macular fibres enter among dendrites of the first order giant cell and those of other large cells it is a tight network of fibres, dendrites and boutons. But at the front of the lobe and in the commissure is a neuropil of much looser texture (figures 58, 59, plate 5). This contains the individual trunks of the sparse medium-sized cells of this part of the lobe, and their collateral dendrites, surrounded by the processes of a large number of smaller cells. The axons of these probably pass to the dorsal magnocellular and lateral pedal lobes.

8.3.4. *Output of the ventral magnocellular lobe* (figure 110, p. 157)

(1) The two first order giant cells lie at the medial borders of the lateral parts of the lobe (figure 54). Their largest diameter is 150 μm, with a nucleus of 60 μm. They contain abundant basophil material, which appears to extend into the axon as tubular structures (figure 55) (Young 1975). These cells have lost the characteristic unipolar structure, they have enormous dendrites spreading throughout the ventral magnocellular lobe (Young 1939). Ventral dendrites extend among the macular nerve fibres almost to the receptor cells (figure 57, plate 6). Lateral dendrites spread out towards the fibres coming from the optic lobe and antero-medial ones into the magnocellular commissure (figure 54). The axon of each cell proceeds upwards and then backwards to the centre of the palliovisceral lobe, where the two are joined by a bridge (figures 69, 71, plate 7; 96, plate 9) and then make synapse with second order fibres.

(2) The first order giant cell is the largest of a set of some 20 others on each side of very large size occupying the ventro-lateral wall of the lobe behind the entry of the crista nerve (figures 55 and 56, plate 5). Each of these cells has a characteristic form, and can be recognized in every individual squid. The largest are over 100 μm in diameter with a nucleus of 30 μm. The difference in the character of the cytoplasm and dendrites between the first order giant cell and the others is very striking. Yet they all have axons of about the same length and the difference suggests special need for metabolic support for the very large dendrites of the giant cell. This is confirmed by the extensions of the Nissl substance (granular endoplasmic reticulum) into the dendrites (Young 1975).

All the other large cells of the ventral magnocellular lobe have the characteristic unipolar form, with collateral dendrites. Their main trunks run across the neuropil, some back to the palliovisceral lobe very close to the first order giant axon (figure 16, p. 114). Others after also coming very close to it turn forward to enter the posterior pedal lobe (figures 17 and 56). Here they turn forwards and may cross in the posterior pedal commissure. Some of them divide up in the posterior pedal lobe, others (or perhaps branches of the same ones) run on forwards into the anterior pedal lobe. Their branches therefore reach to the centres influencing the funnel, fins and arms. These cells are presumably activated by the same inputs as reach to the first order giant cells. Indeed where they pass close to the first order giant axon the last collateral dendrites of the latter occur and there is a complex tangle of fibres in which dendrites of all the trunks may be involved. This could be the site of generation of action potentials in all the large fibres. Their effect would be therefore to produce the reactions of arms and fins that are appropriate to jet propulsion. It may be significant that their endings lie near the middle line, and are thus presumably not concerned with steering.

(3) The third output from the ventral magnocellular lobe comes from the anterior portion and is much more difficult to define. It consists of fibres streaming upwards from the sides of the ventral magnocellular commissure, many having crossed from the opposite sides (figure 53, plate 5). They are mingled with fibres of the static nerves and median basal to ventral magnocellular tract, making it very difficult to find their destination. Some cross the trunks of the cells of the lateral pedal to anterior pedal tract (p. 127). Others probably proceed on to the dorsal magnocellular lobe, and perhaps back to the retractor centre of the anterior palliovisceral lobe. The significance of these fibres and the part of the lobe from which they arise is obscure. This region is very well developed in *Mastigoteuthis* and *Chiroteuthis*, squids with especially developed tactile sense in the tentacles but no giant fibres (Young 1976*a*).

8.3.5. *Input to the ventral magnocellular lobe*

The ventral magnocellular lobe is a region upon which converge fibres from a wide variety of sources. They probably all send fibres to both sides, by crossing in the ventral magnocellular commissure (figure 17, p. 115). (1) The brachio-magnocellular connectives bring influence from the arms. They enter the lobe from in front ventrally (figure 59, plate 5). Many, perhaps all, of the fibres bifurcate to end partly on the same side partly opposite after crossing in the ventral magnocellular commissure (Young 1939). Some of these fibres are very large (35 μm, figure 55) and it has been suspected that some might be efferent from the magnocellular lobe. However, even the largest divide as they enter from in front and none of the branches has been traced to cells of the lobe. It is concluded that all the fibres of the tract run backwards. (2) The medial optico-magnocellular tract of large fibres brings influences direct from the optic lobes (p. 134) and (3) the median basal to magnocellular tract has large fibres (up to 10 μm) from the supraoesophageal centres (figure 49). (4) The postorbital nerve sends a bundle from the surface of the head (figures 31 and 60, plate 5). (5) There is a bundle from each collar nerve (p. 149, figure 30) and (6) many fibres come from the pallial nerve, running forwards through the posterior magnocellular lobe. (7) Fibres enter the front of the lobe from the anterior funnel nerves (p. 132). (8), (9) Numerous fibres enter from the macula and crista nerves. These include branches of the large crista nerve fibres as well as many smaller ones of both nerves (figures 17, 61).

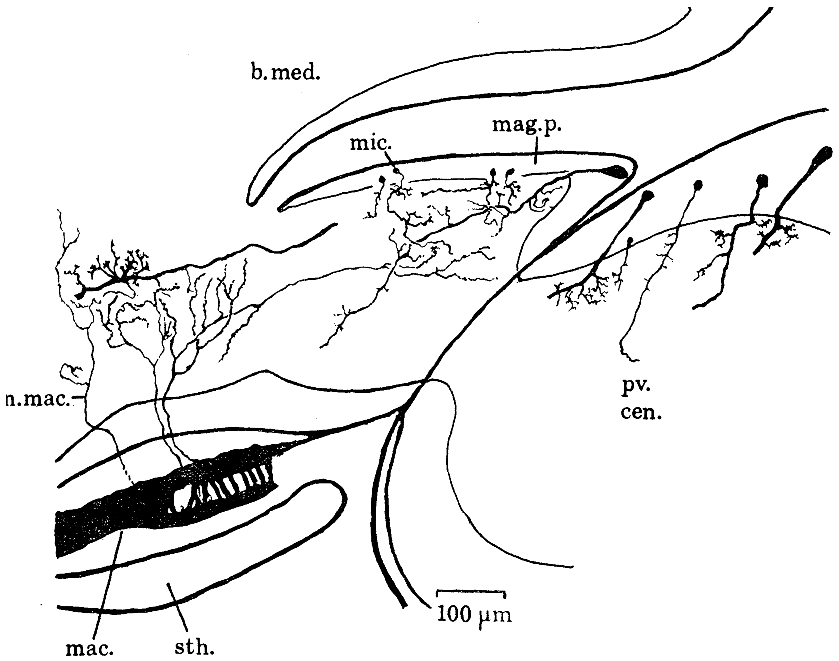


FIGURE 61. *Alloteuthis subulata*. Sagittal section showing fibres from the macula statica and cells of the posterior magnocellular and palliovisceral lobes. Golgi.

8.4. *Posterior magnocellular lobe*

8.4.1. *Position and relations*

This will be described here although it lies in the posterior suboesophageal mass. It is linked functionally both with the other divisions of the magnocellular lobes and with the pallio-visceral lobes. It is a cylinder lying along the sides of the palliovisceral lobe (figures 50, 51, plate 4 and 66, plate 6). The significance of this arrangement may be that it allows fibres from the posterior magnocellular lobe to influence the neurons at the centre of the mass. It is continuous with the dorsal and ventral magnocellular lobes in front. Laterally and ventrally it occupies the edge of the brain and is in contact with cartilage. Dorsal to it lie the fin and chromatophore lobes and the roots of the pallial nerve. Posteriorly the magnocellular lobes of the two sides are joined by the large posterior magnocellular commissure (figures 64 and 67, plate 6). Medially the lobes are partly separated from the palliovisceral neuropil by narrow ridges of cells dorsally and ventrally. Between these ridges however the neuropil of the posterior magnocellular lobe sends fibres to that of the palliovisceral lobe.

8.4.2. *Cells of the posterior magnocellular lobe*

The lobe has a rather uniform wall of small and medium cells. The largest are 20 μm in diameter, with nucleus 10 μm. The axons of these cells proceed across the neuropil, and some turn forwards (figure 13, p. 111). Many of the smaller cells are amacrines, with branches ending within the lobe (figure 61, p. 137).

8.4.3. *Input to the lobe*

(1) The input to this lobe comes largely from the optic lobes as the lateral optic to magnocellular tract (figures 13, 14, 15 and figure 52, plate 5). The fibres of this tract form loose interweaving bundles in which specific topographical relations are probably not preserved (figure 66, plate 6). The more lateral bundles contain the finer fibres and break up in the lateral part of the lobe and must be afferent to it. The more medial bundles contain larger fibres, which enter the posterior magnocellular commissure and pass to the posterior and dorsal magnocellular lobes of the other side and perhaps to the latero-ventral palliovisceral lobe (p. 144). (2) Other fibres come from the postorbital nerve (figure 60, plate 5), perhaps operating escape functions in response to stimulation of the head (3) Many fibres in the bundles running through the lobe come from the median basal and perhaps other supraoesophageal lobes (figure 29, p. 118) and (4) others from the arms via the brachio-magnocellular tract. (5) A small bundle even comes direct from the olfactory lobe (figure 63, plate 6), and (6) another from the collar nerve (p. 149). (7) Fibres from the statocyst are abundant throughout the magnocellular lobe, at least as far back as the transverse septum (figure 61).

This region thus receives afferents from sources of many different types and locations. Perhaps they are all concerned in initiating escape reactions. The actual courses and terminations of the various sorts of fibres are hard to follow. At the front of the posterior magnocellular lobe there are very numerous fine fibres running across the forward-turning trunks of the cells of the lobe, but the significance of this arrangement is not clear.

After passing through the interweaving bundles these fibres reach the hind end of the palliovisceral lobe partly as numerous discrete bundles. Here many fibres leave the magnocellular lobe to terminate in the latero-ventral region of the pallio-visceral lobe (p. 144).

8.4.4. *Posterior magnocellular commissure*

The region of the commissures in the mid-line is a complicated set of fibres, lying between the dorsal and ventral roots of the visceral nerves (figure 82, plate 8). They contain several sets of fibres with very different diameters (figure 64, plate 6). At the front is a compact bundle of very large fibres descending from the dorsal magnocellular region (c.mag.p.a.). Behind this are numerous bundles of fibres of decreasing size, linking the various parts of the magnocellular system (c.mag.p.p.). In front of the posterior magnocellular commissure are numerous other crossing fibres, making a visceral commissure (c.visc.).

8.4.5. *Neuropil and output of the posterior magnocellular lobe*

The neuropil is a characteristic meshwork of bundles of the fine fibres of the lateral optic to magnocellular tract (figure 66, plate 6). The courses of the fibres are complex and their destinations hard to discover. Many are afferent to the lobe and branch as they pass backwards. The trunks of the cells proceed transversely and give off dendritic branches (figure 61, p. 137). They have been hard to trace and probably reach to several destinations. (1) Some of them turn forwards to the dorsal magnocellular lobe and end there, or perhaps run on to the optic lobe. (2) Others turn back and may cross in the commissure. (3) Some run medially and may end in the central palliovisceral lobe (figure 13, p. 111). (4) Some may reach to the latero-ventral palliovisceral lobe (p. 144).

The neuropil of the lobe is not homogeneous but shows three distinct types (figure 62, plate 6). (1) At the centre the texture is loose (pil.cen.), (2) secondly, along much of the margin there is a yellow, small-fibre neuropil (pil.mar.). (3) Thirdly, also around the edges there is a neuropil of very fine fibres (pil.per.) perhaps a continuation of the last but not showing the yellow stain typical of marginal neuropil associated with small cells.

Along the medial side of the lobe the bundles coming from the dorsal magnocellular lobe join to form an especially conspicuous bundle of large fibres, lying at the boundary with the neuropil of the central palliovisceral lobe (figures 50, 51, plate 4). The fibres of these bundles form the compact anterior portion of the posterior magnocellular commissure. Some of these fibres diverge backwards after crossing to end in the latero-ventral palliovisceral lobe of the opposite side. Others continue forwards with the descending bundles of the opposite side and then diverge medially (figure 50) to spread out in the dorsal magnocellular lobe (figure 65, plate 6). The whole posterior magnocellular lobe may thus be largely a commissural system. Fibres of the optico-magnocellular tracts and perhaps of the cells of the dorsal magnocellular lobes descend in the lateral part of the bundle and return in the medial one. This interpretation is not certain but suggests that this tract serves to link the functions of the two dorsal magnocellular lobes. But it may also be relevant that other members of the same set end in the latero-ventral palliovisceral lobes.

9. POSTERIOR SUBOESOPHAGEAL MASS

9.1. *Relations and divisions*

This mass lies above the statocyst and below the oesophagus, at the hind end of the brain. It shows only slight external lobulation, but considerable internal subdivision (figures 1 and 32). Some of the lobules are rather sharply distinct anatomically and functionally (the fin lobes and posterior chromatophore lobes), but the others are interlocking systems. The mass may therefore be taken to include seven partly distinct regions or lobes and we can make a provisional functional analysis.

(i) The anterior palliovisceral lobe. The posterior retractor centre.
(ii) The central palliovisceral lobe. The region for control of the mantle muscles.
(iii) The latero-ventral region. Perhaps concerned with the emission of ink.

(iv) The posterior magnocellular lobe.
(v) The fin lobe, antero-dorsally.
(vi) The posterior chromatophore lobe, postero-dorsally.
(vii) The visceral lobe, in the restricted sense, lying posteriorly.

The posterior suboesophageal mass contains many final motoneurons, running to the muscles of the retractors of the head and funnel, to the valves at the entry to the mantle, to the chromatophores and muscles of the skin of the back and to the viscera. On the pathway to the mantle muscles however there is a further synapse in the stellate ganglion. There are also ganglia along some of the pathways of the visceral nerves.

Not all the cells of the mass are motoneurons. Some regions of the lobe contain only small cells, confined to one lobe or conducting to other regions of the brain. The fin lobes and chromatophore lobes however contain only large motoneurons.

9.2. *Anterior palliovisceral lobe: the posterior retractor centre*

9.2.1. *Position and relations*

The front part of the posterior suboesophageal mass is occupied by the neurons that give rise to the more posterior nerves to the retractors of the head and funnel (figures 66–68, plate 6). These include the posterior funnel nerve and the retractor fibres in the pallial and visceral nerves, the last two sets arising in each case by separate dorsal and ventral roots. There are therefore five roots on each side and they come from cells at the front end of the posterior suboesophageal mass lying both dorsally and ventrally. In the ventral part of this region there is also an antero-ventral lobule whose axons proceed up to the fin lobe (figure 69, plate 7). It is not clear whether this is functionally related to the retractor centre. It perhaps provides the pathway that serves to stop the movement of the fin and to depress it during the process of jet propulsion.

The anterior palliovisceral region is related to the perioesophageal sinus above and the statocyst below. Laterally it is quite sharply marked off from the fin lobe above and the latero-ventral lobe below (figures 68 and 69). Anteriorly it is continuous with the posterior pedal lobe and behind and medially with the palliovisceral lobe, but from this it is not sharply separated, the distinction being made only in terms of the cell types present.

DESCRIPTION OF PLATE 7

FIGURE 69. *A. subulata*. Transverse section showing cells of various parts of the posterior suboesophageal mass.

FIGURE 70. *L. vulgaris*. Horizontal section to show afferent fibres from the mantle connective to the palliovisceral lobe.

FIGURE 71. *L. pealeii*. Horizontal section of palliovisceral and magnocellular lobes.

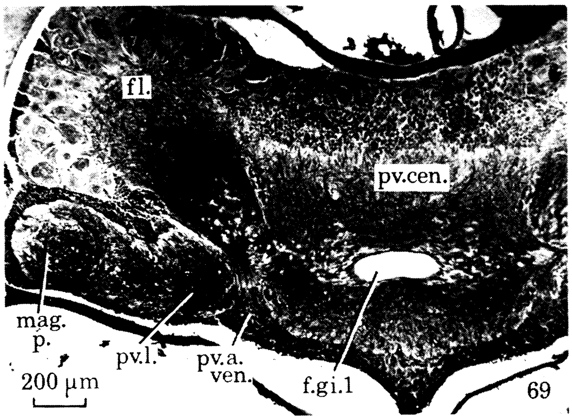
FIGURE 72. *Alloteuthis*. Horizontal section. Latero-ventral palliovisceral and posterior magnocellular lobes.

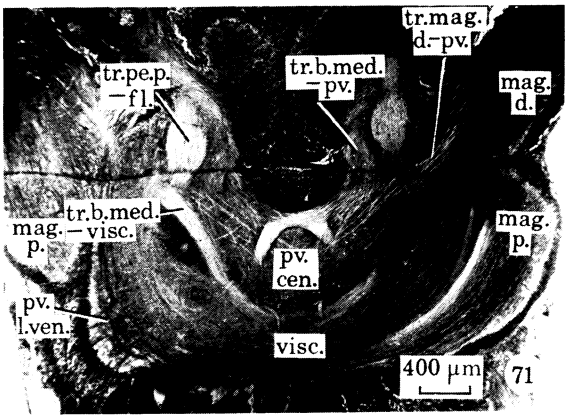
FIGURE 73. Part of figure 72 to show large terminal knobs. Touched up.

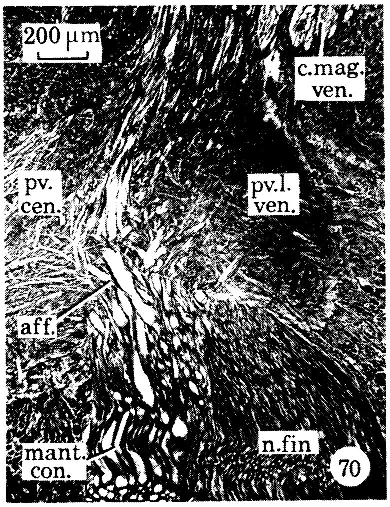
FIGURE 74. *L. pealeii*. Horizontal section latero-ventral palliovisceral lobe to show fibres proceeding to central lobe.

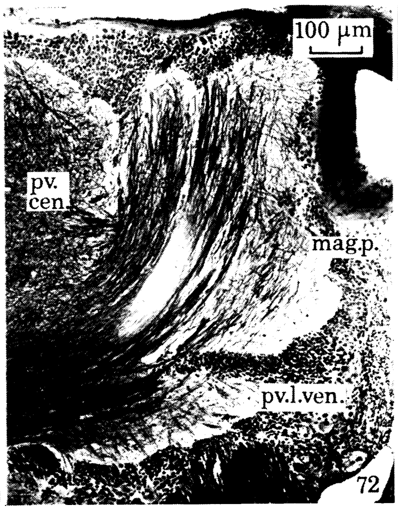
FIGURE 75. *L. pealeii*. Horizontal section latero-ventral palliovisceral lobe showing inputs from collar nerve and olfactory lobe.

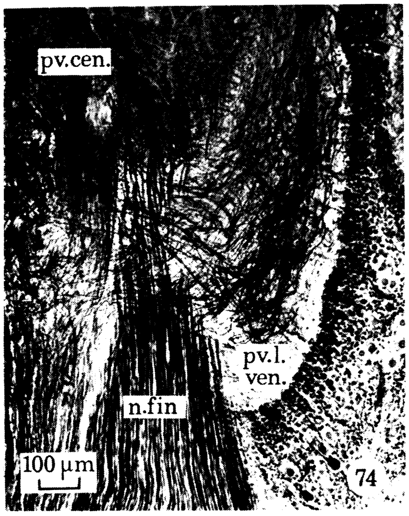
FIGURE 77. *L. pealeii*. Horizontal section of back of visceral lobe to show the very small cells and the origin of the nerve to the anterior vena cava.

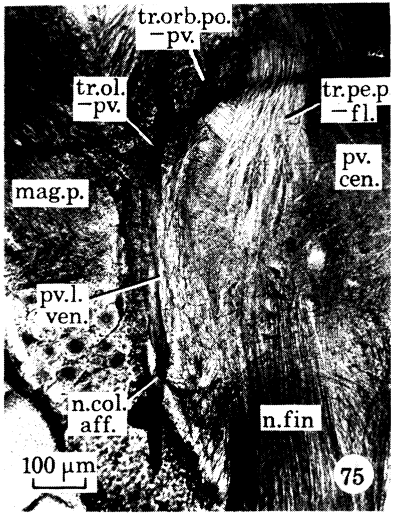


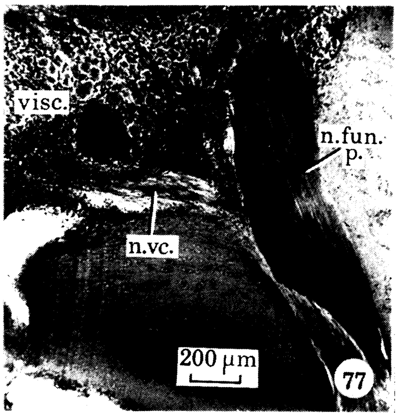






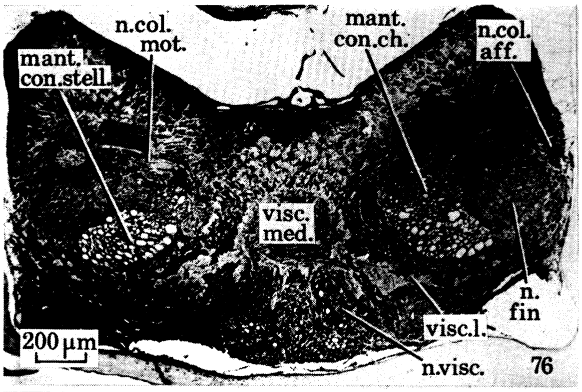


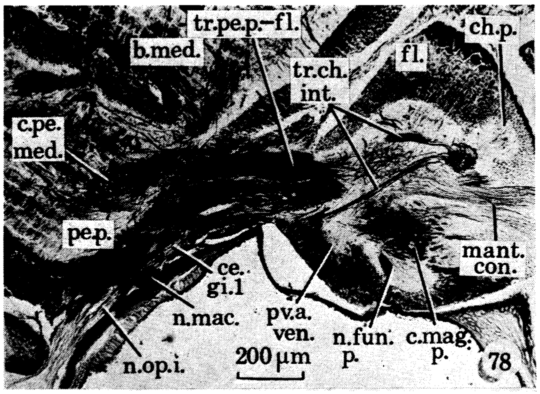


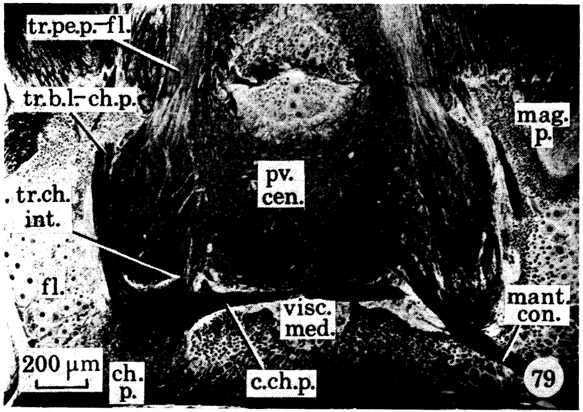


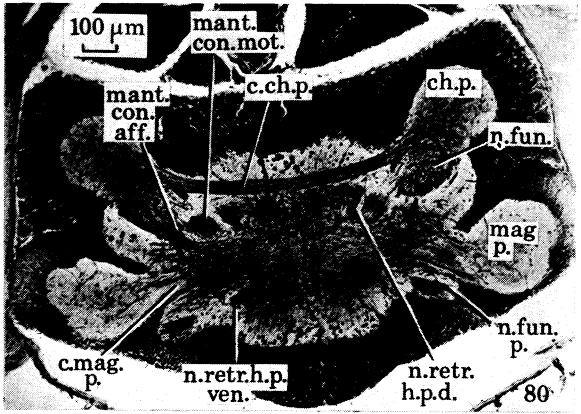
FIGURES 69–75 AND 77. For description see opposite.

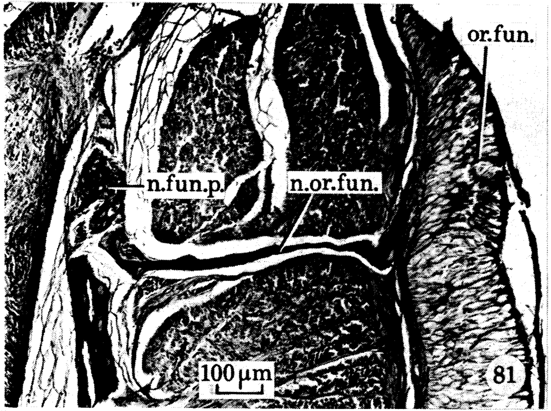
(*Facing p.* 140)

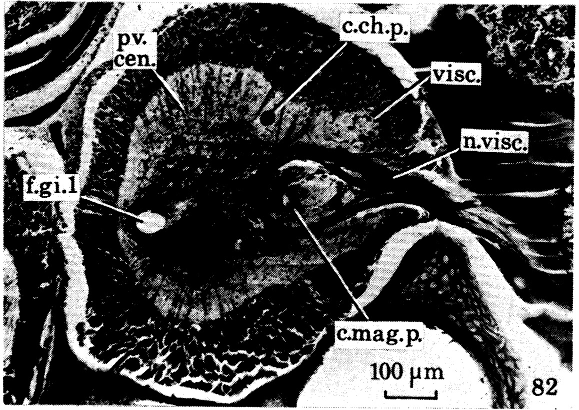


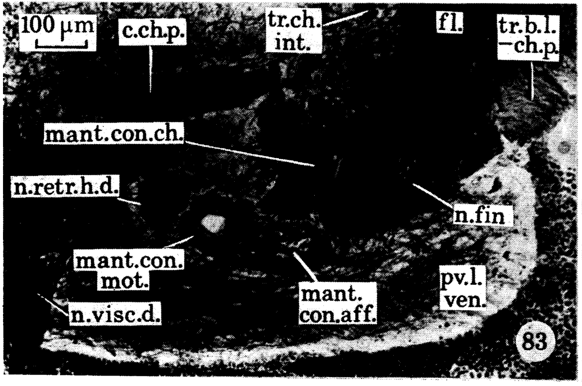


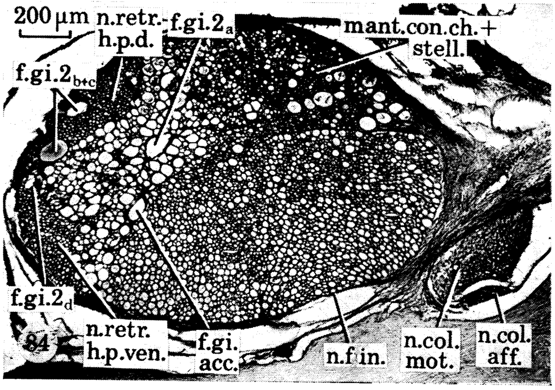












FIGURES 76 AND 78–84. For description see opposite.

9.2.2. *Cells and output of the anterior palliovisceral lobe*

The main part contains a mixture of large and small cells, but the ventral antero-lateral region contains mainly small cells (figure 67). The largest cells of the retractor centre are rather smaller than the largest elsewhere in the mass (20 μm diameter). Their axons go to make up the roots of the retractor nerves (figures 15 and 66). These nerves also contain second order fibres of the giant fibre system.

The dense layers of small cells of the antero-ventral lobe send their axons up to the fin lobe. The trunks of these cells carry collaterals that are characteristically curled, much branched and intertwined with those of neighbouring cells (figure 104). Some of these trunks carry two sets of collaterals, one near to the cell layer and the other at the centre of the palliovisceral lobe. These arrangements are different from those of the motoneurons and are presumably related to the special functions of the lobe. This is the only output from the anterior palliovisceral lobe that has been separately recognized other than the nerve fibres to the retractors. It may be that from its dense neuropil other fibres pass forwards to the posterior pedal or backwards to the central palliovisceral lobe.

9.2.3. *Input to the anterior palliovisceral lobe*

(i) A large tract of fibres reaches this region from the posterior pedal lobe (figures 32 and 68). These fibres probably remain wholly on the same side, and may be concerned with steering by inducing suitable operations of the retractor muscles and raising or lowering the fins.

(ii) Other fibres reach it from the brachio-palliovisceral connective.

(iii) It receives fibres from the anterior funnel nerve by a bundle running up medial to the first order giant cell (p. 132).

(iv) The large median basal to palliovisceral tract probably sends fibres to this region.

(v) There is probably also a further bundle from the small cells of the anterior part of the ventral magnocellular lobe (p. 136).

9.3. *The central palliovisceral lobe*

9.3.1. *Introduction, position and relations*

This is one of the most difficult regions to define, perhaps because it is related to so many operations (figure 69, plate 7). Its connections suggest that it controls the contractions of the mantle, by way of the stellate ganglion. This action is related to respiration as well as locomo-

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DESCRIPTION OF PLATE 8

FIGURE 76. *L. vulgaris*. Transverse section of visceral lobes.

FIGURE 78. *L. pealeii* (juvenile). Sagittal section to show interchromatophore lobe tracts and inferior ophthalmic nerve. The section is slightly oblique (more lateral posteriorly).

FIGURE 79. *A. subulata*. Horizontal section of the posterior suboesophageal mass.

FIGURE 80. *L. pealeii* (juvenile). Transverse section of the posterior chromatophore lobes and commissure.

FIGURE 81. *L. vulgaris*. Transverse section showing branch of the posterior funnel nerve to the funnel organ.

FIGURE 82. *L. pealeii* (juvenile). Sagittal section of roots of visceral nerves.

FIGURE 83. *L. pealeii*. Details of the components of the pallial nerve.

FIGURE 84. *L. vulgaris* (adult). Transverse section of pallial nerve, and collar nerve. The giant fibres in the mantle connective are not well fixed.

tion and obviously requires coordination with the actions of the retractor muscles and those of the fins and the collar, and of course also of the arms. This co-ordination is apparently achieved by a combination of over-riding influences from above with interactions among the motor centres themselves.

The efferent fibres leading to the mantle connective arise from the dorsal and ventral walls of the central part of the posterior suboesophageal lobe. This region is continuous in front with the posterior retractor centre (anterior pallioviscerai lobe) and indeed merges with it. At the sides the central region is rather sharply marked off dorsally from the fin lobe in front and the chromatophore lobe behind, but exchanges fibres with them. Ventrally it is broadly continuous with the latero-ventral lobe, though a ridge of cells marks the boundary. Behind, the lobe merges with the visceral lobe.

FIGURE 104. *Alloteuthis subulata.* T.S. of anterior palliovisceral lobe showing the cells whose axons mostly run to the fin lobe. Golgi.

9.3.2. *Cells of the central palliovisceral lobe*

The largest of these are larger than those of the retractor lobes but smaller than those of the fin lobe (figure 69). They range up to 60 μm diameter, with nuclei of 20 μm. The cell layers are sharply marked off from those of the fin lobe by the presence of numerous small cells in the central lobe. Some of the cell bodies of the second order giant cells lie dorsally, others ventrally, but have not been mapped in detail.

The outputs from the central palliovisceral lobe are (1) fibres to the mantle connective, ending in the stellate ganglion (figure 12, p. 110). These include the second order giant fibre (g.f.2a) and probably several rather smaller fibres that accompany it. The accessory giant fibre (g.f. 2acc.) probably arises separately (p. 150). The smaller fibres to the stellate ganglion may include two sets, one for respiration and the other for locomotion, but these have not been identified. (2) The central palliovisceral lobe gives rise to the fibres of the collar nerves and these are primarily respiratory. They probably arise both dorsally and ventrally (p. 149).

FIGURE 105

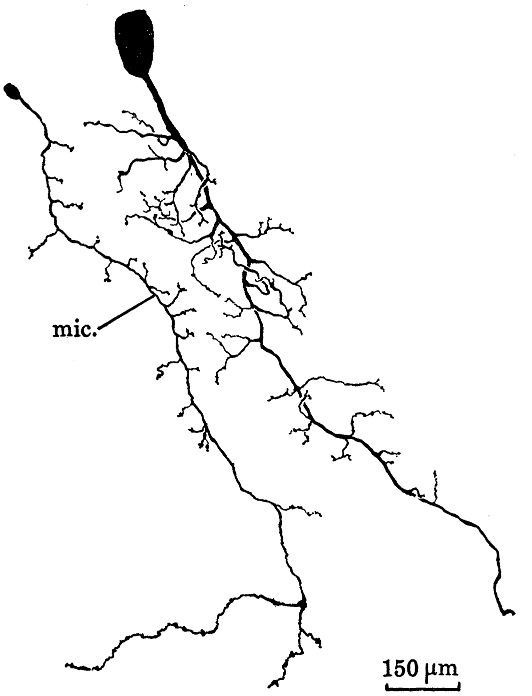

FIGURE 106

FIGURES 105 AND 106. *Alloteuthis subulata*. T.S. Cells of central palliovisceral lobe. Golgi.

There is no evidence that the cells of this central region also send fibres to other lobes of the brain, and it is assumed that they do not do so.

The neuropil shows a dense tangle of fibres, coarser at the centre, finer round the periphery, where presumably the processes of the small cells exert their effects. The giant fibres, their bridge and their synapses are conspicuous at the centre (figures 71 and 96). The trunks of the larger cells of the central palliovisceral lobe carry rather irregular long collateral dendritic branches, thinner than those of the fin lobe and with varicosities and terminal twigs (figure 105; figures 90, 91, plate 9). Some have many twigs on the main trunk, which in others is smooth. The smallest cells, near to the neuropil end in branches in the immediate vicinity. Others, slightly larger, send trunks to the centre of the neuropil, and probably some or all of these end here as microneurons (figure 106).

9.3.3. *Input to the central palliovisceral lobe*

The lobe comes under many influences. (1) The mantle connective brings forward-running fibres (figures 12 and 70, plate 7). These are large and many of them divide, sending one branch into the central region and others to the ventro-lateral region and the posterior magnocellular lobe, through which they may reach to the optic and supraoesophageal lobes.

(2) Fibres enter from the posterior funnel nerves and probably (3) from the visceral nerves. (4) Fibres run from the supraoesophageal lobes in the median basal to pallioviscera! tract (figures 12 and 13; figure 68, plate 6), and (5) precommissural to pallioviscera! tract (figure 12). (6) The lobe also receives part of the brachio-pallioviscera! tract, probably bringing direct influences from the arms. (7) A main factor controlling this lobe is the magnocellular lobe. The first order giant fibres ramify at the centre of the lobe after joining in the inter-axonic bridge (figures 13 and 33; figures 71 and 96). They make connection with the several second order giant fibres arising in the lobe (Young 1939). In addition numerous other large fibres enter the centre of the lobe from the dorsal magnocellular lobe (figure 71, plate 7). It is not clear whether these operate distinct actions or are all part of the same system (Martin 1969). (7) Fibres enter the central pallioviscera! lobe from the latero-ventral lobe (see below).

9.4. *The latero-ventral pallioviscera! lobe*

9.4.1. *Position and relations*

The region along the lower edges of the central pallioviscera! lobe is a distinct entity anatomically and by its connections. However, it is closely interrelated with both the central pallioviscera! and posterior magnocellular lobes. It may serve escape functions, particularly the emission of ink. It stretches back on either side from the transverse septum nearly to the hind end of the brain (figure 71, plate 7).

The lobe lies medial to the posterior magnocellular lobe, from which it is separated by ridges of cells dorsally and ventrally, the neuropils being broadly continuous (figure 69, plate 7). Posteriorly the two latero-ventral lobes are joined by commissural fibres lying beneath the posterior magnocellular commissure (figure 66, plate 6). The lobe lies on either side of the central pallioviscera! lobe and the neuropils are broadly continuous medially. The fin lobe lies dorsal to but separate from the latero-ventral lobe.

9.4.2. *Cells, neuropil and output*

This latero-ventral region has many small cells and among them a few larger ones, only reaching 60 μm diameter (figure 74, plate 7). The trunks of these reach into the central pallioviscera! neuropil. It is not known whether they end there or proceed into the pallial or visceral nerves, but bundles of fibres proceed between the lobe and the roots of both these nerves

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DESCRIPTION OF PLATE 9

FIGURE 85. *L. vulgaris.* Transverse section of the superior and inferior buccal lobes.

FIGURE 86. *L. pealeii* (juvenile). Transverse section of the buccal mass, showing the subradular ganglia.

FIGURE 87. *A. subulata.* Central pallioviscera! lobe to show form of dendrites. Golgi.

FIGURE 87*a*. *A. subulata.* Gliovascular cell with branches, attached to a blood vessel. Golgi.

FIGURE 88. *L. vulgaris.* Sagittal section of anterior pedal lobe. Golgi.

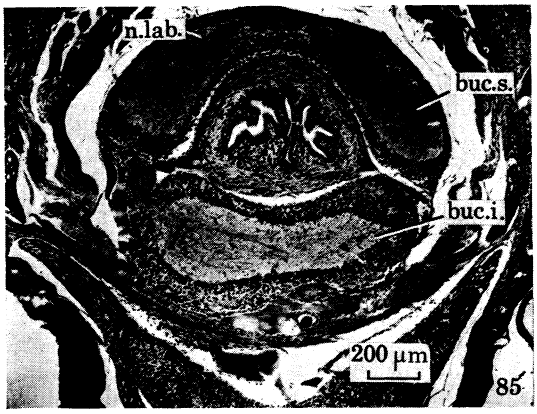
FIGURE 89. *A. subulata.* Sagittal section of posterior suboesophageal mass, showing fibres of the anterior pallioviscera! lobe, fin lobe and posterior chromatophore lobe. Golgi.

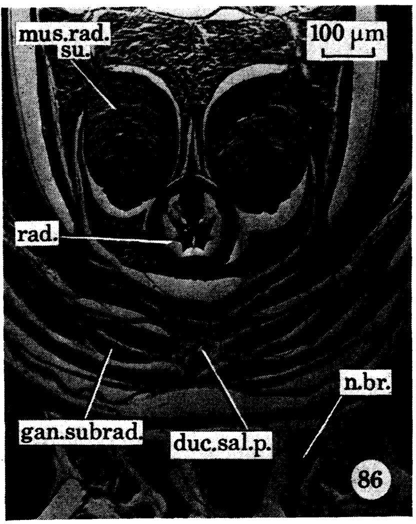
FIGURES 90 AND 91. *A. subulata.* Detail of dendritic branches and trunk of cells of the pallioviscera! lobe.

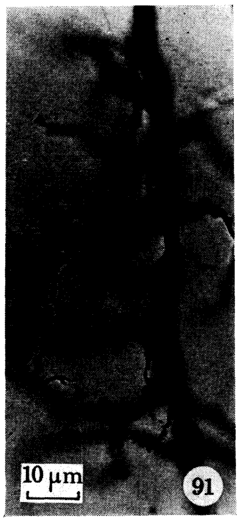
FIGURES 92 AND 92*a*. Detail of dendrites of cells seen in figure 107, p. 146.

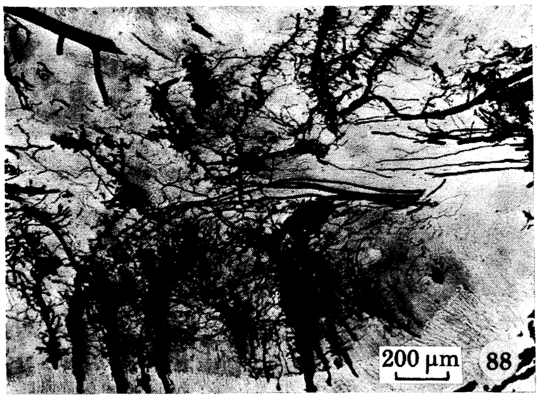
FIGURE 93. *A. subulata.* Sagittal section showing a cell of the fin lobe. Golgi.

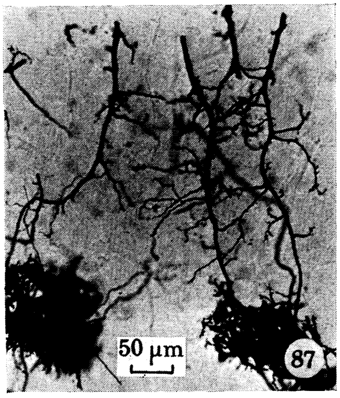
FIGURE 96. *A. subulata.* Horizontal section of the pallioviscera! lobe (Golgi). Note that the stain has taken on the entire pair of first order giant axons.

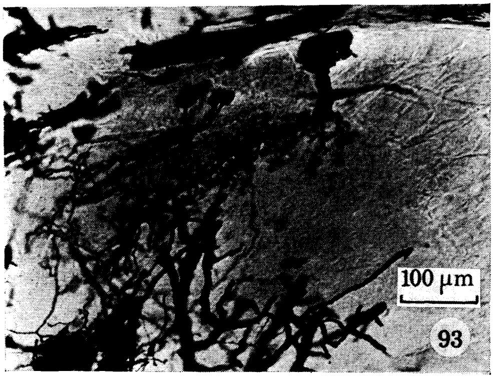


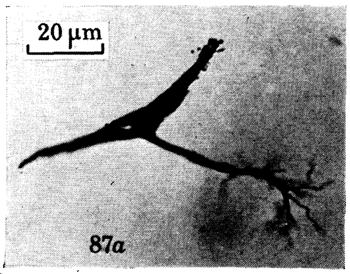


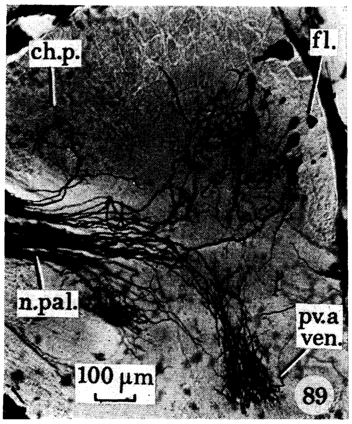


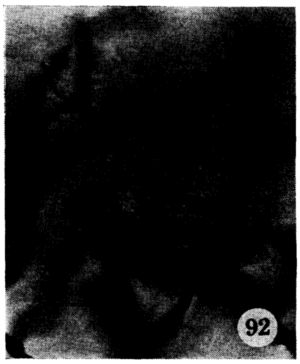


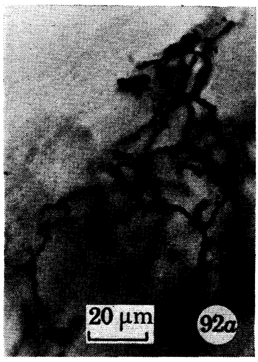


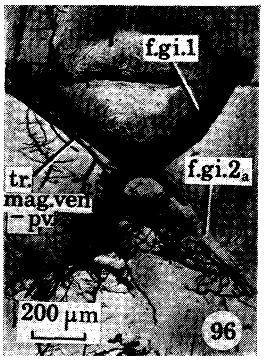




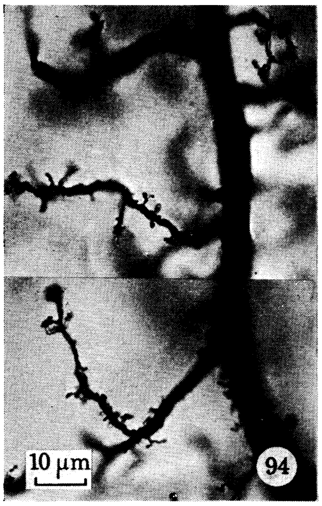


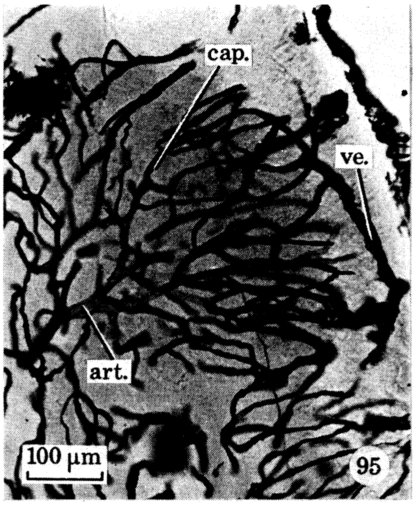


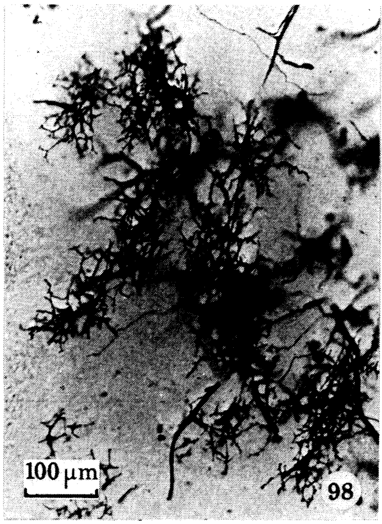


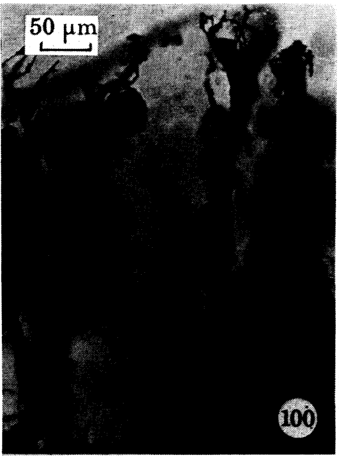


FIGURES 85–93 AND 96. For description see opposite.









