THE CENTRES FOR TOUCH DISCRIMINATION IN *OCTOPUS*

By J. Z. YOUNG, F.R.S.
Department of Anatomy, University College London

(*Received* 21 *July* 1964)

[Plates 12 to 17]

CONTENTS

The inferior frontal system, concerned with learning chemotactile discriminations, shows four distinct regions. The posterior buccal lobes contain both large and small cells and are the centre of the system. They receive fibres from the arms (without interweaving), from the lips, and from the buccal mass. They send fibres downwards to the arm centres and backwards to the optic and superior frontal/vertical systems. This is therefore probably both a reflex centre for response to some simple chemotactile stimuli and also the main output pathway for the whole system.

In the lateral inferior frontal lobes the fibres from the arms interweave and mix with those from other sources. Their efferent fibres pass to the posterior buccal lobes and to the same destinations as the efferent fibres of the posterior buccal lobes. The organization of the lateral inferior frontal thus allows responses to *combinations* of chemotactile inputs.

The median inferior frontal lobe receives the same input as the lateral inferior frontals, and its interweaving bundles allow for further spreading and combination between afferents. Its efferent axons pass only to the subfrontal lobes.

The subfrontal lobes, besides the input from the median inferior frontal lobe, receive fibres from below. Their cells are mostly very small, with axons ending within the lobe A few larger cells with axons running to the posterior buccal lobes carry the output.

The tactile system is thus essentially similar to the visual one, with a pair of lower centres (posterior buccal and lateral inferior frontal) and a pair of upper ones (median inferior frontal and subfrontal). Embryologically these all differentiate from a single lobe, and the small cells of the upper lobes form a continuous layer with the relatively fewer small cells of the lower lobes.

The main difference between the visual and tactile systems is the absence from the latter of a differentiated region corresponding to the optic lobe. From the evidence of Wells the change that constitutes a memory record occurs in the region of the posterior buccal lobe that contains both large and small cells. This region is under the influence of the circuit through lateral and median inferior frontal and subfrontal lobes.

1. Introduction

In recent years there has been much investigation of visual and tactile discrimination in *Octopus*. In their studies of the effects of brain lesions upon tactile learning Wells & Wells (1957) have provided a great deal of information about the effects of removal of various parts of the brain upon the capacity to learn tactile discriminations. Wells (1959*a*, *b*, 1961) has also provided evidence about the effects of removal of parts of the inferior frontal complex of the brain upon feeding activity, as well as more details about tactile learning. A description of the structure of this system was given by Thore (1939), but more detailed information is needed to interpret the learning experiments.

The organization of the inferior frontal system has certain obvious similarities to that of the superior frontal-vertical system. The median inferior and median superior frontal lobes are alike in structure, as are the subfrontal and vertical lobes. Closer examination shows that there are detailed similarities between the systems. In both of them two pairs of lobes can be recognized, arranged in parallel in upper and lower tiers (Young 1963*b*, figure 1). The significance of this arrangement will be discussed later. The purpose of the present paper is to describe in detail the connexions within the inferior frontal system. Some of these facts have become apparent during the preparation of an account of the anatomy of the brain of *Octopus* (Boycott & Young 1965).

A problem of terminology arises because in earlier studies no distinction was made between what are now to be called posterior buccal and lateral inferior frontal lobes, the latter name being previously given to both jointly. It is now clear that the distinction between the two are marked and significant for their functioning.

2. Methods

The plan of the inferior frontal system has been studied by examination of serial sections of brains of octopuses, cut in various planes. Numerous series are available stained with a modification of Cajal's method (Young 1939). Very useful preparations have also been obtained with Golgi's method and especially with the Kopsch modification. The courses of many of the tracts have been studied by making lesions and looking for degeneration of fibres with Cajal's stain. Fibres of the central nervous system break up rapidly during the first 2 days after severance from their cell bodies (at 25 °C) and can be recognized as rows of granules.

Some behavioural results are also reported here, mainly of the effects of removing single parts of the inferior frontal system. All operations were done under anaesthesia (3% urethane in sea water). Cell counts were undertaken using the methods previously described (Young 1963*a*).

3. Plan of the inferior frontal system

The inferior frontal system appears to be involved in at least three types of activity of an octopus. It is convenient to organize description of the system around these presumed functions, although this involves using a hypothesis the evidence for which is incomplete. First, the system is concerned with the regulation of those actions of the arms that include discrimination and learning. Secondly, since such actions mostly involve taking in food or rejecting it the inferior frontal system receives fibres from the lips and buccal mass and sends efferents to the centres for their regulation (superior and inferior buccal lobes). Thirdly, the inferior frontal system has some relation to the mechanism concerned with visual discrimination, in that it sends fibres to the lateral and median superior frontal and to the optic lobes and receives fibres from the subvertical lobes, and perhaps direct from the vertical lobes. As it plays a part in so many activities it is not surprising that the inferior frontal system has a complicated organization, which is difficult to unravel and describe. However, with the assistance of a study of its embryology it can be understood as a development of the feeding system, having the primary function of enabling the animal to learn to discriminate between objects by touch.

In an adult octopus four centres can be recognized in the inferior frontal system, arranged in parallel as lower and upper pairs (figure 1). The posterior buccal lobes are the centre of the system in the sense that many of the outgoing axons arise from them (but not all). They contain relatively large cells as well as small ones, and an 'unspecialized' tangled neuropil. In these respects they are similar to the superior buccal and subvertical lobes, with which they are continuous in front and behind respectively.

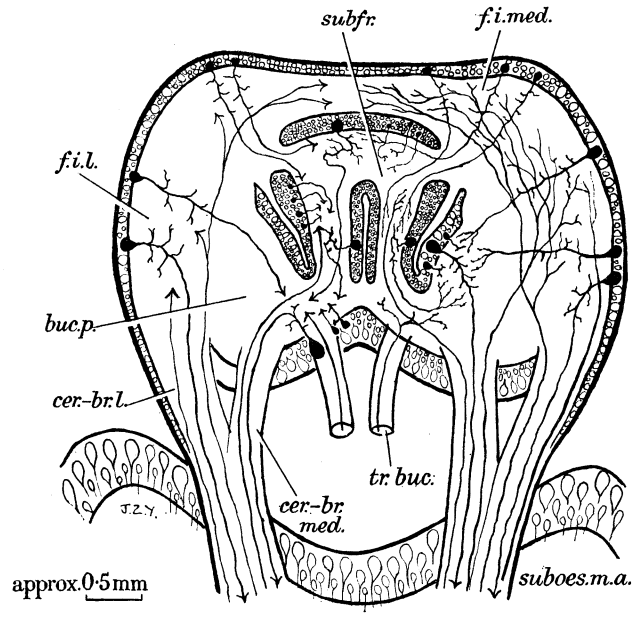


FIGURE 1. Diagram compiled from several transverse sections to show the four lobes of the inferior frontal system and the main types of neurons that they contain. For abbreviations see end of preceding paper, p. 44).

The posterior buccal lobes receive many afferent fibres from the buccal mass, lips and arms. However, other pathways to them from the arms come indirectly, either through the lateral inferior frontals or through the upper tier, the median inferior frontal and subfrontal lobes. The posterior buccal lobes send efferent fibres down to the centres for the arms in the anterior suboesophageal mass, backwards to the visual system (lateral superior frontal lobes) and forwards to the superior buccal lobe.

The lateral inferior frontal lobes receive inputs from the same sources as the posterior buccal lobes (arms, lips and buccal mass) but the characteristic feature of the lateral inferior frontals is that the incoming fibres interweave before making synapse with the output cells. The axons of the latter lead either to the posterior buccal or to the same centres that are reached by the fibres of the posterior buccal. The suggestion that will be made as to the significance of this arrangement is that the posterior buccal lobes serve for reflex responses to simple stimuli, perhaps primarily those of pain. The lateral inferior frontal lobes mediate responses to complex patterns of inputs, especially those involving the association of touch with food.

The lobes of the upper tier, median inferior frontal and subfrontal, are concerned with providing further opportunities for interaction between the inputs from the arms (Wells 1959*a*) and with learning tactile discriminations (Wells 1961). The median inferior frontal lobe receives its fibres from the arms and from the lips, after they have passed through the lateral inferior frontal lobes, probably mainly without synapse. The fibres interweave within the median inferior frontal lobe and make synapse with its cells, all of whose axons proceed to the subfrontal lobes. The latter consist of a vast number of very small cells and a few larger ones, whose axons pass to the posterior buccal lobes.

The arrangement by which the upper lobes send signals back into the lower circuit is the result of the fact that the four lobes develop from one lobe during ontogeny. The lateral inferior frontal, median inferior frontal and subfrontal lobes are all special developments of the small-celled inner layers of this region of the supraoesophageal cord. The posterior buccal lobes are the only ones of the set that retain the primitive arrangement of large outer and small inner cells, and their small cells can be seen to be continuous with the cell layers of the other lobes. Study of the organization and function of the system therefore throws light upon the significance of small cells, especially for discrimination and learning.