FIGURES 94, 95 AND 97–103. For description see opposite.

(figure 74). This region has a characteristic neuropil containing many large swellings along the course of the axons and also many large terminal masses. These are at the end of branches of the large fibres that run round the lobe, coming from various sources, including the magnocellular and pedal lobes and probably the pallial nerves. The knobs end against the main trunks of the larger cells of the lobe (figure 73, plate 7).

9.4.3. *Input to the latero-ventral lobe*

(1) The region receives numerous bundles from the same and the opposite magnocellular lobes (figure 66, plate 6). This is obviously one of its chief sources of excitation. In a sense this region is a part of the posterior magnocellular lobe, and the latter brings to it fibres from the optic lobes of both sides. (2) Numerous fibres enter from the mantle connective division of the pallial nerve (figure 70, plate 7). These fibres divide within the lobe. (3) This lobe also receives bundles of fibres that bring signals of changes in the contents of the water, from the olfactory lobe in front and (4) the collar nerve behind (figure 75, plate 7). (5) Fibres from the postorbital nerve (surface of the head) also reach into this lobe. (6) Fibres reach back to this region from the arms, in the brachio-palliovisceral connectives. Fibres from supraoesophageal lobes may reach here through the magnocellular lobes.

9.5. *The visceral lobes*

9.5.1. *Position and relations*

These are considered separately from the rest of the posterior suboesophageal mass because they contain cells with functions connected with internal rather than external adjustments. Their cells are correspondingly different, but the boundaries of the lobes are not easy to define anatomically.

These lobes occupy the posterior and ventral part of the posterior suboesophageal mass, behind the posterior magnocellular commissure (figures 15, 82, plate 8). There are thick walls of cells grouped around a central neuropil from which irregular extensions proceed laterally and ventrally (figure 76, plate 8). These lobes are not clearly detectable externally but their cell layers are distinctly marked off from those of the central palliovisceral lobe by the large number of small cells and smaller size of the largest (40 μm). However in this region there are a small number of extremely large cells (> 100 μm), probably four on each side, presumably giving rise to the giant nerve fibres of the visceral nerves. At the lateral ventral edges of the brain is a mass of very small cells (figure 77, plate 7). These lie around the hind ends of the magnocellular and lateral palliovisceral lobes and above the exit of the posterior funnel

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DESCRIPTION OF PLATE 10

FIGURE 94. Detail of dendrites of the cell of figure 93.

FIGURE 95. *A. subulata.* Sagittal section. Blood vessels of the pedal lobe. Golgi.

FIGURES 97 AND 98. *A. subulata.* Transverse section of brachial lobe, showing branched gliovascular cells. Golgi.

FIGURES 99 AND 99*a*. *L. vulgaris.* Vessels of the pedal lobe, showing gliovascular cells wrapping around them and also sending branches into the neuropil. Golgi.

FIGURE 100. *L. vulgaris.* Pedal lobe showing nerve cell bodies wrapped by gliovascular tissue. Golgi.

FIGURE 101. *A. subulata.* Transverse section of the prebrachial lobe showing very long glial processes. Golgi.

FIGURES 102 AND 103. *A. subulata.* Fibrous glia cells of brachial lobe. Golgi.

nerves. Bundles of fine fibres run among them and form the two parts of the anterior vena cava nerves (p. 149). This is a characteristic 'extra-cortical neuropil' (Thore 1939), presumably supplying cells of neurovenous tissue in the wall of the vein (Alexandrowicz 1964, 1965).

The cells of the main lobules of the visceral lobes send their trunks in to the neuropil at the back of the posterior suboesophageal lobe. This region provides the roots of the visceral nerves (figure 82, plate 8). It receives input from a wide variety of sources but largely in the form of diffuse bundles from other parts of the palliovisceral lobes. It is not possible therefore to give any satisfactory list of the sources of stimulus to this region. They no doubt include afferents from the visceral and other nerves (p. 149). Large bundles reach here in the median basal to visceral lobe tract (figure 71, plate 7). This bundle runs partly outside the brain (figures 29 and 30) suggesting some particular phylogenetic origin (see Young 1971).

9.6. *The posterior chromatophore lobe*

9.6.1. *Position and relations*

The posterior chromatophore lobe is distinctly marked at the back of the posterior suboesophageal mass dorsally (figures 1, 30, 32 and figure 80, plate 8). It is related to the fin lobe in front but exchanges no fibres with it. The pallial nerve enters below it and to this it sends most of its output fibres. There is no published evidence that this lobe innervates the chromatophores but electrical stimulation of it produces expansion of the chromatophores of the back.

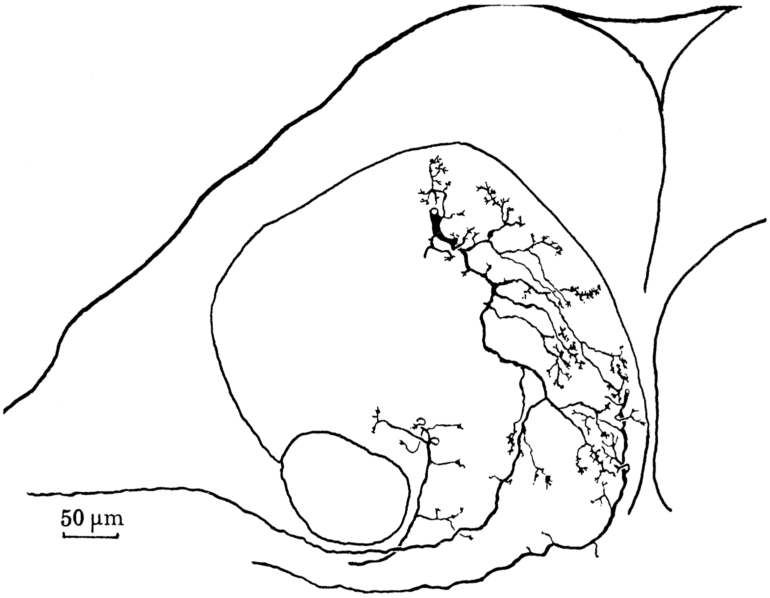

FIGURE 107. *Alloteuthis subulata.* Sagittal section showing dendrites of the cells of the posterior chromatophore lobe. Golgi.

9.6.2. *Cells, neuropil and output*

The lobe innervates the muscles of the chromatophores and skin of the mantle and fins, by fine fibres running to them through the pallial, collar and fin nerves without further synapse. These final motoneurons are of medium size (80 μm being the greatest diameter). They are arranged in characteristic rather regular rows. There are no inner layers of small cells or small-fibre neuropil. Presumably there are no short-axon cells, all send fibres to the periphery. The neuropil does not show the complications seen in other cephalopods that have elaborate colour patterns, such as *Octopus* or *Sepia*. The large fibres entering the lobe from in front divide and run mainly tangentially round in the transverse plane, across the trunks of the cells of the lobe. These trunks give a series of collateral dendrites, which branch repeatedly forming a series of twigs carrying further collateral spines (figure 107). Each cell thus comes under the influence of a considerable part of the neuropil of the lobe. The dendrites are also swollen at intervals into masses of various sizes and shapes (figures 92 and 92*a*, plate 9), some rather large and appearing to be pitted, perhaps by incoming synaptic endings. Electron microscopy should show the significance of these various formations. The collaterals continue to come off the main trunk until the axon leaves the lobe, but the more distal ones are small. The axon is narrower than the main trunk within the lobe, but there is no sign of a sudden narrowing or 'axon hillock'. The axons of these cells mostly pass to the skin through the mantle connective or fin nerve, some probably in the collar nerve. Probably none run to the opposite side but some perhaps pass to the anterior chromatophore lobe (see below).

9.6.3. *Input to the lobe*

(1) The lobe receives the lateral basal to chromatophore lobe tract (figures 12 and 30 and figure 79, plate 8), which is the main source of control of colour and is under the influence of the visual system. (2) There are a few fibres entering the lobe from in front from the central palliovisceral lobe but their source and significance are not known.

The lobe is joined to its fellow by a posterior chromatophore lobe commissure (figures 79, 80, 82). This does not carry axons arising from cells of the lobe but from the lateral basal to chromatophore lobe tract. Many or all of these divide, giving one branch on the same side and another crossing in the commissure (figure 79). (3) and (4). Two further bundles join the lobe from in front (figures 32 and 79). They run back from the pedal lobe one dorsally and the other ventrally but it has not been possible to be certain of their origins because they become confused with the brachio-palliovisceral and posterior pedal to fin lobe tracts. They will be presumed to be dorsal and ventral tracts of interchromatophore lobe fibres, but some of them may perhaps come from the arms. There are certainly fibres in these tracts running backwards and dividing at the front of the posterior chromatophore lobe, one branch then crossing in the commissure (figure 79). It is not clear whether there are also fibres running forwards. It is possible that fibres from this lobe reach to the superior or inferior ophthalmic nerves to control the colour around the eyes (p. 124). In *Octopus* these areas are innervated from the anterior chromatophore lobes (Young 1971).

9.7. *The fin lobe*

9.7.1. *Position and relations*

The fin lobe occupies the dorsal part of the posterior suboesophageal mass on each side, in front of the posterior chromatophore lobe (figures 1–2, 30–32, and 60 and 68). It lies dorsal to the magnocellular lobe and lateral to the central palliovisceral lobe.

9.7.2. *Cells, neuropil and output*

The fin lobe contains much larger cells than the chromatophore lobe, up to 120 μm, and all are motoneurons, (figure 69, plate 7). The inner cells are somewhat smaller than the outer ones (*ca.* 40 μm) but it is characteristic of this lobe, like the chromatophore lobes, that there are no very small cells. The neuropil is also characteristic, with the large trunks of the cells clearly showing among the incoming fibres of the posterior pedal to fin lobe tract. There are numerous terminal boutons in the neuropil, but no bundles of fine fibres such as occur where there are small cells with axons confined to a lobe. The cells are all final motoneurons and make axons that run in the fin nerve (p. 150). There is no evidence for any reverse projection from this lobe to higher centres. The trunks of the cells run circumferentially round the neuropil on their way to the nerve. They give off characteristic dendritic collaterals (figure 93, plate 9). All are stout, of similar length and rather short, with little secondary branching. They are covered with many fine terminal spines (figure 94, plate 10) but rather few of the larger masses so prominent on the dendrites in the chromatophore lobes.

9.7.3. *Input to the fin lobe*

(1) The greater part of the input comes by the posterior pedal to fin lobe tract (figures 31 and 32, and figure 79, plate 8). This is a large bundle composed of numerous similar large fibres (10 μm). They run parallel in the tract and then begin to divide to form a criss-crossing of bundles passing backwards through the lobe. There is no evidence that this tract carries fibres in the opposite direction.

(2) Where the fin lobe neuropil meets the central palliovisceral lobe medially there is an interchange of numerous fibres (figure 79). Many of these are small but there are also a few very large ones (> 20 μm) coming from the centre of the palliovisceral lobe. Some of these are members of the set that accompanies the first order giant nerve fibre, arising therefore in the dorsal or ventral magnocellular lobe. They perhaps operate actions of the fins appropriate to jet propulsion, such as folding.

(3) Some fibres reach the fin lobe from the brachio-palliovisceral tract, their direction is not known.

(4) A large bundle reaches the lobe from the smaller cells of the antero-ventral part of the anterior palliovisceral lobe (figure 69, plate 7).

There is no clear evidence of a tract proceeding direct from the median basal to the fin lobe, but such fibres may exist. The median basal to palliovisceral tract passes to the neuropil that exchanges fibres with the fin lobe (figure 68, plate 6). Since the fins are almost continually active the operation of the control of this centre is especially interesting. Presumably action of the fins is coordinated with that of the funnel (from the posterior pedal lobe) and with the jet system (by way of the magnocellular and palliovisceral lobes). The former is perhaps the steering mechanism, whereas the latter pathways may simply stop the fins and fold them.

9.8. *The brachio-palliovisceral tract*

This is a set of fibres running between the anterior suboesophageal mass and the palliovisceral and magnocellular lobes, some conducting in each direction. Its fibres probably arise at least in part within the arms (or run to them) but there is no definite proof of this because of the difficulty of analysing the fibres in the brachio-pedal connectives (p. 110).

The tract runs back at the side of the middle suboesophageal mass and there a brachio-ventral magnocellular bundle separates from it (p. 137). More posteriorly it receives a branch from the postorbital nerve (p. 131). The main tract continues backwards to the hind end of the pedal lobe and bends dorsally, passing medial to the magnocellular root of the postorbital nerve and the first order giant fibre. Here its fibres diverge, some run more ventrally into the postero-lateral palliovisceral lobe others form more dorsal bundles running to the central palliovisceral and fin lobes (joining the posterior pedal to fin lobe tract).

9.9. *Nerves arising from the posterior suboesophageal mass*

A study of the components of the nerves leaving the mass provides the basis for a functional analysis.

9.9.1. *Collar nerve* (*n. collaris*)

This nerve carries efferent and afferent fibres for the collar, whose movements regulate the intake of water to the mantle. The nerve lies above the main root of the pallial nerve and it divides into medial and lateral roots at entry. (figure 12, p. 110) The medial bundle contains large fibres and is presumably mainly efferent. It runs in to the centre of the palliovisceral lobe (figure 76, plate 8). Here its fibres turn some dorsally, some ventrally to arise from cells of the walls of the lobe. Since the collar is concerned wholly with respiration this enables us to identify this region as the respiratory centre. The same region also gives conspicuous bundles of fibres to the mantle connective and visceral nerves, which are also concerned in respiration.

The lateral root of the collar nerve runs along the side of the brain below the fin lobe (figure 76). It turns medially and divides into one part to the latero-ventral palliovisceral lobe (figure 75, plate 7) and another to the posterior magnocellular lobe (figure 30, p. 119). This turns down to enter the ventral magnocellular lobe in the region of the first order giant cell. Presumably this nerve contains afferents signalling the presence of noxious matter in the water intake over the surface of the valves of the mantle.

The collar nerve contains medium-large fibres, but no giant fibres. It runs dorso-laterally through the retractor muscles of the head, to which it supplies fibres. The rest of the nerve passes through the retractor muscles to end in the muscles of the valves of the mantle apertures, whose respiratory movements it operates.

9.9.2. *Posterior funnel nerve and anterior vena cava nerve*

The funnel nerve arises from the neuropil of the antero-ventral palliovisceral lobe (p. 140). The trunk runs backwards below the posterior magnocellular lobe and leaves the brain at the extreme hind end, being there joined by the fibres of the anterior vena cava nerve (p. 146, figure 77, plate 7). Together they run through the cartilage round the back of the statocyst and turn sharply down to the funnel. The anterior vena cava nerve then turns medially to the vein. The funnel nerve innervates the muscles of the funnel and sends a branch to the glandular funnel organs. This branch contains some quite large fibres (25 μm). It innervates muscles at the base of the glands and perhaps also sends secretomotor fibres to the gland cells themselves (figure 81, plate 8). The main part of the posterior funnel nerve innervates the dorsal muscles of the funnel. It contains large fibres and a giant fibre (g.f2e) under control of the first order giant cell (Young 1939). It also has small fibres, presumably afferents.

9.9.3. *Visceral nerves* (*n. visceralis*)

These arise by dorsal and ventral roots above and below the magnocellular commissure (figure 33, p. 122). The significance of this double origin is not known. These are not purely 'visceral' nerves since they innervate the retractor muscles of the funnel. These retractor fibres arise in the anterior or central palliovisceral lobe and each root includes a fibre of the giant fibre system (g.f.2d of Young, 1939). The nerves also contain afferent fibres and these may divide at entry, sending one branch to each root.

The strictly 'visceral' parts of the nerves are made up from bundles of fine fibres arising from the small-celled visceral lobes at the back of the brain (figure 15, p. 113). The two visceral nerves leave the brain close together and run for a considerable way through the digestive gland and then turn ventrally. They give branches to the retractor muscles of the funnel and muscles of the body wall and then come to lie on either side of the cephalic aorta. From there the visceral fibres run backward to supply the vena cava, hearts, gills and other viscera. It is not known whether they make anastomoses with branches of the sympathetic system and gastric ganglion as in *Octopus* (Young 1971).

9.9.4. *Pallial nerve* (*n. pallialis*)

This is a complex carrying at least five different sets of fibres and forming three major nerves, the posterior head retractor nerve, the mantle connective and the fin nerve. The fibres for these three arise as separate bundles (figures 12 and 31–33).

The fibres to the posterior head retractor (*n. retractor capitis posterior*) are the most medial. They include three second order giant fibres (figure 84, g.f.2b, c and d of Young 1939). The largest of these innervates the hinder part of the funnel retractor muscle, the other two the hinder parts of the retractor muscle of the head. The fibres of the posterior head retractor nerve arise by two roots, one dorsal and the other ventral to the posterior magnocellular commissure (figure 32, p. 121). This nerve runs with the rest of the pallial nerve as it passes through the hepatopancreas. Anteriorly it lies ventro-medially, ventral to the fibres of the mantle connective and medial to those of the fin nerve. Farther back it comes to lie laterally and leaves the main trunk shortly in front of the stellate ganglion to pass into the retractor muscles.

The fibres for the fin nerve (*n. pinnae*) arise from the fin lobe, and form a compact bundle occupying the lateral part of the pallial nerve as it leaves the brain (figures 76 and 83, plate 8). They are of relatively large and uniform diameter, and include no giant fibres. They continue back with the rest of the nerve as far as the stellate ganglion, which they pass without synapse. The maximum diameter of the fibres is about 15 μm as measured after fixation in a small squid of 5 cm mantle length (figure 84).

The mantle connective (figures 76, 83 and 84) includes three components (1) pre-ganglionic fibres that end in the stellate ganglion and thus activate the mantle muscles (2) fibres for the chromatophores and skin muscles, which run through the stellate ganglion without synapse (3) afferent fibres. Strictly only those in the first class should be said to constitute the mantle connective. They arise from the centre of the palliovisceral lobe, perhaps from both dorsal and ventral walls. They include the large second order giant fibre (f.gi.2a) and the accessory giant fibre (f.gi.acc.). The former arises just behind the bridge between the first order axons, probably from cells lying dorsally (Martin 1969). The origin of the accessory fibre is not known. There are also several other quite large fibres in this part of the nerve – probably also concerned in activating the third order giant fibres (Miledi 1967).

The fibres for the skin and chromatophores arise in the posterior chromatophore lobe and form a compact bundle of small fibres lying in the dorsal part of the pallial nerve at its origin, between the pre-ganglionic fibres medially and those of the fin nerve laterally (figure 83, plate 8).

The afferent fibres of the mantle connective have been described on p. 143. Many of them are large and they form a bundle below the chromatophore fibres, between the pre-ganglionic fibres and the fin nerve. Passing forwards they enter a complicated plexus and some pass into the bundles of the magnocellular lobe branching as they go (figure 70, plate 7). Some of these reach to the region of the first order giant cell, others run more dorsally and perhaps reach the optic lobe. Other afferent fibres of the mantle connective pass to the centre of the palliovisceral lobe and to its latero-ventral lobule (p. 145). Some may reach forward to the pedal lobe (p. 131).

10. Nerves to the buccal mass

10.1. *Buccal ganglia*

The superior buccal ganglion is a narrow band of tissue above the oesophagus (figures 1 and 2 and figure 85, plate 9). It contains an outer layer of cells up to 30 μm in transverse diameter in a *Loligo* of 15 cm mantle length, and a dense layer of small cells near the neuropil. The labial nerves arise from it in front. At each side it gives rise to the inter-buccal connectives and to a small bundle that by-passes the inferior buccal ganglion. Part of this runs to the subradular ganglion and part probably to the posterior salivary gland, but the details have not been analysed.

The inferior buccal ganglion contains more numerous large cells, extending up to 50 μm in the *Loligo* of 15 cm mantle length. At the back of the ganglion is a complex system of lobules, mainly of small cells, with a few scattered larger ones. The sympathetic nerve trunks probably arise from this region and run up near the mid-line to the oesophagus (figure 32, p. 121). This ganglion contains large amounts of noradrenaline (Juorio 1971). It is interesting that no mass of juxta-ganglionic tissue arises here as it does in *Octopus* (Young 1971).

10.2. *Subradular ganglia*

These are minute collections of a few nerve cells at the base of the salivary papilla (figures 1, p. 106 and 86, plate 9). They are joined by a commissure below the salivary duct and they send fibres forward to the papilla.

The origin of the nerve was traced to the sides of the salivary duct, and presumably comes from the superior buccal ganglion, with the posterior salivary nerve, which is also minute.

11. Blood supply and gliovascular tissue

Each of the suboesophageal centres is provided with a system of arteries and veins communicating by capillaries (figure 95, plate 10). The arteries mostly run through the centres of the lobes, giving off branches approximately at right angles. The capillaries collect towards the outside of each lobe, joining the larger veins at angles less than a right angle. The main veins run over the surface of the lobes.

The capillaries thus do not come very close to the tissues. Nourishment is probably passed by the set of cells called the gliovascular tissue by Bogoraze & Cazal (1945). The nuclei of these cells may lie independently in the neuropil or attached to an arteriole or capillary. The cell sends branches that wrap around the vessel (figures 87*a*, plate 9, and 108, p. 152). Indeed it may be that the spaces around all vessels are completely covered by the cytoplasm of these cells (figures 99 and 99*a*, plate 10). From these perivascular sheaths bundles proceed outwards among the tissues. The processes may be short, giving the vessel a covering looking like a mat of hairs (figure 99). Other processes, especially near the ends of the finer vessels, are stout (5 μm) but break up into exceedingly fine branches at the tips (figures 87*a*, plate 9 and 108). These branches presumably carry material from the vessel to the tissues or from the tissues to a vein. The fine branches are varicose and are interposed among the fine neural twigs, whose pattern of branching they therefore resemble. It is not clear whether these are hollow tubes communicating with the lumen or perivascular space of the larger vessel to which they are attached. The finest branches extend below the level of optical resolution. It might be that diffusion to and from the nervous tissues occurs around these fine processes, rather than within them. Further study with the electron microscope is needed.

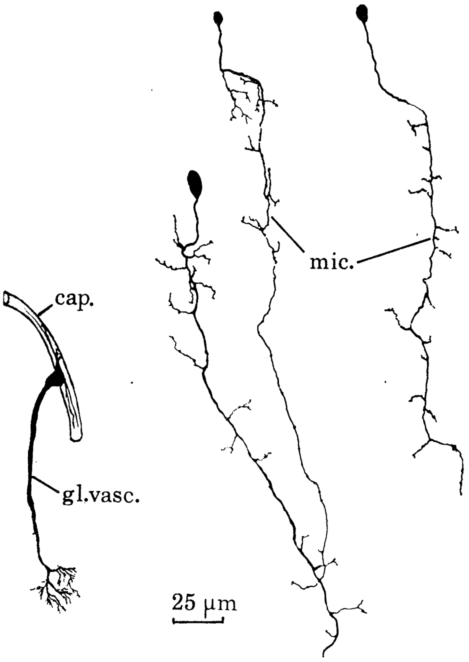

FIGURE 108. *Alloteuthis subulata*. Anterior pedal lobe. Microneurons and a branched gliovascular cell attached to a blood vessel. Golgi.

In other regions cells similar to the above have a star shape with characteristic rather straight branches making anastomosis with those of other cells (figures 97 and 98, plate 10). Finer lateral branches are given off from these main trabeculae and terminate among the tissues. There are also end feet attached to the vessels. In these respects the cells resemble those described above, but there are obvious differences. They recall some aspects of the glia (Young 1971). In some places bushy formations attached to vessels recall the formations called 'lymph spaces' in *Octopus*.

Some Golgi preparations show stained material all around nerve cell bodies and their trunks (figure 100, plate 10). Some of this material presumably belongs to the glia cells, whose nuclei are numerous in the cell layers. It is not clear how these cells are related to the blood vessels. Their cytoplasm lies very close to the surface of the neurons and indeed penetrates the latter as a system of channels. These 'Holmgren's canals' are especially well developed in these large neurons of *Loligo*.

12. Fibrous glia

There are many of these very large cells in the suboesophageal ganglia (figures 101–103, plate 10). They may be spherical, with numerous, fine, varicose fibres radiating out approximately straight through the neuropil. The cell bodies are large, often more than 50 μm in diameter and filled with granular material as seen in Golgi preparations, but the nuclei are small. Each fibrous process arises separately from the cell body and runs directly, with little branching and only gradual tapering to its tip. The diameters are only about 1 μm at the base and the varicosities are about 2 μm. The fibres run for hundreds of micrometres, sometimes accompanying tracts but often in all directions through the neuropil.

These cells are also related to blood vessels, indeed the cell body is generally attached to a vessel (perhaps always). Around them there are often shorter processes of the gliovascular cells attached to the same vessel.

13. Dendritic collaterals

13.1. *Various types of dendritic apparatus*

Except for the first order giant cells all synapses in the suboesophageal lobes are made by dendrites collateral to the main trunk of unipolar cells. These show different patterns of branching in the various lobes and have many interesting variations. Certain features are common to all. All the larger neurons carry collaterals over quite a long stretch between the cell body and the centre of the neuropil. The form of the collaterals varies considerably. In the anterior pedal and lateral pedal lobes they come off at right angles to the main trunk and run for up to 100 μm tangentially (figures 27, p. 116 and 33, p. 123). These cells are motoneurons and each is activated by a cylinder of neuropil. The collaterals of neighbouring neurons certainly overlap. Afferent fibres entering the lobe run tangentially across the dendrites and presumably activate the cells simultaneously or sequentially. Other cells that are certainly motoneurons are similar, e.g. those in the fin lobe (figure 93, plate 9). However, those of the central palliovisceral lobe have more sparse collaterals, not all at right angles to the main trunk (figure 87, plate 9). It is possible that distinct collaterals are connected with particular specific inputs but no regularities have been seen. The motoneurons of the chromatophore lobes have long collaterals with many terminal branches as well as some at the base (figure 107, p. 146).

Some large neurons appear to carry very numerous short collaterals on the main trunk (figure 91, plate 9), but in others this trunk is smooth. Many of the collaterals have a long thin base, with few or no secondary branches and then numerous twigs and knobs at the tip (figure 27, p. 116). If the synaptic points are thus collected at the end of a branch it may be that those of each branch can act independently as has been suggested for dendritic spines in vertebrates (Diamond, Gray & Ysargil 1971). The very long collaterals in the chromatophore lobes may act in this way (figure 107, p. 146).

Some neurons carry bushes of dense collaterals in the outer layer of neuropil (figure 105, p. 143). These may be in special relation with the processes of short axon cells. Others on the contrary may have only short collaterals proximally, then a few long ones and then short again.

With all these variations one constant feature is that each large neuron is in relation to a large volume of neuropil of irregular shape. The incoming fibres usually spread widely and it would be interesting to discover whether the various separate neurons in any one region can differ greatly in the connections they receive. It may be that large numbers all work together, or at least are activated serially.

The larger neurons that are not motoneurons but end within the suboesophageal mass may differ somewhat from the motoneurons. Those shown in figure 28, p. 117 have rather few dendrites, widely scattered in the magnocellular lobe but others in this lobe have more. The cells in figure 104, p. 142 are from the lobule of the anterior palliovisceral lobe that sends fibres to the fin lobe (p. 140). They make an interlacing mass of curled dendritic collaterals. On many of these fibres there are two sets of collaterals, one near the cell layer and the other further away. We cannot yet say whether these correspond to two sources of input.

The differing patterns of dendrite branching must surely be significant. For instance the long thin dendrites of the chromatophore lobes (figure 107) presumably act differently from the short stout ones of the cells of the fin lobe in figure 93. And there are many intermediates.

13.2. *Synaptic points*

Many of the Golgi preparations show much detail of the finer branches of the dendrites. These are presumably the actual points of contact, though only one member of the synaptic union is stained. However from these terminal points an estimate of the number of contacts can be made. Thus the oculomotor neurons are estimated to have at least 500–1000 contacts (p. 125), those in the anterior pedal lobe more than 2000. These figures are probably too low but they show that thousands of contacts on each neuron are usual throughout the suboesophageal ganglia. Of course it is not known how many input fibres contribute to the contacts to each cell. Nor can we say whether all contacts contribute equally to excite or inhibit it.

Many of the contacts seem to be made by tiny collateral twigs, sometimes with a swollen base (figures 92 and 92*a*, plate 9).

Some dendrites have stout main trunks carrying numerous small spines, presumably each a synaptic contact. Others consist of quite short branching tufts and some are single spines on the main trunk. The spines may be carried all along (figure 94, plate 10) or grouped at the base or end of the collateral or both. The spines may consist of a swelling, from which a small terminal twig stands out, sometimes less deeply stained with silver (figures 92 and 94). Swelling may occur at branch points or elsewhere along the dendrites. They seem to be especially marked on the dendrites of cells of the chromatophore lobes (figure 92).

With all these variations investigation of the synapses in the different lobes by electron microscopy should be very rewarding. Until we know more of the anatomy and physiology there is still too little information available for any clear statement about the functioning of the neuropil. It may be that each neuron is independently excited or inhibited by the combination of incoming impulses. But we do not know to what extent there are synapses between branches of the cells themselves. Certainly the processes of many of the smaller cells are restricted to a small volume of neuropil. It is even possible that a whole volume of neuropil acts as an integrated whole, with the propagation of activity through it. The fact that the neuropils of neighbouring centres is fully continuous without obvious breaks suggests a functional unity.

14. DISCUSSION

14.1. *Microneurons*

The Golgi preparations have shown many details of the smaller cells of the suboesophageal lobes. Many of them are shown to be microneurons, in the sense that they carry no long axon but end within the neuropil of their own lobe (Young 1972). The question of the natures of the various types of small cell and the naming of them remains controversial (Gray 1974). The smaller of them are amacrines with a few branches in the outer layers of the neuropil (figure 61, p. 137). Others proceed to the centre, giving collaterals on the way and tapering to a fine termination (figures 33*a–c*, p. 123). In some of these the final part is varicose and has the appearance of an axon. But there is no sharp distinction between this terminal region of the fibre and the more proximal part carrying collaterals that are presumably dendritic. These collaterals are few and mostly quite short (20 μm) and nearly always unbranched. Each consists of a spine with a few varicosities and a blunt tip. Their sparse distribution is in marked contrast to the abundance of collaterals on the motoneurons. Some of those shown seem to have only about 20 synaptic points, compared to the thousands on large cells nearby.

Study of these microneurons is a first requirement for the understanding of the actions of the suboesophageal lobes. They are of course vastly more numerous than the larger cells, but each of them seems to make fewer contacts. Do they carry specific signals from point to point in the neuropil or serve to produce some general effect around themselves? It is particularly intriguing that short axon cells are absent from the chromatophore lobes and fin lobes. It has already been shown that they are present in the dorsal half of the stellate ganglion but not the ventral (Young 1972). It is possible that they do not occur on pathways where the synapses are simple relays, acting always to produce the same action. Where they do occur, these cells may be involved in reciprocal reflex action, perhaps serving for inhibition of the unwanted movement. A striking example of the contrast between regions with and without them is between the central palliovisceral lobe and the nearby fin lobe (figure 69, plate 7).

14.2. *The oculomotor centres, lateral pedal lobes*

The system for the control of eye movements is clearly marked off from other systems (figure 109, p. 156). The motoneurons of the eye-muscle nerves are influenced directly by fibres from both the macula and crista of the statocyst. No fibres from the optic lobes reach them directly, but there are large sets from the peduncle lobe, and anterior basal and median basal lobes (p. 126). These are all lobes that also have extensive optic and statocyst inputs and return pathways to the optic lobes. The systems of efference copies involved will be discussed in the next paper of this series. Electrical stimulation of these basal lobes in *Sepia* produces movements of the eyes, arms and head (Boycott 1961). The question of whether there are proprioceptive fibres from the eye muscles is difficult to resolve because of uncertainty as to the destination of the fine fibres that accompany some of the eye and muscle nerves (p. 120). There is no evidence of a reverse pathway from the lateral pedal to the higher visual centres either in *Octopus* or *Loligo*, but neither can it be rigorously excluded.

The oculomotor centres of the two sides are connected by a suprapedal commissure (p. 125). This suggests that these centres are essentially ‘cerebral’, as might be expected from their connection with the eyes.

There are considerable differences between the optic and ophthalmic nerves of octopods and decapods, connected with differences in the lids and perhaps dioptric systems. However, some of these nerves seem to contain only large fibres and it is provisionally concluded that there are no proprioceptors.

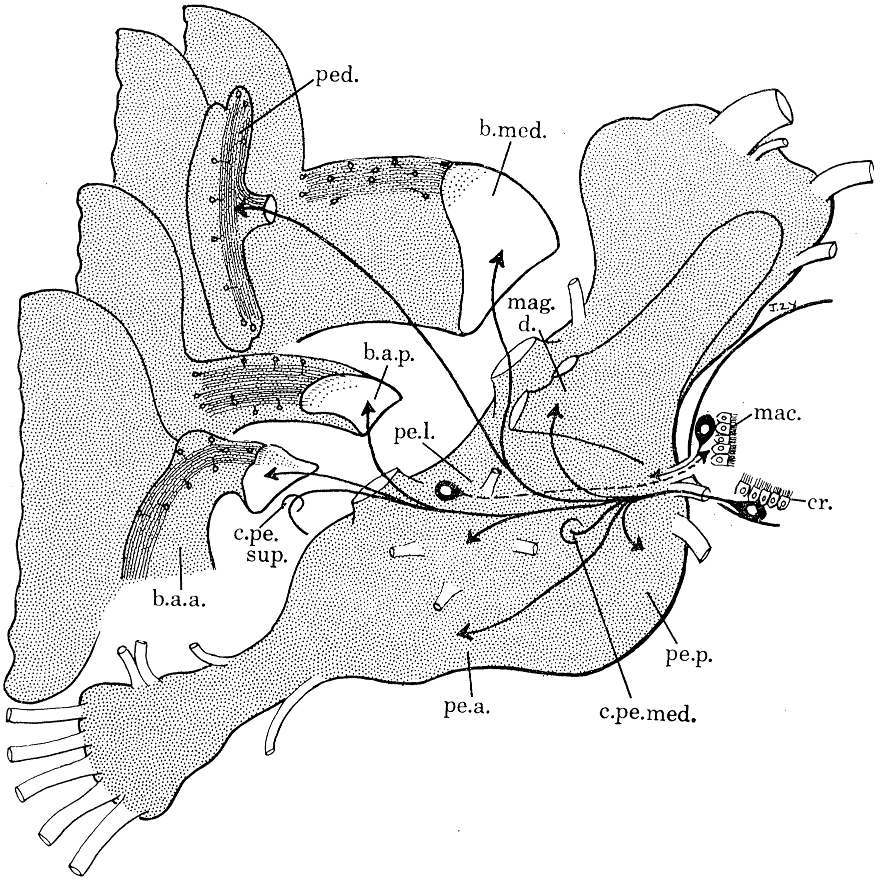

FIGURE 109. Diagram of the distribution of nerve fibres from the statocyst. They are shown as if all come from the crista nerve. The separate distribution of the fibres of the macula nerve are not well understood. The efferent fibres are shown running to the macula (dotted line) but of course they also run to the crista. In this and figures 110 and 111 the optic lobes are shown as sections exploded apart.

14.3. *Control of movement*

The various components of the locomotor system are separately controlled from suboesophageal centres and are called into play partly by the higher ones, partly by direct local reflex responses. This is especially well shown by the giant fibre system, originating in the first order giant cells (figure 110). The ventral magnocellular lobes receive inputs from many sources, from the optic lobes, from supraoesophageal centres and directly from the macula and crista of the statocyst and skin of the head (p. 137). The direct influences provide for escape reactions to contact or sudden disturbance (from the macula). Electrical stimulation of the skin of the back of the head produces giant fibre contractions following the frequency of stimulation (unpublished results). In attack or escape reactions to visual stimuli the input is first analysed by the optic and basal lobes before initiating the jet action.

The retractors of the head and funnel are presumably brought into action with the jet but are also used in steering and they are separately innervated from retractor centres in the posterior pedal and anterior palliovisceral lobes. Large fibres from the ventral magnocellular lobe pass to the posterior pedal and palliovisceral lobes and are presumably activated with the first order giant cell, ensuring activation of the retractors when necessary.

The fins are continually active, except when jetting, but no anatomical basis for this continuous action has been seen. The tract from the antero-ventral palliovisceral lobe to the fin lobe may be concerned with stopping the fins during the jet (p. 140). In *Sepia* it is known that the isolated suboesophageal centres produce continuous action of the fins, perhaps generated by rhythmical activity in the fin lobes (Boycott & Young 1950). Unilateral lesions of the anterior basal lobe produce circling in *Sepia* and in *Octopus* (unpublished results).

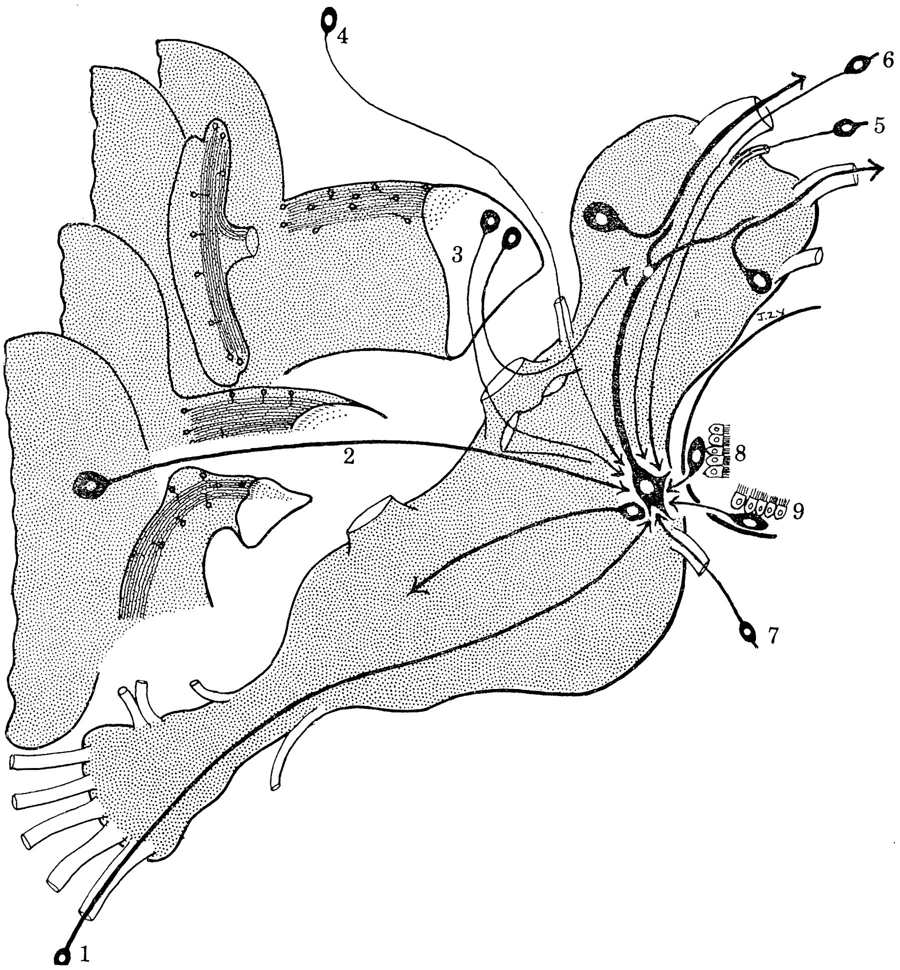

FIGURE 110. The final common path through the giant fibre system. The numbers indicate the inputs to the first order giant cell as listed in the text from (1) the arms, (2) the optic lobes, (3) the median basal lobe, (4) the surface of the head, (5) the collar, (6) the mantle, (7) the funnel, (8, 9) the macula and crista. Output fibres of the ventral magnocellular lobe also go to the anterior pedal lobe and there is a third set to the dorsal magnocellular lobe (not shown). Only two of the second order giant cells are shown.

The intermediate centre for control of steering seems to be in the posterior pedal lobe (figure 111). The forward-backward control of the funnel is probably by the nerve to the median funnel adductor, and control of turning with the fins is through the large posterior pedal to fin lobe tract. Turning is also effected by directing the funnel, by the anterior and perhaps also posterior funnel nerves, and probably also by the retractors of the head and funnel. The arms are also involved in steering movements by way of the connections from posterior to anterior pedal lobes.

The input to this steering centre is obviously of special importance (figure 111). Large fibres come direct from the crista and are presumably especially concerned with angular acceleration. It is significant that there is no direct pathway from the optic lobe, but a very large input comes through the peduncle lobes and median basal lobe and 'interbasal' regions, which are already known to be concerned with swimming and other actions (Boycott 1961). No other pathways from supraoesophageal centres have been identified but it is not possible to exclude them. Fibres also reach this centre from the arms and mantle.

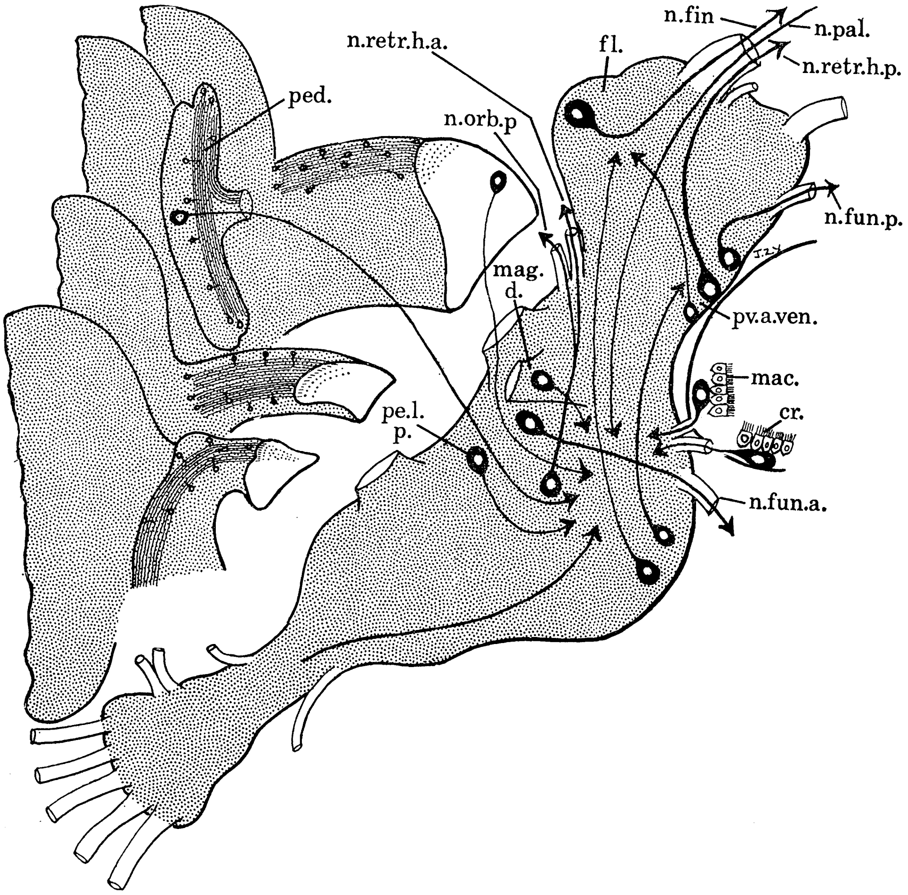

Figure 111. Pathways leading to and from the anterior swimming centre in the posterior pedal lobe. It sends fibres to (1) the fin lobe, (2) the anterior palliovisceral lobe, (3, 4) the anterior and median funnel nerves, (5, 6) the muscles of the neck (postorbital and anterior head retractor nerves).

It receives fibres from (1) the median basal lobe, (2) the crista and macula, (3) the magnocellular lobes, (4) the posterior lateral pedal lobe, (5) the palliovisceral lobe and (6) the arms.

This set of connections suggests that the functioning of the fins, retractors and funnel muscles of the two sides are controlled partly by influences direct from the periphery, partly by the statocyst and partly from higher centres. The optic influence passes mainly through the peduncle and median basal lobes. It may seem curious that no direct pathway is recorded to the posterior pedal lobe from the anterior basal, although fin movements occur on stimulating the latter (in *Sepia*, Boycott 1961). Probably this effect is produced indirectly through the large pathways from the anterior to the median basal. Boycott noted that movement of the fins was more easily produced by stimulation of the median basal lobe than the anterior basal. However it is important to recognize the difficulty of tracing connections and a direct pathway from anterior basal to posterior pedal lobe cannot be wholly excluded.

14.4 *Control of attack*

The large fibres running from the back of the lateral pedal lobe to the anterior pedal probably provide the lower part of the mechanism for control of the tentacles in capture of the prey (p. 128). They lie at the back of the oculomotor centre and it may be that they are brought into action when the image of the prey falls on the appropriate parts on the back of the retina. The attack also involves actions of the other arms, which are presumably controlled from the anterior pedal lobe, perhaps by direct fibres by-passing the anterior suboesophageal mass (p. 111). The relation between this pathway from the posterior lateral pedal and that from the magnocellular to the anterior pedal lobe remains to be discovered. Both consist of large fibres and presumably exercise command of important movements either in attack or retreat or in both.

14.5. *Can the system be described as a hierarchy?*

In some respects the nervous system of cephalopods compares well to the scheme of a Jacksonian hierarchy (see Phillips 1973). There are lower reflex centres, which often act autonomously but are dominated by a succession of higher centres. The scheme applies best at the lower levels considered in this paper. It is more doubtful whether the basal lobes, which will be considered later in this series, can usefully be considered as a hierarchy.

The innervation of the arms shows the clearest evidence. Actions of individual suckers are regulated by sucker ganglia (Graziadei 1971), though we know little of their detailed physiology. They are presumably dominated by the ganglia of the main arm nerve cord and these in turn by the pre-brachial and brachial ganglia. Again little is known of these operations, but here for the first time we find large numbers of small neurons with axons ending within the lobe. These lobes probably control actions in which all the arms work together, as in manipulating prey after seizure.

The brachial ganglia are themselves influenced not only by the supraoesophageal centres but also by fibres from the pedal lobes, which certainly also influence the arms by direct paths (p. 111). The signals for the attacks with the tentacles pass from the optic via the basal lobes to the pedal lobes and this involves suitable actions at the three lower levels. These suboesophageal centres from the arms thus include four clearly distinct levels of control, involving increasingly large sections of the animal. All are in turn subordinate to the optic and supraoesophageal centres.

The significance of a hierarchical organization also appears rather clearly in the pedal, palliovisceral and magnocellular lobes. They allow for use of the lower centres for mantle, fins and arms in various combinations. The jet produced by the giant fibre system can be used to go forwards or backwards or to turn, and either for escape or attack. How the 'decisions' are made is a more difficult question and involves consideration of the organization of the basal supraoesophageal lobes. An elaborate interplay of afference and 'efference copy' or 'corollary discharge' is involved (see Sperry 1950; Holst 1973). However in the lower levels of execution considered in this paper we can detect a hierarchy. The final motoneurons are 'decomposed' into separate sets, and these are brought into action by intermediate centres allowing for various combinations according to commands issued from still higher centres above.

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ABBREVIATIONS USED ON FIGURES

aff.	afferents from connective
anticr.	anticrista
art.	artery
art.pe.le.	left pedal artery
b.a.	anterior basal lobe
b.a.a.	anterior anterior basal lobe
b.a.p.	posterior anterior basal lobe
b.d.	dorsal basal lobe
b.int.	interbasal lobe
b.l.	lateral basal lobe
b.med.	median basal lobe
br.	brachial lobe
br.a.	anterior brachial lobe
br.intra.-pe.con.	intra-brachial–pedal connective
br.po.	postbrachial lobe
br.pr.	pre-brachial lobe
br.-mag.con.	brachial–magnocellular connective
br.-pe.con.	brachial–pedal connective
br.-pv.con.	brachial–palliovisceral connective
buc.i.	inferior buccal lobe
buc.int.con.	interbuccal connective
buc.s.	superior buccal lobe
buc.-br.con.	buccal–brachial connective
cap.	capillary
c.br.int.	interbrachial commissure
c.ch.p.	posterior chromatophore commissure
c.mag.	magnocellular commissure
c.mag.p.	posterior magnocellular commissure
c.mag.p.a.	anterior part of posterior magnocellular commissure
c.mag.d.as.	ascending posterior magnocellular commissure
c.mag.d.de.	descending posterior magnocellular commissure
c.mag.p.p.	posterior part of posterior magnocellular commissure
c.mag.ven.	ventral magnocellular commissure
c.opt.	optic commissure
c.pe.med.	middle pedal commissure
c.pe.p.	posterior pedal commissure
c.pe.sup.	supra-pedal commissure
c.pv.l.ven.	ventral lateral palliovisceral commissure
c.visc.	visceral commissure
ce.f.gi.1.	cell of giant fibre 1
ce.gi.	giant cell
ce.gi.1	giant cell 1
ce.gi.2a	giant cell 2a

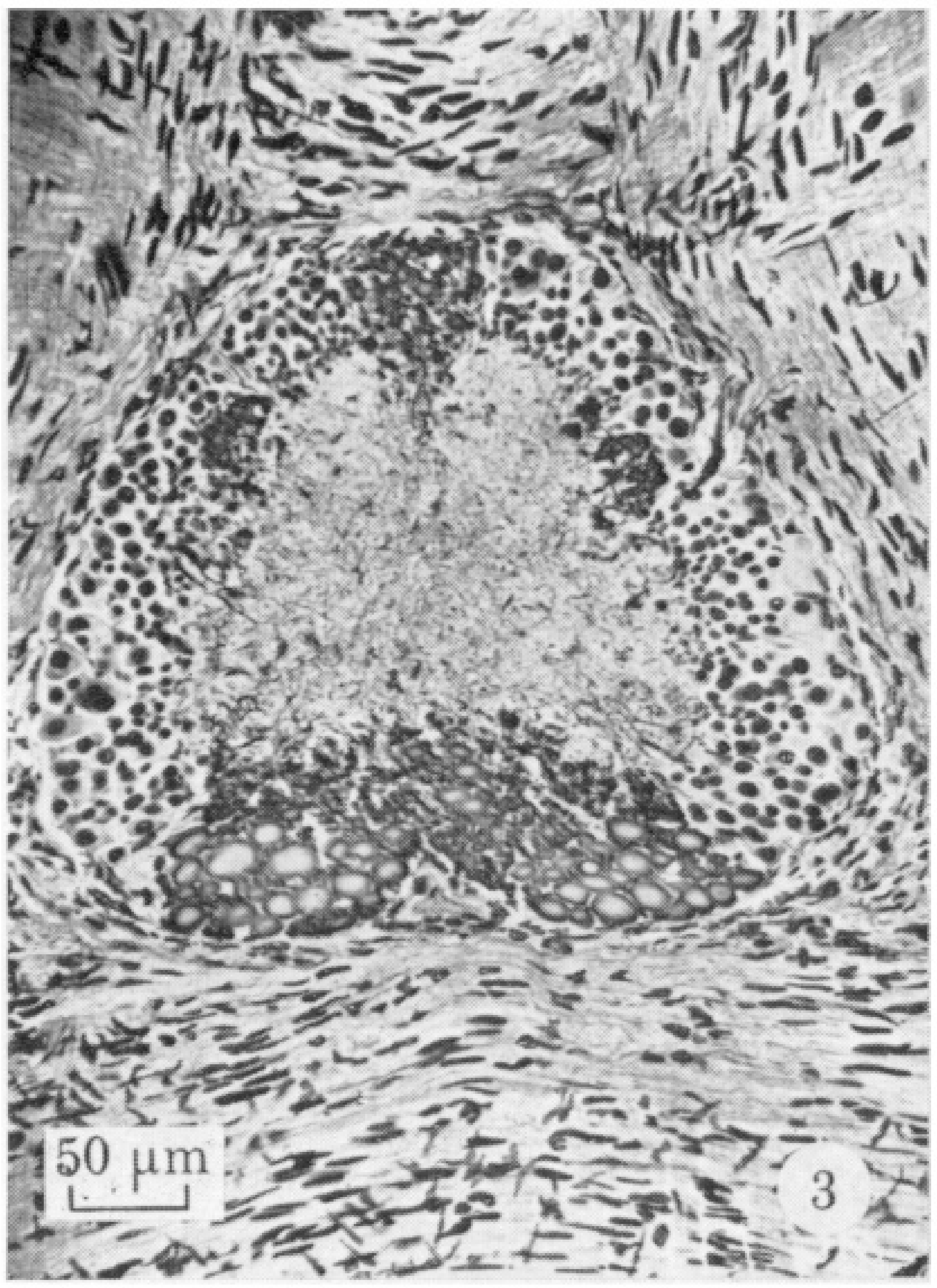
ce.gi.2d	giant cell 2d
ce.mag.-pe.	cell of magnocellular to pedal lobe tract
ce.pe.l.	cell of lateral pedal lobe
ce.sm.	small cell
cer.-br.con.	cerebro–brachial connective
cer.-buc.con.	cerebro–buccal connective
cer.-subrad.con.	cerebro–subradular connective
(+n.sal.p.)	(plus posterior salivary gland nerve)
ch.a.	anterior chromatophore lobe
ch.p.	posterior chromatophore lobe
col.	collar
cr.	crista
cr.trans.	transverse crista
cr.v.	vertical crista
den.a.	anterior dendrite of giant cell 1
den.ven.	ventral dendrite of giant cell 1
duc. sal.p.	posterior salivary gland duct
f.gi.acc.	giant fibre accessory
f.gi.1	giant fibre 1
f.gi.2a	giant fibre 2a
f.gi.2b	giant fibre 2b
f.gi.2b + c	giant fibres 2b + c
f.gi.2d	giant fibre 2d
fl.	fin lobe
fr.i.	inferior frontal lobe
fr.s.	superior frontal lobe
fun.	funnel
g.opt.	optic gland
gan.br.intra.	intrabrachial ganglion
gan.buc.mem.	ganglion of buccal membrane
gan.subrad.	subradular ganglion
gl.vasc.	gliovascular channel
mac.	macula
mag.	magnocellular lobe
mag.d.	dorsal magnocellular lobe
mag.p.	posterior magnocellular lobe
mag.ven.	ventral magnocellular lobe
mag.ven.a.	anterior ventral magnocellular lobe
mag.ven.p.	posterior ventral magnocellular lobe
mant.con.	mantle connective
mant.con.aff.	mantle connective, afferent
mant.con.ch.	mantle connective, chromatophore
mant.con.ch. + stell.	mantle connective, chromatophore + stellar
mant.con.mot.	mantle connective, motor
mant.con.stell.	mantle connective, stellar

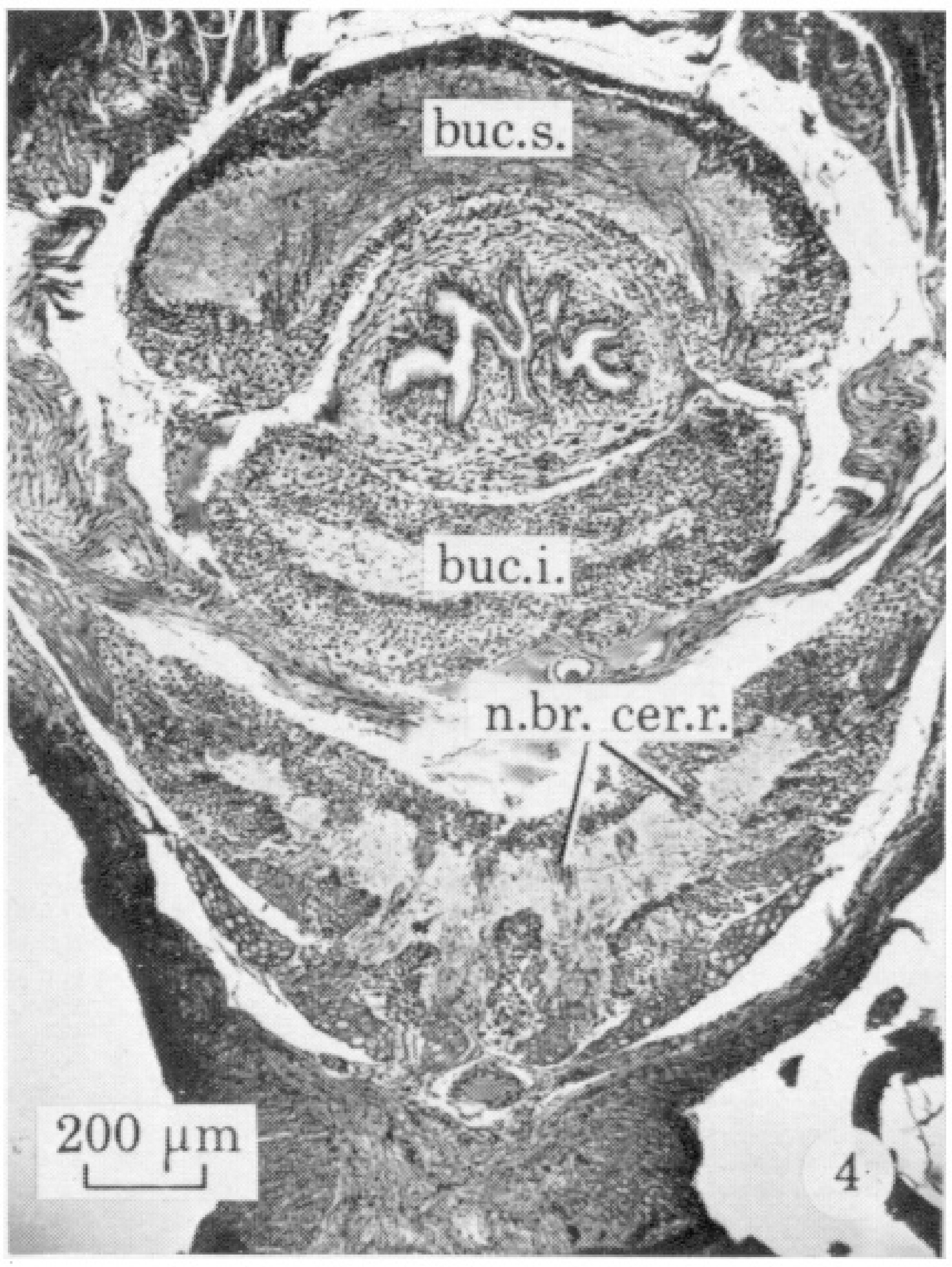
mic.	microneuron
mus.fun.add.med.	median funnel adductor muscle
mus.ocul.	oculomotor muscle
mus.rad.su.	radular support muscle
mus.retr.h.	head retractor muscle
n.antorb.i.	inferior antorbital nerve
n.antorb.s.	superior antorbital nerve
n.br.1–4	brachial nerves 1–4
n.br.l.r.	lateral root of brachial nerve
n.br.cer.r.	cerebral root of brachial nerve
n.br.med.r.	medial root of brachial nerve
n.br.pe.r.	pedal root of brachial nerve
n.col.	collar nerve
n.col.aff.	afferent collar nerve
n.col.eff.	efferent collar nerve
n.col.mot.	collar nerve, motor part
n.col.-mag.	collar nerve fibres–magnocellulular lobe
?n.cr.	? crista nerve
n.cr.	crista nerve
n.cr.d.	dorsal crista nerve
n.cr.f.1–3	fibre of crista nerve branches 1–3
n.cr.ven.	ventral crista nerve
n.cr.-pe.l.	crista–lateral pedal nerve
n.cr.-pe.p.	crista–posterior pedal nerve
n.fin	fin nerve
n.fun.	funnel nerve
n.fun.a.	anterior funnel nerve
n.fun.med.	median funnel nerve
n.fun.p.	posterior funnel nerve
n.lab.	labial nerve
n.mac.	macula 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.oc. + op.p.s.	superior posterior oculomotor and ophthalmic nerves
n.ol.	olfactory nerve
n.op.i.	inferior ophthalmic nerve
n.op.p.i.	inferior posterior ophthalmic nerve
n.op.p.s.	superior posterior ophthlamic nerve
n.op. + oc.p.s.	superior posterior oculomotor and ophthalmic nerves
n.or.fun	funnel organ nerve
n.orb.po.	post-orbital nerve
n.pal.	pallial nerve
n.pal.-mag. + pe.	pallial nerve to magnocellular and pedal lobes

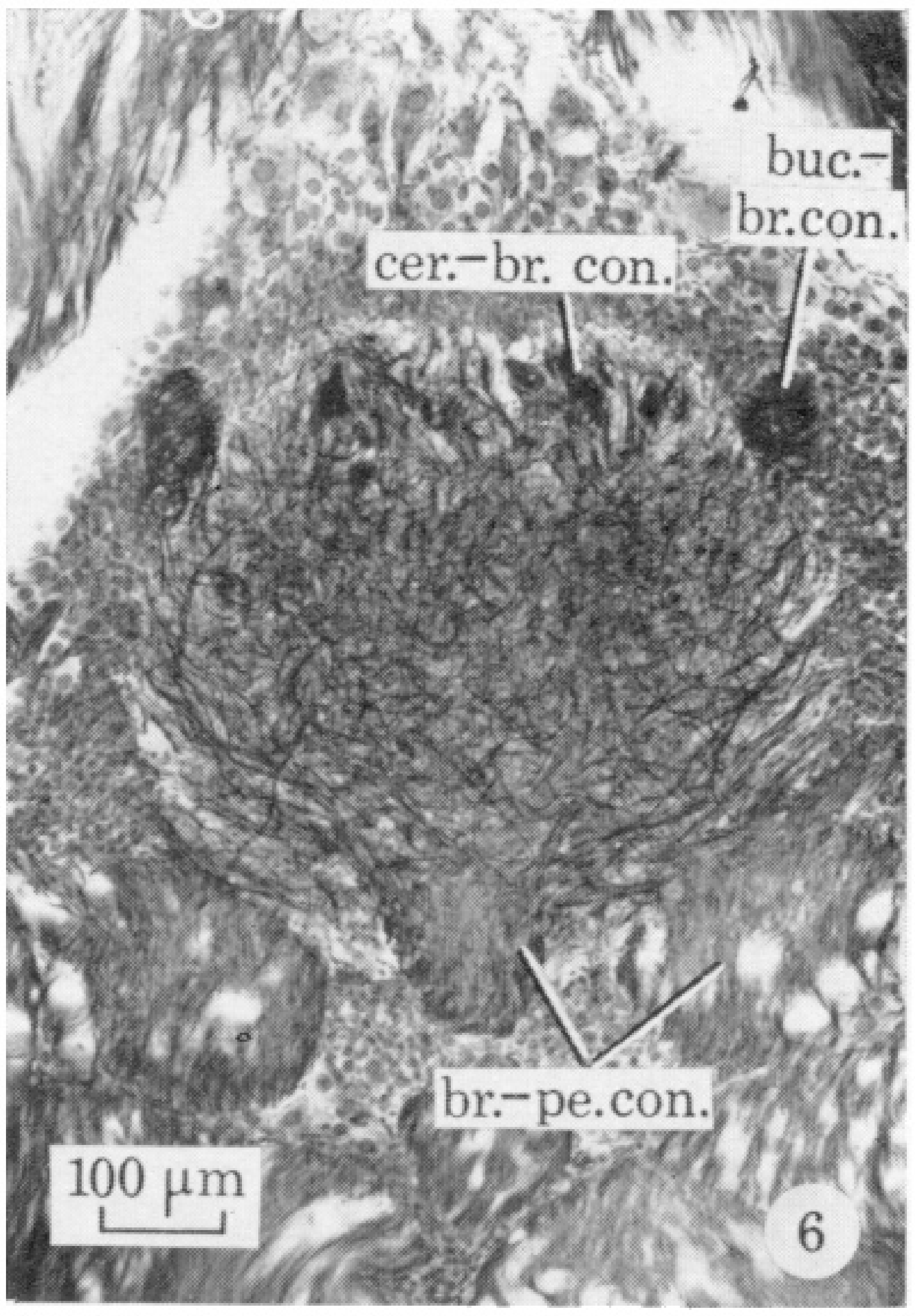
n.retr.h.a.	anterior head retractor nerve
n.retr.h.d.	dorsal head retractor nerve
n.retr.h.p.	posterior head retractor nerve
n.retr.h.p.d.	dorsal posterior head retractor nerve
n.retr.h.p.ven.	ventral posterior head retractor nerve
n.st.	static nerve
?n.st.-b.a.	? static nerve fibres–anterior basal lobe
n.st.-b.a.	static nerve fibres–anterior basal lobe
?n.st.-b.med.	? static nerve fibres–median basal lobe
n.st.-b.med.	static nerve fibres–median basal lobe
n.st.-ped.	static nerve fibres to peduncle lobe
n.st.-ped. + tr.ped.-pe.l.	static nerve fibres to peduncle lobe + peduncle to lateral pedal lobe tract
n.symp.	sympathetic nerve
n.tent.	tentacle nerve
n.vc.	vena cava nerve
n.visc.	visceral nerve
n.visc.d.r.	dorsal root of visceral nerve
n.visc.ven.r.	ventral root of visceral nerve
oes.	oesophagus
ol.	olfactory lobe
opt.	optic lobe
or.fun.	funnel organ
or.ol.	olfactory organ
pe.a.	anterior pedal lobe
pe.l.	lateral pedal lobe
pe.l.a.	anterior lateral pedal lobe
pe.l.p.	posterior lateral pedal lobe
pe.p.	posterior pedal lobe
pe.-pv.con.	pedal–palliovisceral connective
ped.	peduncle lobe
pil.cen.	central neuropil
pil.mar.	marginal neuropil
pil.pf.	peripheral neuropil
prec.	precommissural lobe
pv.a.	anterior palliovisceral lobe
pv.a.ven.	ventral anterior palliovisceral lobe
pv.cen.	central palliovisceral lobe
pv.l.	lateral palliovisceral lobe
pv.l.p.	posterior lateral palliovisceral lobe
pv.l.ven.	ventral lateral palliovisceral lobe
pv.p.	posterior palliovisceral lobe
rad.	radula
sth.	statolith
subped.	subpedunculate lobe

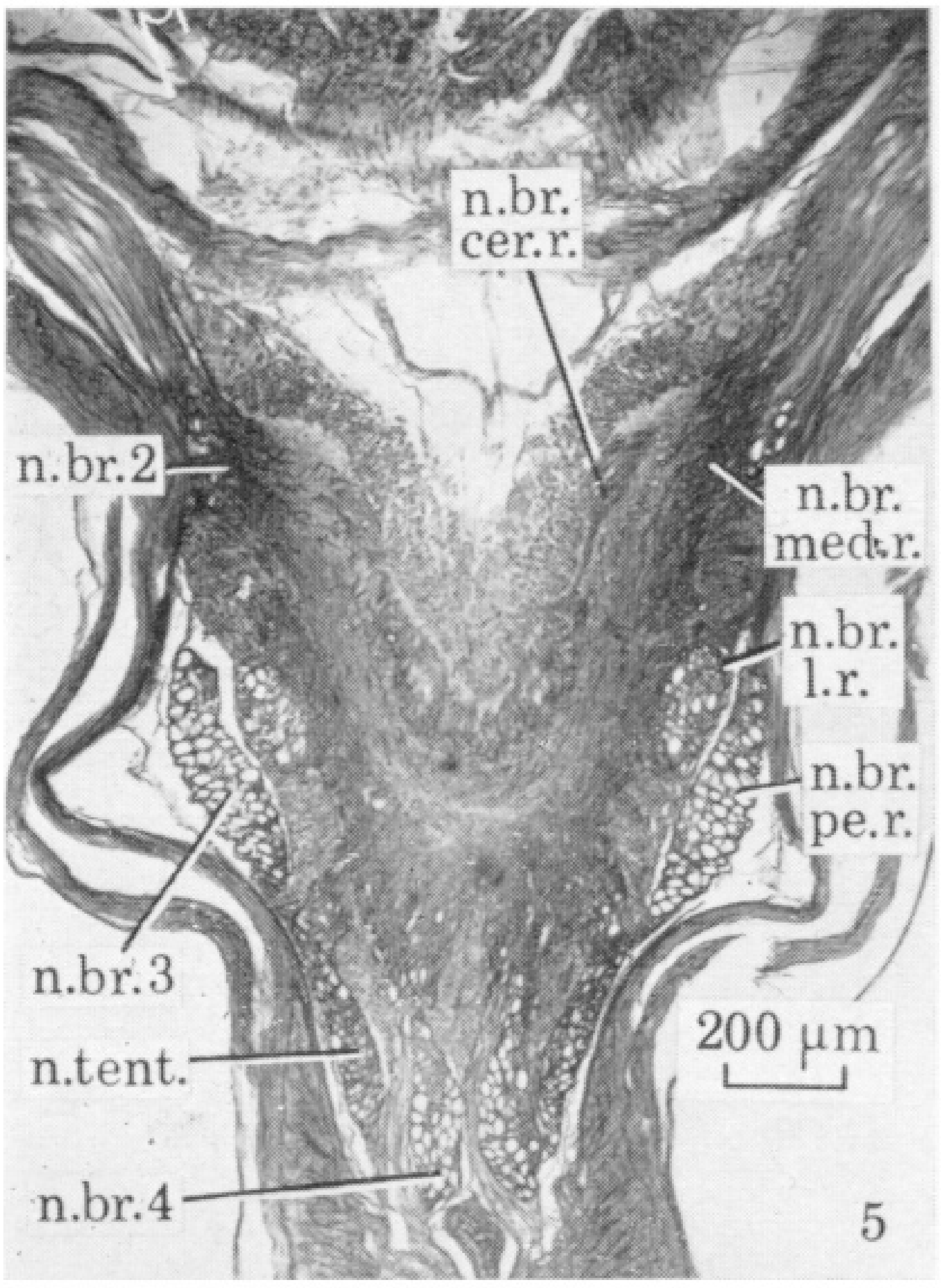
subv.	subvertical lobe
tr.b.a.-b.med.	anterior basal–median basal lobe tract
tr.b.a.-pe.a.	anterior basal–anterior pedal lobe tract
tr.b.a.-pe.l.	anterior basal–lateral pedal lobe tract
tr.b.l.-ch.a.	lateral basal–anterior chromatophore lobe tract
tr.b.l.-ch.p.	lateral basal to posterior chromatophore lobe tract
tr.b.med.-br.	median basal–brachial lobe tract
tr.b.med.-mag.d.	median basal–dorsal magnocellular lobe tract
tr.b.med.-mag.ven.	median basal–ventral magnocellular lobe tract
tr.b.med.-pe.	median basal–pedal lobe tract
tr.b.med.-pe.a.	median basal–anterior pedal lobe tract
tr.b.med.-pe.l.	median basal–lateral pedal lobe tract
tr.b.med.-pe.p.	median basal–posterior pedal lobe tract
tr.b.med.-pv.	median basal–palliovisceral lobe tract
tr.b.med.-pv.cen.	median basal–central pallioviscer al lobe tract
tr.b.med.-pv.(ext.)	median basal–pallioviscer al lobe tract (external)
tr.b.med.-visc.	median basal–visceral lobe tract
tr.br.-mag.	brachial–magnocellular lobe tract
tr.br.-pe.	brachial–pedal lobe tract
tr.br.-pv.	brachial–pallioviscer al lobe tract
tr.cer.	cerebral tract
tr.ch.int.	inter-chromatophore tract
tr.fr.i.-fr.s.	inferior frontal to superior frontal lobe tract
tr.fr.i.-pv.	inferior frontal to pallioviscer al lobe tract
tr.fr.s.-subv.	superior frontal–subvertical lobe tract
tr.fr.s.-v.	superior frontal–vertical lobe tract
tr.mag.pe.	magnocellular–pedal lobe tract
tr.mag.-pe.a.	magnocellular–anterior pedal lobe tract
tr.mag.-pe.p.	magnocellular–posterior pedal lobe tract
tr.mag.-pv.	magnocellular–pallioviscer al lobe tract
tr.mag.d.-pe.	dorsal magnocellular–pedal lobe tract
tr.mag.d.-pe.p.	dorsal magnocellular–posterior pedal lobe tract
tr.mag.d.-pv.	dorsal magnocellular-pallioviscer al lobe tract
tr.mag.d.-pv.cen.	dorsal magnocellular–central pallioviscer al lobe tract
tr.mag.p.-mag.d.	posterior magnocellular–dorsal magnocellular lobe tract
tr.mag.ven.-pe.	ventral magnocellular–pedal lobe tract
tr.mag.ven-pe.a.	ventral magnocellular–anterior pedal lobe tract
tr.mag.ven.-pe.p.	ventral magnocellular–posterior pedal lobe tract
tr.mag.ven.-pv.	ventral magnocellular–pallioviscer al lobe tract
tr.ol.-mag.	olfactory–magnocellular lobe tract
tr.ol.-pv.	olfactory–pallioviscer al lobe tract
tr.opt.-b.a.	optic–anterior basal lobe tract
tr.opt.-b.a.(cruc.)	crossed optic–anterior basal lobe tract
tr.opt.-b.a.(rect.)	uncrossed optic–anterior basal lobe tract
tr.opt.-fr.s.	optic–superior frontal lobe tract

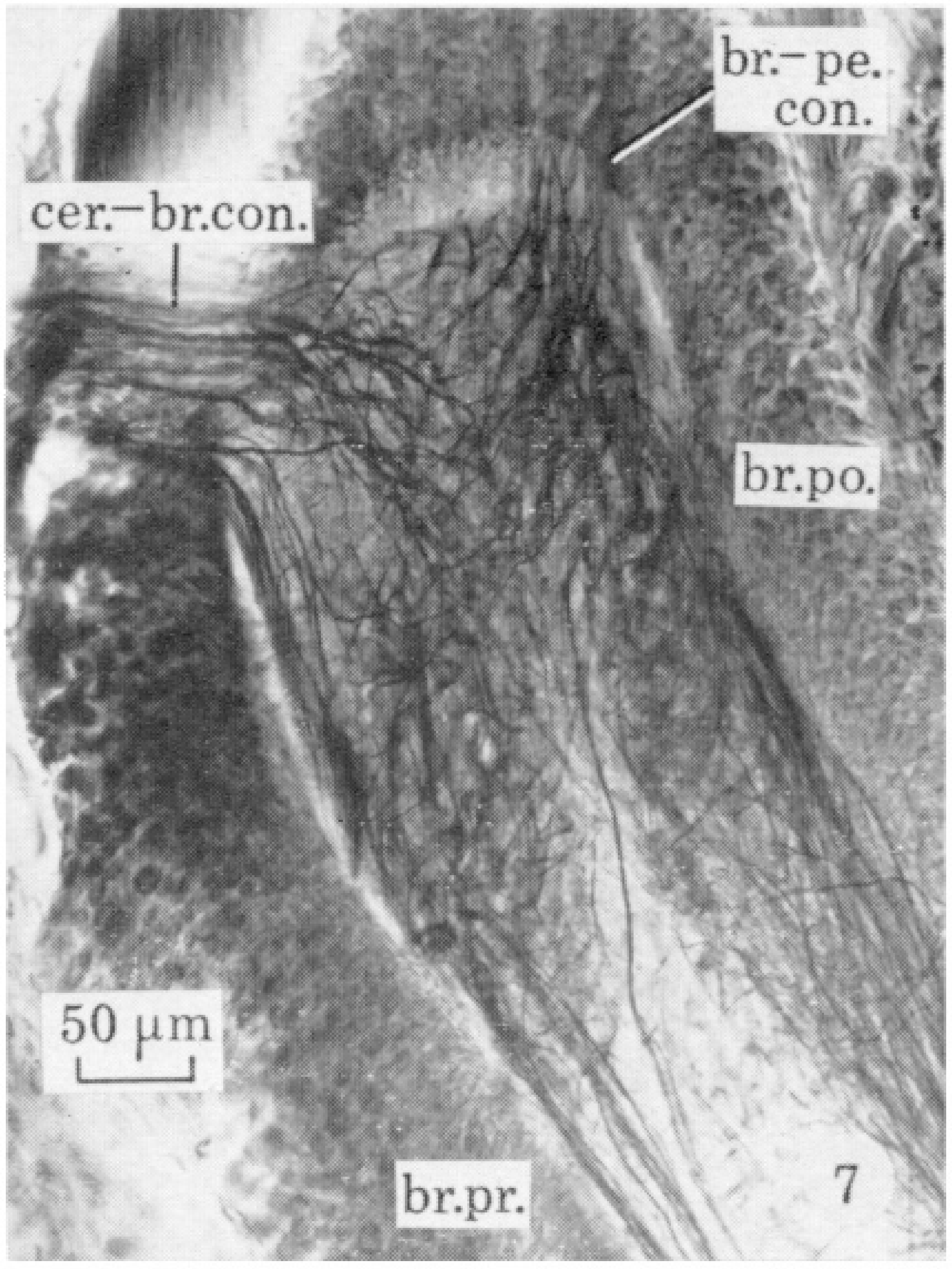
tr.opt.-mag.ven.	optic–ventral magnocellular lobe tract
tr.opt.-prec.	optic–precommissural lobe tract
tr.opt.l.-mag.	lateral optic–magnocellular lobe tract
tr.opt.med.-mag.	median optic–magnocellular lobe tract
tr.orb.po.-pv.	post-orbital–pallioviscral lobe tract
tr.pe.-pv.	pedal–pallioviscral lobe tract
tr.pe.l.-pe.a.	lateral pedal–anterior pedal lobe tract
tr.pe.p.-fl.	posterior pedal–fin lobe tract
tr.pe.p.-pv.	posterior pedal–pallioviscral lobe tract
tr.pe.p.-pv.a.	posterior pedal–anterior pallioviscral lobe tract
tr.ped.-pe.l.	peduncle–lateral pedal lobe tract
tr.prec.-b.med.	precommissural–median basal lobe tract
tr.prec.-br.	precommissural–brachial lobe tract
tr.prec.-pe.	precommissural–pedal lobe tract
tr.prec.-pe.a.	precommissural–anterior pedal lobe tract
tr.prec.-pv.	precommissural–pallioviscral lobe tract
tr.subv.-opt.	subvertical–optic lobe tract
tr.v.-fr.s.	vertical–superior frontal lobe tract
v.	vertical lobe
vc.	vena cava
ve.	vein
ves.pho.	photosensitive vesicles
visc.	visceral lobe
visc.l.	lateral visceral lobe
visc.med.	median visceral lobe
visc.ven.	ventral visceral lobe