4. Posterior buccal lobes

(*a*) *Form, relations and effects of removal*

This pair of lobes corresponds to the hind parts of the 'buccal lobe' as described by Thore (1939). He called each of them the 'Pons buccalo-frontalis inferior' and recognized that their connexions were different from those of the anterior part of the buccal lobe. The differences are indeed considerable and it is necessary to have separate names for the lobes, especially in view of their wide separation in the decapods (Young 1963*b*).

In *Octopus* the posterior buccal lobes are continuations from the superior buccal lobe (figures 2 and 3, plate 12). In the superior buccal lobe the neuropil is continuous across the mid-line but the posterior buccal lobe is a distinctly paired structure and may be said to begin anteriorly at the level where the neuropil is no longer continuous across the mid-line. Posteriorly the posterior buccal lobes pass above the anterior basal lobes to join the subvertical lobe. Their hinder part is mainly occupied by fibre bundles, which will be called the cerebral tracts (figures 5 and 6, plate 12). There are large nerve cells in the walls around the tracts and these will be included as part of the posterior buccal lobes.

The subpeduncular nerves run down between the hind ends of the posterior buccal lobes (figure 5, plate 12). Just behind them a pair of bundles enters the lobes from below (figures 9, 10, plate 13). These are the palliovisceral-buccal tracts and perhaps contain pain fibres (p. 55). Their position marks the hind ends of the posterior buccal lobes.

The ventral sides of the posterior buccal lobes are in contact with the peri-oesophageal sinus (except posteriorly) (figures 5 and 6, plate 12). Laterally they are broadly continuous with the lateral inferior frontal lobes (figures 6 and 7, plate 12). The lateral inferior frontal and posterior buccal lobes are, however, rather sharply distinguished by their cells and neuropil (figure 8, plate 12). The walls of the posterior buccal lobes consist of large cells peripherally and smaller ones adjacent to the neuropil (figures 12 to 14, plate 13), whereas the lateral inferior frontals have much thinner walls, including moderately large and small cells (figure 8, plate 12 and figure 15, plate 13). The neuropils of the two lobes are even more markedly different; that of the posterior buccals is an apparently irregular tangle, whereas the lateral inferior frontal lobes contain a web of interweaving bundles of incoming fibres. This difference is the basis for the suggestion that the lobes serve to produce responses to simple and complex input patterns respectively (p. 64).

The front parts of the dorsal walls of the posterior buccal lobes lie beneath the median inferior frontal lobe. The neuropil of these lobes is continuous laterally, but it is doubtful whether there is any interchange of fibres. The hind parts of the posterior buccal lobes lie beneath, and more posteriorly between, the subfrontals, with which they exchange fibres in both directions. A commissure joins the two posterior buccal lobes, below the subfrontal lobes (figure 6, plate 12).

It is clearly impossible to remove the posterior buccal lobes alone without seriously interrupting many important pathways and damaging other lobes. However, since something is known of the effects of damage to the median inferior frontal and subfrontals (p. 58) we can say that when the posterior buccals and lateral inferior frontals are damaged, in addition to the median inferior frontal and subfrontal, there is interference with the mechanisms for release of the suckers and for the manipulation of crabs (v. Uexküll 1895). Separate removal of the lateral inferior frontals however is anatomically possible (p. 56), and produces this phenomenon of 'sticky suckers'. Since this operation deprives the posterior buccals of a large part of their input we cannot be certain how the posterior buccal and lateral inferior frontal lobes co-operate in the control of sucker release.

(*b*) *Cell layers and neuropil of the posterior buccal lobes*

The posterior buccals are less homogeneous than the other lobes of the system. At the front their cell layers and neuropil resemble those of the superior buccal lobes (figures 11 and 12, plate 13). There are large cells in the outer layers, with nuclei up to 20 μm in diameter and smaller ones down to about 5 μm near the neuropil. Passing backwards the 'large' cells become rather smaller and the 'small' cells relatively more numerous and smaller until the structure typical of the subfrontals is reached (figures 12 to 14, plate 13). This change probably corresponds to the transition from a tissue capable only of reflex functions to one that is able to learn (p. 65). The fact that there is no sharp division

---

Description of plate 12

(Abbreviations used on the figures and plates are listed at the end of the preceding paper, p. 44.)

Plate 12

Figure 2. Sagittal section of brain nearly in the mid-line.

Figure 3. Sagittal section slightly to one side of the mid-line, showing the continuity of posterior buccal and subvertical lobes.

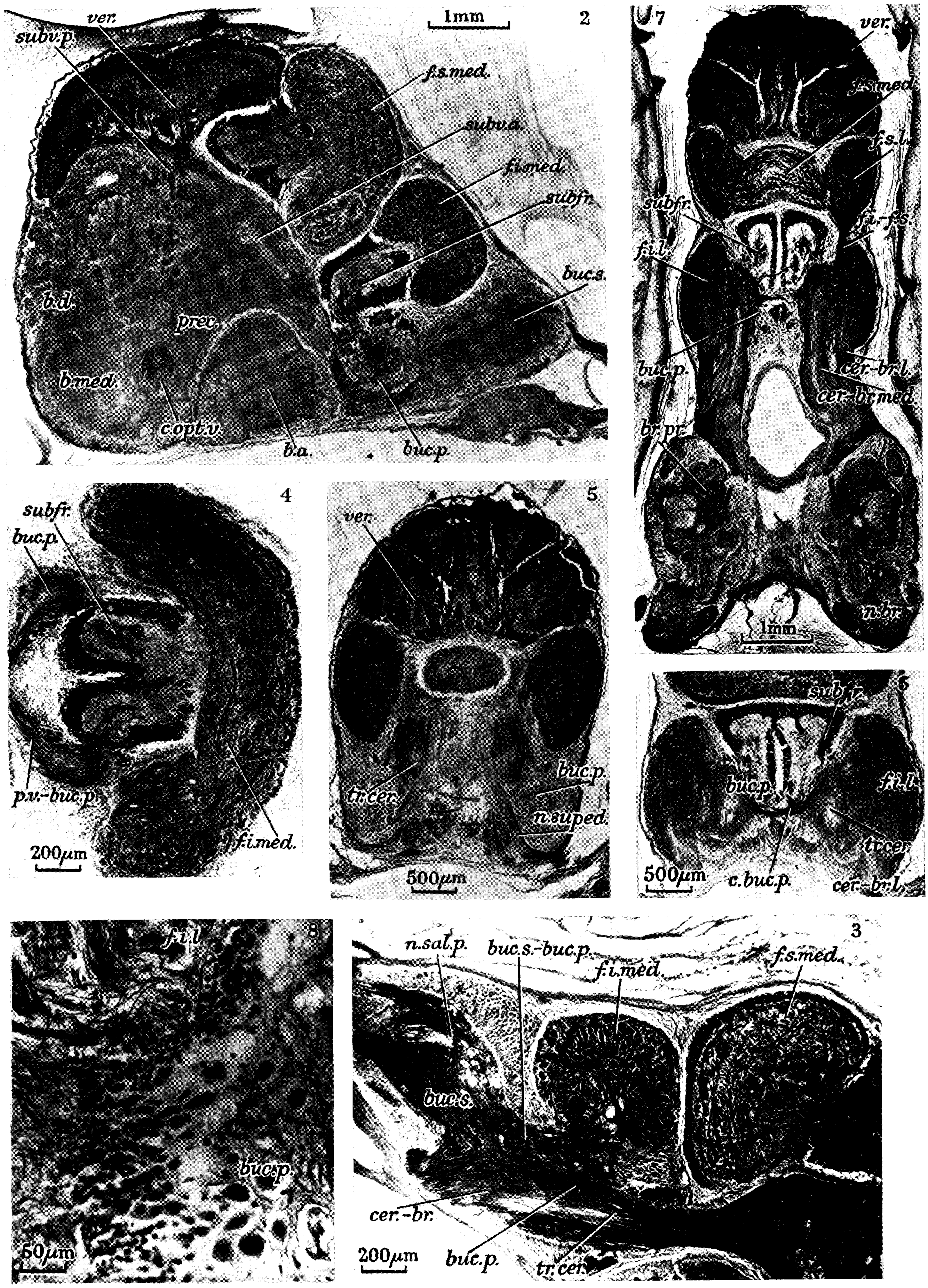
Figure 4. Horizontal section showing the palliovisceral to posterior buccal tracts.

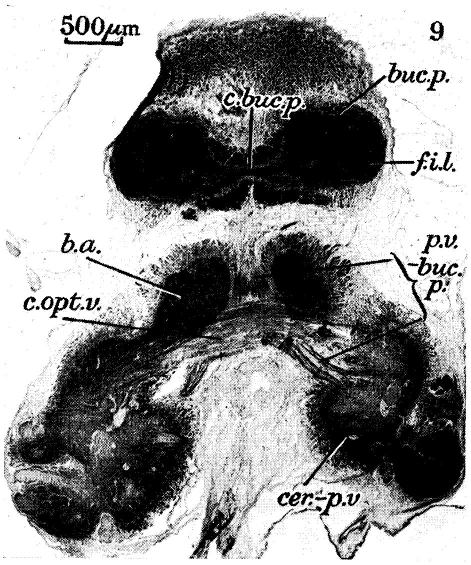
Figure 5. Transverse section through the extreme hind end of the posterior buccal lobes.