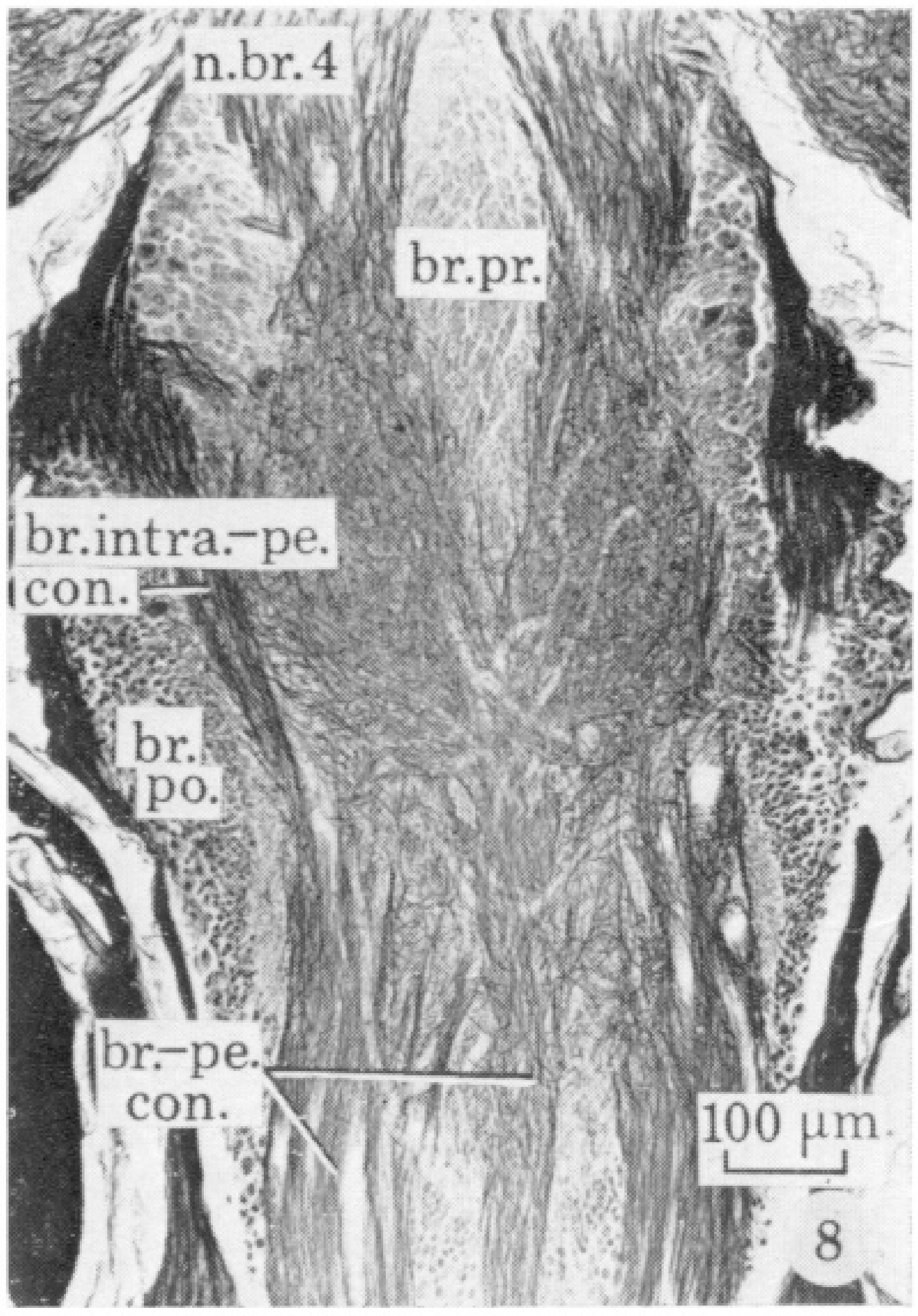


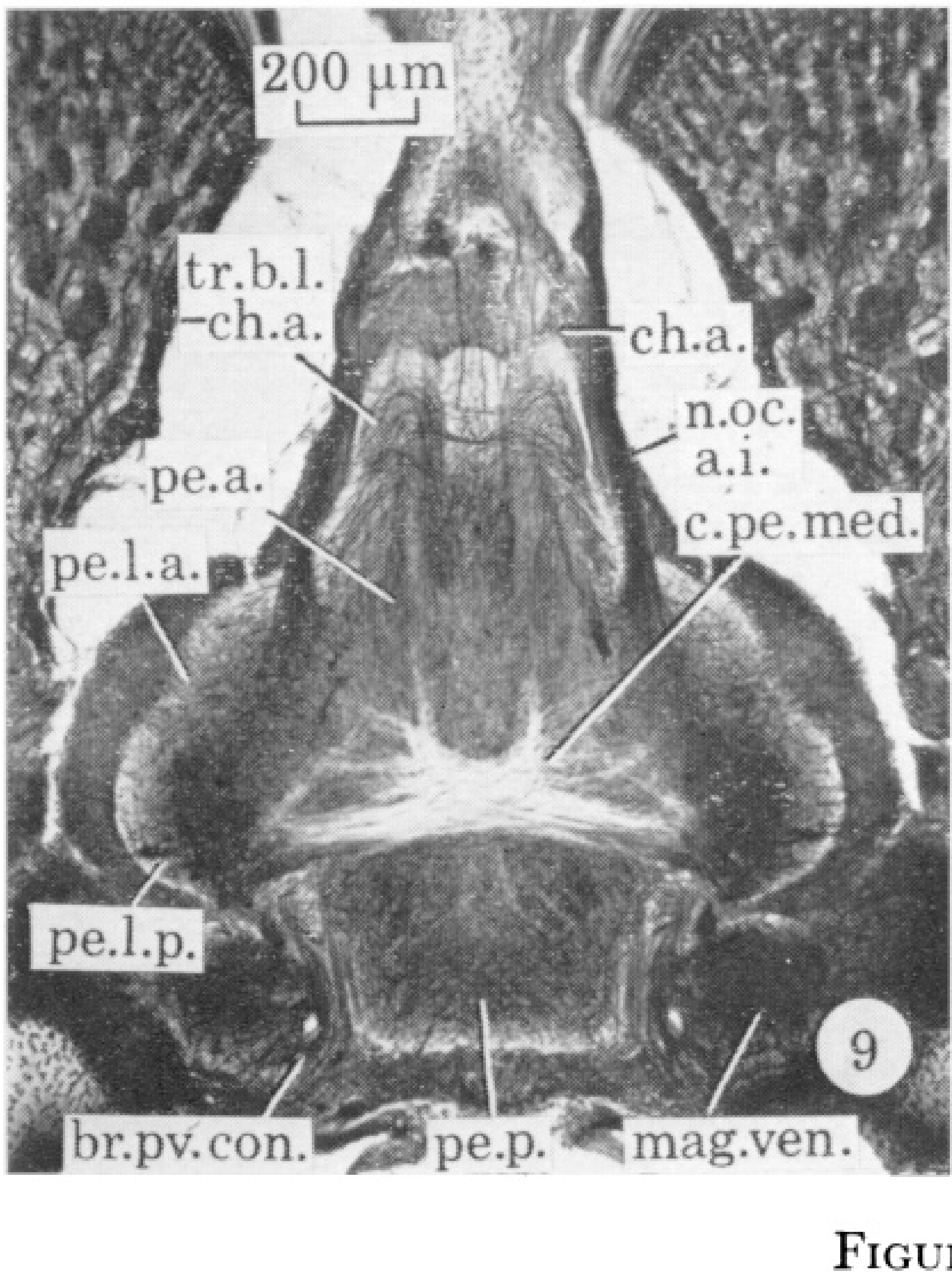


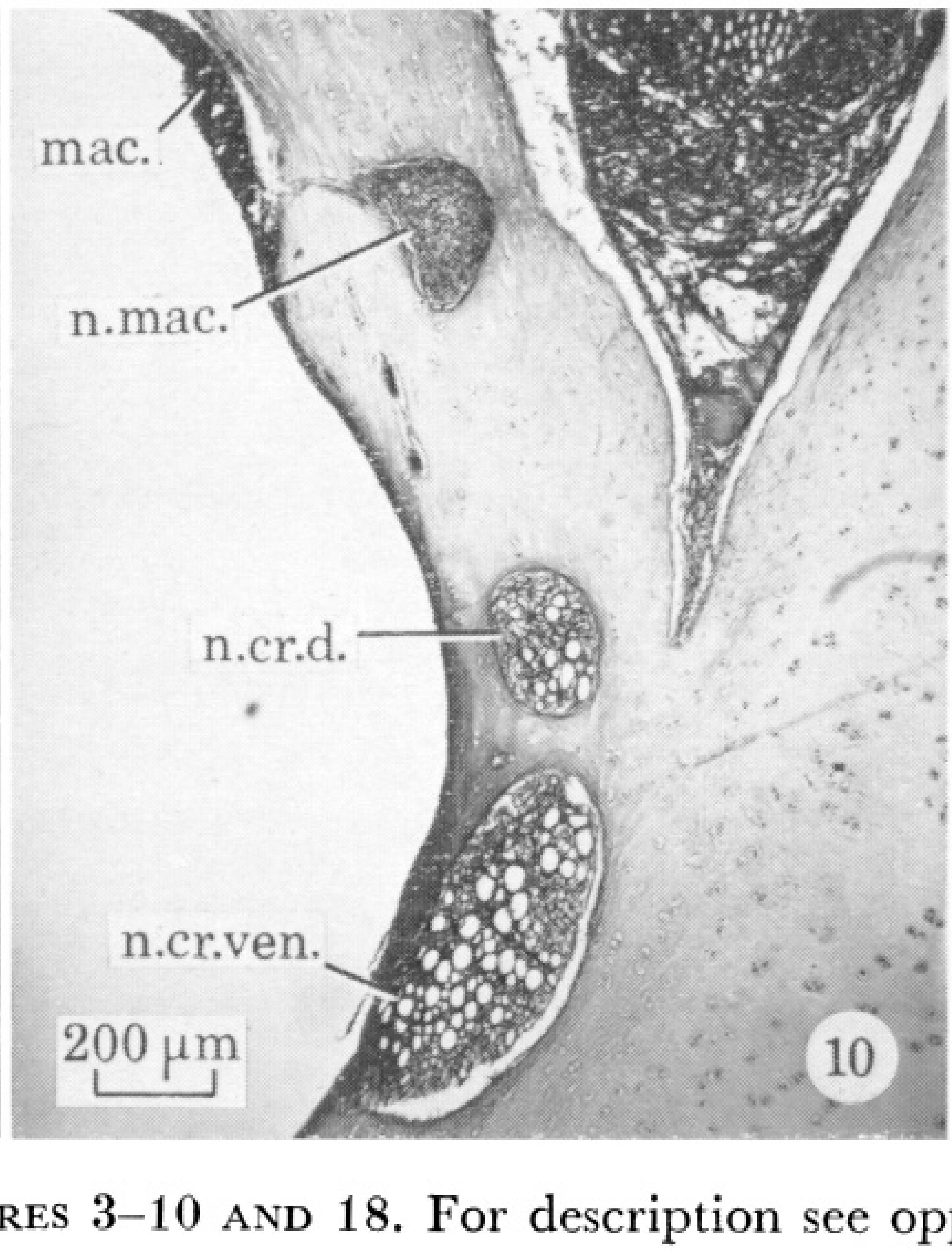


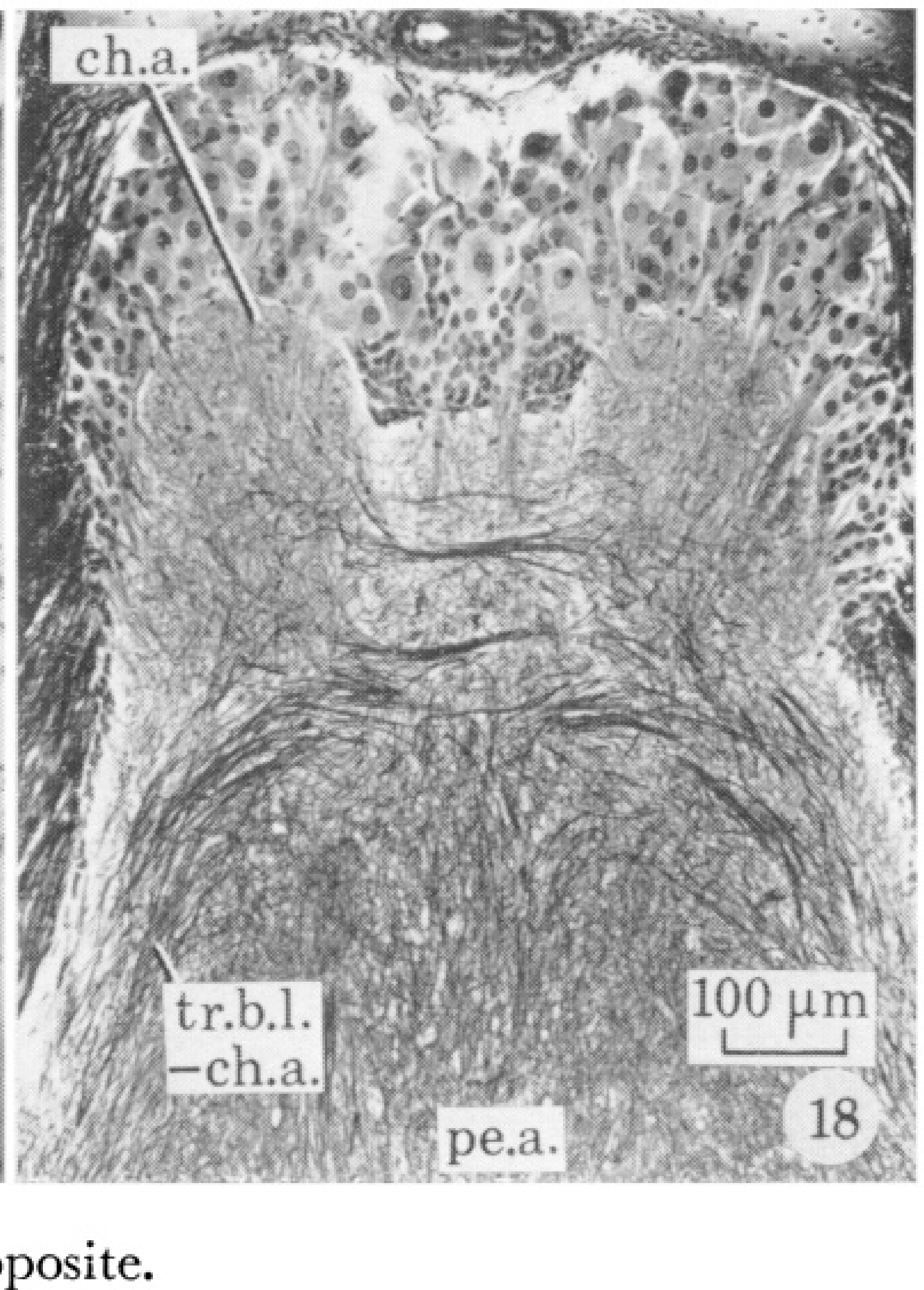




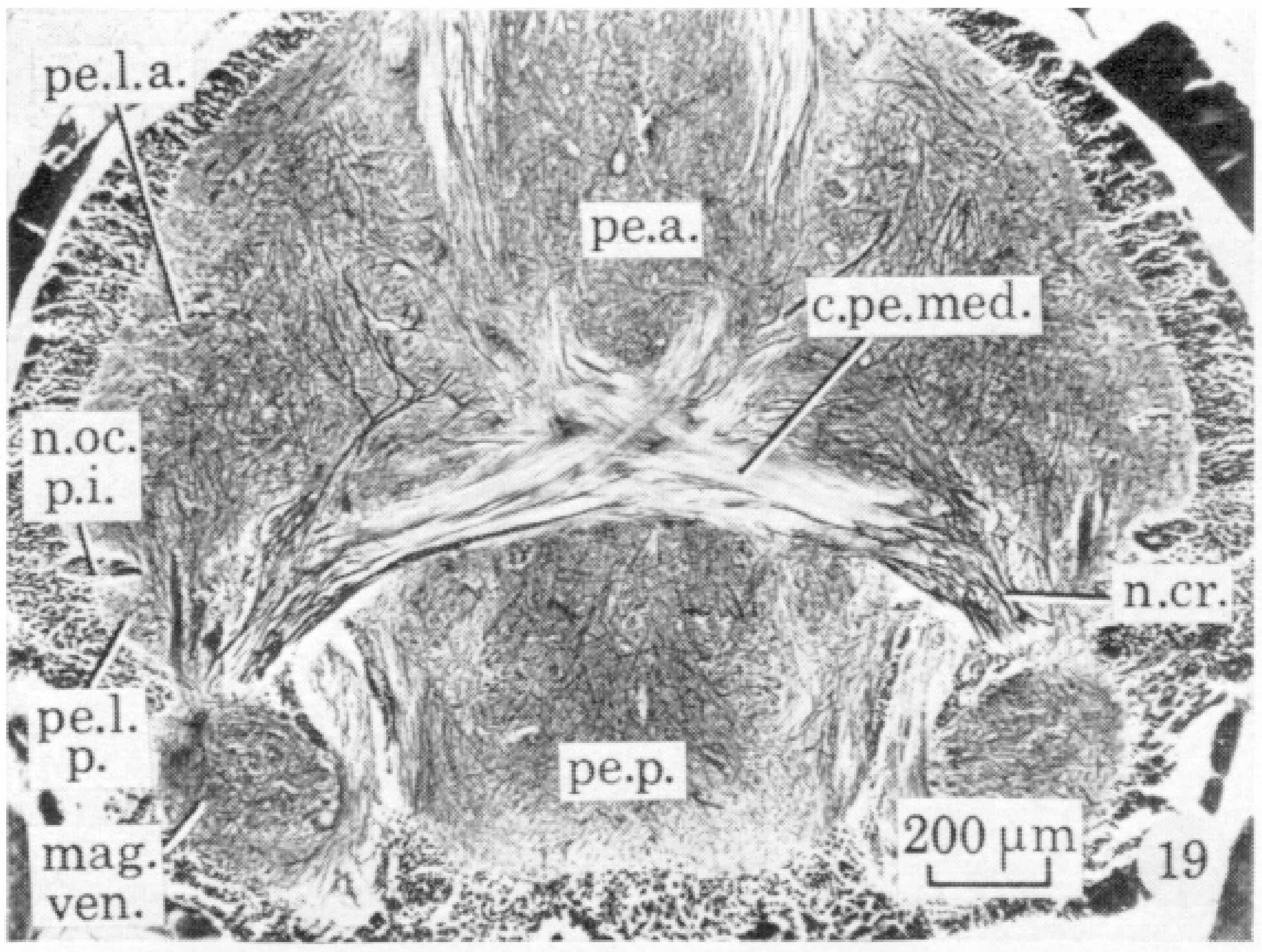


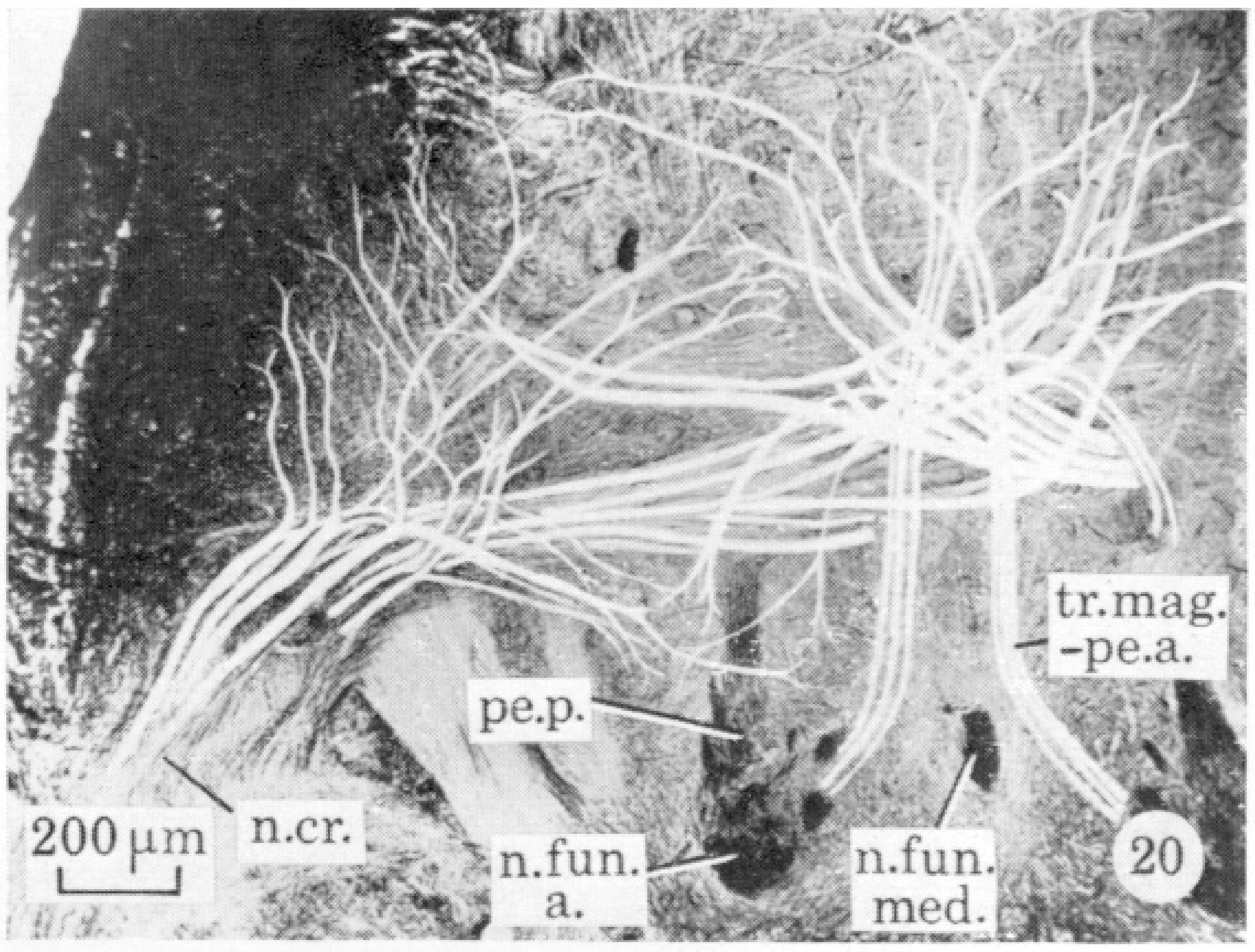


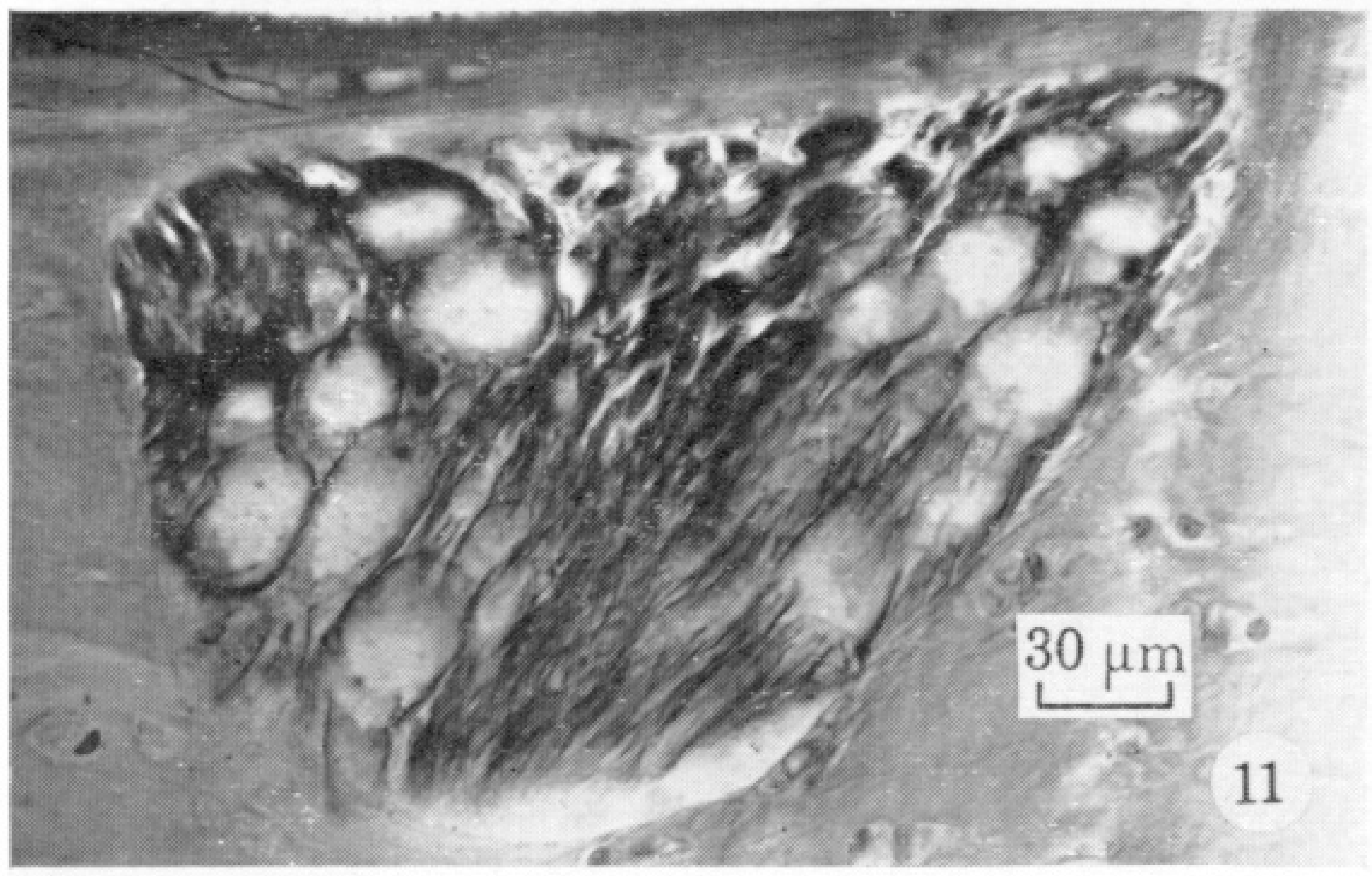


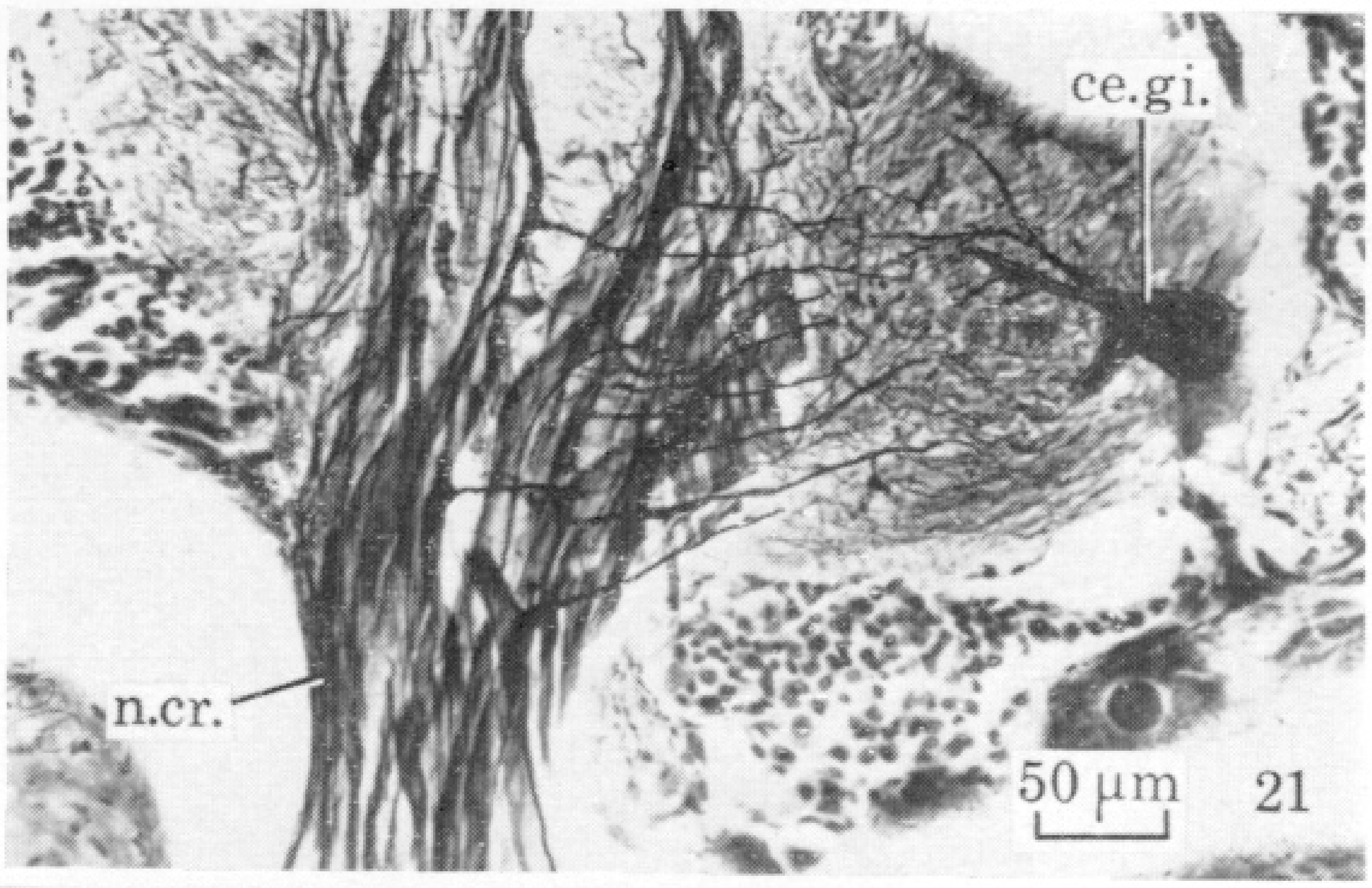


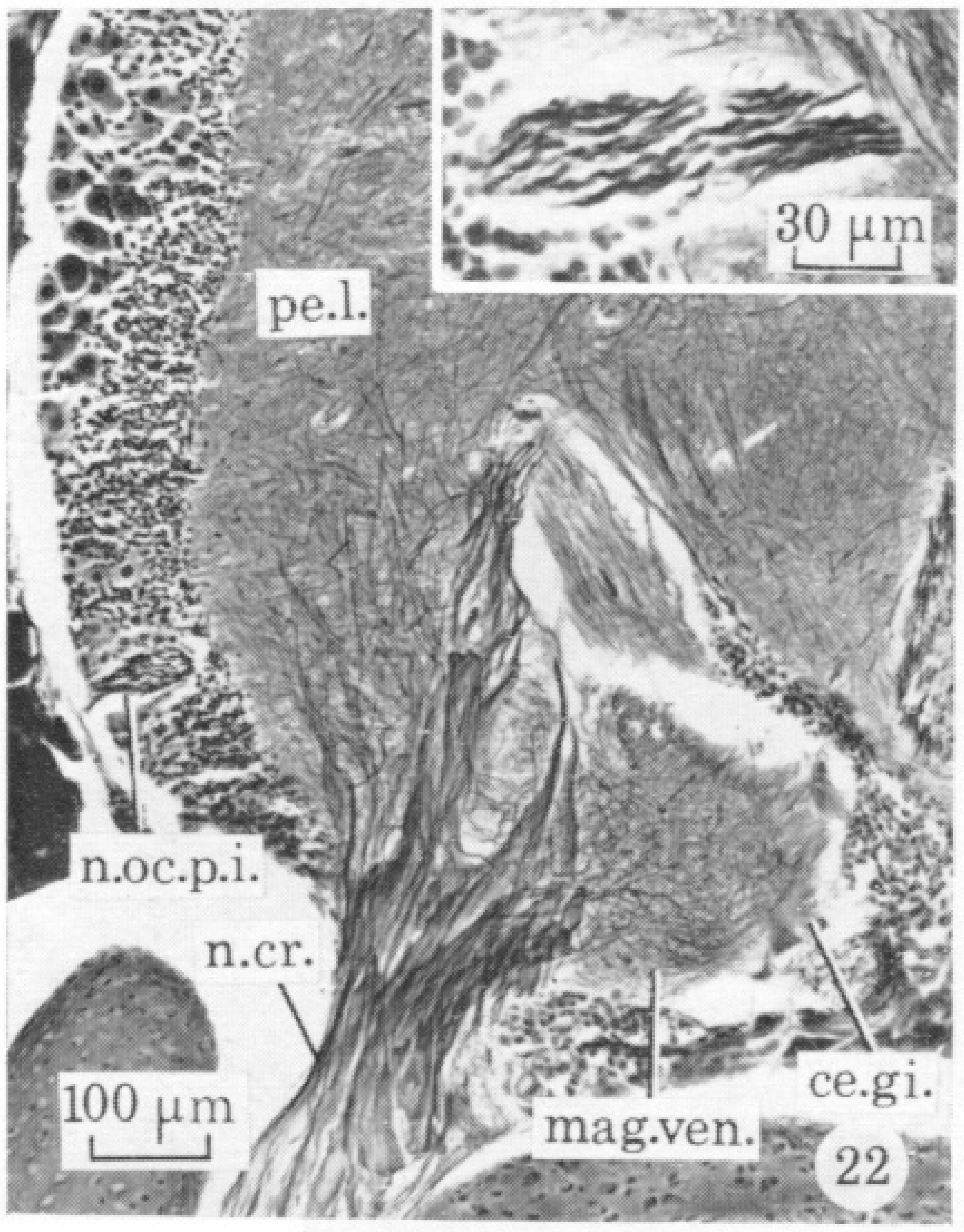
FIGURES 3–10 AND 18. For description see opposite.

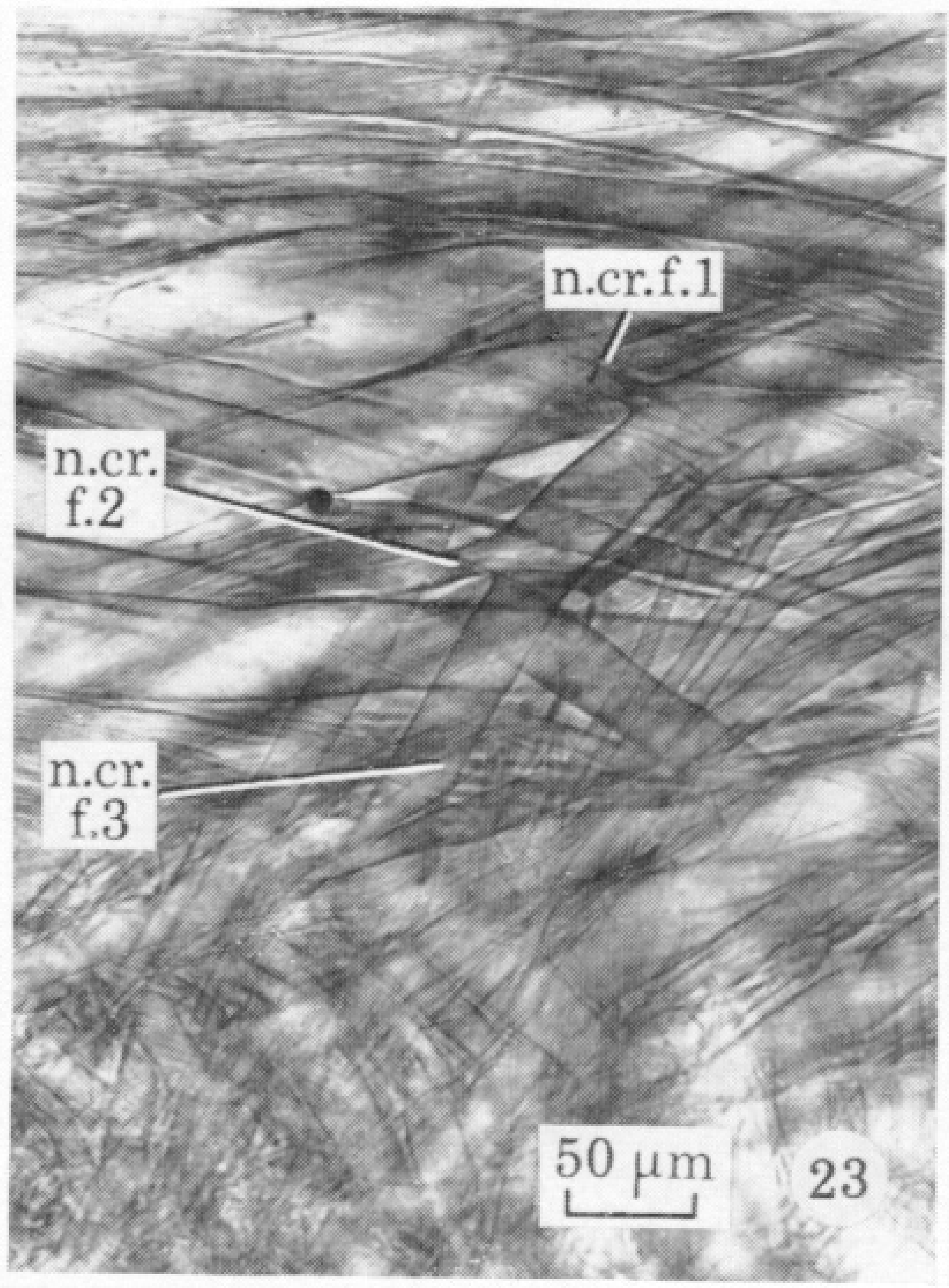


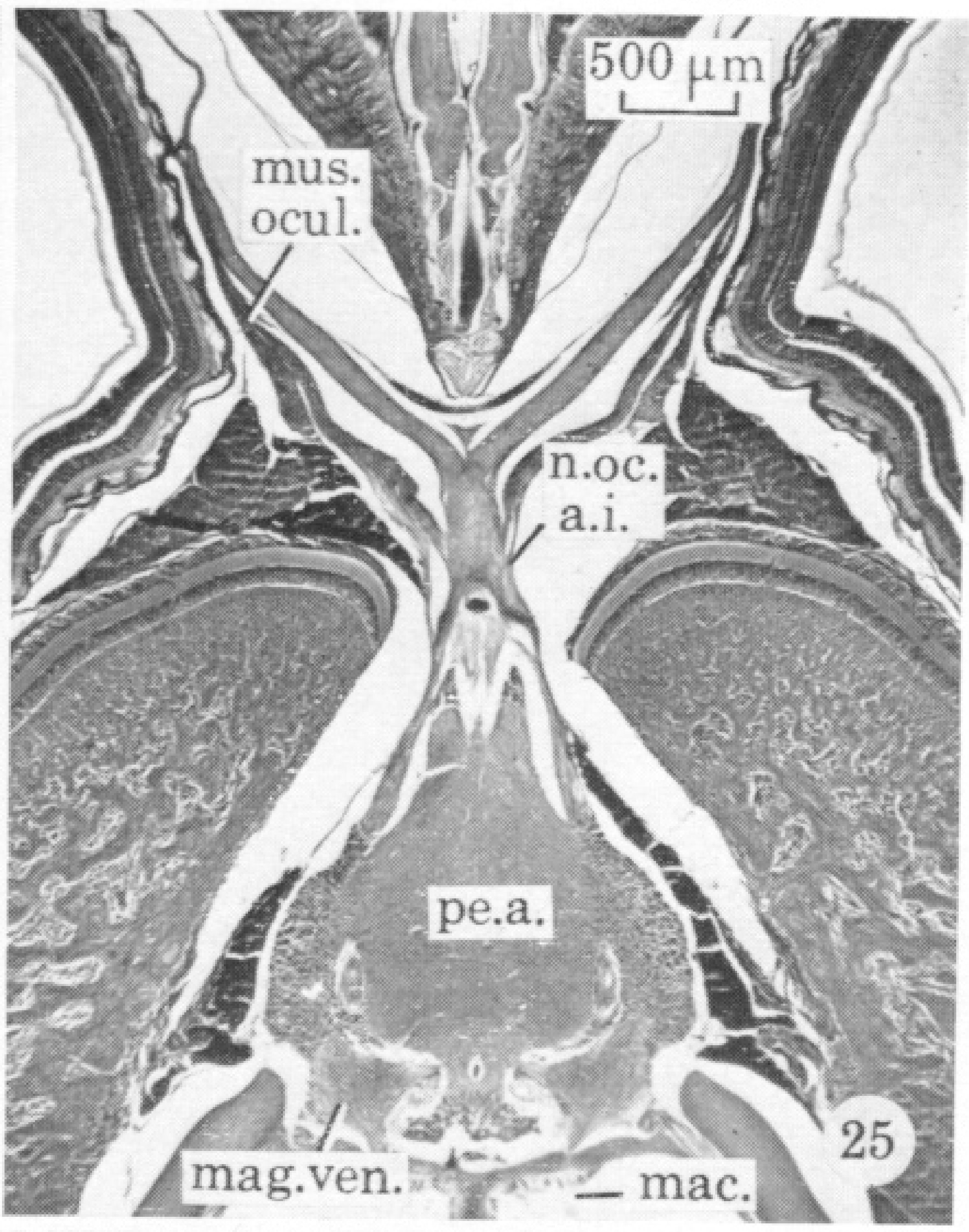


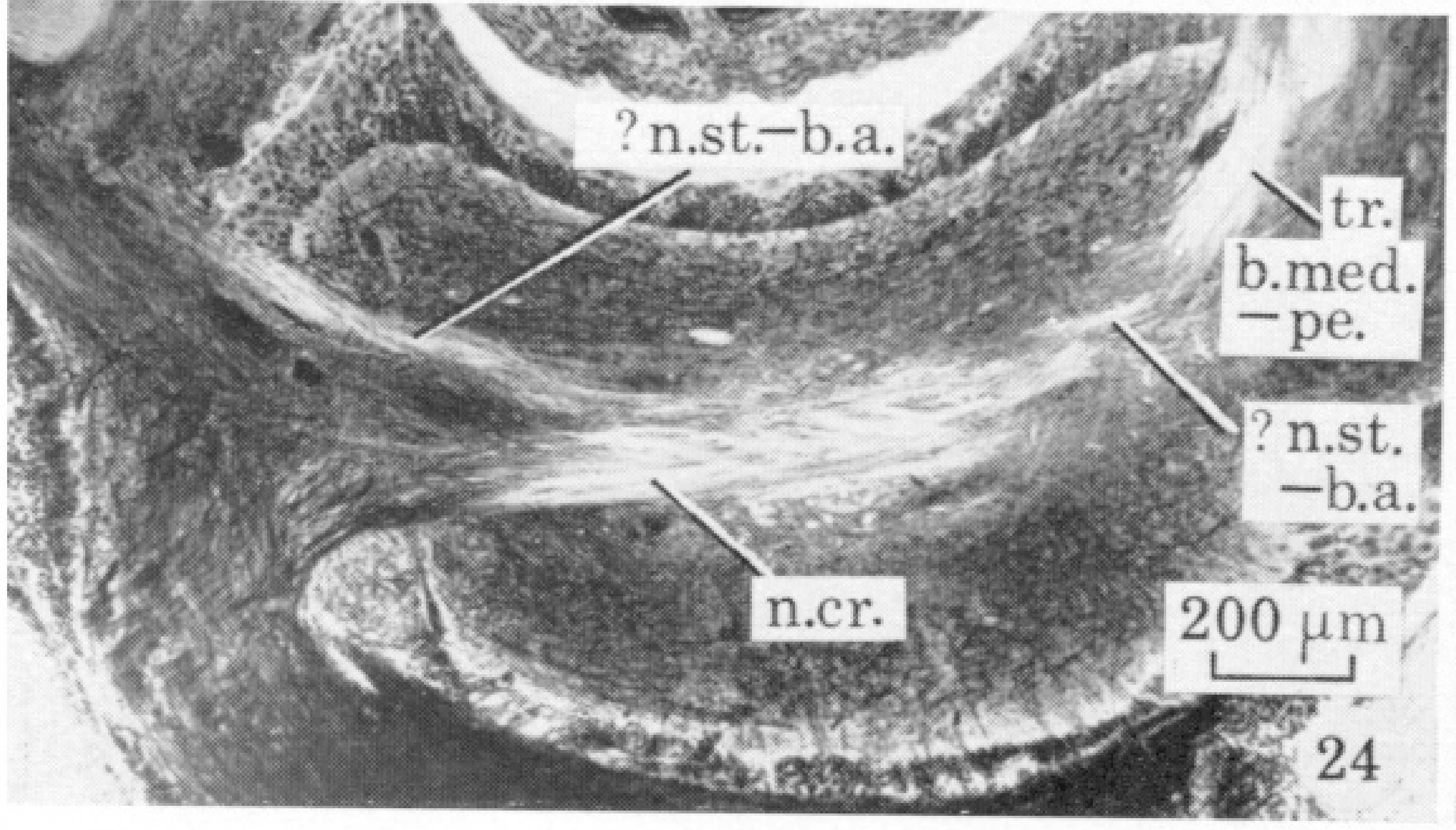


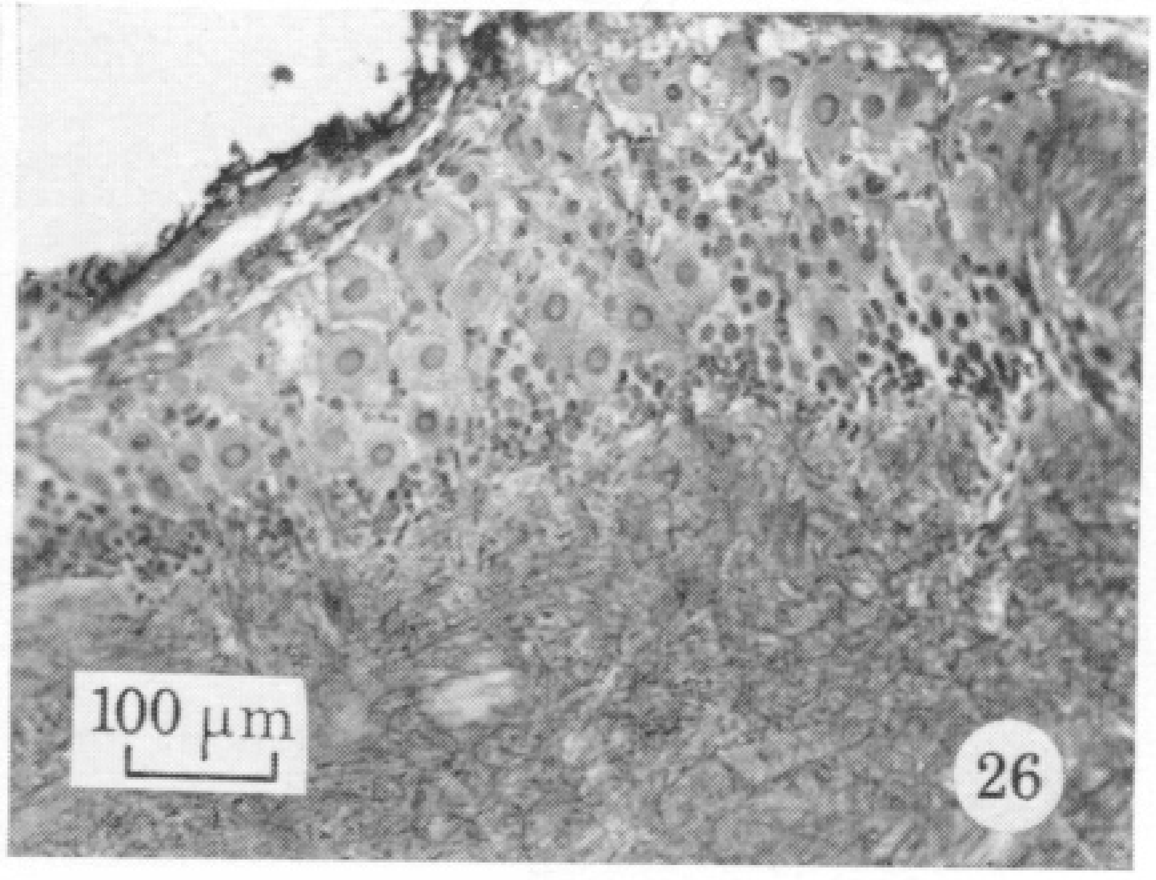




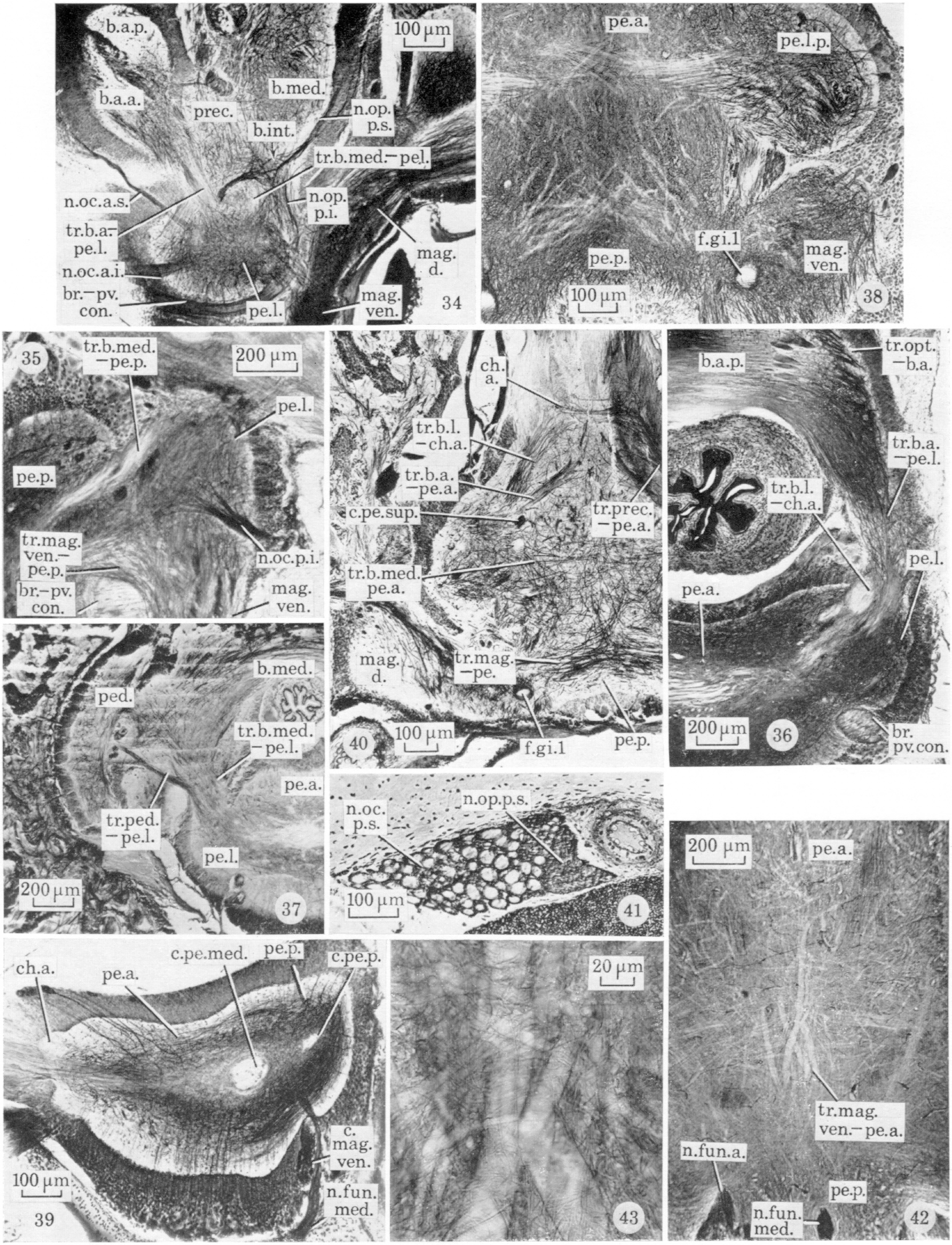




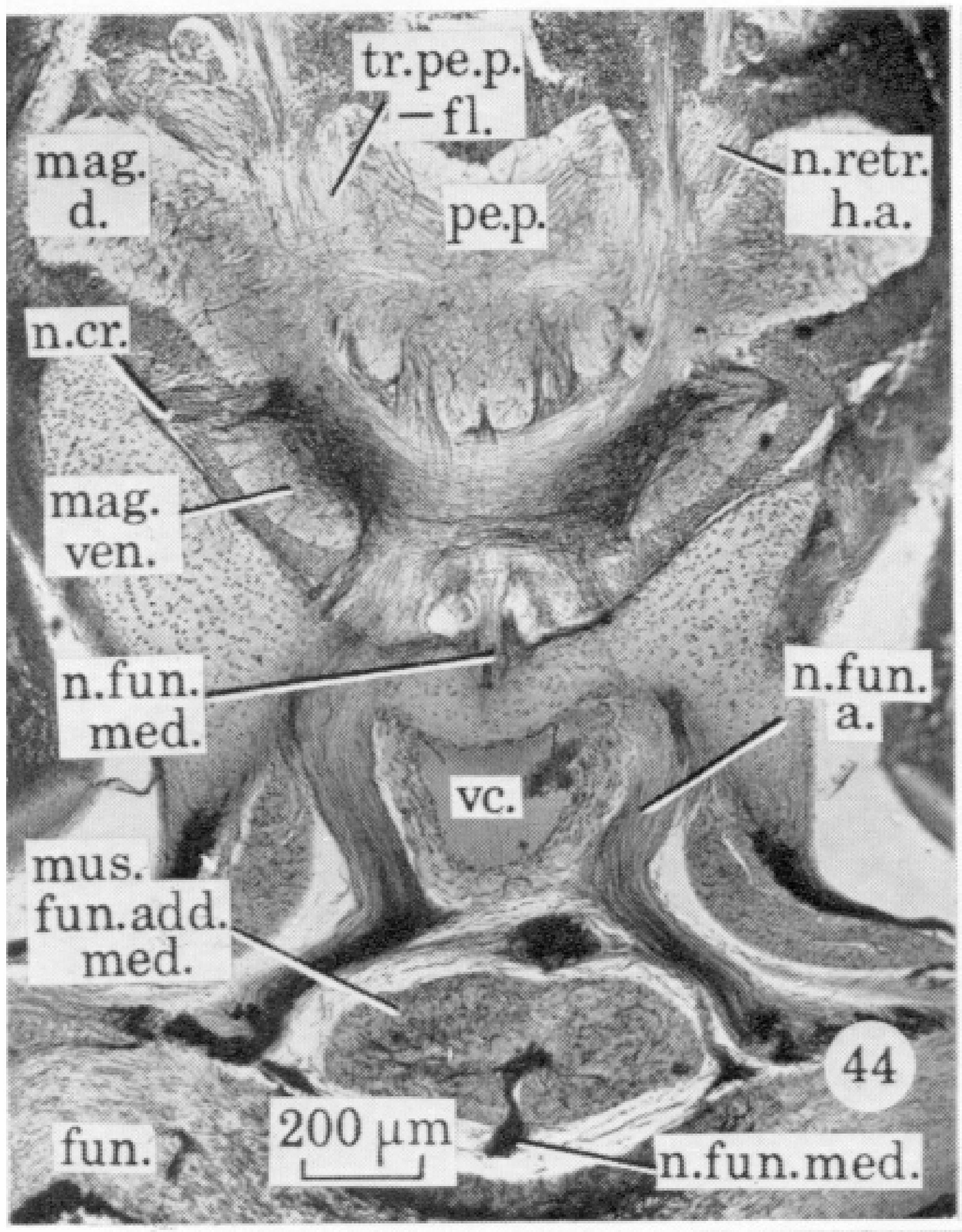


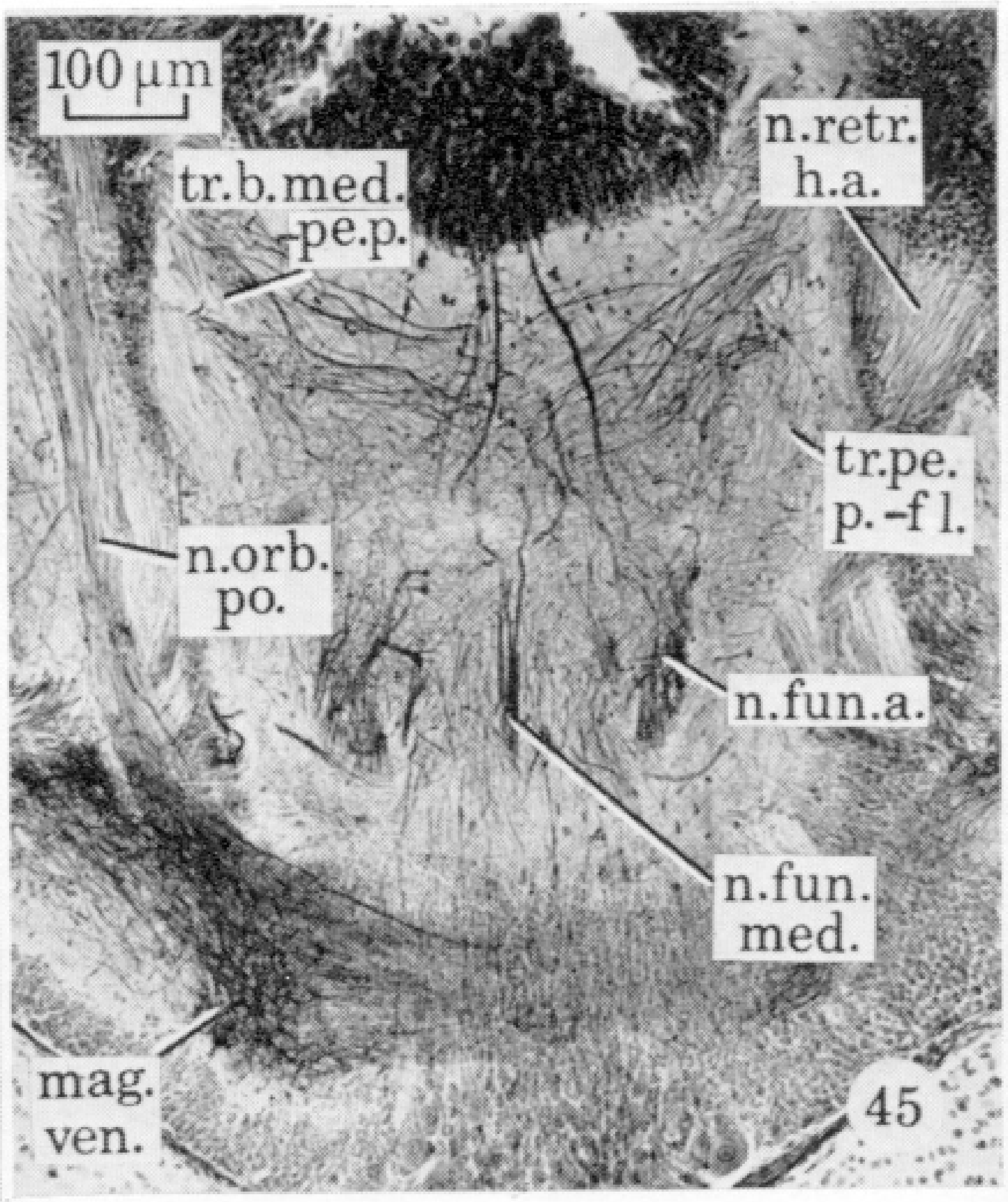


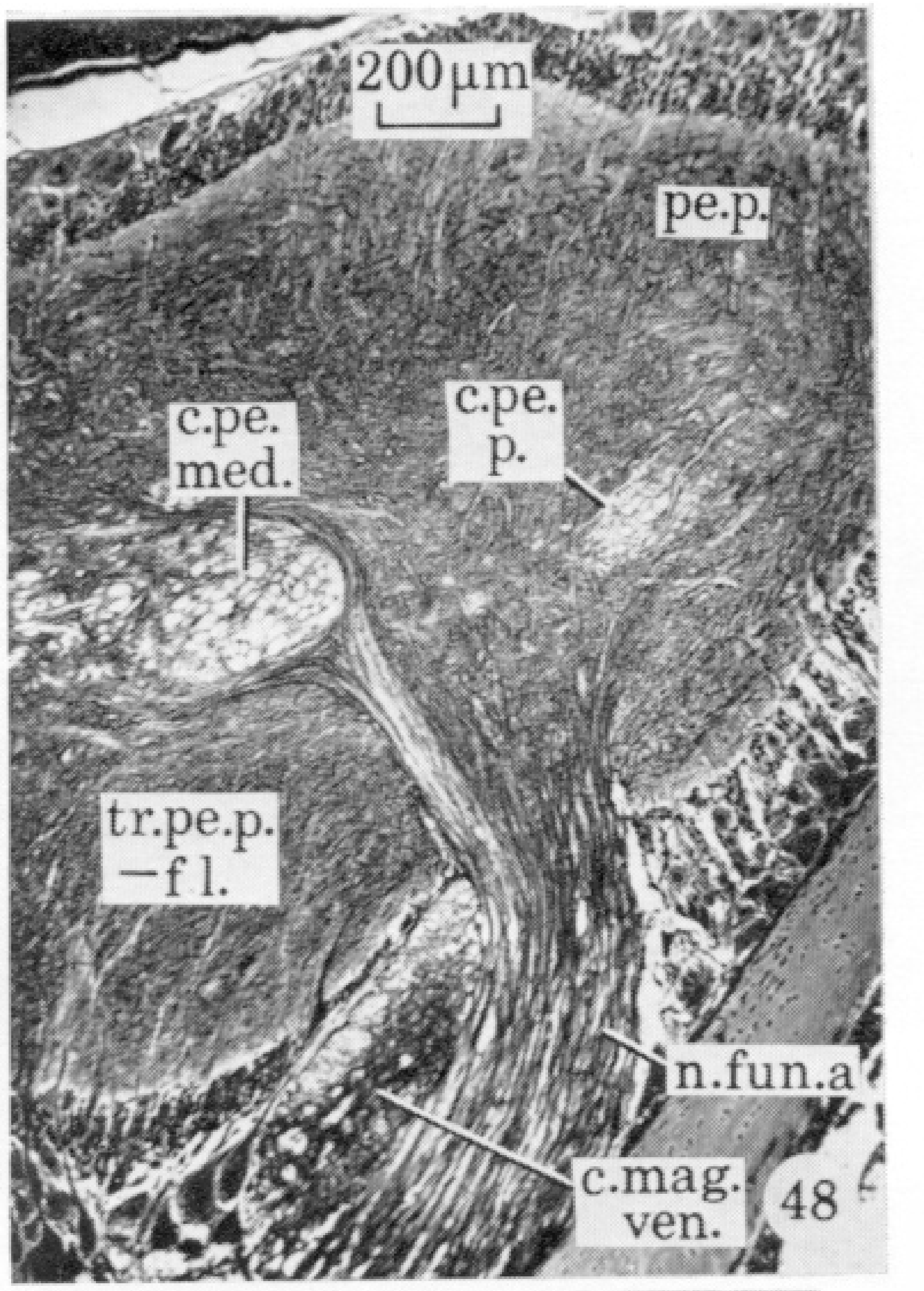
FIGURES 11 AND 19–26. For description see opposite.