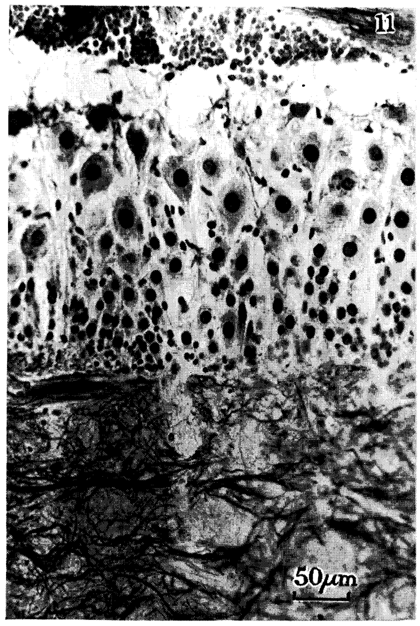
Figure 6. Transverse section farther forward than figure 5, showing the commissure joining the two sides of the posterior buccal lobes below the subfrontals.

Figure 7. Oblique transverse section showing the cerebro-brachial tracts.

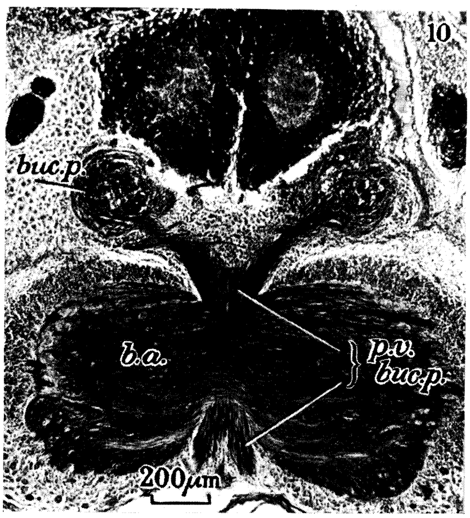
Figure 8. Transverse section showing the transition from posterior buccal to lateral inferior frontal lobes.

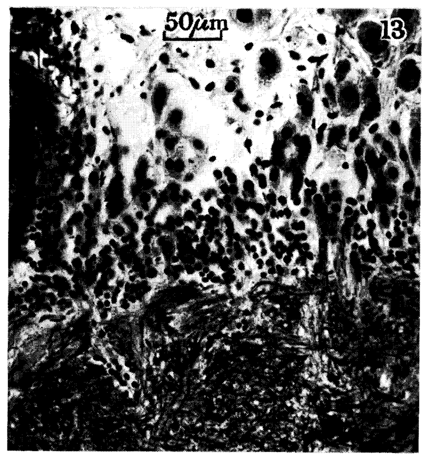

2
1mm
ver.
subv.p.
f.s.med.
subv.a.
f.i.med.
subfr.
buc.s.
b.d.
prec.
b.med.
c.opt.v.
b.a.
buc.p.
7
ver.
f.s.med.
f.s.l.
subfr.
f.i.-f.s.
f.i.l.
buc.p.
cer.-br.l.
cer.-br.med.
br.pr.
n.br.
1mm
4
subfr.
buc.p.
p.v.-buc.p.
f.i.med.
200μm
5
ver.
buc.p.
tr.cer.
n.suped.
500μm
6
sub.fr.
buc.p.
f.i.l.
tr.cer.
500μm
c.buc.p.
cer.-br.l.
8
f.i.l.
buc.p.
50μm
3
n.sal.p.
buc.s.-buc.p.
f.i.med.
f.s.med.
buc.s.
cer.-br.
200μm
buc.p.
tr.cer.


500μm
9
c.buc.p.
buc.p.
f.i.l.
b.a.
c.opt.v.
p.v.
buc.
p.
cer.-p.v.

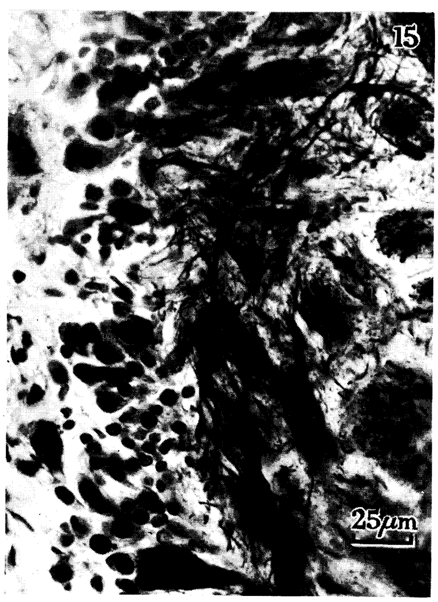

11
50μm


12
50μm


10
buc.p.
b.a.
p.v.
buc.p.
200μm


50μm
13


50μm
14


15
25μm


16
25μm


17
25μm

Plate 13

Figure 9. Horizontal section at the base of the supra-oesophageal mass showing the course of the palliovisceral to posterior buccal tract, passing below the optic commissure.

Figure 10. Transverse section at the extreme hind end of the posterior buccal lobe, showing the palliovisceral to posterior buccal tract running up in front of the anterior basal lobe.

Figures 11 to 14. Transverse sections showing the transition from tissue with the structure of the superior buccal in front, through the posterior buccal to the subfrontal type tissue behind. All at the same magnification.

Figure 15. Transverse section of the cell layers and neuropil of the lateral inferior frontal lobes.

Figure 16. Transverse section of the cell layers and neuropil of the median inferior frontal lobe.

Figure 17. Transverse section of the cell layers and neuropil of the subfrontal lobes.

Plate 14

Figure 18. Sagittal section showing the buccal tract running to the posterior buccal lobe.

Figure 19. Transverse section at the hind end of the posterior buccal lobe showing a large cell surrounded by many small ones. The outer part of the neuropil shows the fine-grained structure that is characteristic of the subfrontals.

Figure 21. Sagittal section to show the buccal tract separating from the interbuccal connective.

Figure 22. Sagittal section to show the part of the buccal tract that passes through the posterior buccal lobe and on to the subvertical lobe.

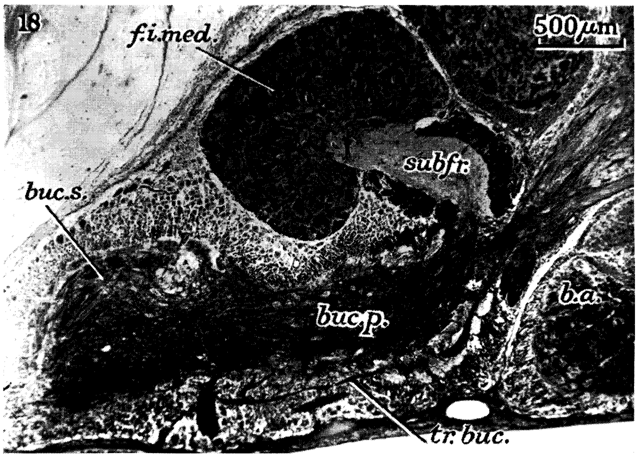
Figure 23. Sagittal section to show the fibres running between the superior buccal and posterior buccal lobes.

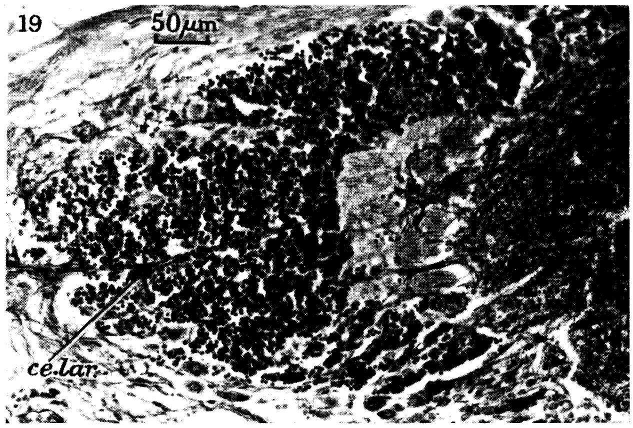
Figure 24. Sagittal section to show the fibres running between the posterior buccal and subvertical lobes. A cut was made between the posterior and superior buccal lobes 2 days previously (19 °C), and the connexions between the posterior buccal and subvertical lobes perhaps show more clearly because of the degeneration of other fibres.