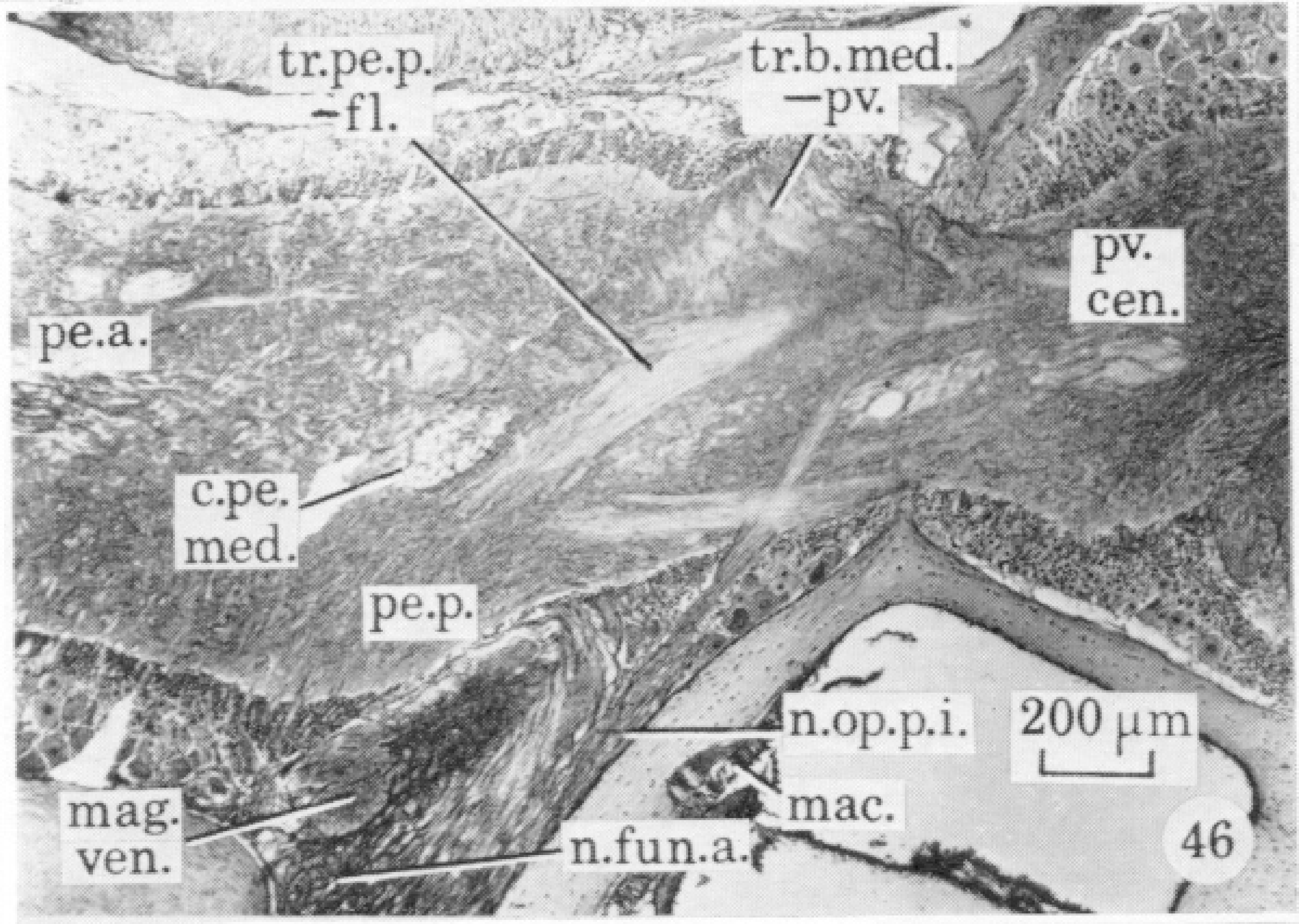


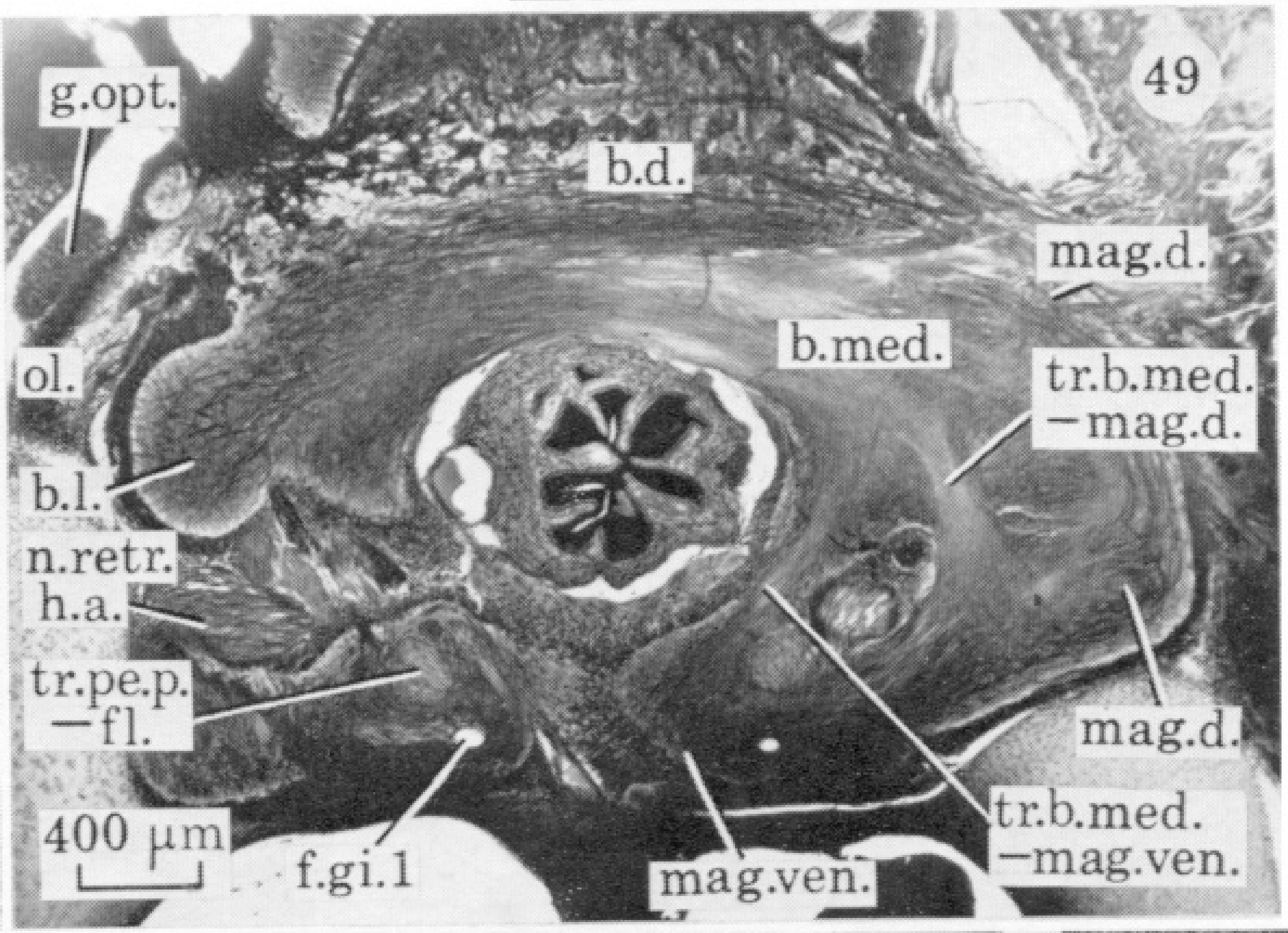
FIGURES 34–43. For description see opposite.

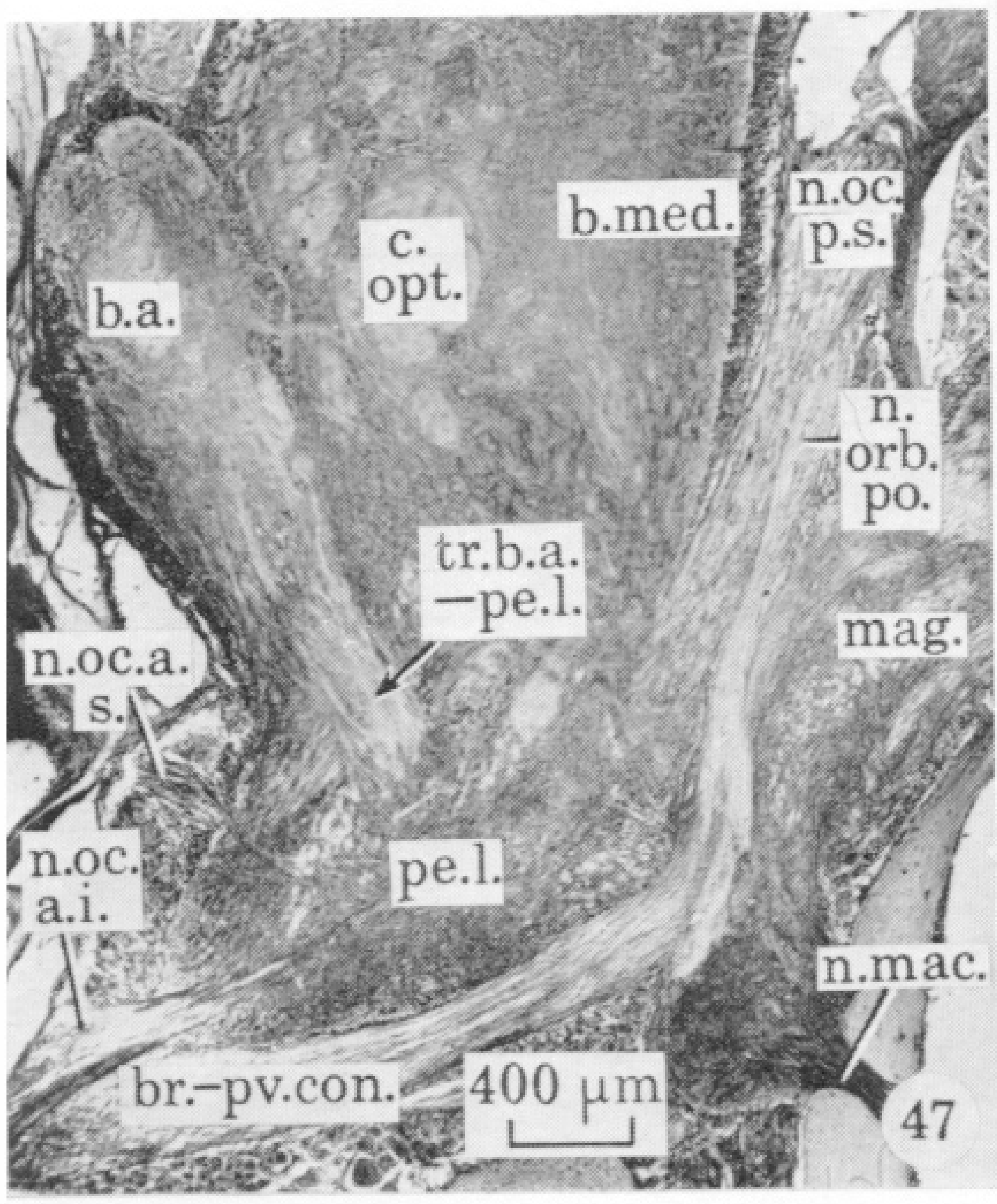


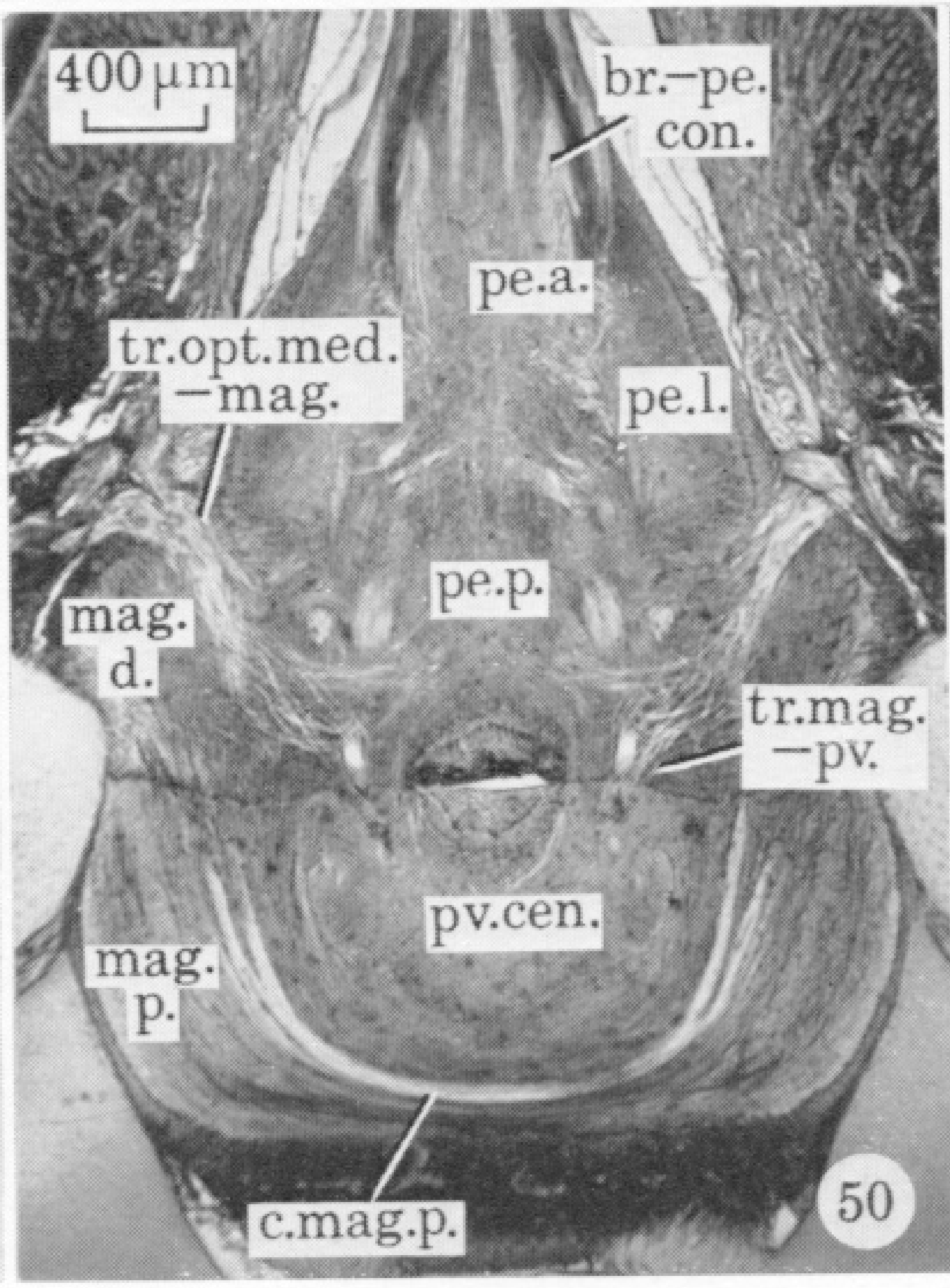


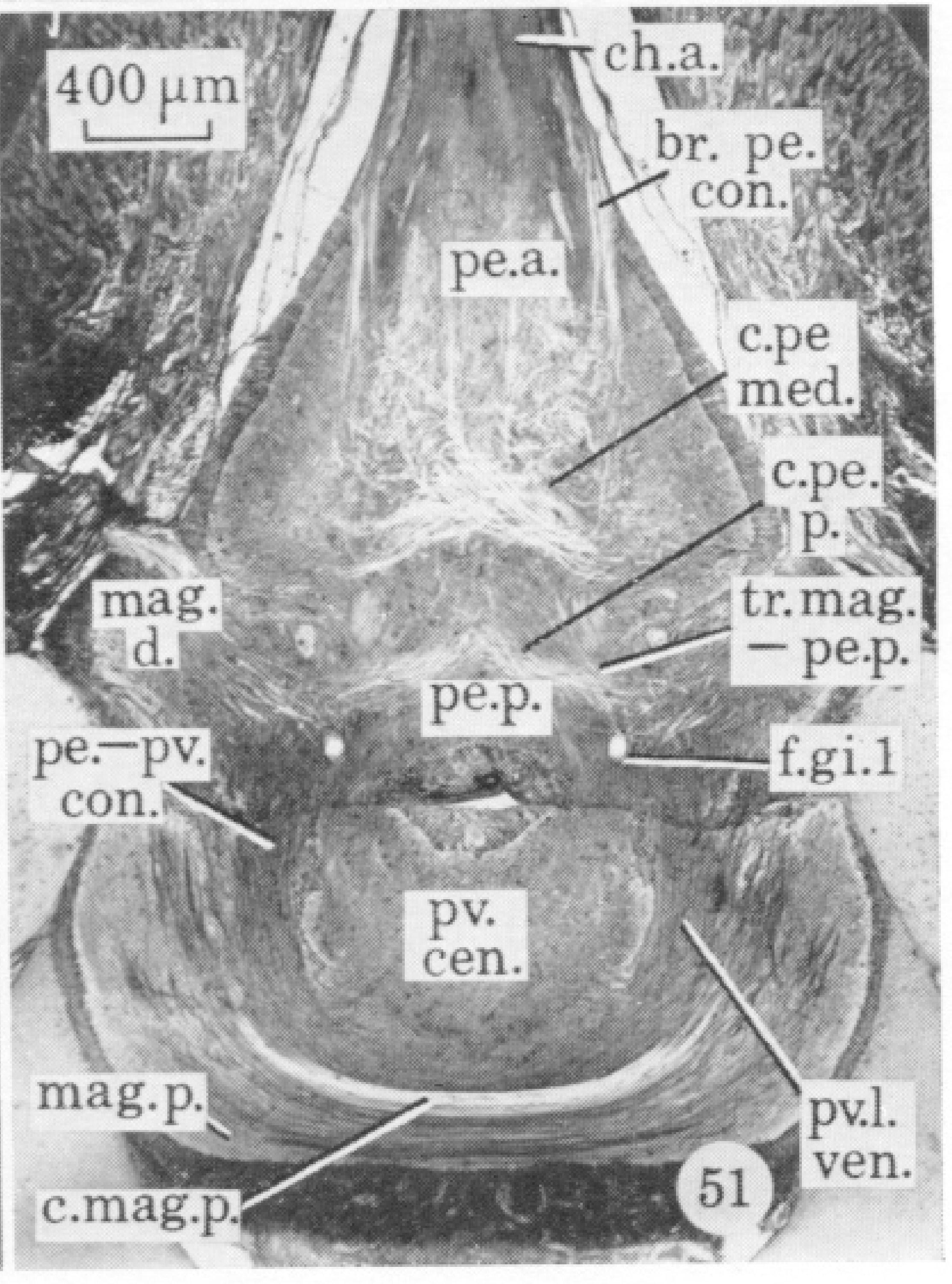




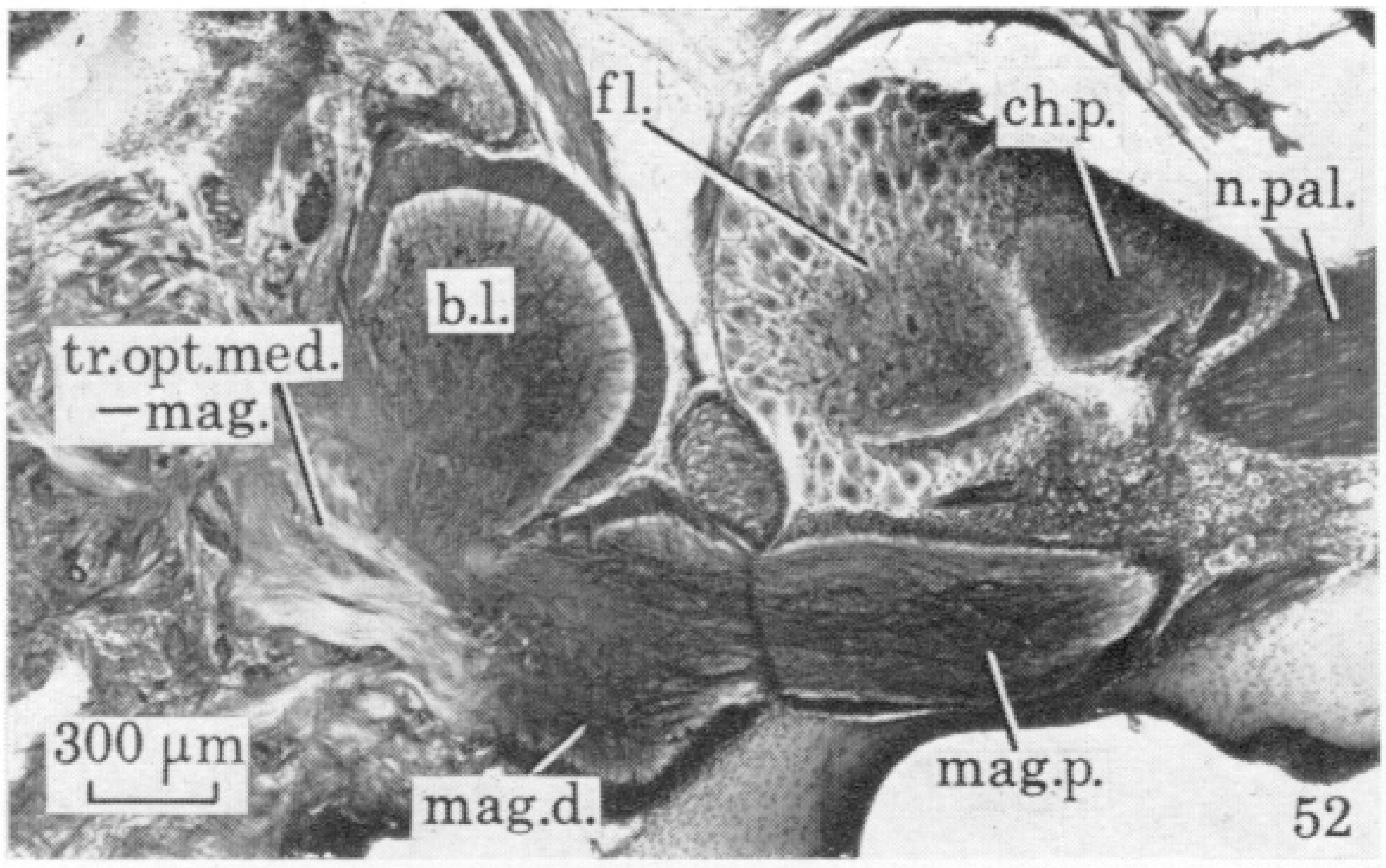


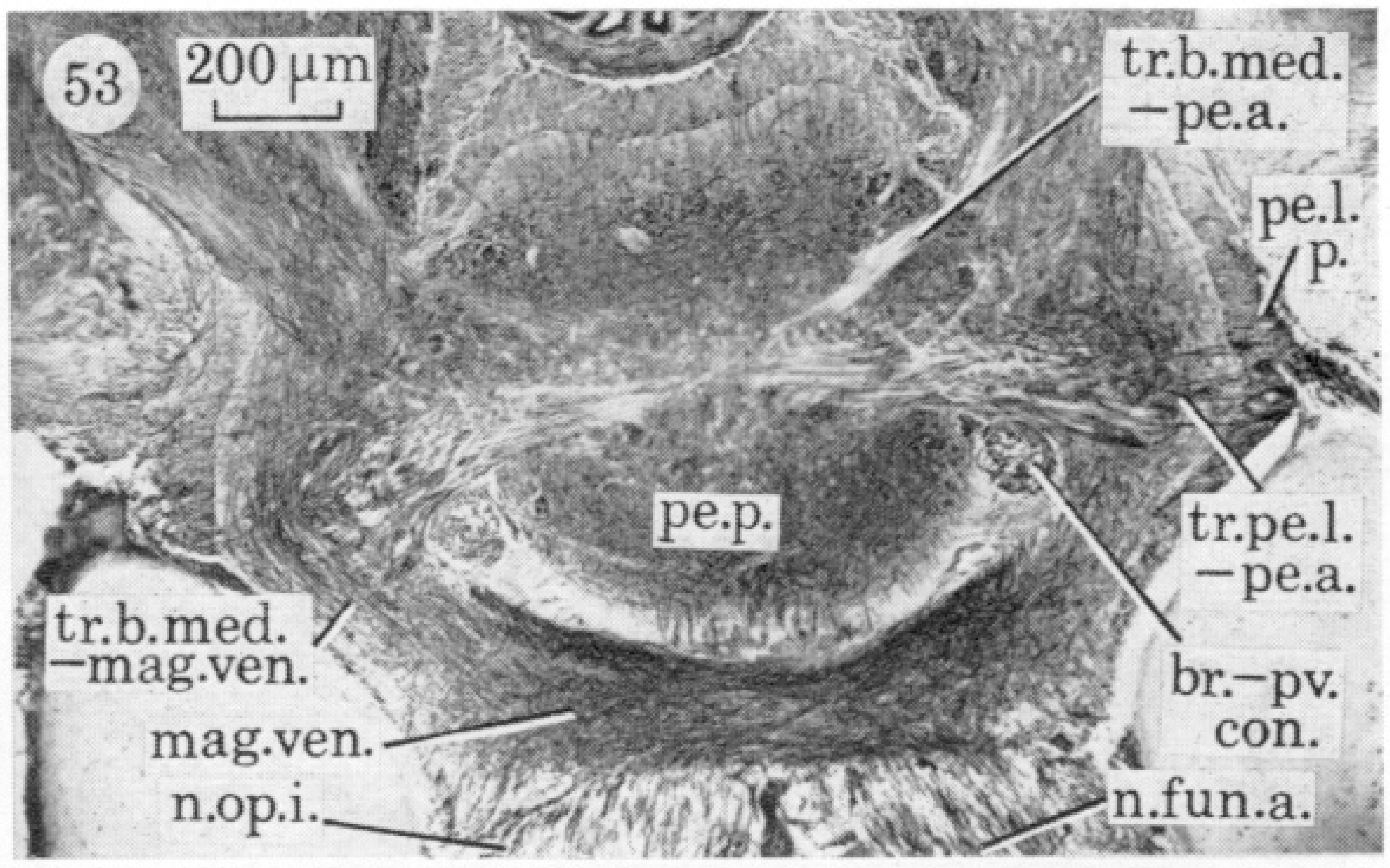


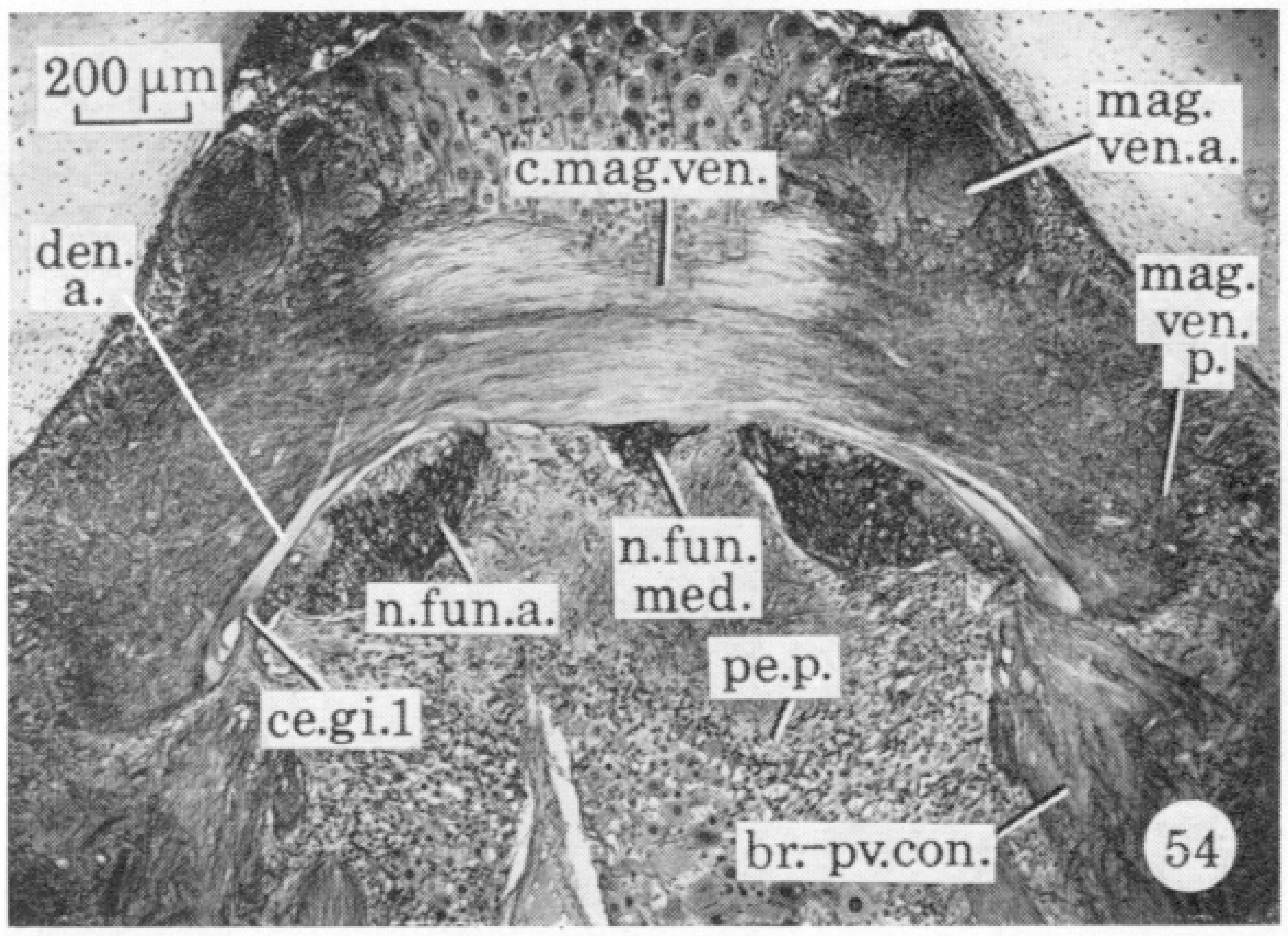


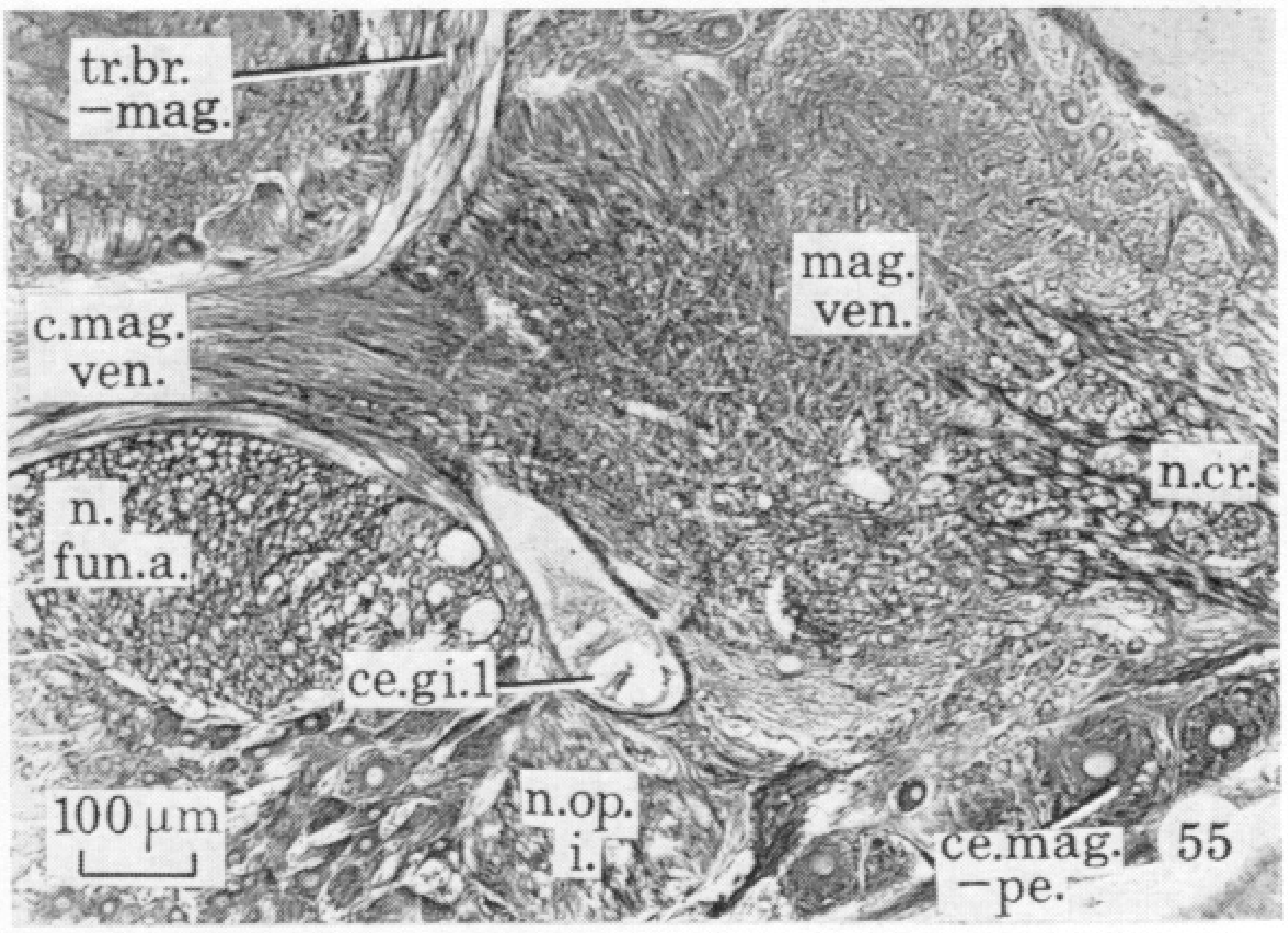


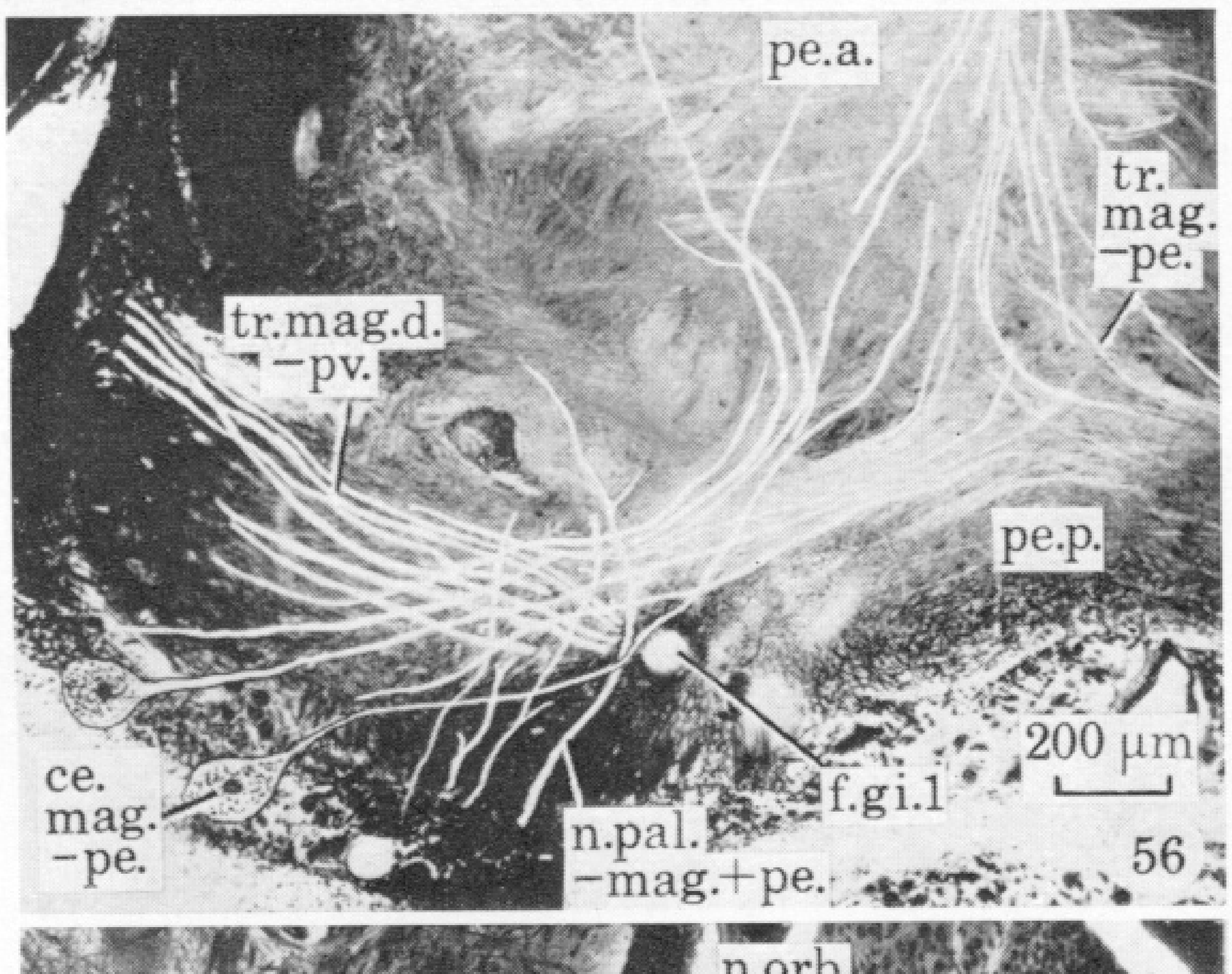
FIGURES 44–51. For description see opposite.