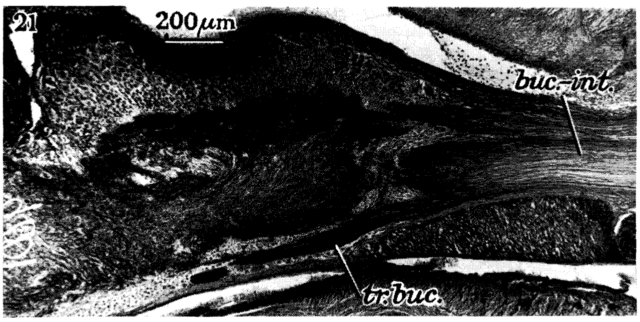
Figure 25. Transverse section to show the bundles of fibres running from the lateral inferior frontal to the posterior buccal lobes.

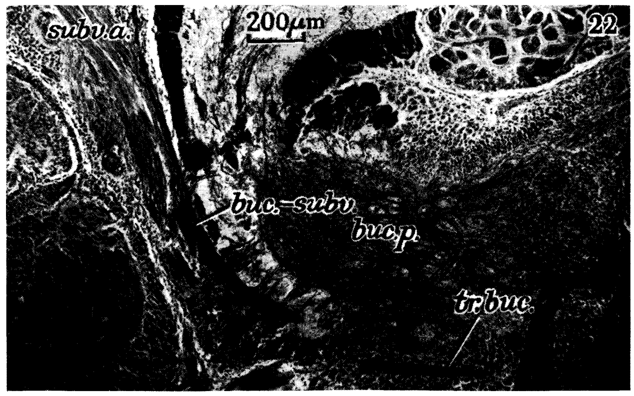
Figure 26. Sagittal section to show the subvertical to posterior buccal tract and the relation of the subfrontal lobes to the median inferior frontal and posterior buccal lobes.

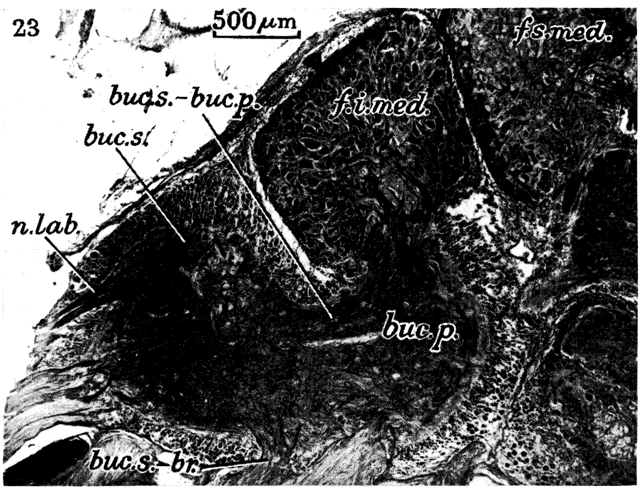
Figure 27. Fibres of the subvertical-posterior buccal tract ending in the latter lobe. Anterior is to the left.

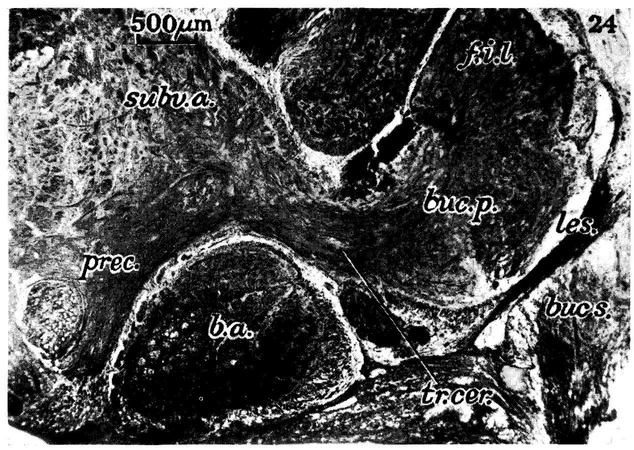

18
500 μm
f.i.med.
subfr.
buc.s.
b.a.
buc.p.
tr. buc.

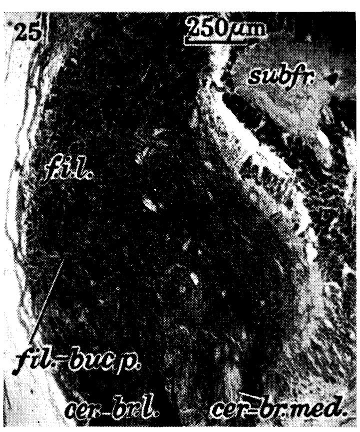

19
50 μm
ce.lar.

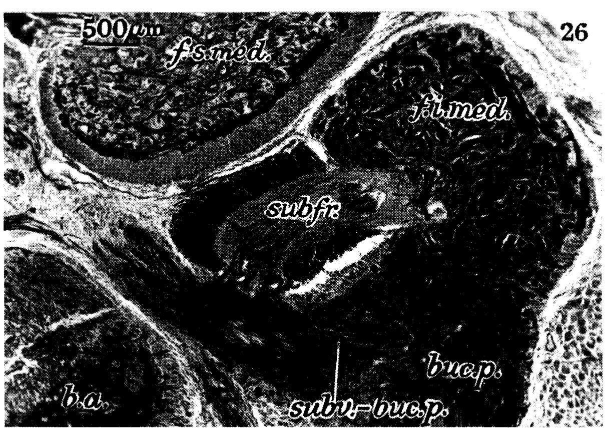

21
200 μm
buc.-int.
tr.buc.


subv.a.
200 μm
22
buc.-subv
buc.p.
tr.buc.


23
500 μm
f.s.med.
bucs.-buc.p.
f.i.med.
buc.s.
n.lab.
buc.p.
buc.s.-br.


500 μm
24
f.i.l.
subv.a.
buc.p.
les.
prec.
b.a.
buc.s.
tr.cer.


25
250 μm
subfr.
f.i.l.
f.i.l.-buc.p.
cer.-br.l.
cer.-br.med.


f.s.med.
26
f.i.med.
subfr.
buc.p.
b.a.
subv.-buc.p.