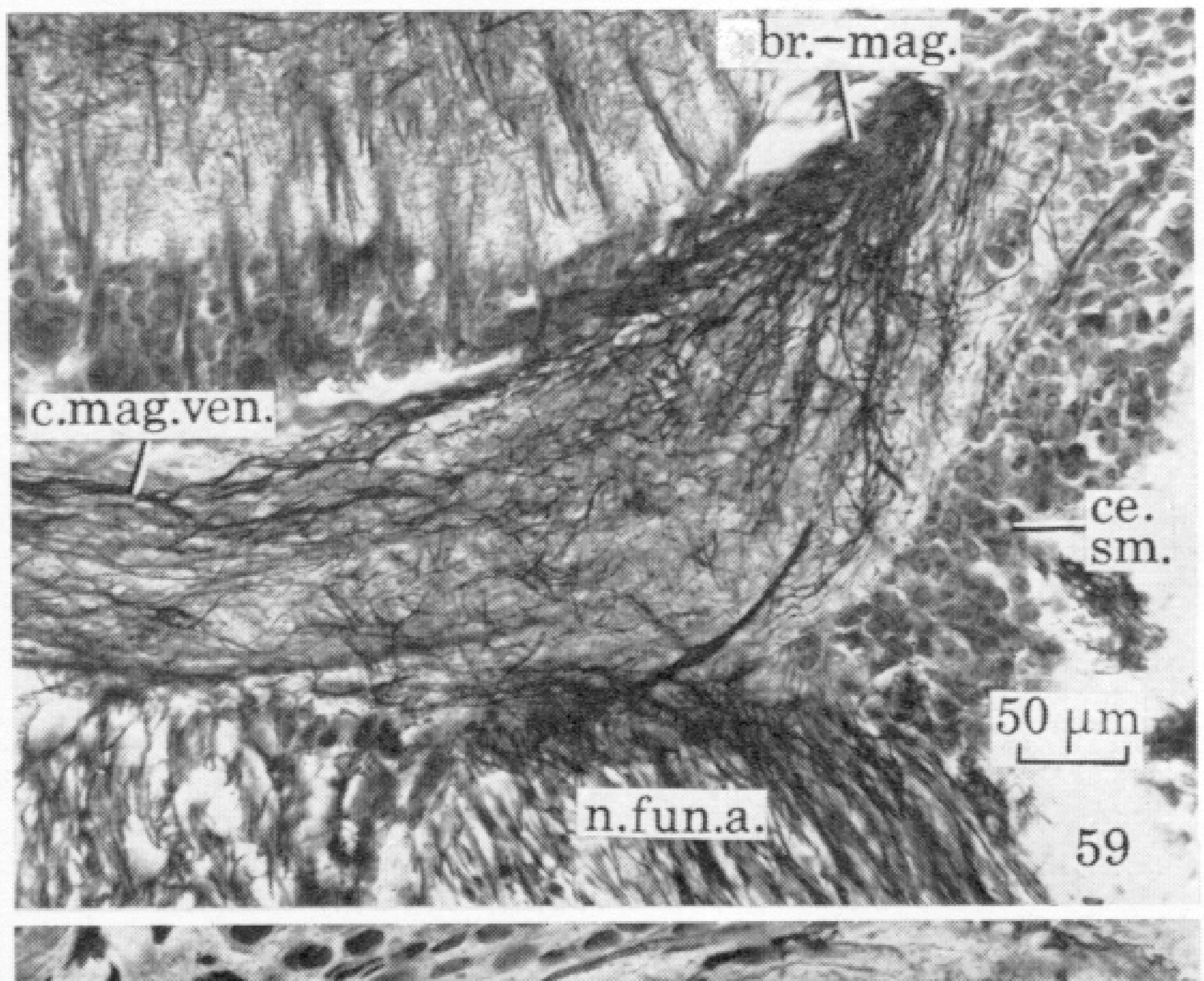


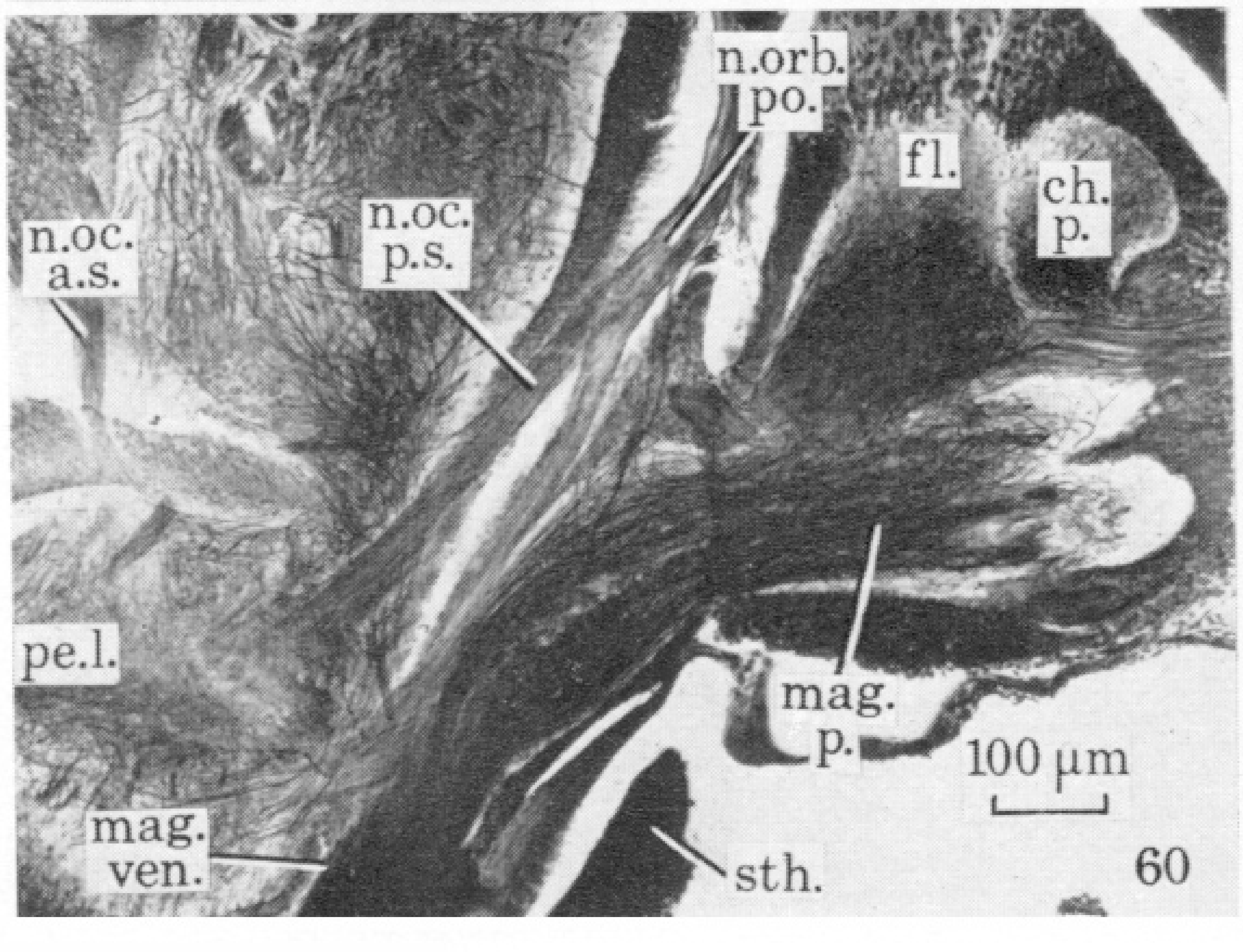


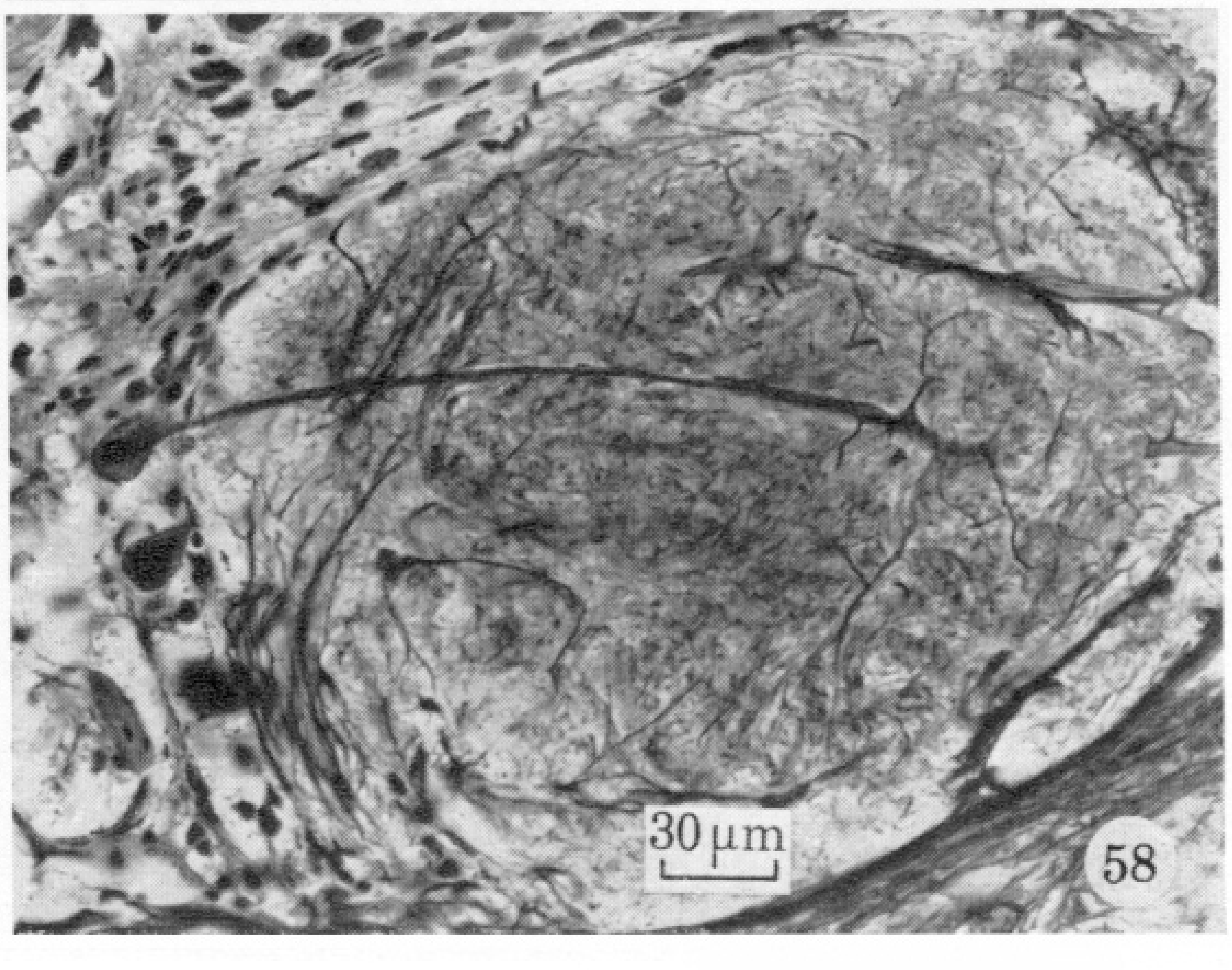




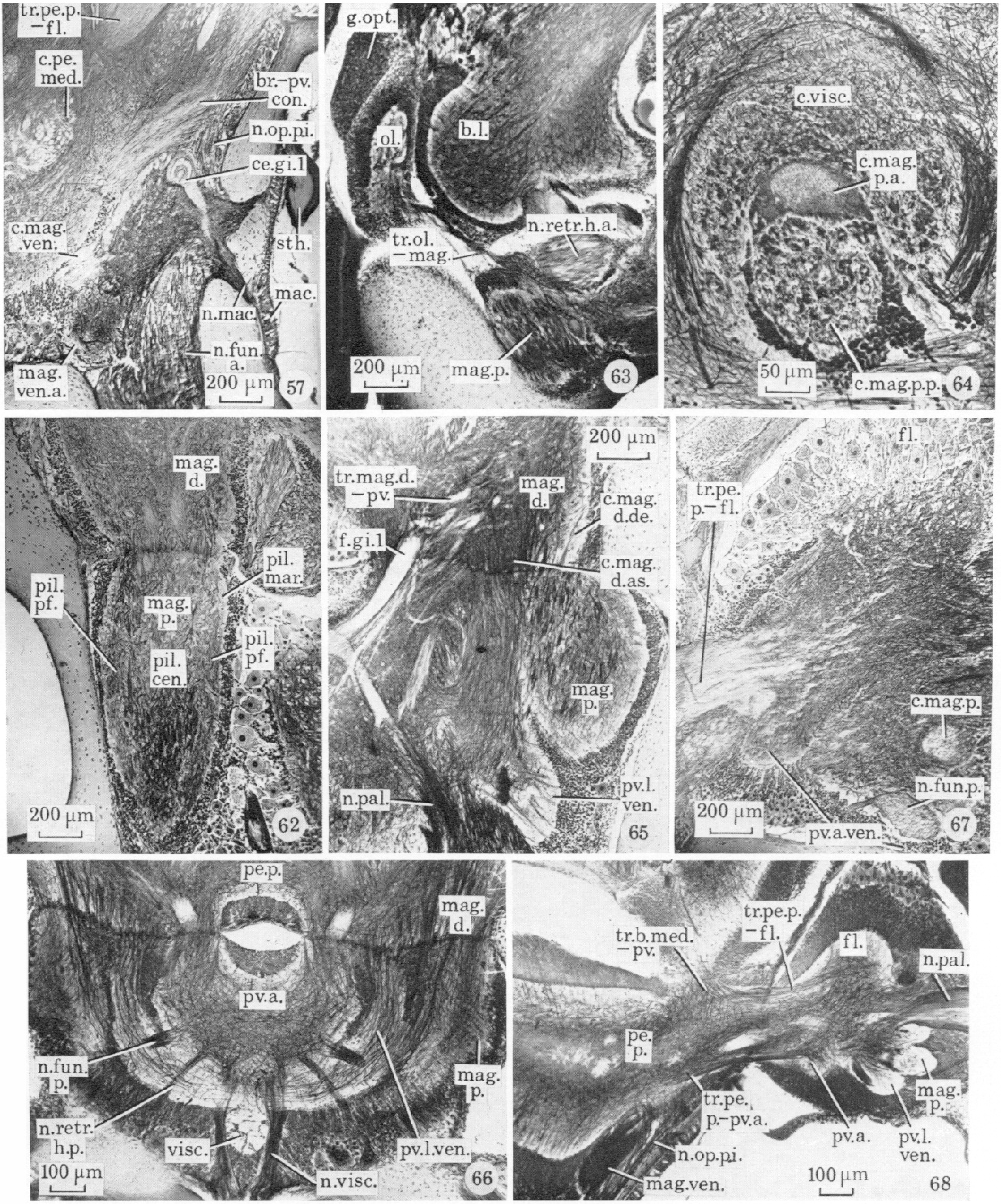




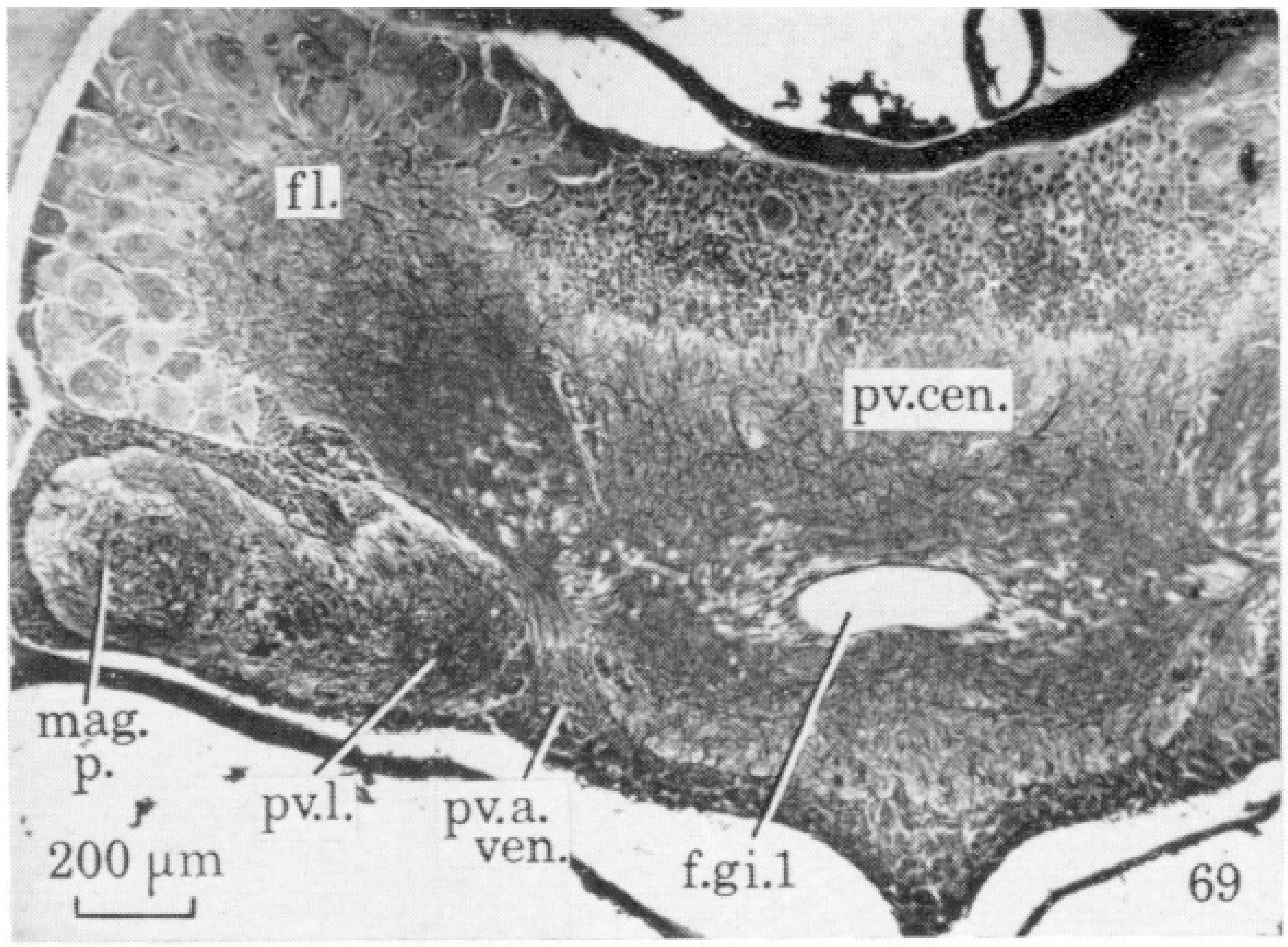


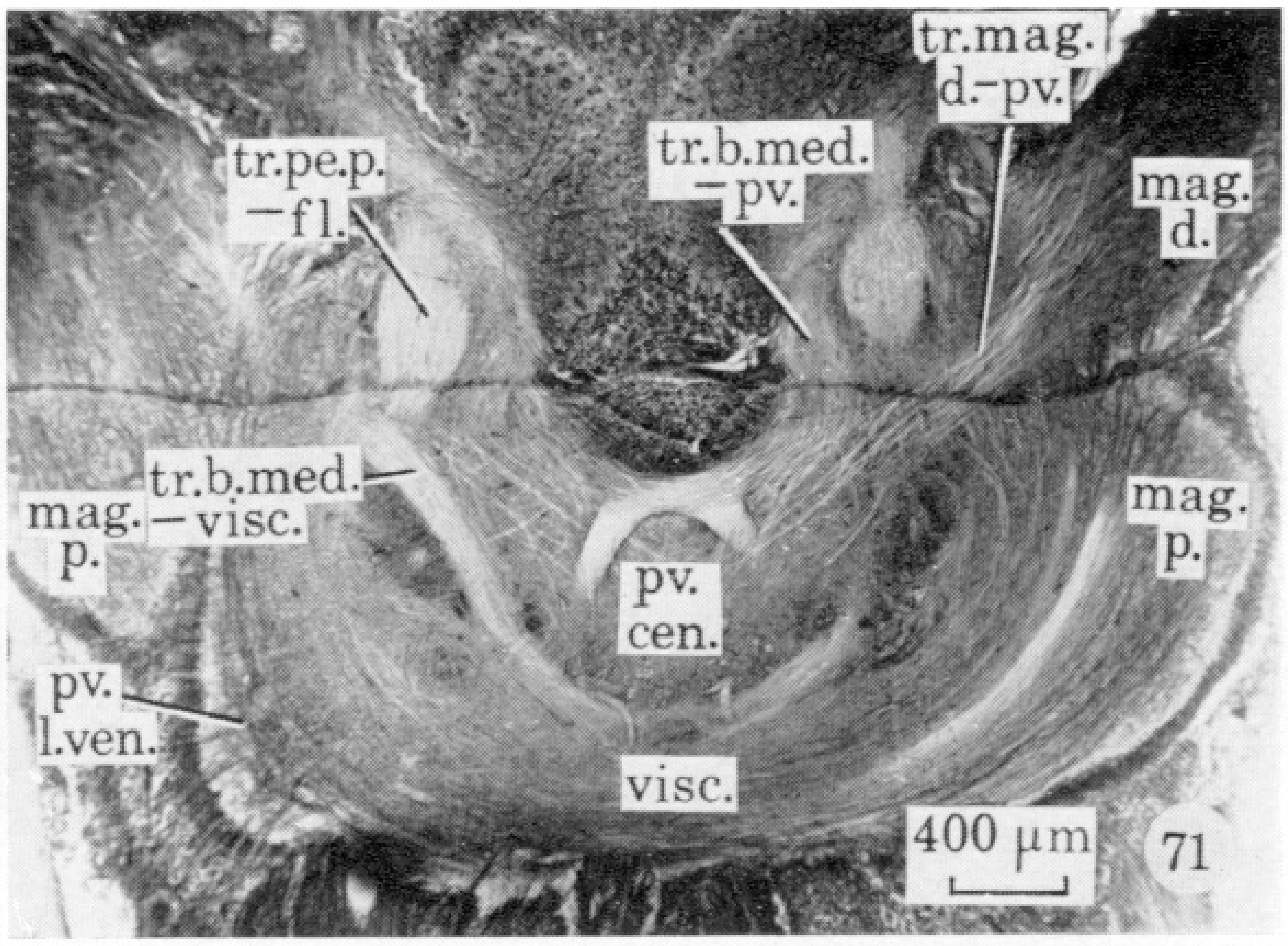


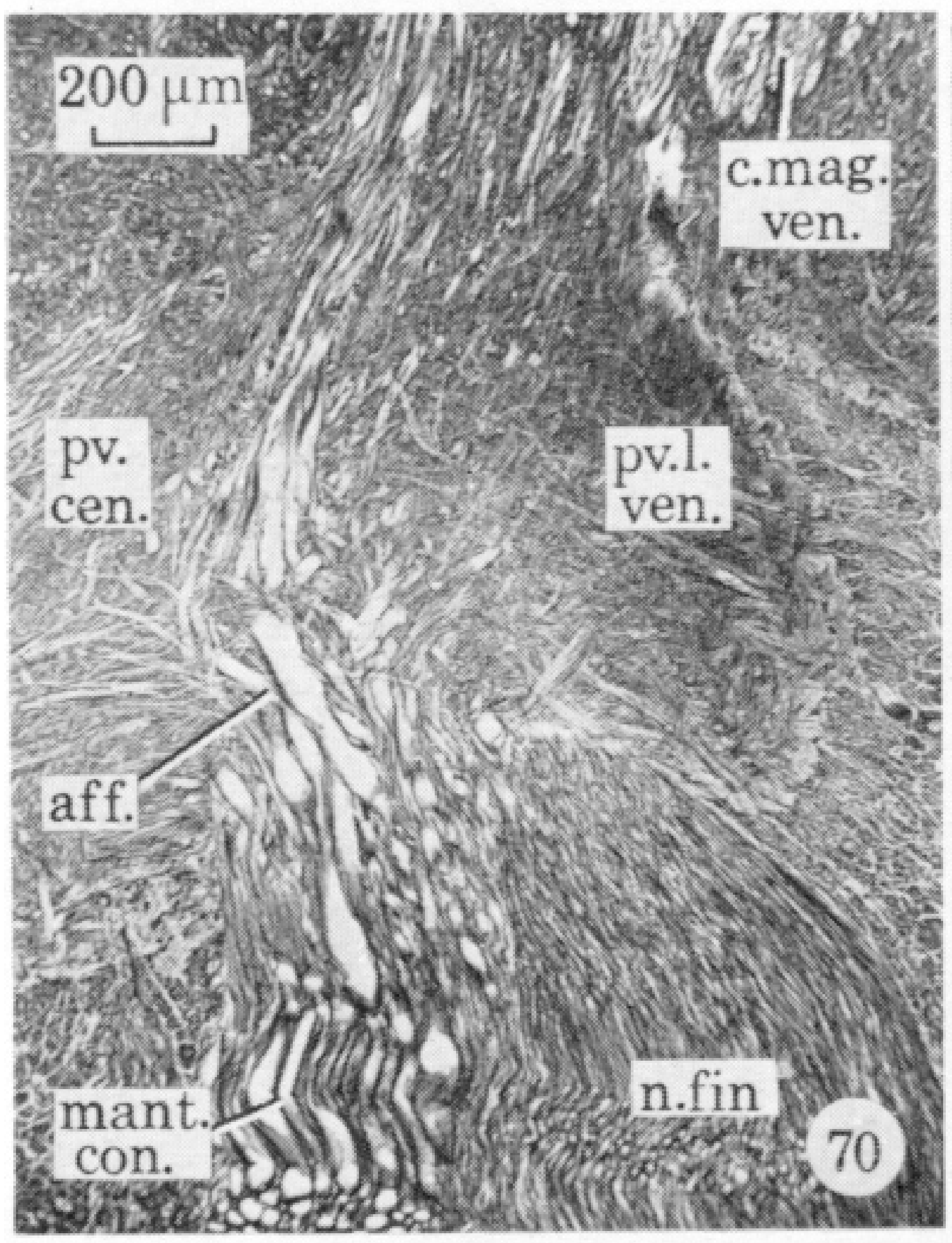
FIGURES 52–56 AND 58–60. For description see opposite.

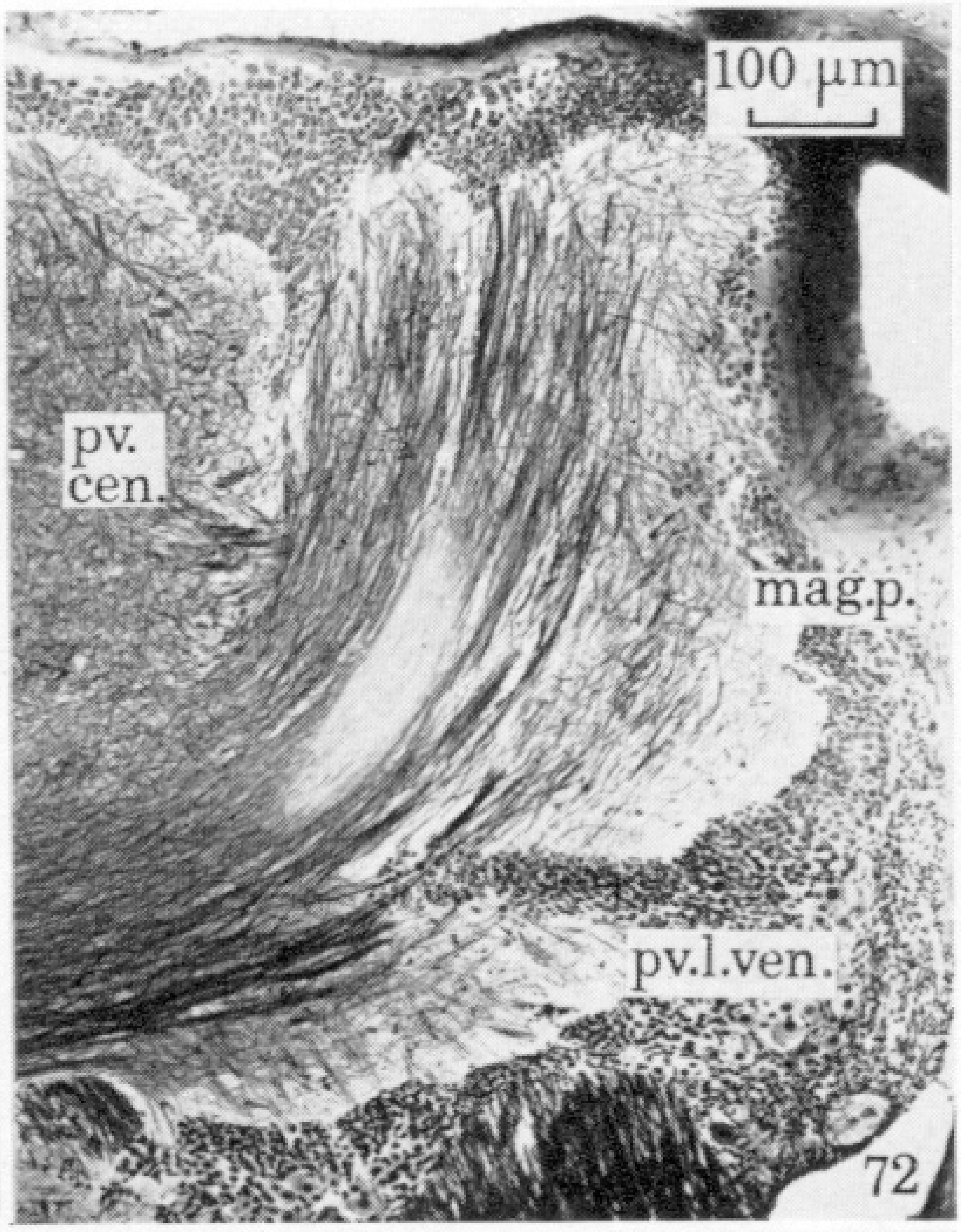


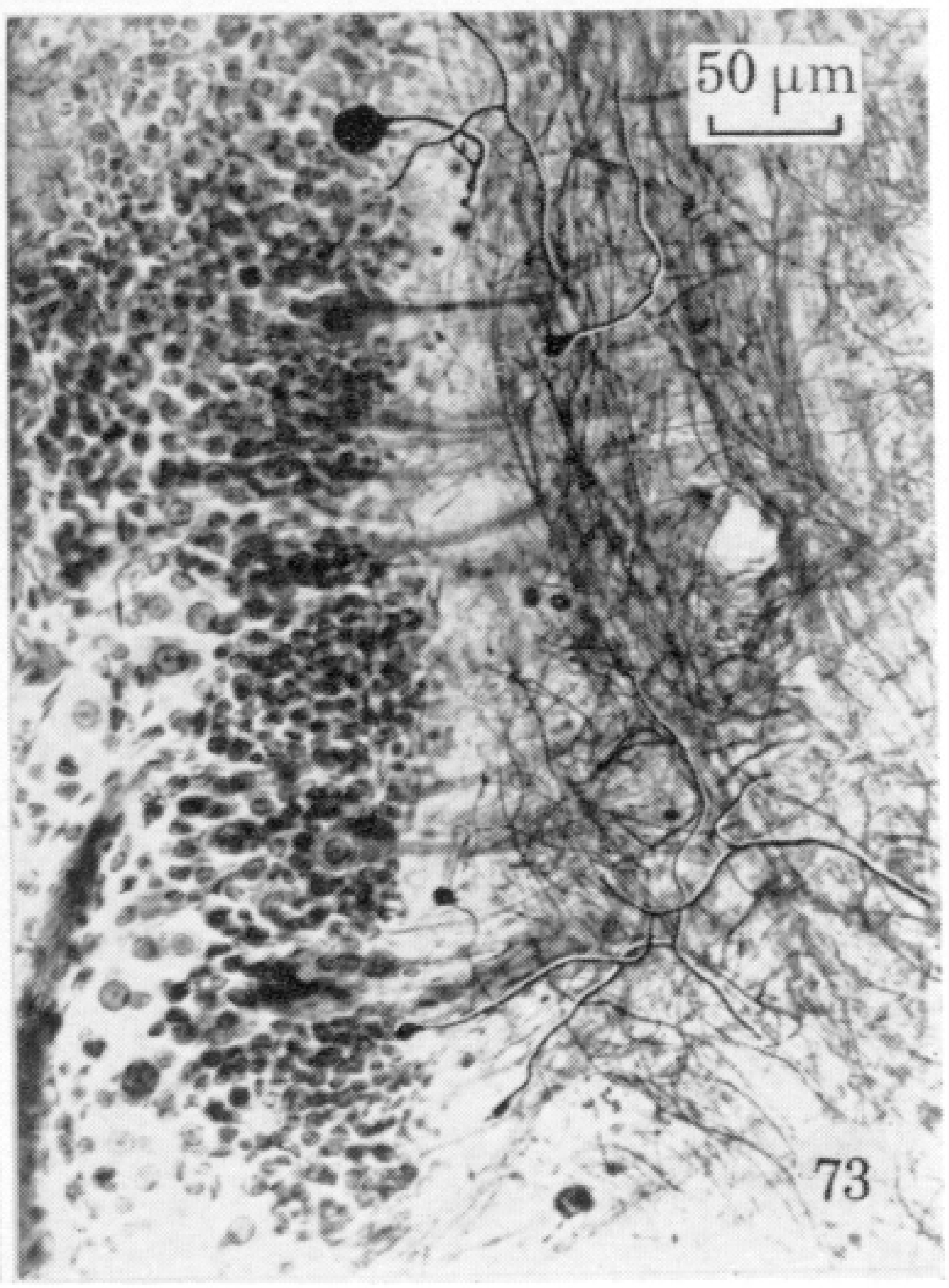
FIGURES 57 AND 62–68. For description see opposite.