10 μm
27

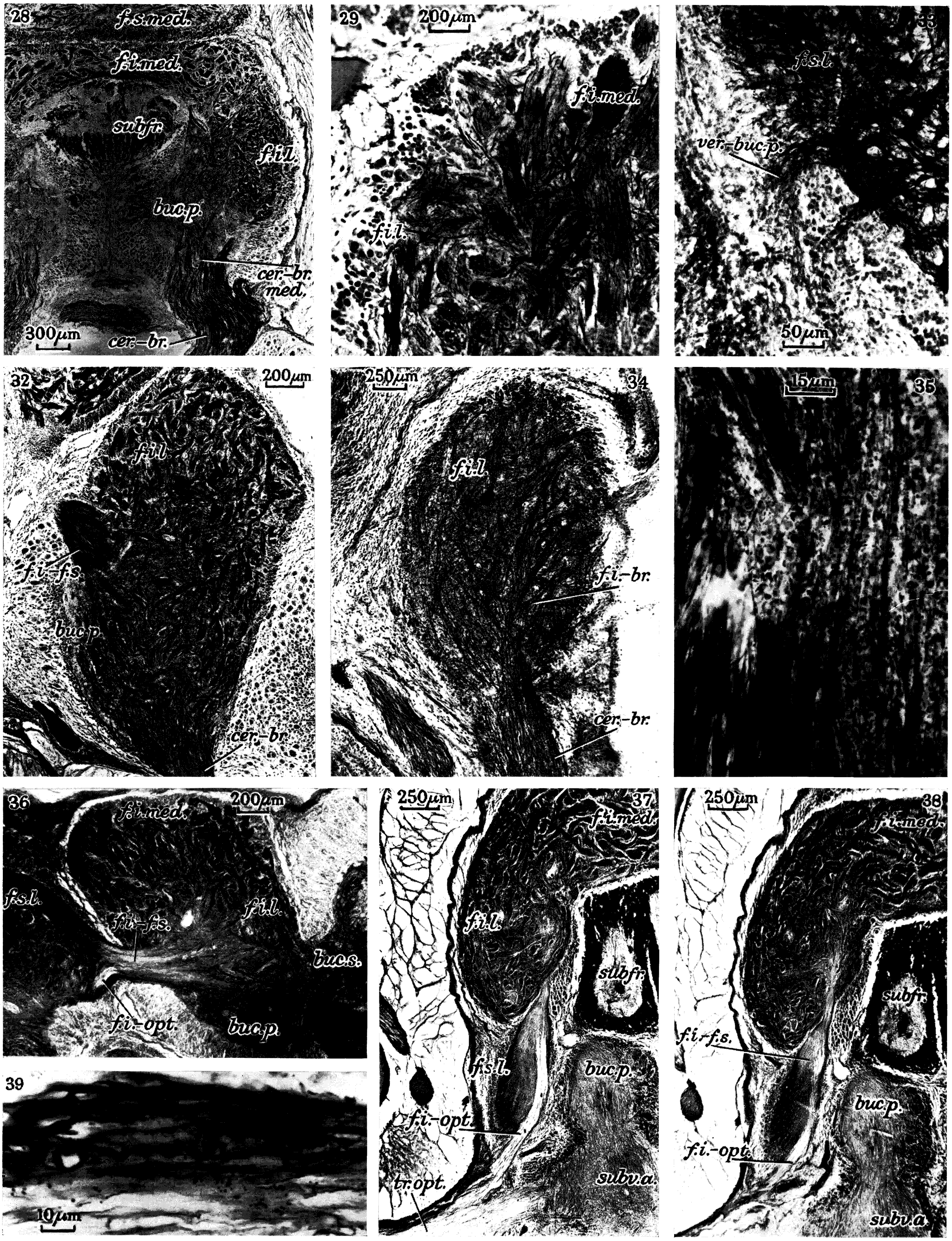

28
f.s.med.
f.i.med.
subfr.
f.i.l.
buc.p.
cer.-br. med.
300μm
cer.-br.
29
200μm
f.i.med.
f.i.l.
f.s.l.
ver.-buc.p.
50μm
32
200μm
f.i.l.
f.i.-f.s.
buc.p.
cer.-br.
250μm
34
f.i.l.
f.i.-br.
cer.-br.
15μm
35
36
f.s.med.
200μm
f.s.l.
f.i.-f.s.
f.i.l.
buc.s.
f.i.-opt.
buc.p.
39
10μm
250μm
37
f.i.med.
f.i.l.
subfr.
f.s.l.
buc.p.
f.i.-opt.
tr.opt.
subv.a.
250μm
38
f.i.med.
subfr.
f.i.-f.s.
buc.p.
f.i.-opt.
subv.a.

Plate 15

Figure 28. Transverse section to show relations of lateral inferior frontal and posterior buccal lobes and the medial cerebro-brachial tract.

Figure 29. Transverse section at junction of lateral and median inferior frontal lobes, showing the sharp difference in cell layers of the two lobes and the lesser difference between their neuropils.

Figure 32. Sagittal section showing the origin of the inferior frontal-superior frontal tract from many parts of the lateral inferior frontal and posterior buccal lobes.

Figure 33. Sagittal section from an animal 7 days after removal of the whole inferior frontal lobe system (25 °C). The fibres of the inferior frontal-superior frontal tract have degenerated, leaving intact the fibres that are presumed to be the vertical-inferior frontal tract.

Figures 34 and 35. Sagittal sections from an animal 3 days after severing the cerebro-brachial connective at the level of the oesophagus (20 °C). The ascending fibres form abundant granules but intact descending ones can be seen in both figures.

Figure 36. Sagittal section showing the inferior frontal and posterior buccal to superior frontal tract, and the inferior frontal and posterior buccal to optic tract.

Figures 37 and 38. Serial horizontal sections showing the course of the inferior frontal and posterior buccal to optic tract.

Figure 39. Large degenerating fibres in the inferior frontal and posterior buccal to optic tract 4 days after removal of the inferior frontal lobe system (16 °C).

Plate 16

Figure 40. Transverse section of a Golgi preparation showing cells of the median inferior frontal lobe with their axons directed towards the subfrontal lobe.

Figure 41. Cells of the median inferior frontal lobe, showing their collaterals.

Figure 42. Sagittal section showing the median inferior frontal to subfrontal tract and the subfrontal to posterior buccal tract. (The buccal to subfrontal tract runs with the latter.)

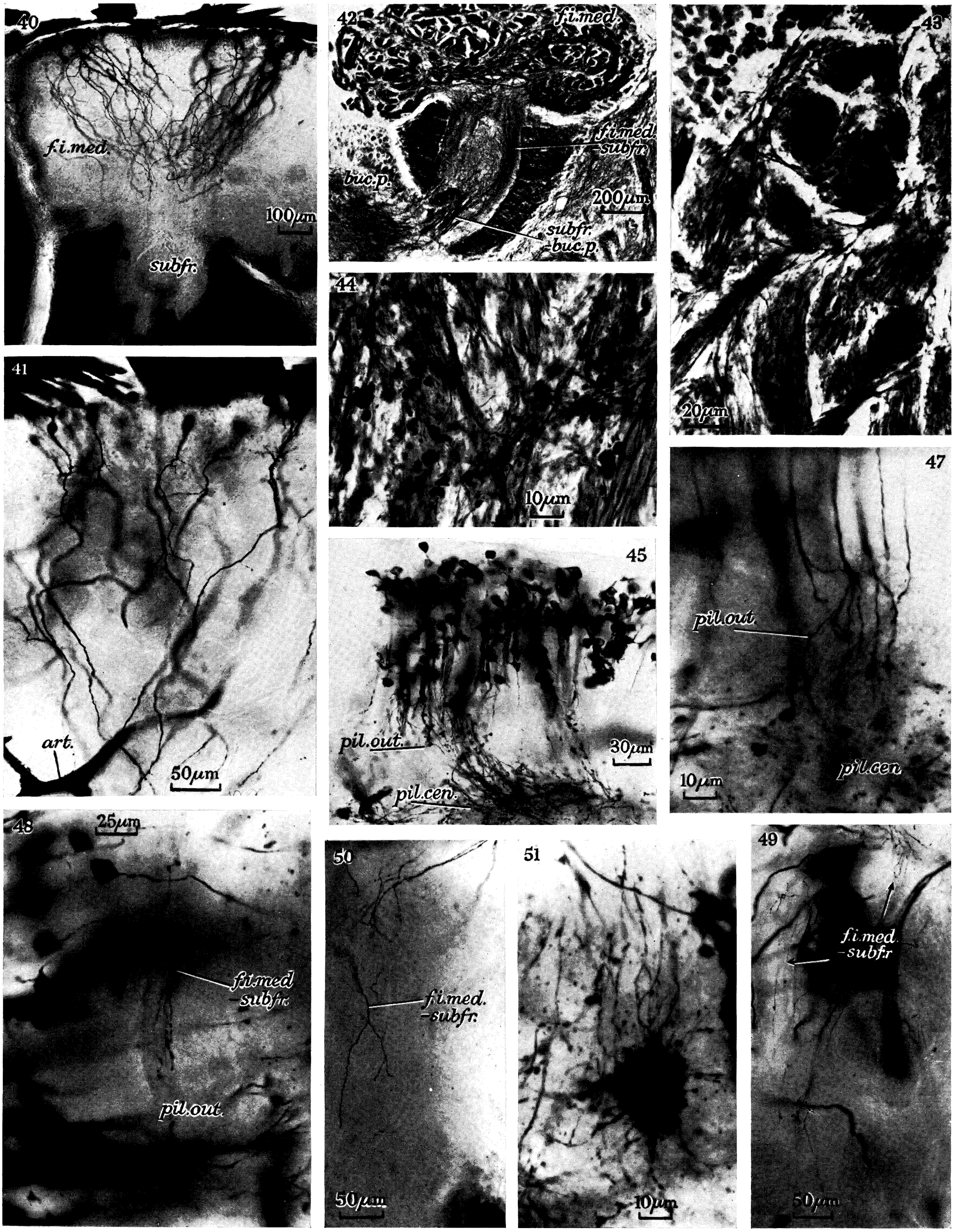
Figures 43 and 44. Sagittal sections showing the organization of the neuropil of the median inferior frontal lobe and the large masses of axoplasm that are often seen there.

Figure 45. Transverse section of Golgi preparation of the subfrontal lobe showing the numerous minute cells with their trunks proceeding through an outer neuropil to end in the central neuropil.

Figure 47. Transverse section of Golgi preparation of a subfrontal lobe showing the swellings that appear on the trunks of the small cells in the outer neuropil.

Figures 48 to 50. Transverse sections of Golgi preparations of the subfrontal lobe showing the beaded terminations of the fibres of the median inferior frontal to subfrontal tract. They divide a few times before ending.

Figure 51. Glia cell from the subfrontal lobe (Golgi). The cell lies in the neuropil with long processes reaching upwards into the cell layer.


40
f.i.med.
100 µm
subfr.
42
f.i.med.
f.i.med.-subfr.
buc.p.
200 µm
subfr.-buc.p.
43
20 µm
41
art.
50 µm
44
10 µm
45
pil.out.
30 µm
pil.cen.
47
pil.out.
10 µm
pil.cen.
48
25 µm
f.i.med.-subfr.
pil.out.
50
f.i.med.-subfr.
50 µm
51
10 µm
49
f.i.med.-subfr
50 µm


52
30μm
pil.cen.
pil.out.
53
f.i.med.
subfr.
les.
buc.p.
200μm
54
30μm
55
50μm
ce.lar.
t.r.buc.
56
subv.
ver.
f.s.med.
f.i.rud.
buc.s.
gan.buc.i.
b.d.
b.med.
ba.
buc.p.
rad.
ped.
suboes. m.a.
p.v.
50μm
gan.subr.
57
f.i.med.
f.i.rud.
opt.
cer.-br.
suboes. m.a.
50μm
58
subv.
f.s.l.
f.i.l.
buc.p.
subfr.
cer.-br. med.
cer.-br.l.
n.br.
suboes.m.a.
50μm
59
ver.
f.s. med.
subv.
f.s.l.
subfr.
f.i.l.
buc.p.
cer.-br. med.
100μm

between the tissue of the posterior buccal and subfrontal lobes is of great interest for consideration of their functions, and should not be obscured in the search for a convenient nomenclature.

For the purpose of counting the cells, all the areas that contained masses of minute cells were considered to belong to the subfrontals. Subject to this convention there is no great difference between the total cell composition of the superior buccal and posterior buccal lobes (table 1). However, only one posterior buccal area near the front end was used for the count. The estimate of 260000 cells for the two posterior buccal lobes together is probably rather high since it was difficult to exclude all areas of subfrontal structure.

TABLE 1. NUMBERS AND NUCLEAR DIAMETERS OF CELLS IN VARIOUS GANGLIA OF AN OCTOPUS OF ABOUT 500 g (BOTH SIDES TOGETHER $\times 10^3$)

Measurements made using the methods of Young (1963 *a*)

	area mm^2	total	< 5 μm	5 to 10 μm	10 to 15 μm	15 to 20 μm
posterior buccal	3·16	264	106 40·0 %	130 50·0 %	26 9·9 %	2 0·1 %
superior buccal	5·70	201	97 48 %	78 39 %	26 13 %	— —
inferior buccal	5·58	331	120 36 %	187 57 %	24 7 %	— —
subradular	1·77	65	21 33 %	39 60 %	5 7 %	—
gastric	8·96	614	280 46 %	320 52 %	14 4·4 %	—

DESCRIPTION OF PLATE 17

FIGURE 52. Transverse section of subfrontal lobe 9 days after removal of median inferior frontal lobe (25 °C). The bundles of the median inferior frontal to subfrontal tract have disappeared and been replaced by numerous cells (? macrophages).

FIGURES 53 and 54. Degeneration of fibres ascending into subfrontal lobe after a lesion passing between the superior buccal and posterior buccal lobes 2 days previously (19 °C). The descending fibres of the subfrontal to posterior buccal tract remain intact. Figure 53 shows the site of the lesion and figure 54 shows the degenerating fibres in a high power view of part of figure 53.

FIGURE 55. Sagittal section showing the fibres of the buccal tract spreading out at the base of the posterior buccal lobe and turning up towards the subfrontal lobe.

FIGURE 56. Sagittal section of whole central nervous system of an unhatched larva of *O. vulgaris*. The inferior frontal system appears as a single lobe, barely marked off from the superior buccal lobe. The vertical lobe system is beginning to differentiate in the dorsal wall of the subvertical lobe.

FIGURE 57. Transverse section of unhatched larva of *O. vulgaris*. The inferior frontal system appears as a single pair of lobes joined by a dorsal commissure, which will develop into the median inferior frontal lobe.

FIGURE 58. Transverse section of newly hatched *O. briareus*. The lateral inferior frontal and posterior buccal lobes are beginning to differentiate, but the subfrontals appear only as slight evaginations of the dorsal wall of the posterior buccal lobes.

FIGURE 59. Transverse section of newly settled young *O. vulgaris* (0·32 g). The inferior frontal lobes appear as a differentiated region of the median wall of the posterior buccal lobes.

The neuropil of the posterior buccal lobes has a general similarity to that of the superior buccal, as seen with Cajal's stain. It is similar to the unspecialized neuropils of the suboesophageal motor centres rather than to the special neuropils such as those of the inferior frontal or subfrontal lobes. At the centre, fibres run in a chaotic manner in which no obvious pattern appears. The trunks of the cells do not enter continuously all round the edge but in bundles (figure 14, plate 13). Several trunks of large cells run together into the neuropil, accompanied by the nuclei of glia cells and of small neurons. The larger cell bodies thus tend to be collected in groups, separated by columns of smaller cells. It is not possible to discern from Cajal preparations exactly what relationship the branches of the small cells have to those of the larger ones. Probably such relations occur mainly in the outer parts of the neuropil.

Passing backwards the composition of the neuropil changes, especially the outer neuropil of the ventral region (figure 18, plate 14). This area has structural similarities with the subfrontal lobes in that it contains numerous minute cells, although unlike the subfrontals, where larger cells occur only in the inner layers, there are large ones lying at all levels (figure 19, plate 14). Wherever this tissue occurs the neuropil shows an outer layer that stains light yellow with Cajal's stain. This is similar to the neuropil of the subfrontal, and presumably consists mainly of the trunks of the small cells (p. 61).

The neuropil of the subfrontal and vertical lobes can thus be regarded as the expanded outer portions of the neuropil of parts of the posterior buccal and subvertical lobes respectively. The tissue with very small cells is quite distinct and characteristic but it can be seen to be continuous with the inner small cell area of the posterior buccal lobes (figure 14, plate 13).

Golgi preparations (figure 20) show that many of the large and the medium small cells of the posterior buccals are of a typical form with a single main trunk carrying dendritic collaterals proceeding through the neuropil. A considerable proportion of the cells are T-shaped, having two equal or nearly equal branches proceeding in opposite directions. However, it is not easy to be sure whether both are axons, one of them may be a large dendrite. One branch may pass down towards the suboesophageal centres and the other either towards the lateral inferior frontal lobes or backwards to the subvertical lobe, though it has not been possible to follow both the fibres of one cell to their terminations. It may be that these are cells that can produce alternative effects, say acceptance or rejection by the arms. Both main branches have been seen to carry dendritic collaterals, which is perhaps evidence of their axonal rather than dendritic nature.

Unfortunately little detail of the small cells of this region has yet appeared in Golgi preparations.

(c) *Afferent connexions of the posterior buccal lobes*

(1) *Labial to posterior buccal tract*

This consists of numerous fibres, running in the upper part of the neuropil that unites the superior and posterior buccal lobes (figure 3, plate 12 and figure 23, plate 14). After a cut has been made between the lobes degeneration granules appear in the posterior buccals. They also appear here after severance of the labial nerves. It is assumed that afferents reach the posterior buccal lobes direct from the lips and not after relay in the superior buccal lobe.

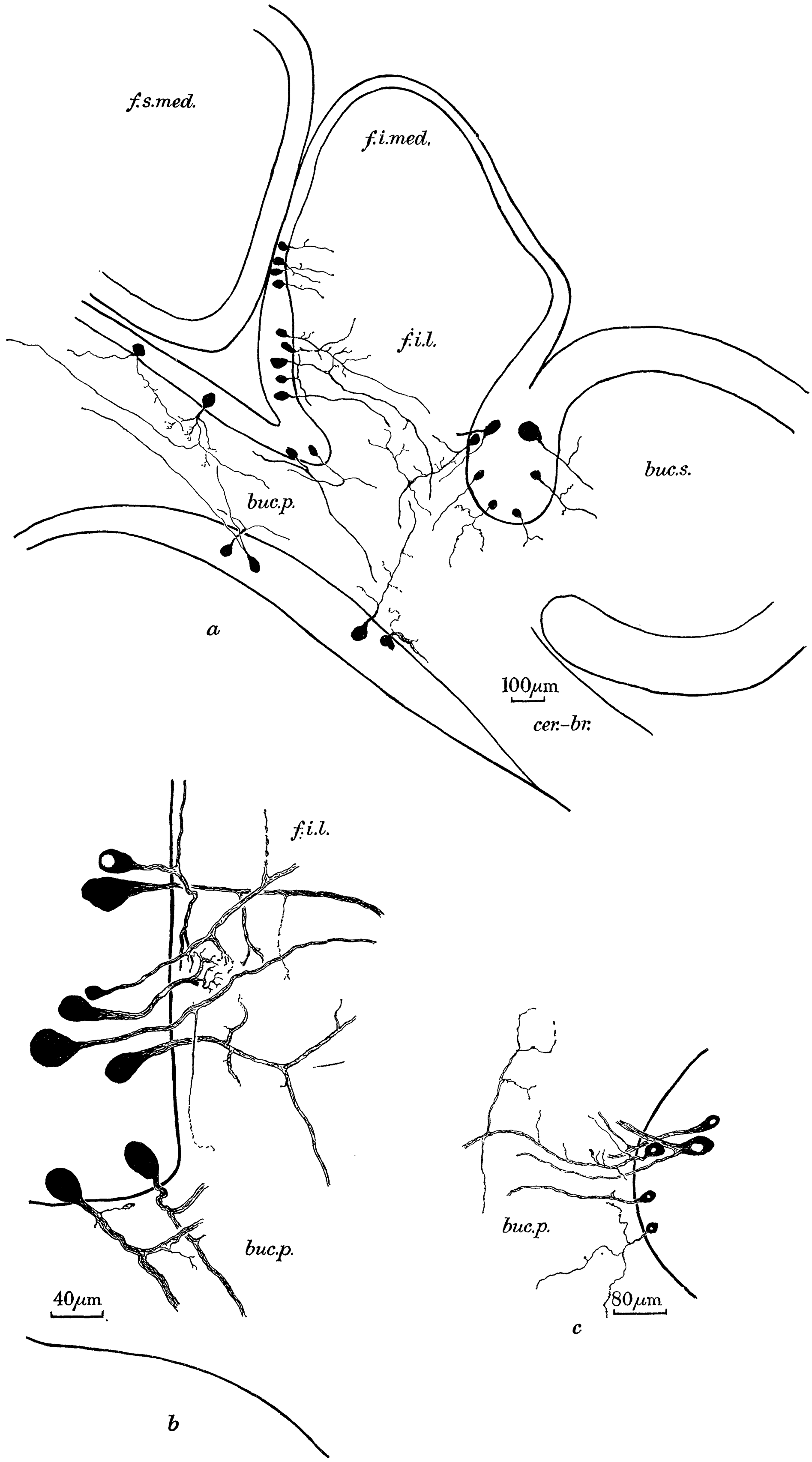


FIGURE 20. (*a*) Cells of the posterior buccal and lateral inferior frontal lobes as seen with Golgi staining. (*b*) Cells from the back of the posterior buccal lobe, showing characteristic bifurcation. (*c*) Cells from the front of the posterior buccal lobe.