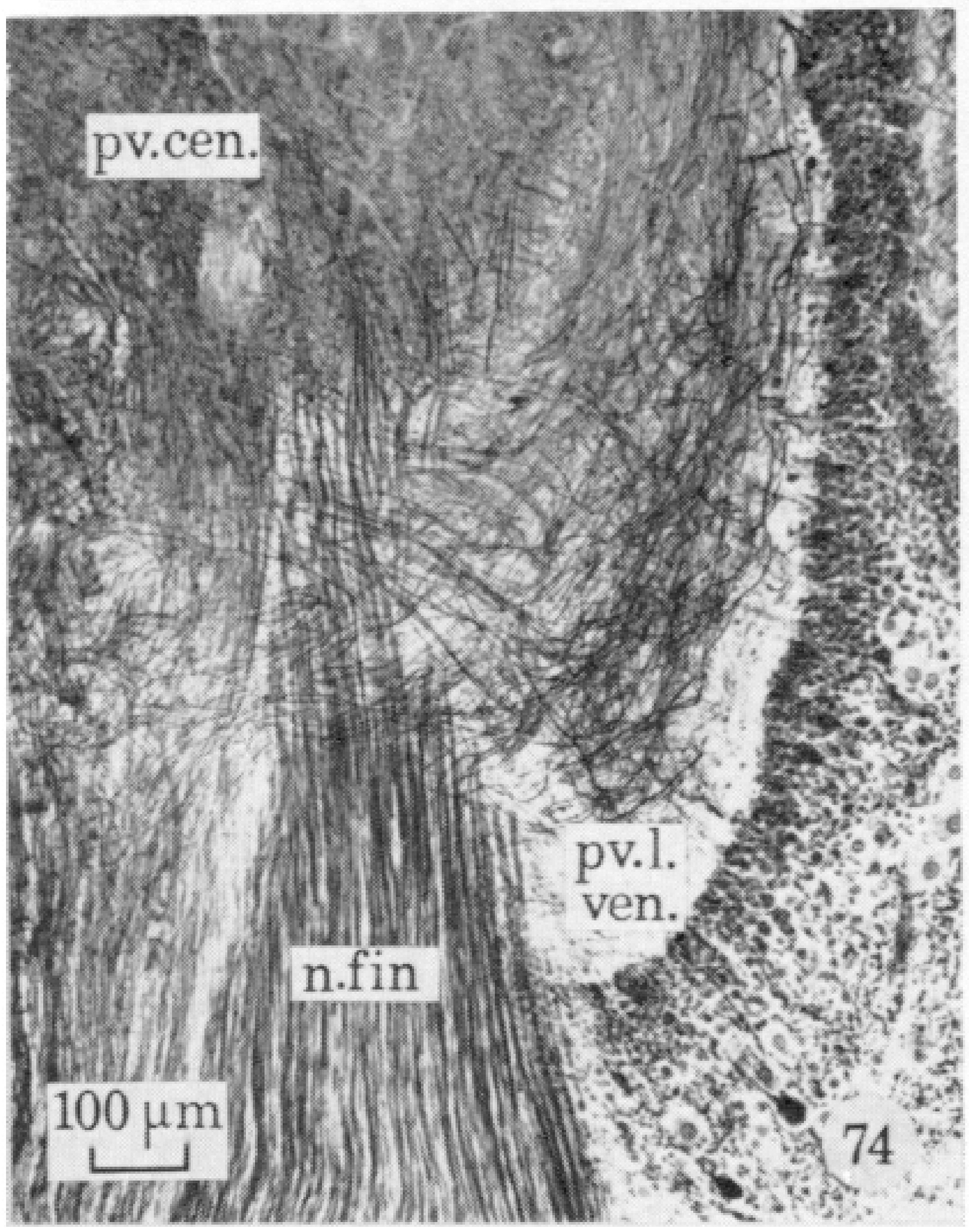


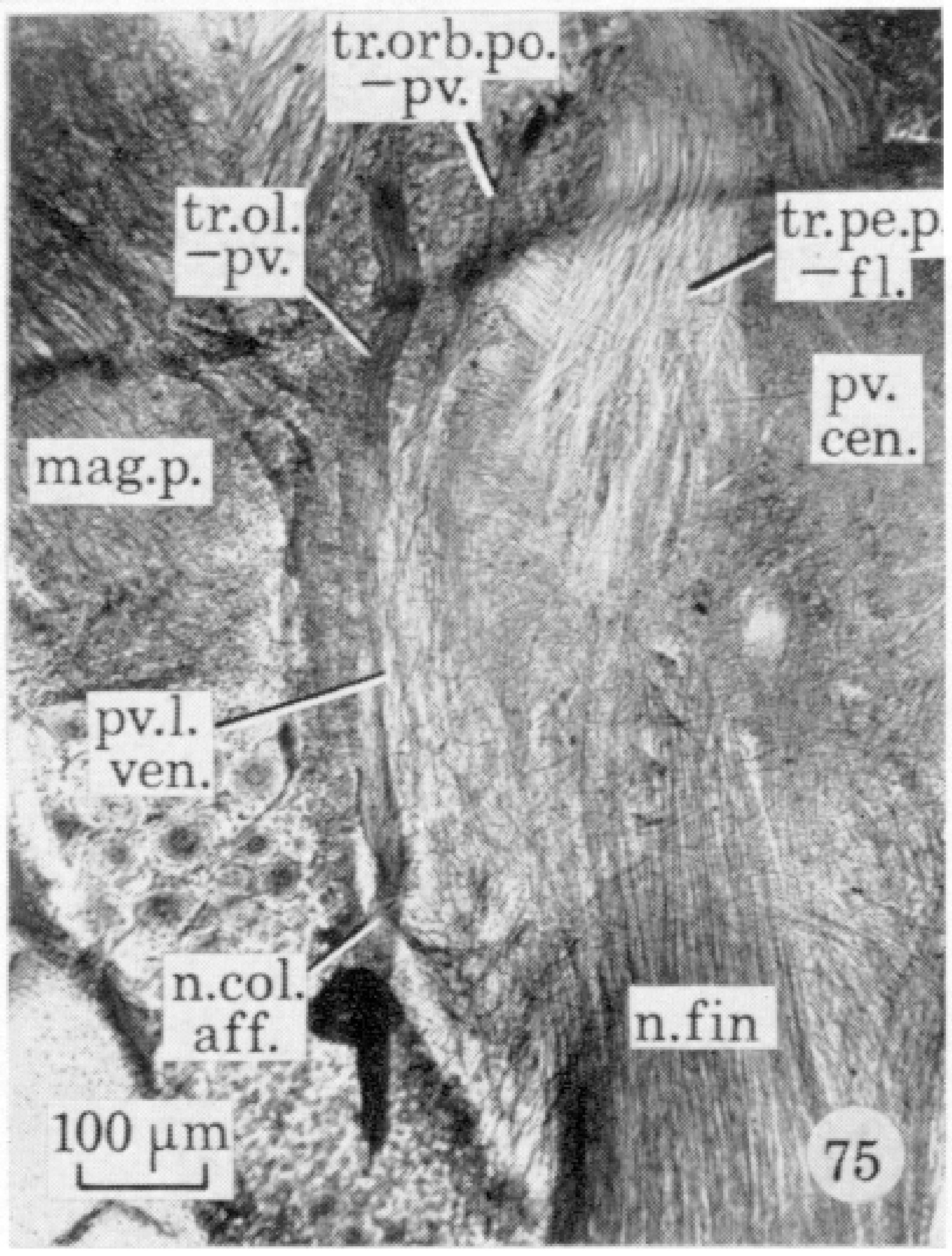


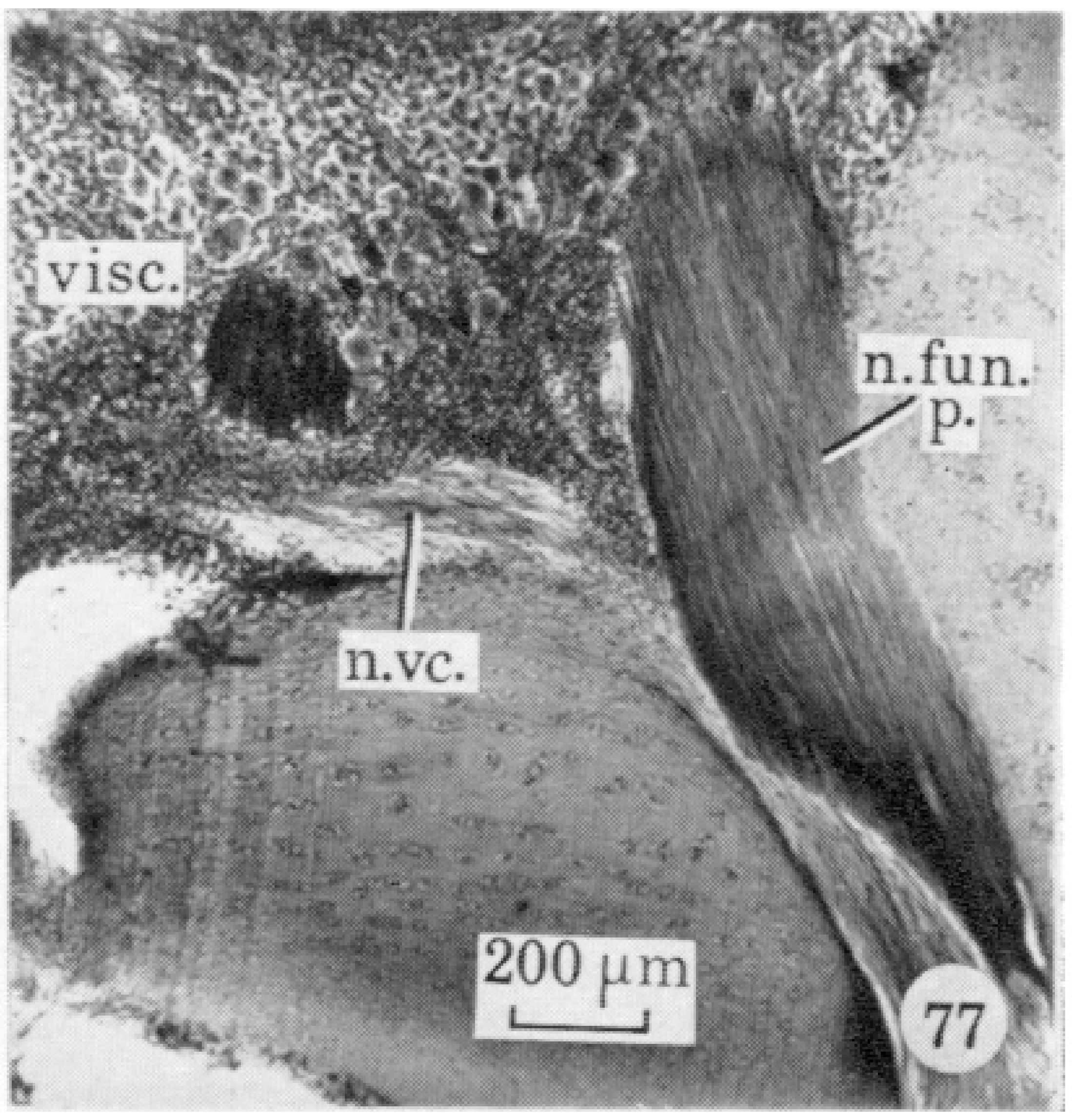




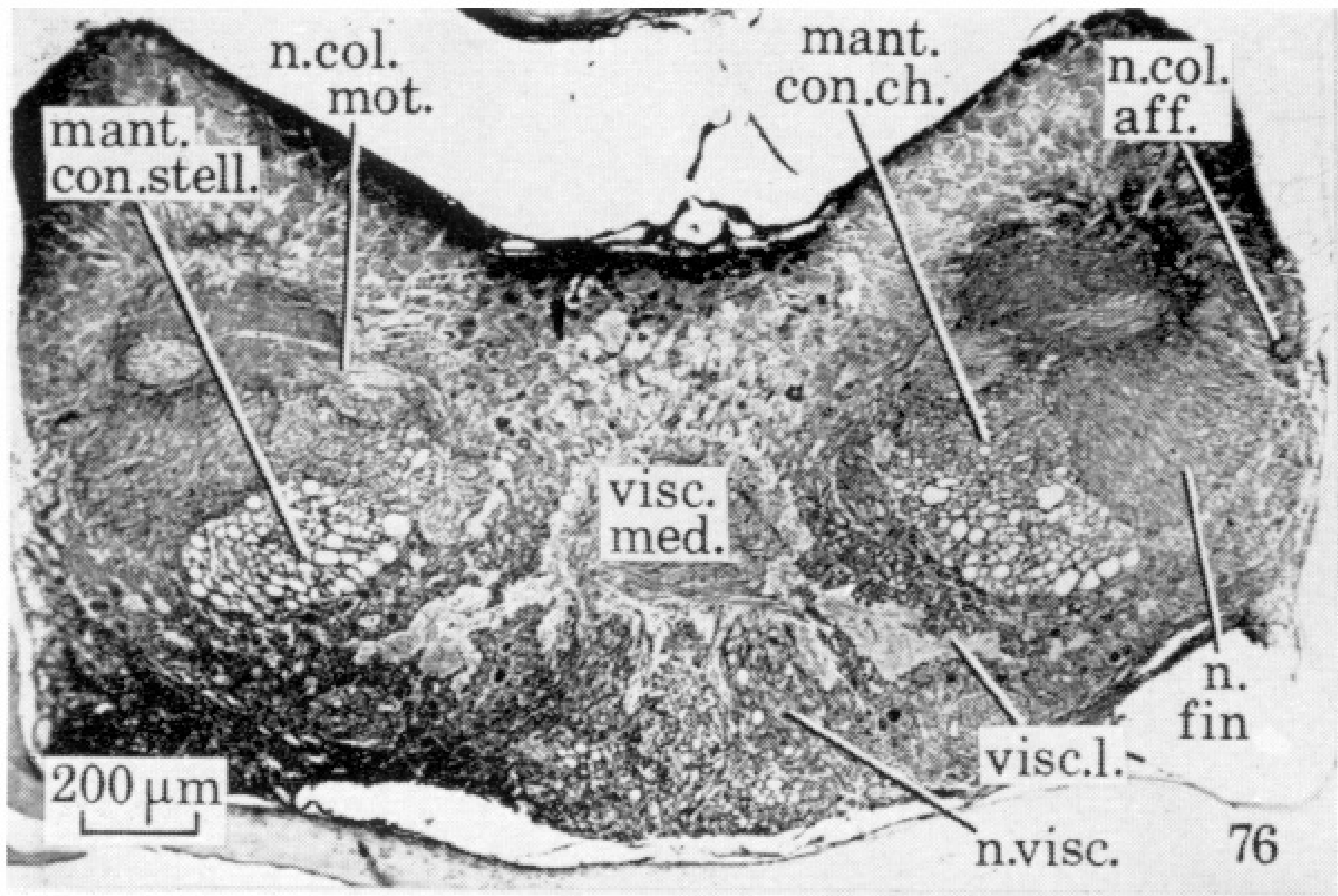


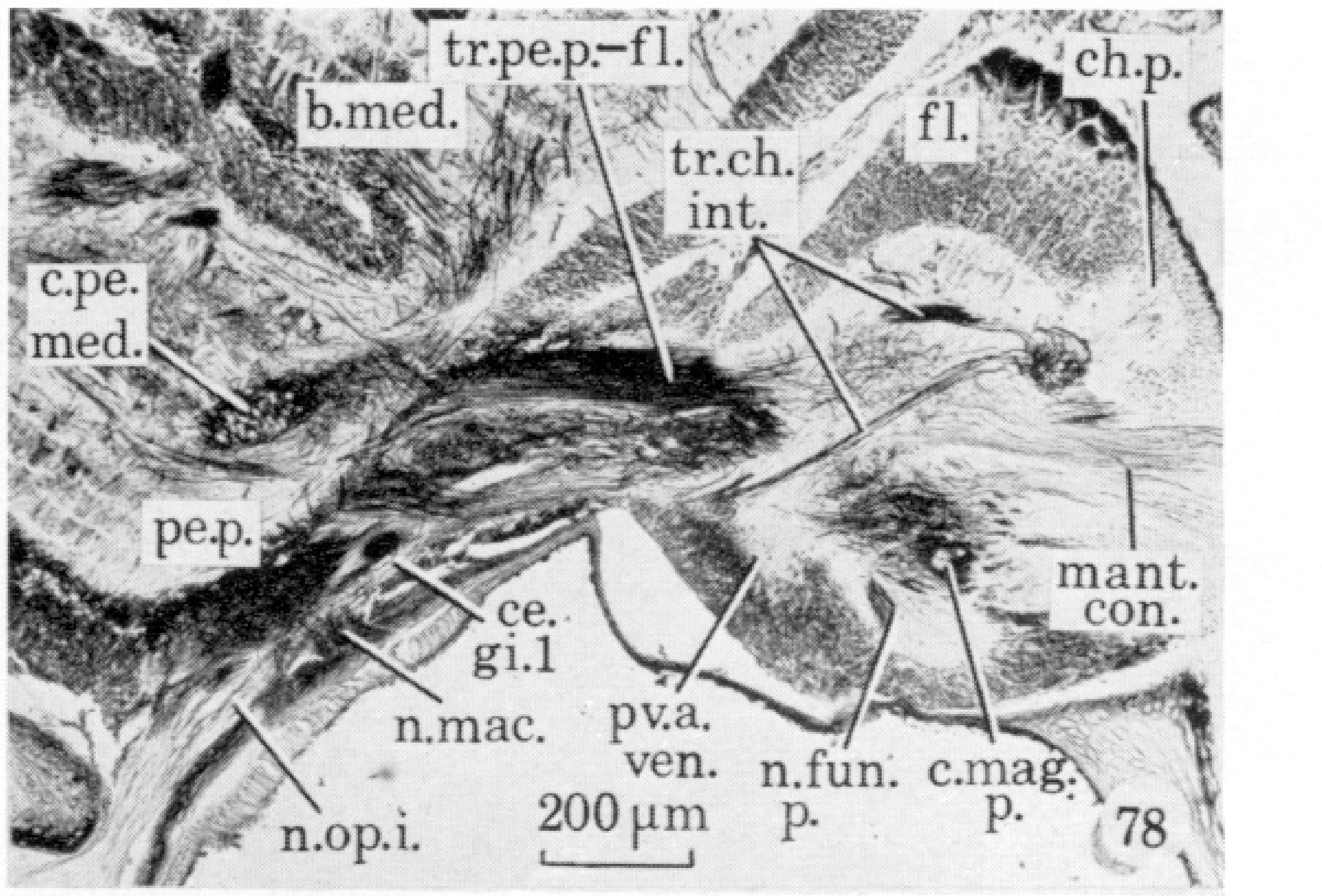


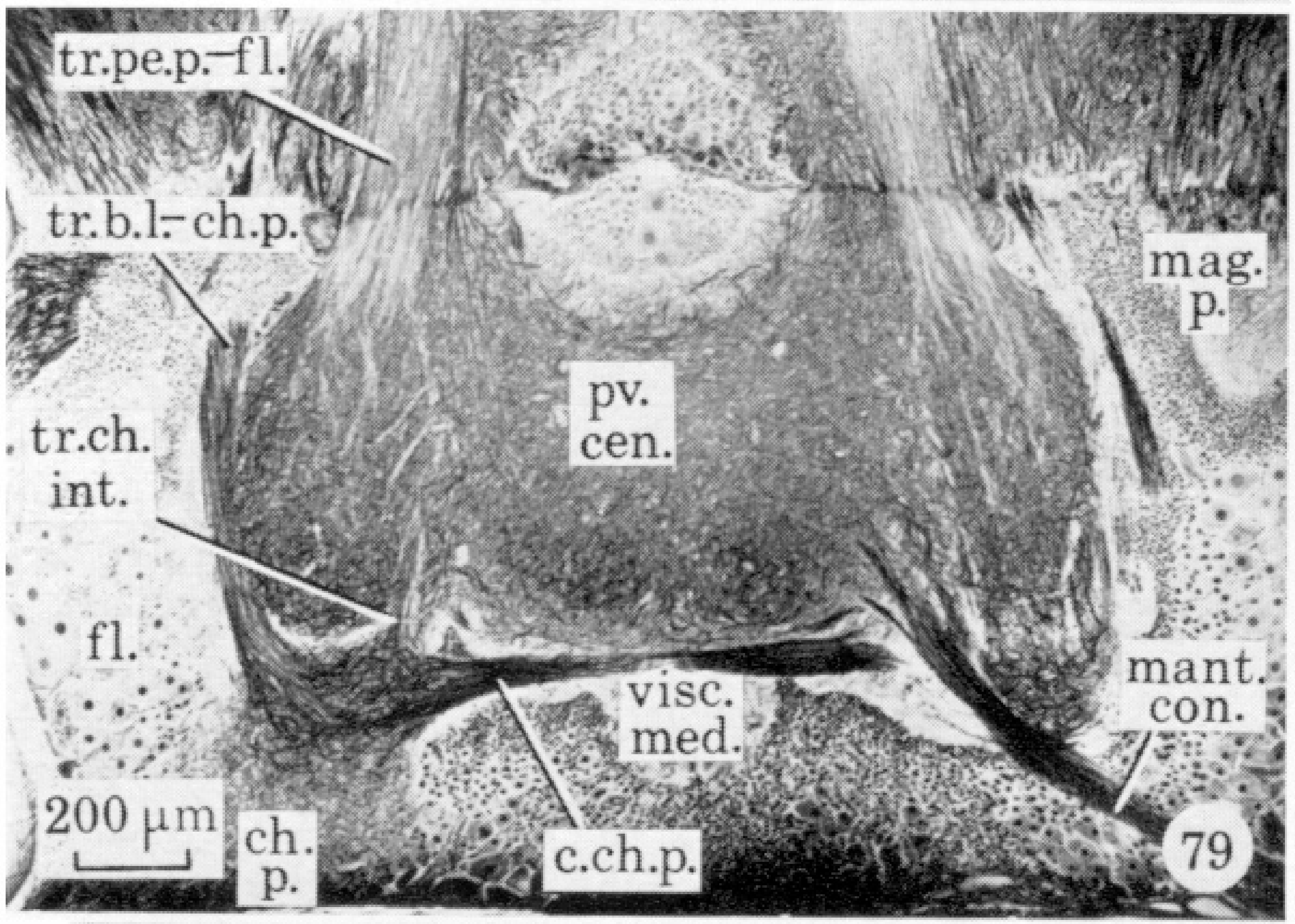


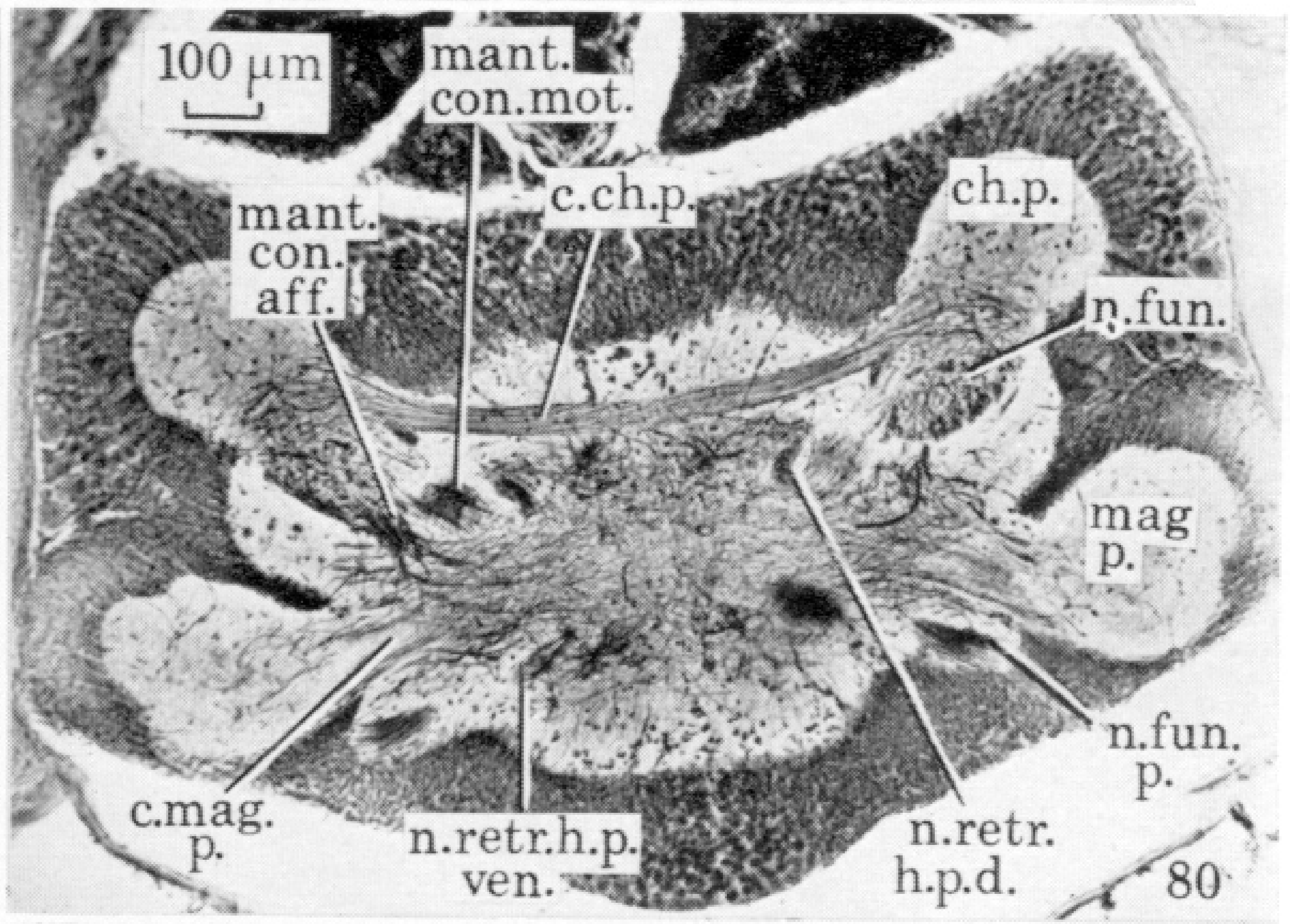


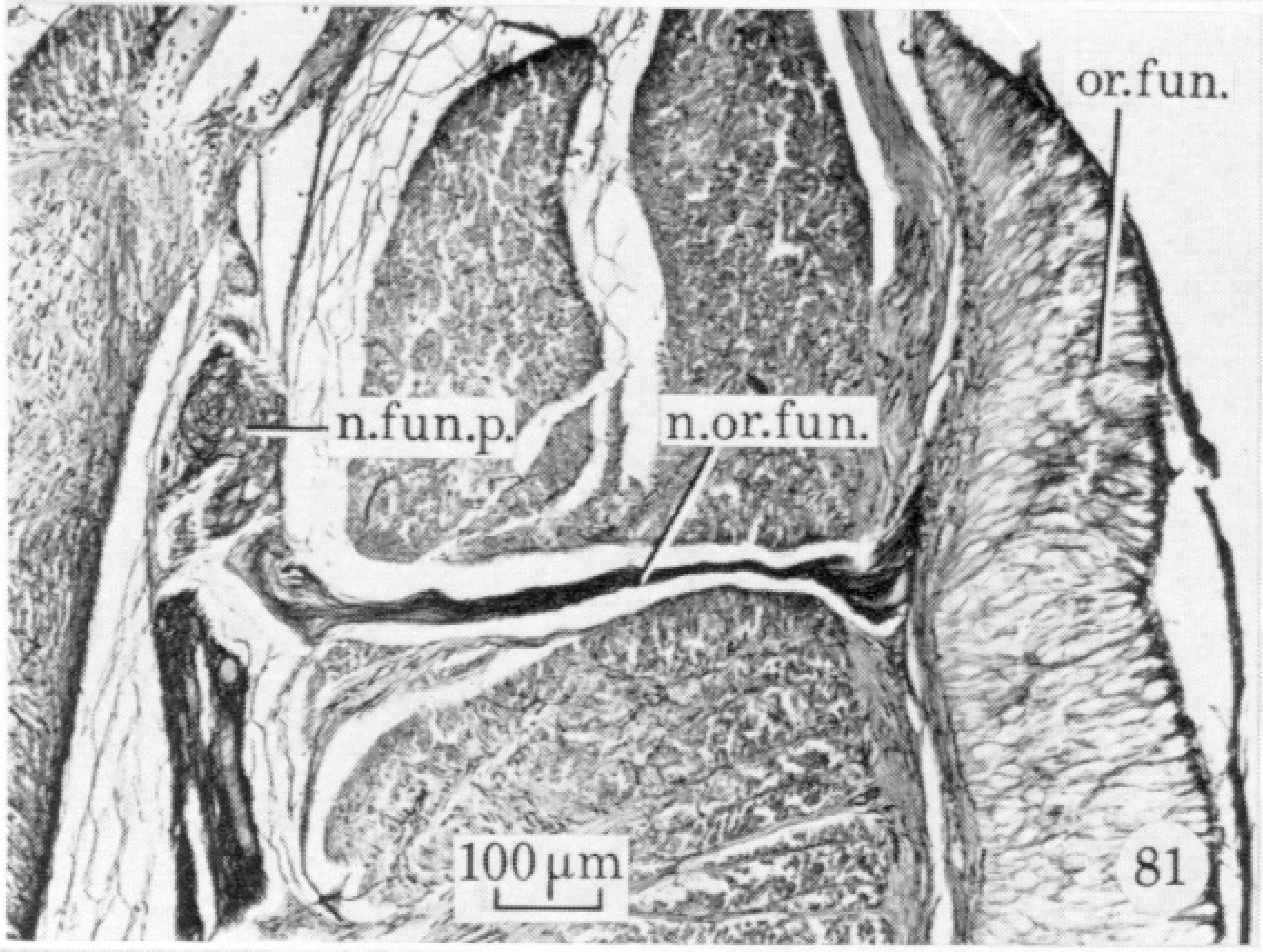
FIGURES 69–75 AND 77. For description see opposite.

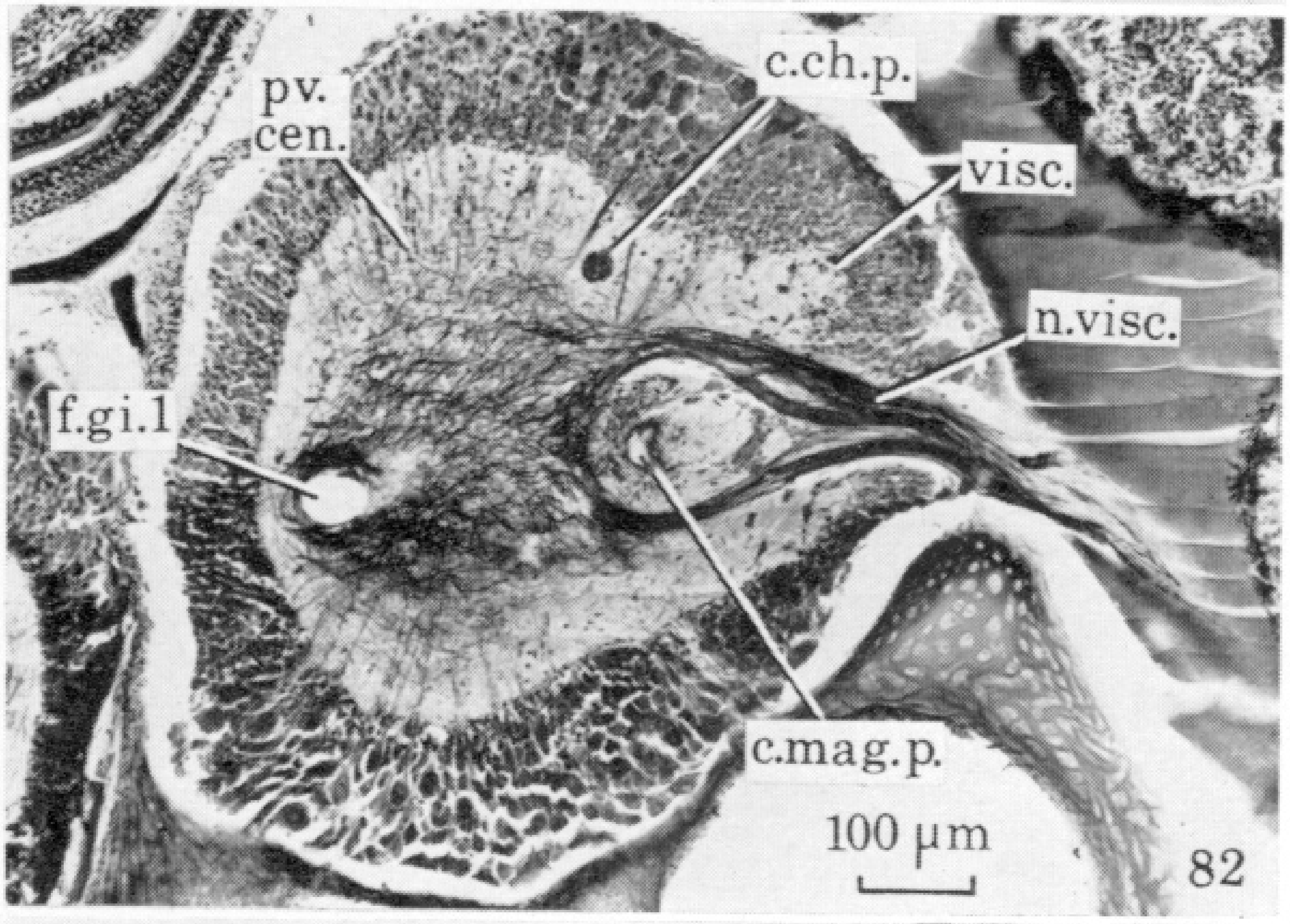


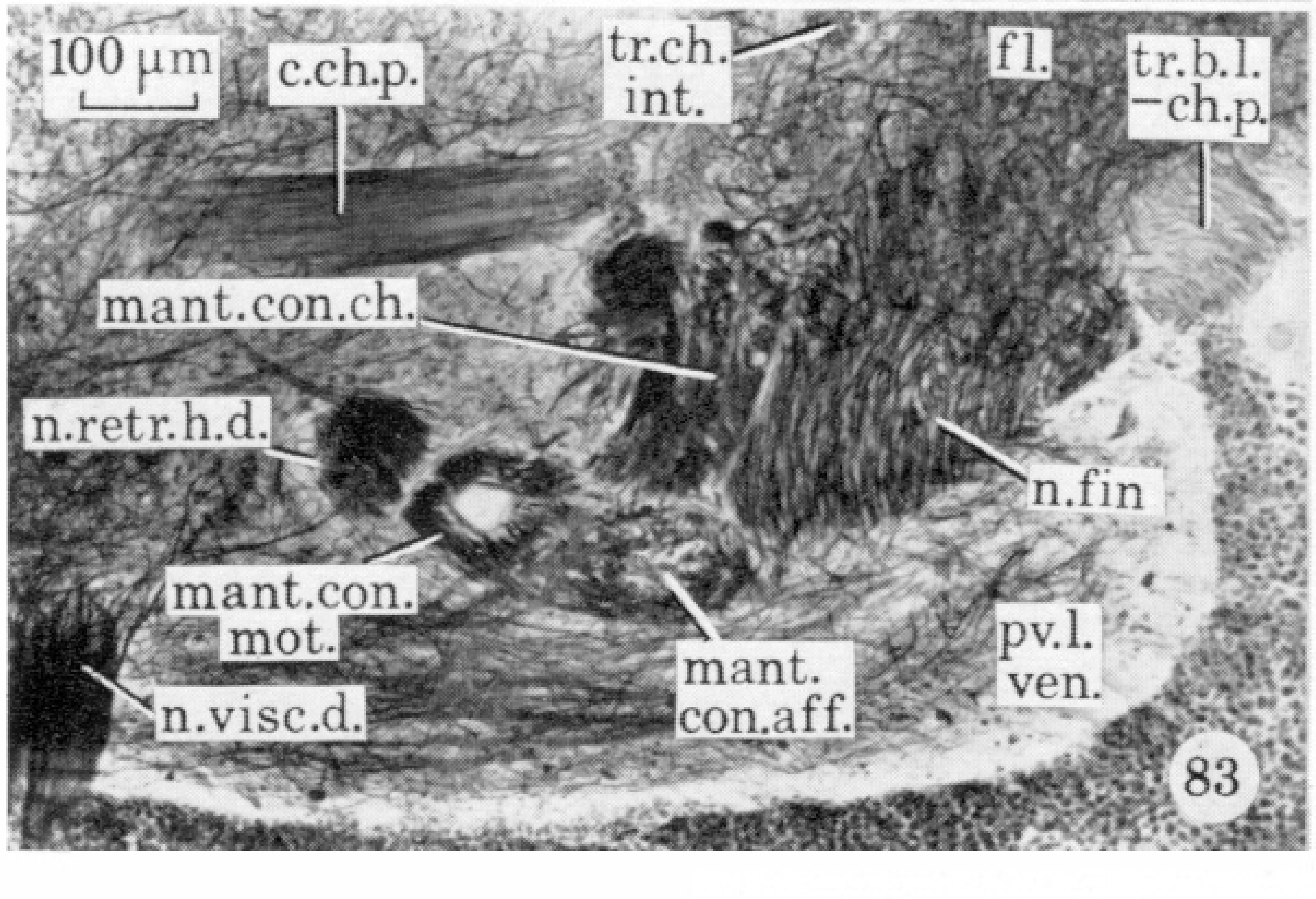


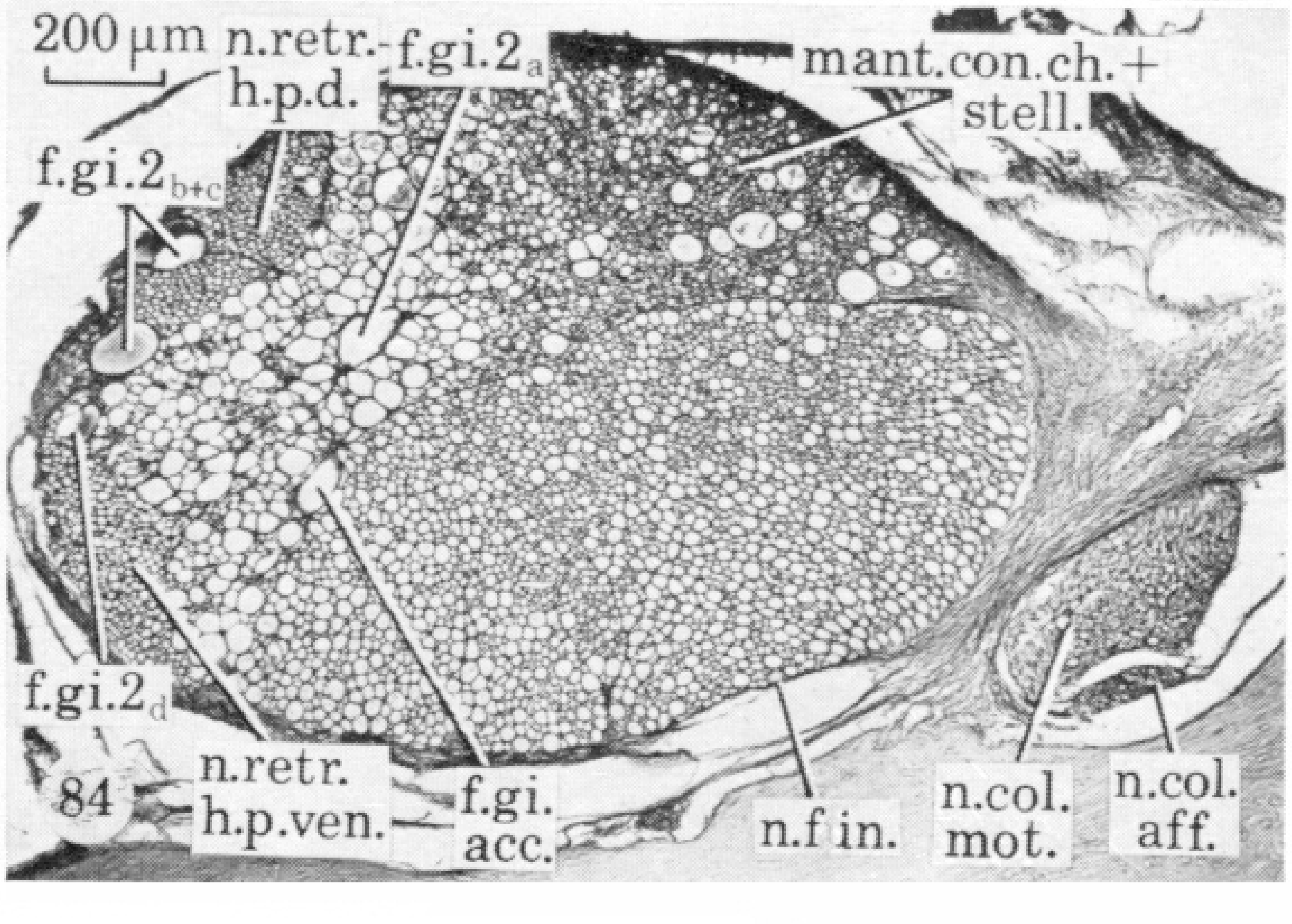




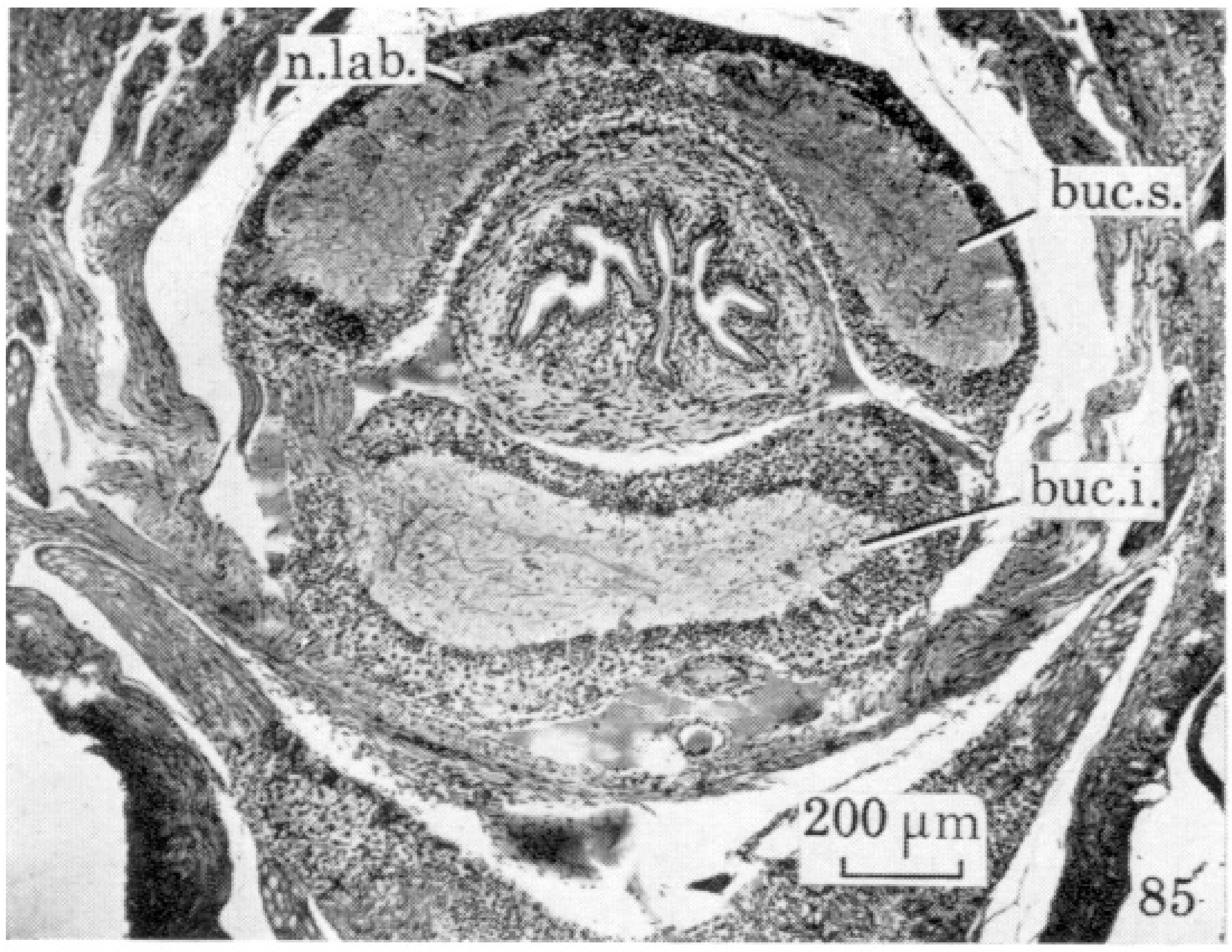


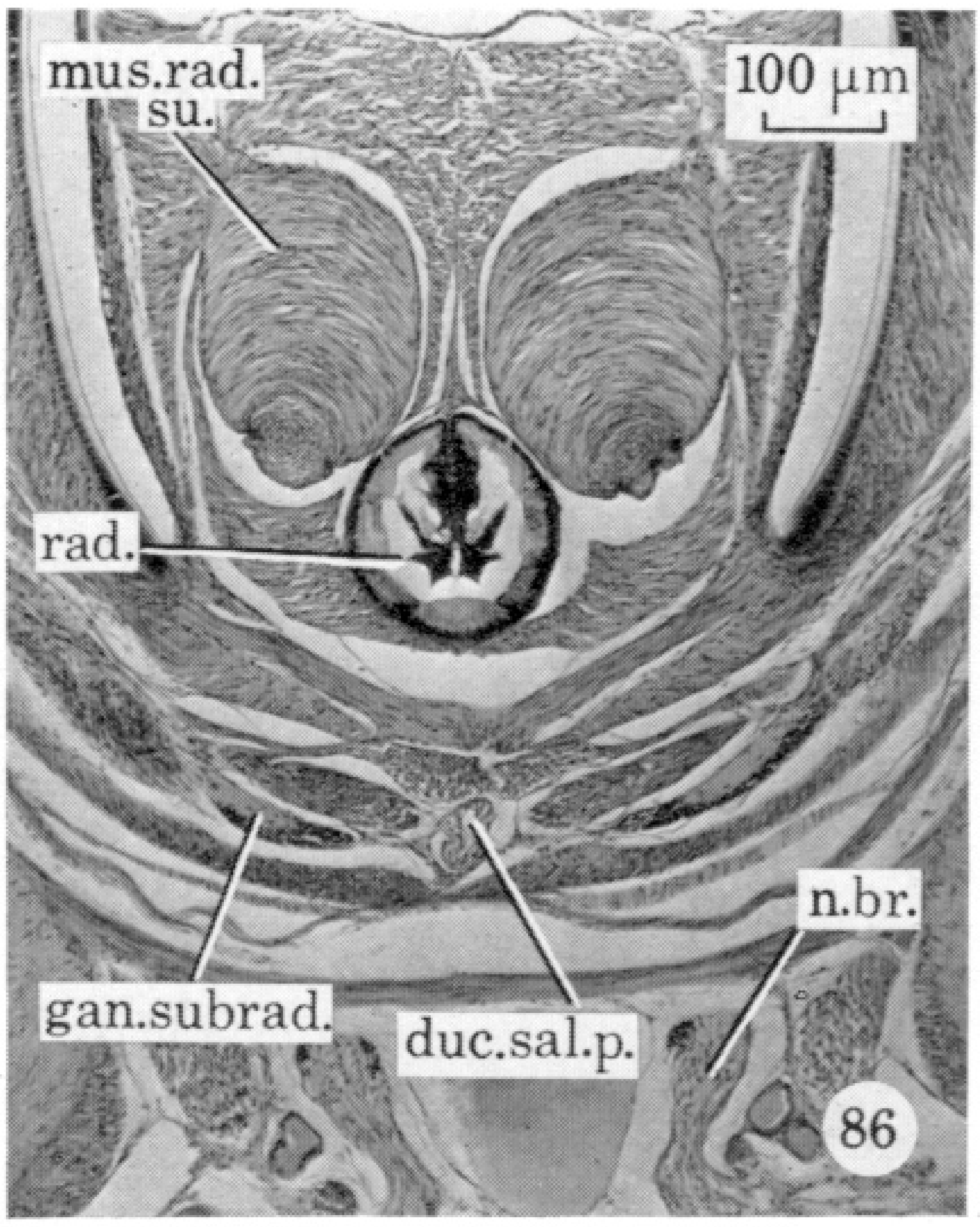


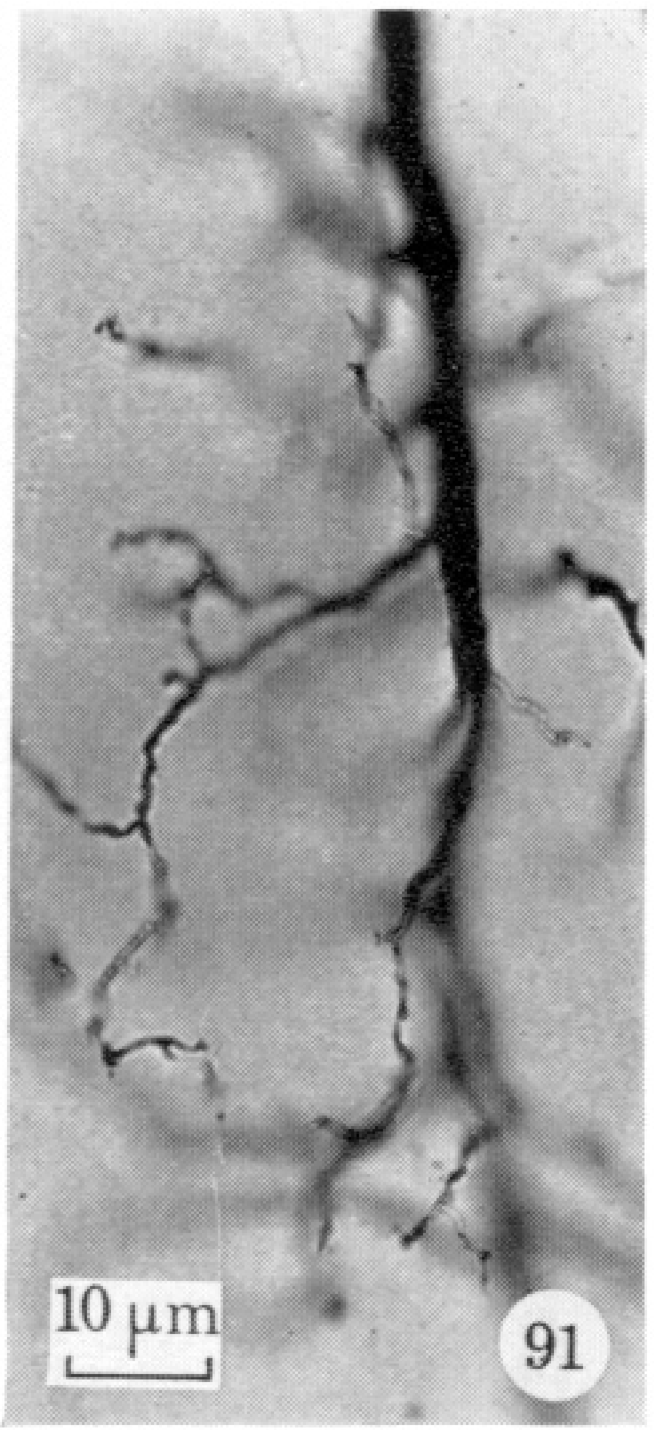


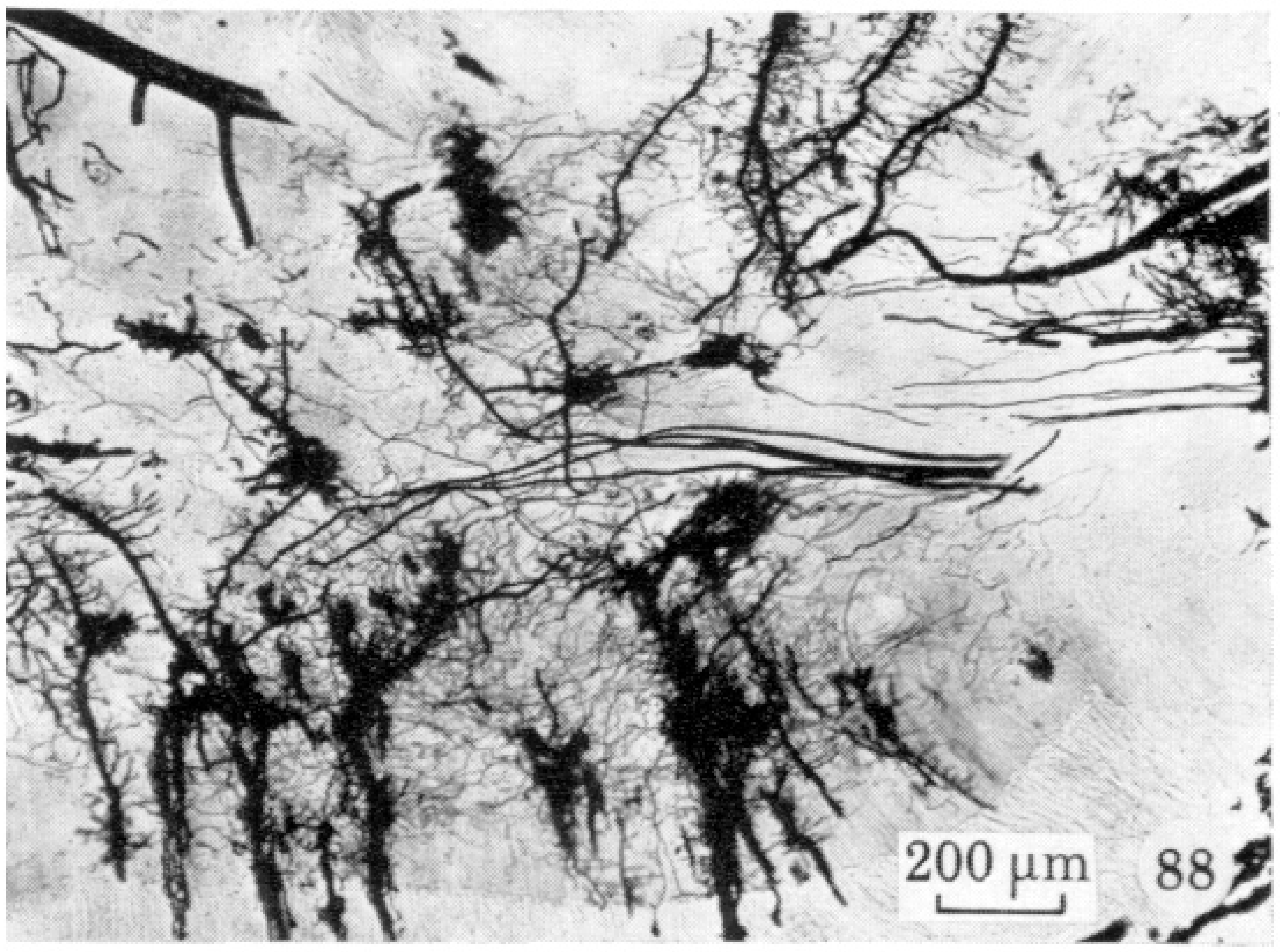


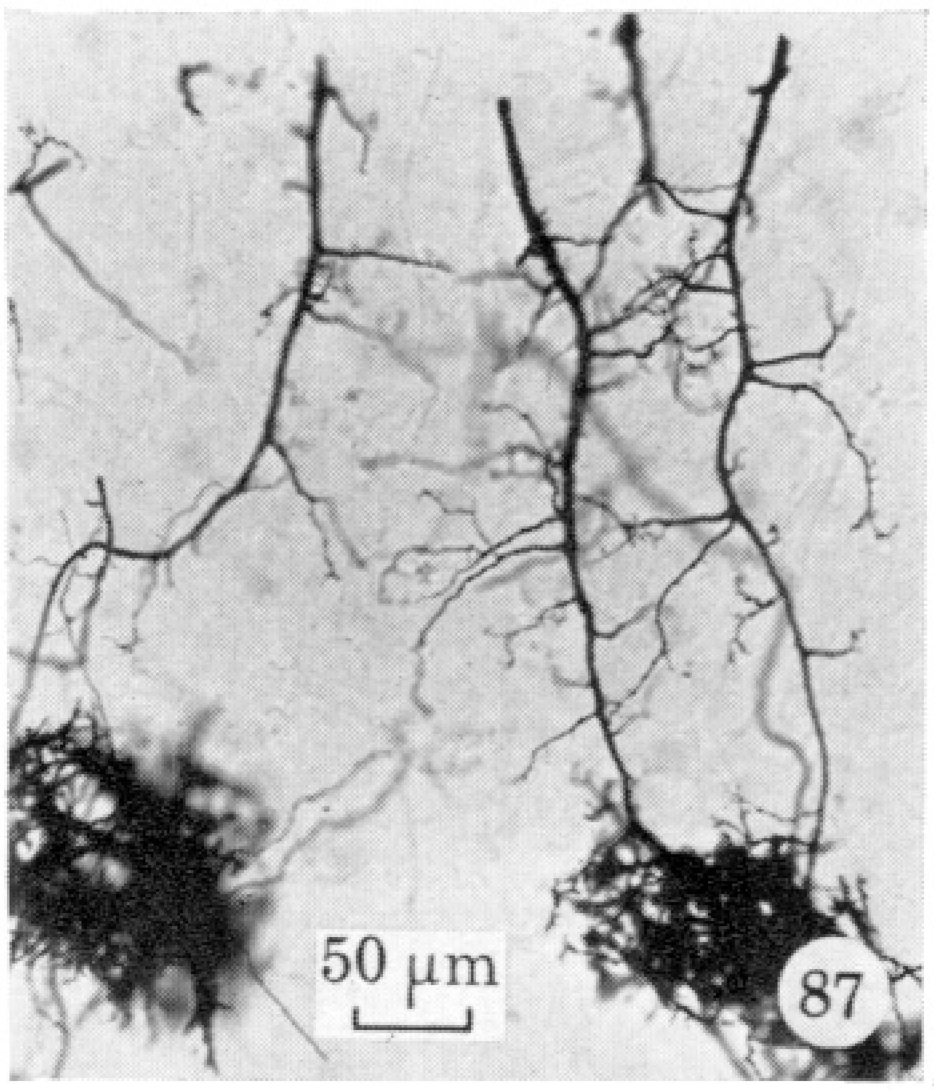
FIGURES 76 AND 78–84. For description see opposite.