(2) *The buccal tract*

A bundle of fibres leaves the interbuccal connective (which unites the superior and inferior buccal lobes) and runs backwards to give fibres to the superior and posterior buccals and also to the subfrontals and subvertical (figures 18, 21, 22, plate 14). Degeneration has been seen in this tract following severance either at its anterior or posterior end. The backward-running fibres are presumably afferents that arise somewhere in the buccal mass. They may include afferents from the surface of the lateral buccal palps in the floor of the mouth, which though cuticularized are richly innervated (Young 1965). There may also be fibres from the oesophagus and crop, since degeneration has been seen in these connectives after severing the sympathetic nerves. These fibres may signal taste, hunger or pain.

The buccal tract runs through the region of small cells that lie at the base of the posterior buccal lobes and continues into the tissue of subfrontal structure that occupies the floor of the posterior buccals in this region (figure 18, plate 14). Some of the fibres end here; others pass as a distinct bundle to form part of the cerebral tract and run on to the subvertical lobe (figure 22, plate 14).

(3) *Brachial (anterior suboesophageal) to posterior buccal tract*

The medial division of the cerebro-brachial connective runs to the posterior buccal lobes (figure 7, plate 12 and figure 25, plate 14). After severing one or more brachial nerves degenerating fibres appear in this division (which also contains efferent fibres that do not degenerate).

(4) *Lateral inferior frontal to posterior buccal tract*

This tract consists of bundles crossing the brachio-inferior frontal roots (figure 25, plate 14), and is the main pathway available for tactile impulses through the lower of the two circuits of the system.

(5) *Subfrontal to posterior buccal tract*

This consists of bundles of darkly staining fibres (Cajal), very similar in appearance to the fibres that run from the vertical to the subvertical lobe (figure 26, plate 14). Most of these fibres run into the front part of the posterior buccal lobes, but a few of them pass into the hinder part, as far back as their junction with the subvertical lobe. Following lesions causing damage to the subfrontal lobes, degeneration granules are seen in these bundles and throughout the posterior buccal lobes. This is the main output pathway of the upper loop of the inferior frontal system.

(6) *Subvertical to posterior buccal tract*

This consists of numerous fibres, some of which are large (figure 2, plate 12 and figure 27, plate 14), passing in the cerebral tracts (figure 24, plate 14). Granules appear in the posterior buccal lobes after lesions of the subvertical lobe. This is presumably a main pathway by which the vertical lobe system enters into tactile learning processes (Wells & Wells 1957).

(7) *Pallioviseral to posterior buccal tract*

These are conspicuous bundles entering the posterior buccal lobes from behind (figure 4, plate 12 and figures 9 and 10, plate 13). They pass in front of the anterior basal lobe and more posteriorly become compressed below the supraoesophageal mass (figure 10, plate 13), and then run immediately beneath the ventral optic commissure, continuing backwards across the bundles of the cerebro-pallioviseral connective. They turn downwards with the latter, but their course could not be followed further. It has not been possible to determine their origin or prove their afferent fibre content. They may contain pain fibres from the hind part of the body.

(*d*) *Efferent fibres of the posterior buccal lobes*

It is not easy to distinguish between the output pathways of the posterior buccal and lateral inferior frontal lobes. It is possible that all the tracts mentioned arise in part from both lobes.

(1) *Posterior buccal to brachial tract*

This runs in the medial division of the cerebro-brachial connective (figure 7, plate 12; figure 25, plate 14, figure 28, plate 15). Most of the fibres of this division degenerate below a cut made at the level of the oesophagus. However, this degeneration does not extend into the brachial nerves. All the fibres therefore run to the brachial and prebrachial lobes.

(2) *Posterior buccal to subvertical and precommissural tract*

This runs in the cerebral tract (figure 24, plate 14). It would only be possible to distinguish between these fibres and those of the superior buccal to subvertical and brachial to subvertical tracts if appropriate lesions could be made in which each part was severed separately. After section of the whole cerebral tract behind the posterior buccal lobes, degeneration granules are very abundant throughout the ventral part of the anterior subvertical lobe and the precommissural lobe, which is continuous with it. The granules become less numerous passing dorsally and backwards in the subvertical lobe. They do not extend into the bundles that run from the subvertical to the vertical lobe. It is assumed that these degenerating fibres come from all of the three sources mentioned above.

(3) *Posterior buccal to superior buccal tract*

Since the neuropils of the posterior buccals and superior buccal are continuous it is assumed that an efferent tract runs from the former to the latter. Granules are found in the superior buccal after lesions involving the posterior buccals, but these might be produced by fibres descending from the subvertical lobe.

The fibres running from the posterior buccals to the subfrontal lobes are probably fibres that arise more distally (see p. 62). It is not considered that there is a specific posterior buccal to subfrontal tract, but the possibility cannot be excluded.

(4) *Efferent fibres of buccal tract*

The bundles of fibres running from the posterior buccal lobes to join the superior to inferior buccal connectives contain fibres that degenerate if one of the tracts has been severed close to its origin. The destination of these fibres is not known. They may end in the inferior buccal ganglia, or somewhere in the salivary system, the radula or the crop, or even further down the alimentary tract.

After separation of the superior and posterior buccal lobes there is no degeneration in the labial nerves. There is therefore no posterior buccal to labial tract.

5. The lateral inferior frontal lobes

(a) *Form, relations and effects of removal*

The lateral inferior frontal lobes cover the sides of the brain from the base of the supraoesophageal lobes to about the level of the base of the median superior frontal lobe (figure 28, plate 15). Each lateral lobe is broadly continuous medially with the posterior buccal lobes (figure 6, plate 12). Removal of the two lateral lobes can in principle be performed without damage to other structures. However, the posterior buccal lobes would inevitably be disturbed, the cerebro-brachial tract damaged, and the median inferior frontal lobe deprived of all input. It is therefore not possible at present to distinguish between the functions of the lateral inferior frontal and the neighbouring lobes (p. 50).

(b) *Cell layers and neuropil of lateral inferior frontal lobes*

The distinction between lateral and median lobes is clear, as regards both the connexions and cell structure (figures 15 and 16, plate 13). The boundary between them is sharp (figure 29, plate 15). The walls of the lateral lobes are composed of a thin layer of cells, many of which are large (figure 15, plate 13). Their axons pass to various destinations, some a considerable distance from the lobe (see below). There are calculated to be altogether (both sides) 20000 cells with nuclei of less than 5 μm in diameter, 72000 of 5 to 10 μm and some 8000 of more than 10 μm (Young 1963*a*). The walls of the median inferior frontal lobe are much thicker and composed of numerous smaller cells whose axons all pass to the subfrontal lobes (p. 60).

The cell compositions of the two lobes thus differ in the same way as do those of the lateral and median superior frontal lobes (Young 1963*a*). However, the distinctions between the neuropils is less sharp than in that case. In both lateral and median inferior frontals there is a network of bundles of interweaving fibres.

The large cells of the lateral inferior frontal lobes give off numerous dendritic collaterals throughout the neuropil (figure 30). They do not show a tendency to form large branches running in opposite directions like those found in the posterior buccal lobes. There is no evidence at present about the form of the smaller cells of the lateral inferior frontal lobes.

The afferent fibres entering the lobe from below branch repeatedly (figure 31). They become thinner and thinner as they do so and finally terminate or pass beyond the resolution of the light microscope. The thinnest branches seen are often finely beaded and are probably near their termination. No elaborate bushy terminations with many twigs were seen.

The lateral inferior frontal neuropil often shows lumps and terminal knobs with Cajal's stain. These are discussed with similar objects found in the median inferior frontal lobe on page 60.