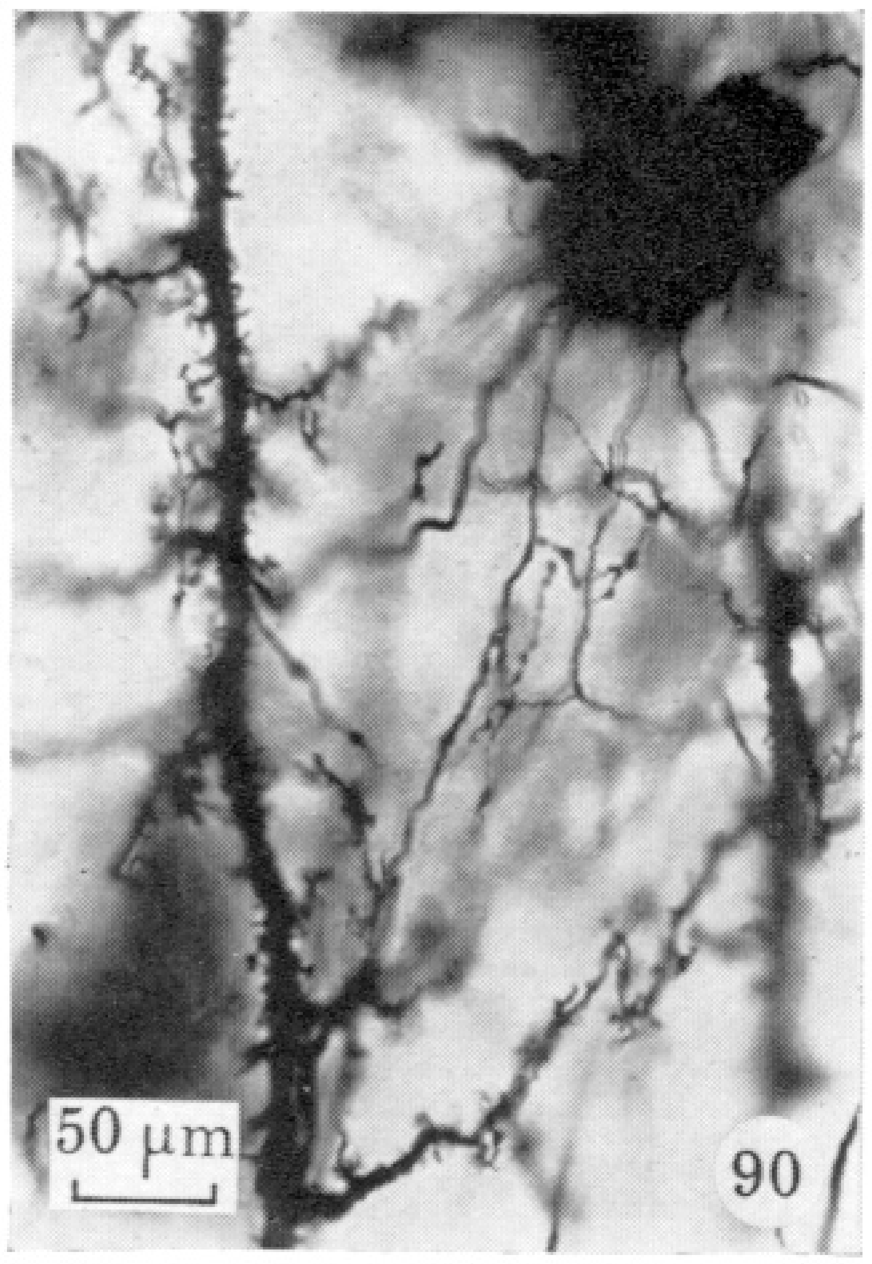


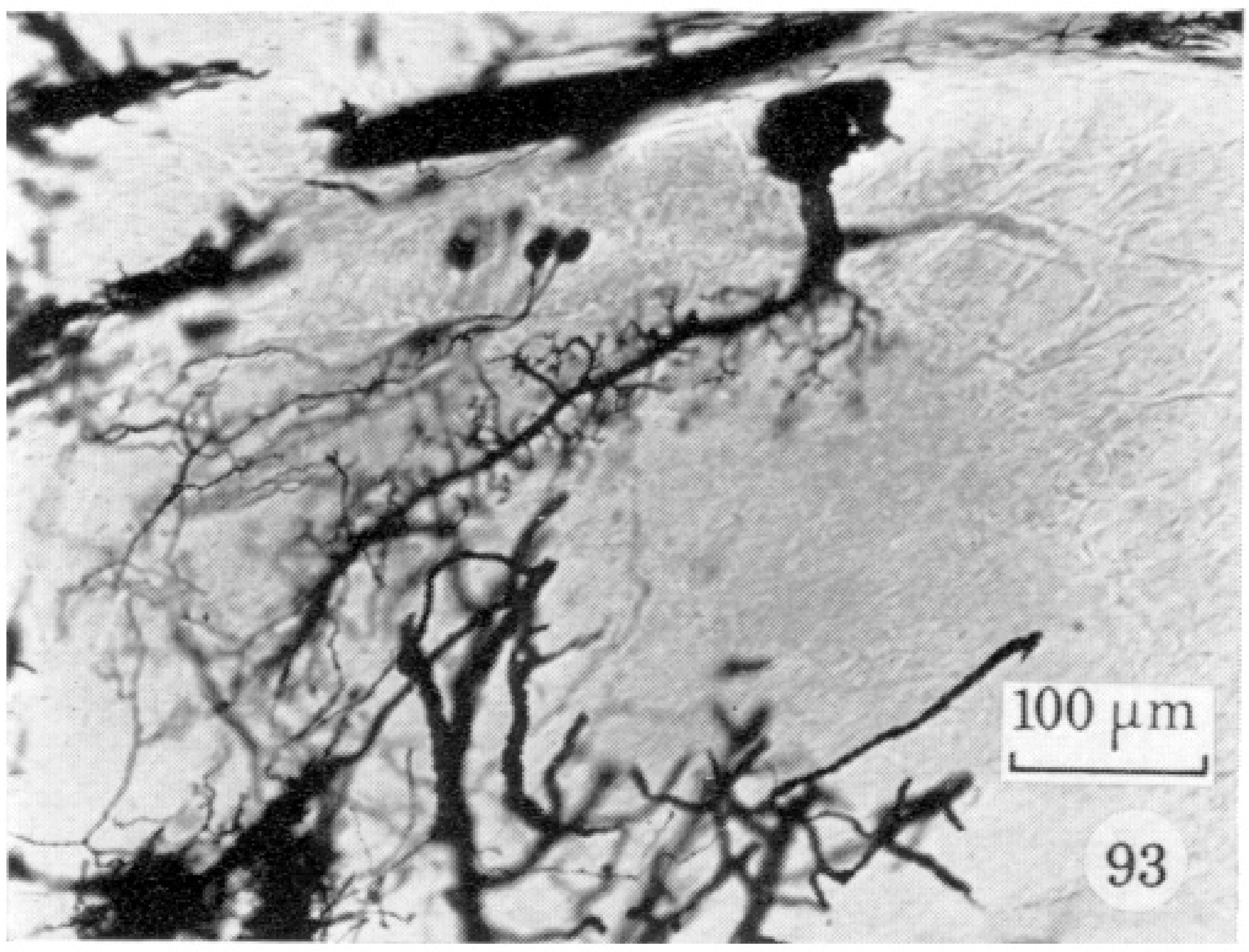


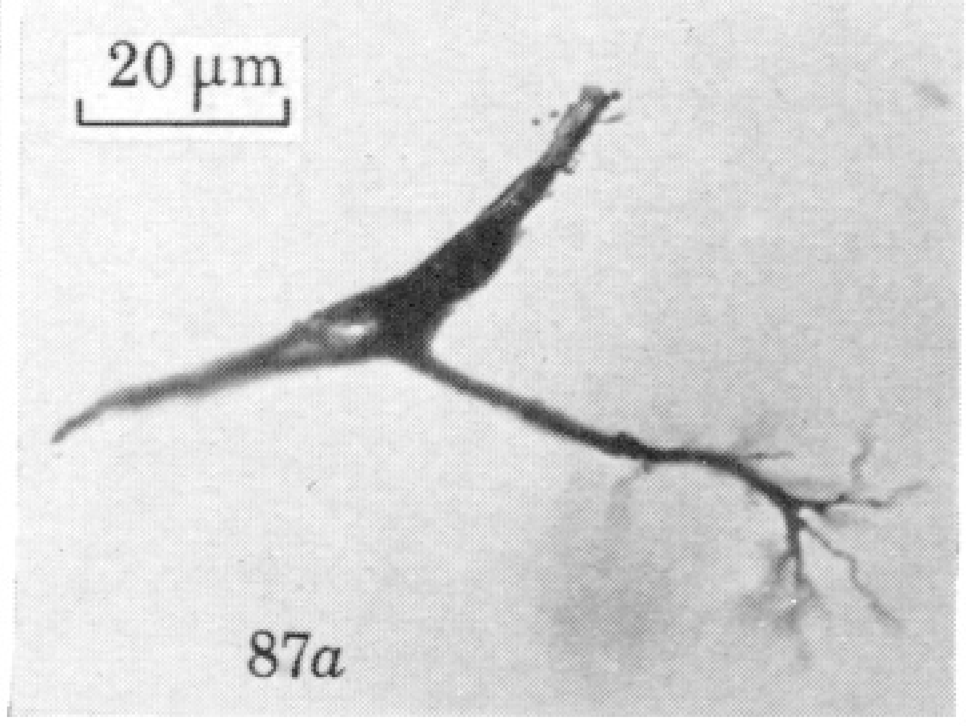


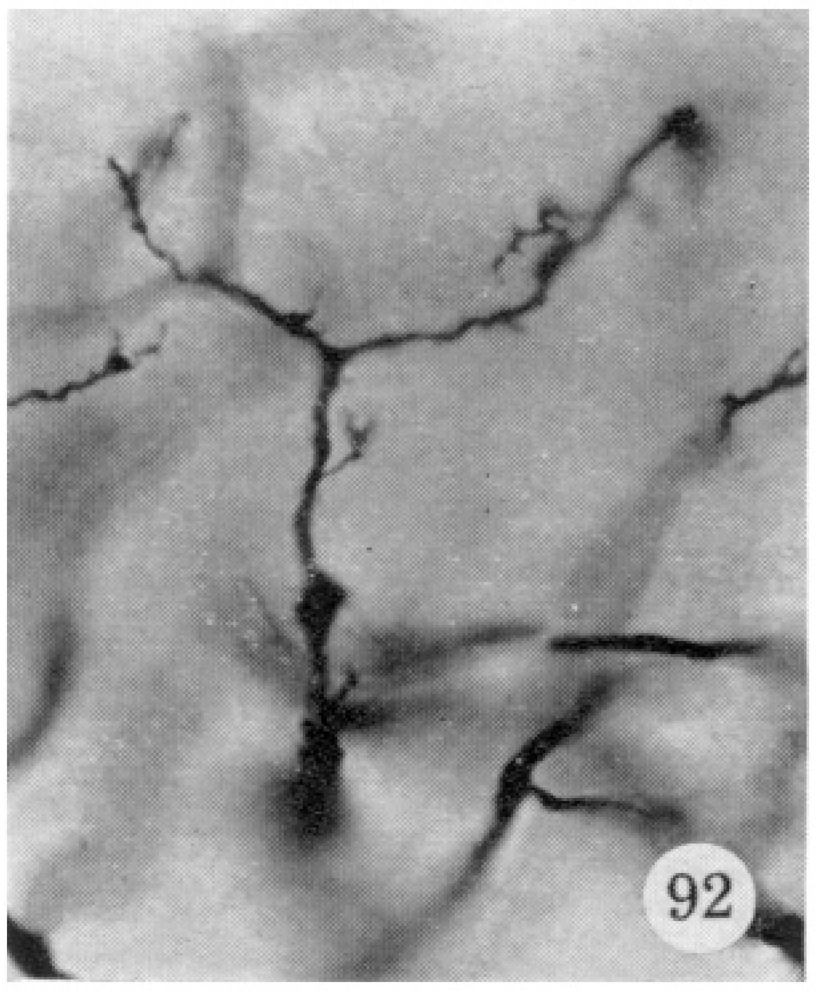


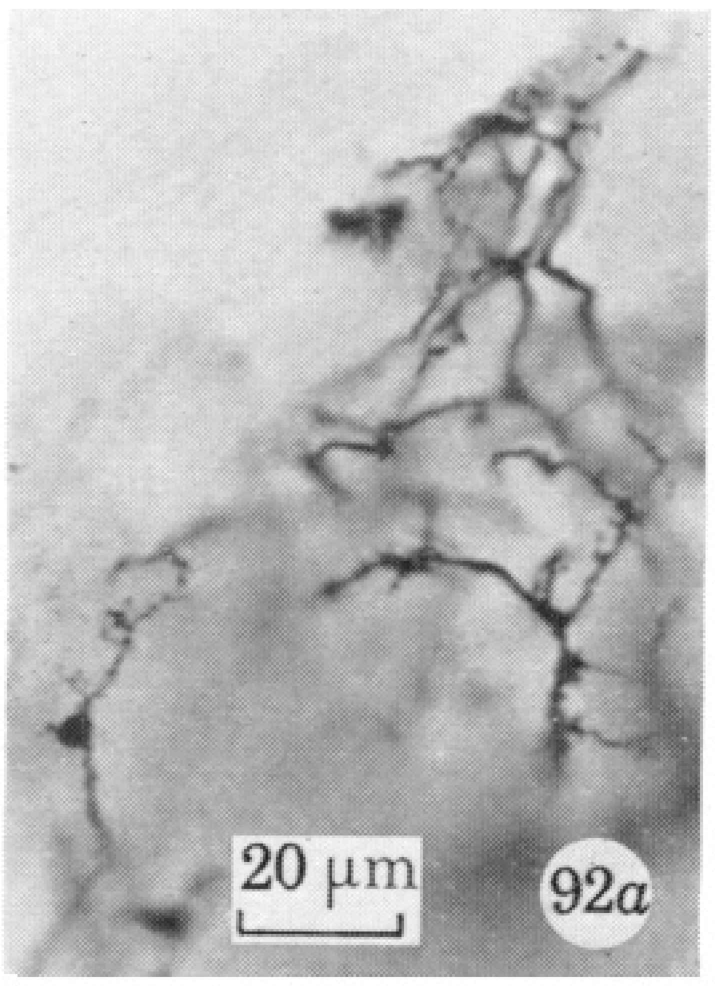


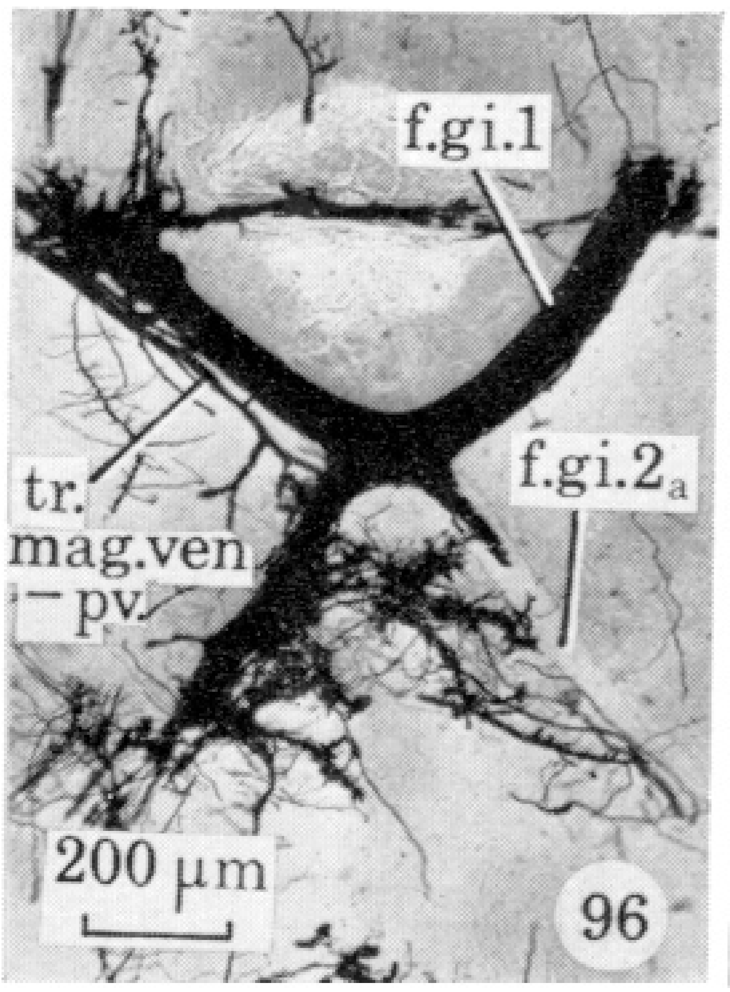


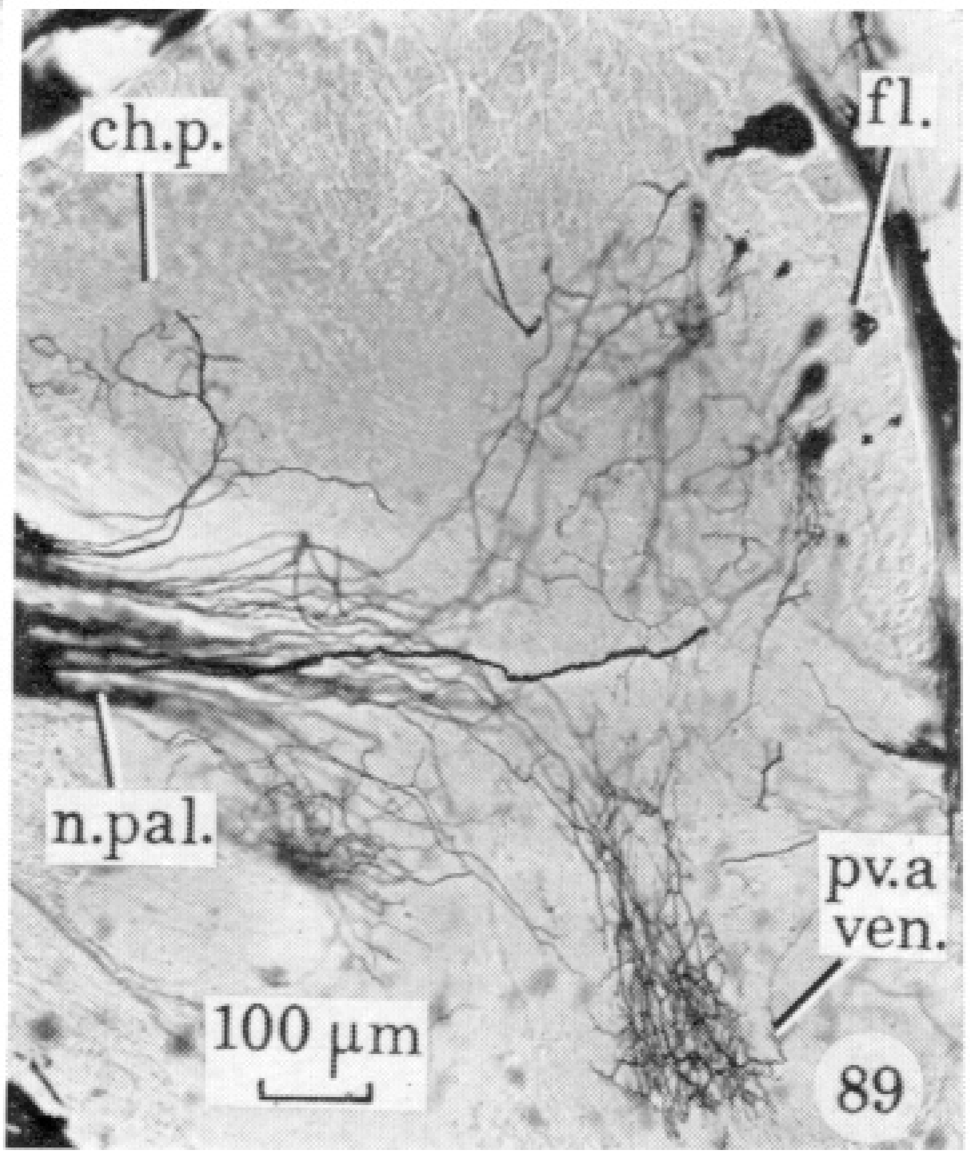






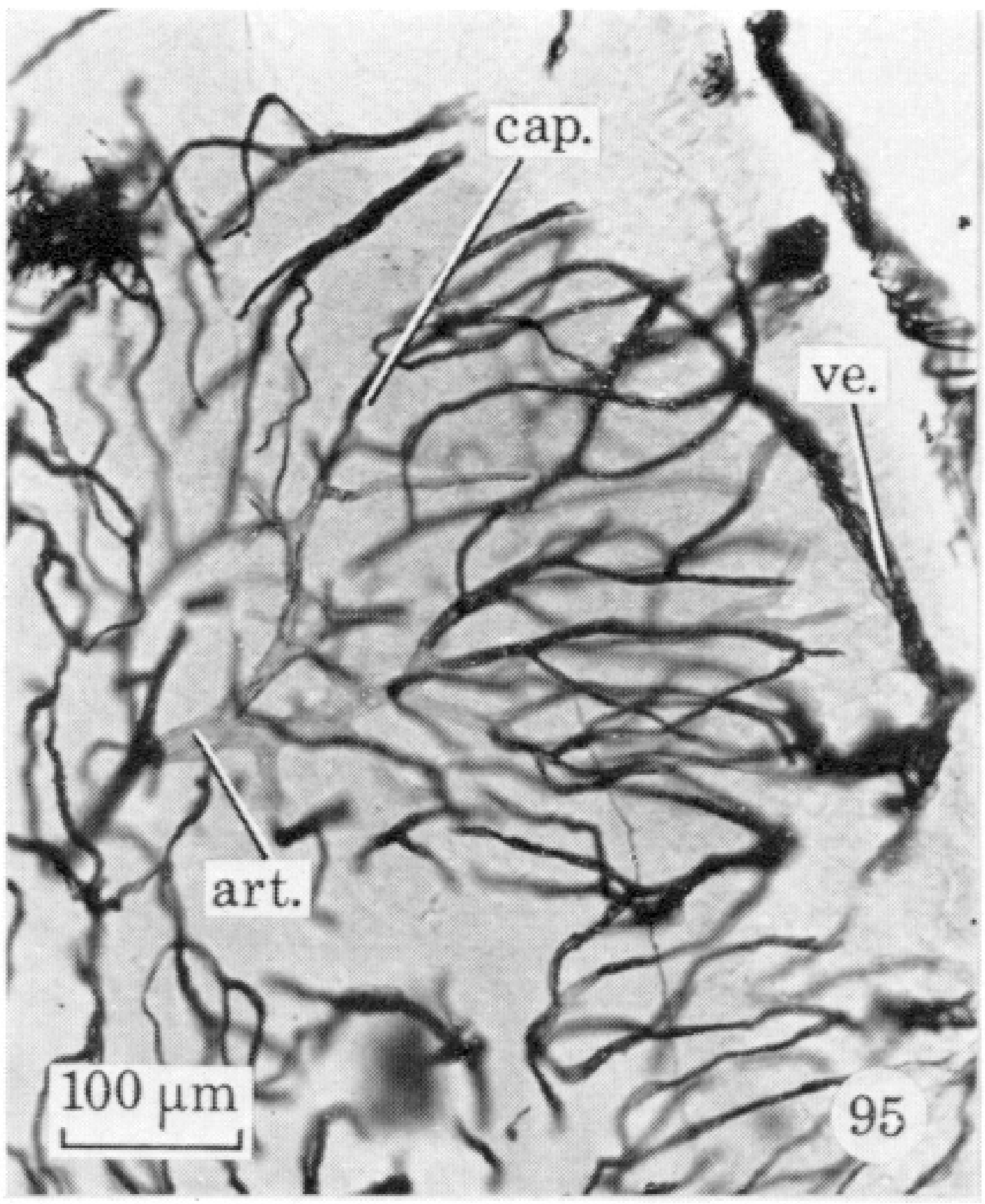




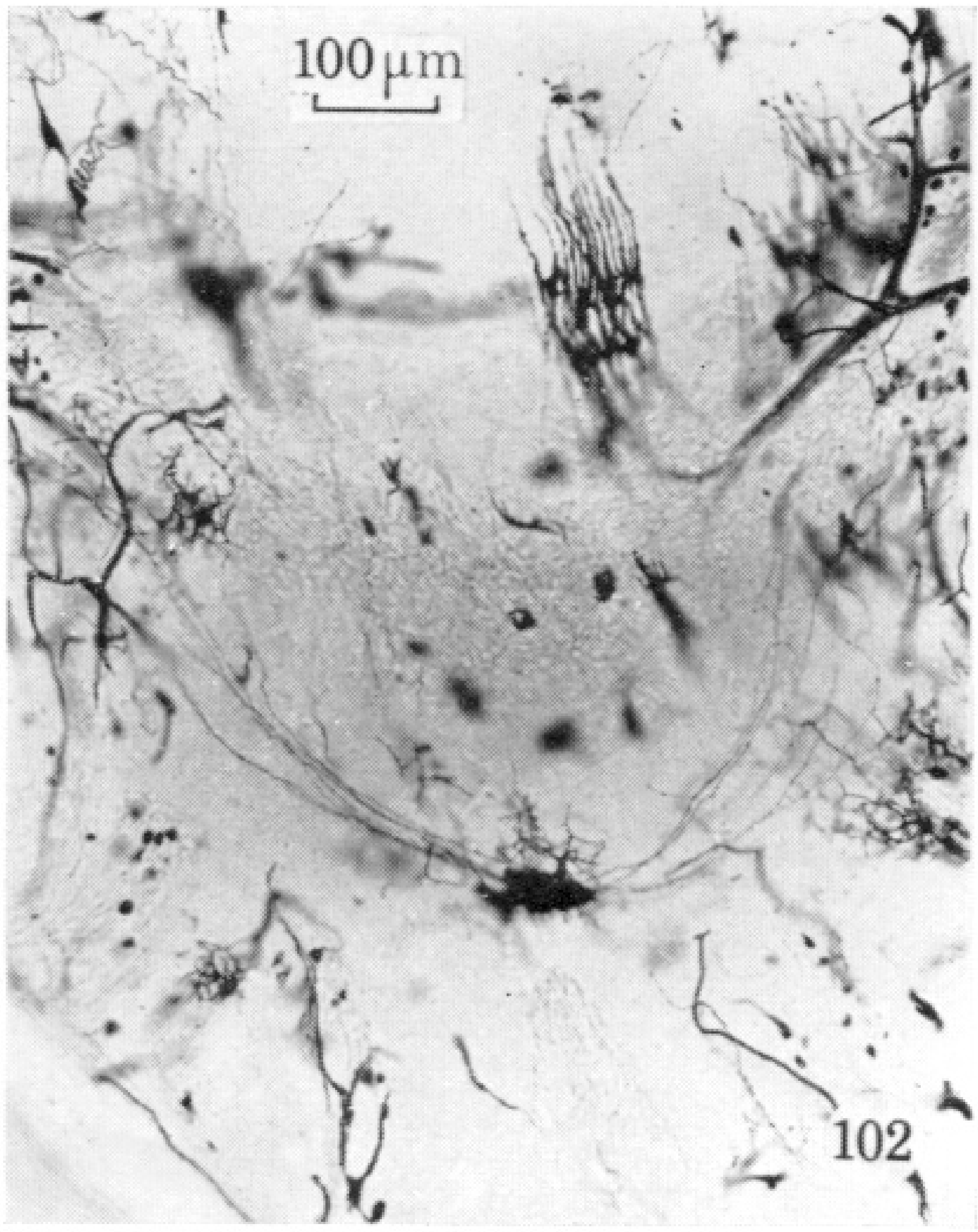


FIGURES 85–93 AND 96. For description see opposite.

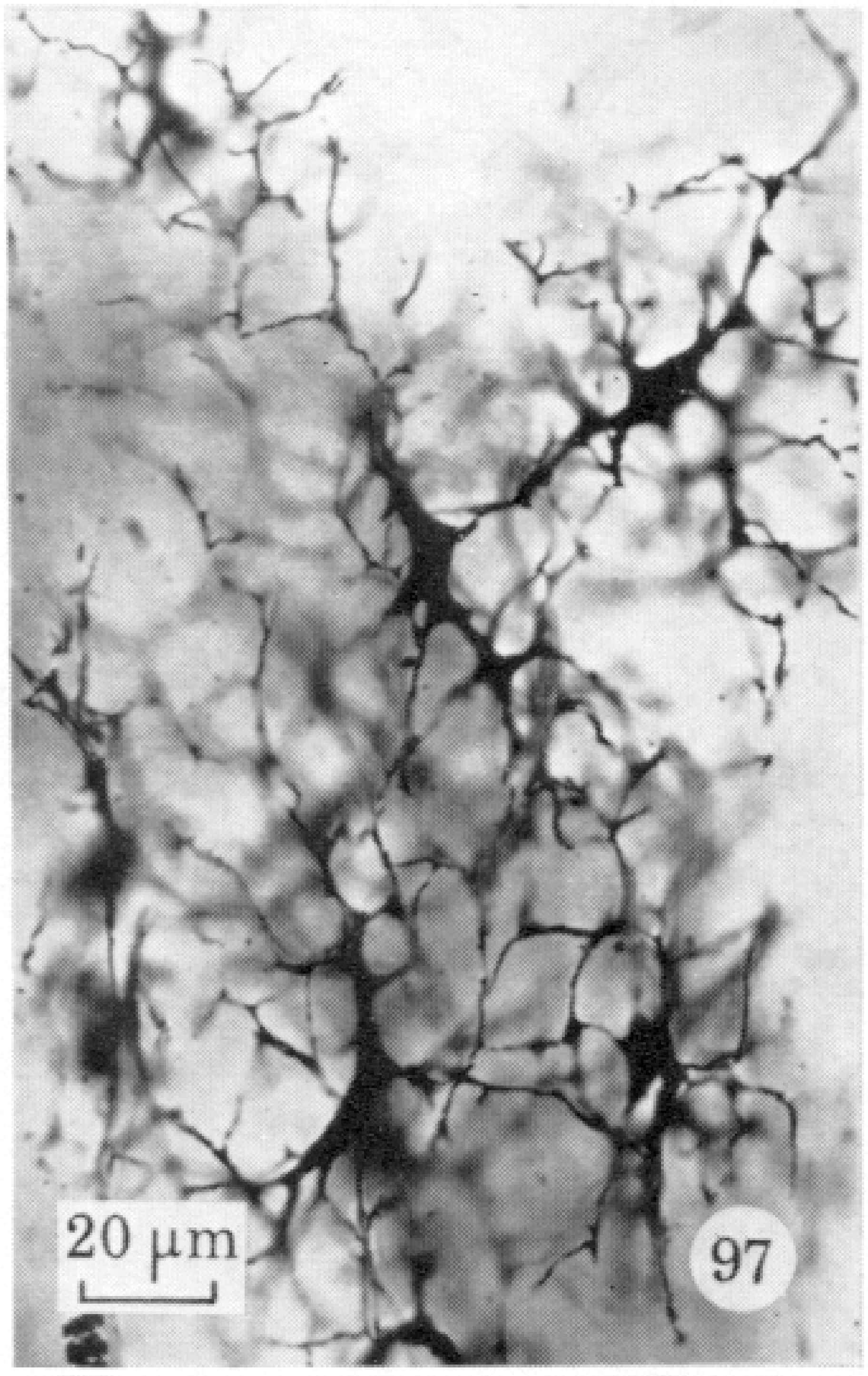
94



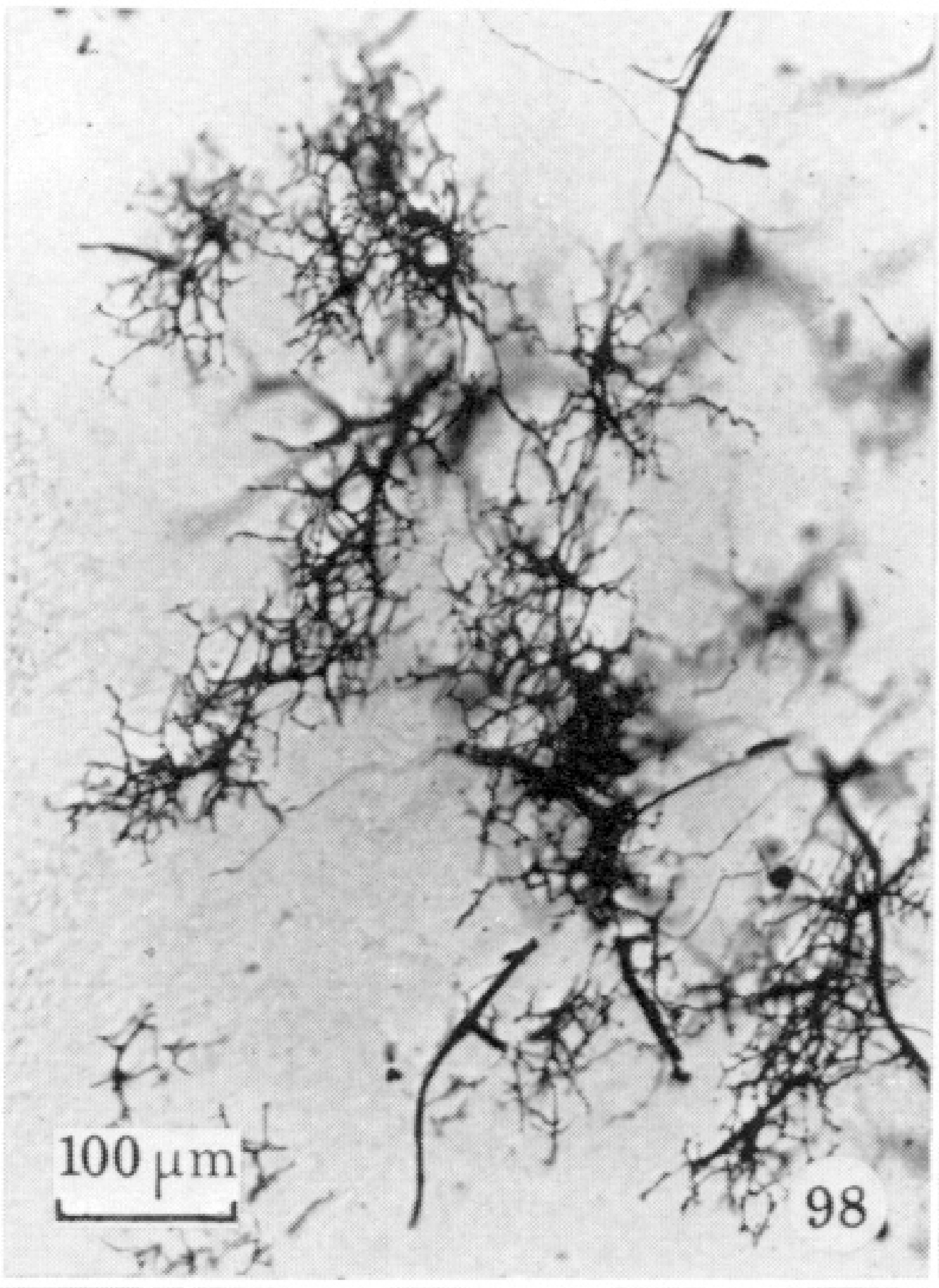
95



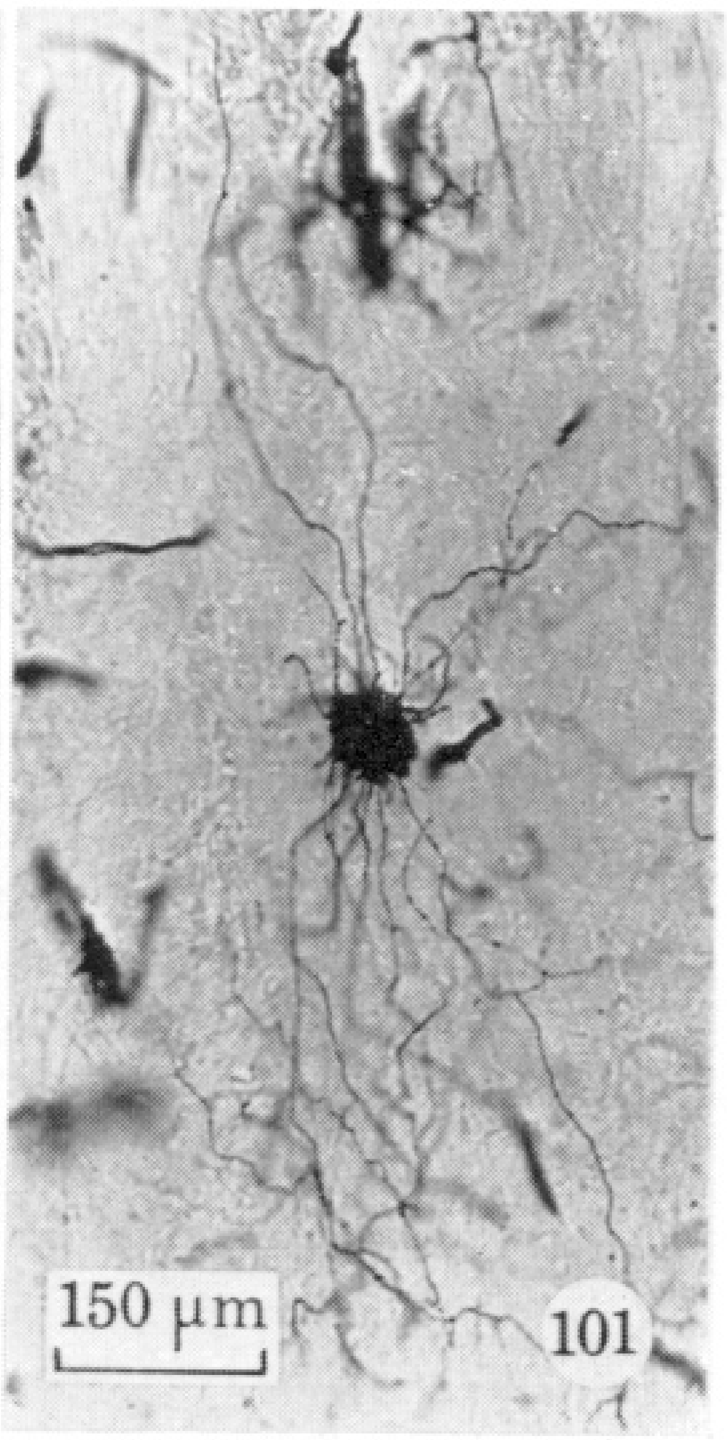
102



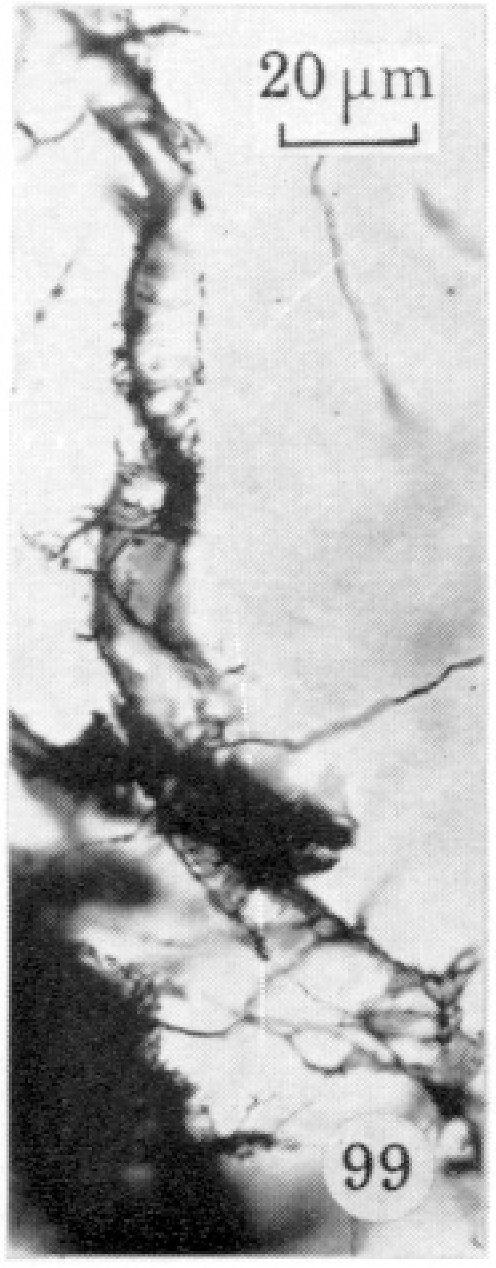
97



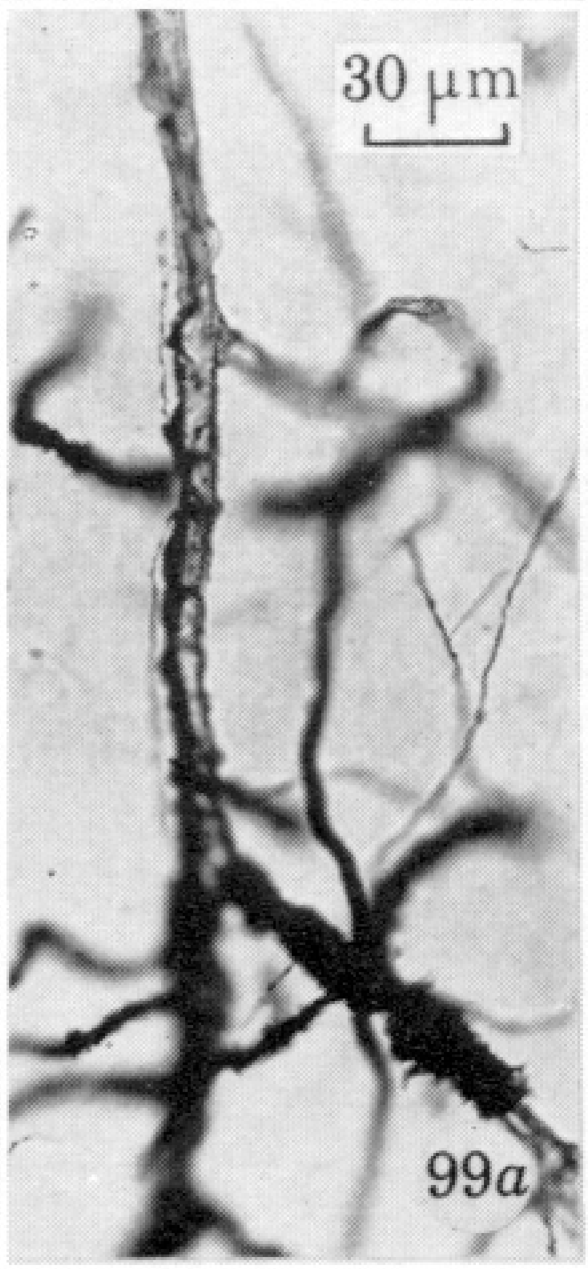
98



101

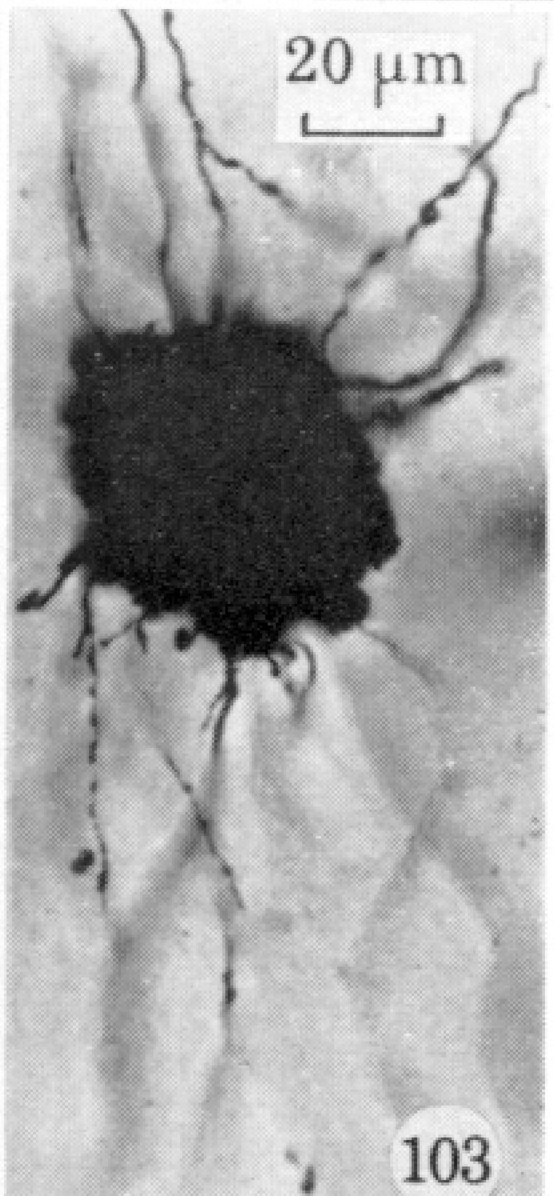


99



99*a*

100



103

FIGURES 94, 95 AND 97–103. For description see opposite.