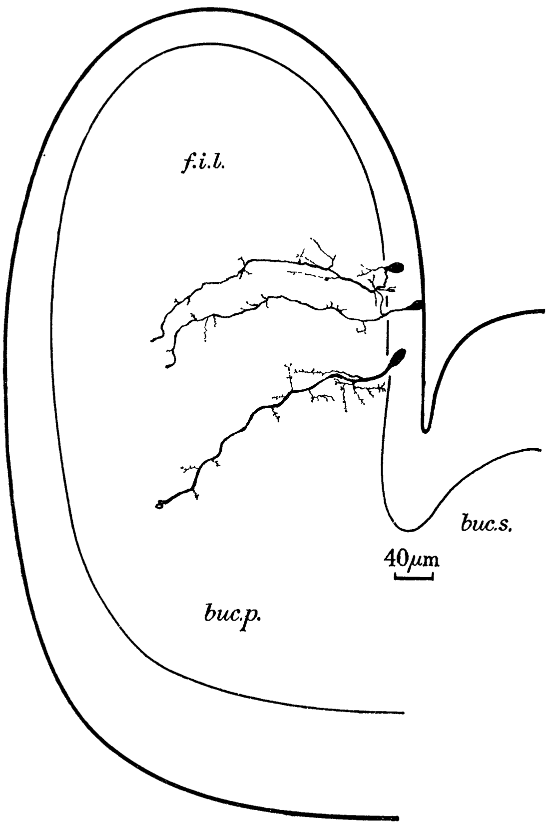


FIGURE 30. Cells of the lateral inferior frontal lobe (sagittal section).

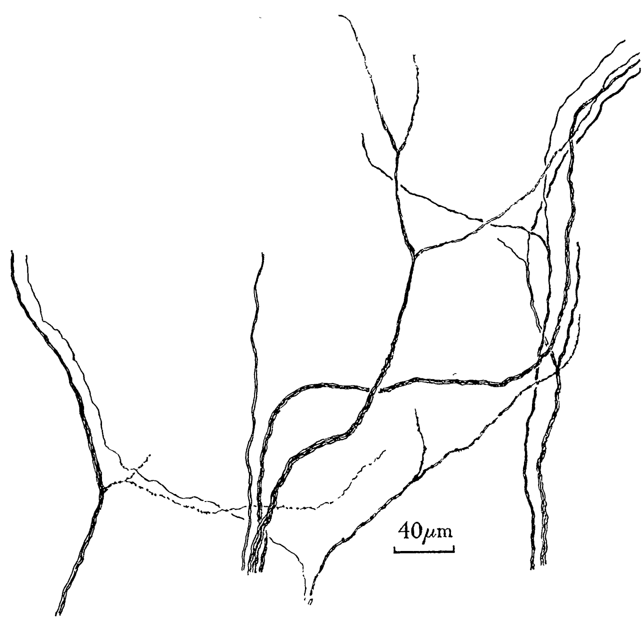


FIGURE 31. Fibres of the lateral cerebro-brachial connective running up into the lateral inferior frontal lobe and dividing as they go (sagittal section, Golgi).

(c) *Afferents to the lateral inferior frontal lobes*

(1) *Brachial to lateral inferior frontal tract*

The input from the arms consists of numerous fibres running direct from the medial roots of the brachial nerves to the lateral divisions of the cerebro-brachial connectives. The fibres of this brachio-inferior frontal tract are parallel as they enter the lateral inferior frontal lobe, but then the bundles divide by multiple branching (figure 32, plate 15). The smaller bundles join each other and then divide again. This process continues as the tract runs throughout the lateral and median inferior frontal lobes. This arrangement allows re-sorting, so that fibres at first widely separated are brought together, and vice versa. That these interweaving bundles are afferent is shown by the fact that most of their fibres degenerate after section at the level of the oesophagus. The descending fibres do not interweave (see below).

(2) *Labial to lateral inferior frontal tract*

The second main source of input is from the labial nerves. These fibres pass with the bundles to the posterior buccal lobes that have already been described (p. 52). They interweave with the fibres of the brachial to lateral inferior frontal tract and continue on into the median inferior frontal lobe.

(3) *Vertical and subvertical to lateral inferior frontal tracts*

The vertical and subvertical lobes probably both send fibres to the lateral inferior frontals as well as to the posterior buccals. These run partly in the cerebral tracts but also in the bundle of fibres that joins the inferior and superior frontal lobes. Degeneration granules have been seen here following vertical lobe removal, but the fibres are very fine and the degeneration granules not clear. More convincing evidence of this pathway is the persistence of its fibres after removal of the inferior frontal lobes (figure 33, plate 15).

(d) *Efferent fibres of the lateral inferior frontal lobes*

A large number of tracts arises in this region. These pathways are probably important in signalling occurrence of combinations of chemotactile and taste signals to the centres concerned in memory storage, including the posterior buccal, superior frontal, and optic lobes and possibly also the brachial lobes.

(1) *Lateral inferior frontal to brachial tract*

The fibres of this pathway stand out very clearly following degeneration of the brachial to lateral inferior frontal tract (figures 34 and 35, plate 15). They run in the lateral divisions of the cerebro-brachial connectives and end in the brachial and prebrachial lobes, none passing direct to the brachial nerves. The significance of this pathway is not known.

(2) *Lateral inferior frontal to posterior buccal tract*

This has already been described.

(3) *Lateral inferior frontal to superior buccal tract*

Some of the fibres in the neuropil joining the lateral inferior frontal and superior buccal lobes probably run forwards.

(4) *Lateral inferior frontal to superior frontal tract*

This is a conspicuous bundle. Fibres run to the centre of the lateral inferior frontal and collect, with others from the superior buccal into a tract entering the antero-lateral border of the lateral superior frontal lobes (figures 32 and 36, plate 15).

(5) *Lateral inferior frontal to optic tract*

This is a bundle of large fibres arising and leaving with the tract last mentioned and passing through the ventral part of the lateral superior frontal lobes to the optic tract (figures 37 and 38, plate 15). After section of the latter the fibres do not degenerate, but they do so after removal of the lateral inferior frontal lobes (figure 39, plate 15). The position within the lobe of the cells of origin of this tract has not been precisely determined.

(6) *Lateral inferior frontal to subvertical and precommissural tract*

This is a large bundle of fibres passing from the posterior buccal and lateral inferior frontal lobes to the cerebral tract, together with fibres running in the opposite direction (figure 24, plate 14). After removal of the lateral inferior frontal lobe, degeneration granules appear throughout the two hinder lobes.

6. Median inferior frontal lobe

(*a*) *Form, relations and effects of removal*

The median inferior frontal lobe is a band of tissue occupying the lower anterior part of the brain (figures 2 and 3, plate 12). It lies between the two lateral inferior frontal lobes at the sides, the median superior frontal above and behind, and the superior buccal below and in front. The subfrontal lobes lie below and behind it. The front parts of the posterior buccal lobes lie beneath (figure 18, plate 14) but these lobes communicate with each other only at the sides (p. 50).

There is therefore no serious difficulty in removing the median inferior frontal lobe alone, without damage to any other lobe or tracts. After the operation the animals do not show any obvious disorders or movement or use of the arms but there are various forms of impairment of the chemotactile learning mechanism (Wells 1959*a*). There is, however, no detectable damage to the visual learning mechanism (Wells 1961; Young 1964).

(*b*) *Cells and neuropil of the median inferior frontal lobe*

The cells of the lobe are all small (figure 16, plate 13) and all send their axons to the subfrontal lobes (figures 40 and 41, plate 16). There are about 140000 cells with nuclei of less than 5 μm, and 90000 of 5 to 10 μm. None of them is as small as the minute cells of the subfrontal lobe.

The form of the trunks of the cells and processes is closely similar to that of the cells of the median superior frontal lobe (Young 1964). They have thin trunks running to the centre of the lobe, with collaterals arising throughout their course, as far as the hilum. The collaterals are either simple, or have a few branches, ending in the islands of neuropil.

At the hilum the trunks change their character, becoming fine beaded threads as they enter the subfrontal lobe. They interweave at this level, so that fibres originating together in the median inferior frontal may end far apart in the subfrontals and vice versa (figures 40 and 42, plate 16).

The neuropil of the median inferior frontal lobe shows a highly characteristic pattern of interweaving bundles (figure 4, plate 12; figures 42 and 43, plate 16). These continue the pattern of branching of the fibres that is found in the lateral inferior frontal lobes. The bundles become smaller and smaller, forming a layer of small units running in various, but mainly transverse, directions.

Between the bundles of fibres are islands of synaptic neuropil. Terminal knobs, often of quite large size, are common here (figure 44, plate 16). Some of them are irregular in outline and give the appearance of degeneration rather than of normal terminal boutons. Some are smaller and more regular. Others appear to be swellings along the courses of the fibres.

These structures give to the inferior frontal neuropil an appearance that is seen only in one other place, namely the front part of the anterior suboesophageal mass. Masses of axoplasm are present in variable amounts in both of these situations in all octopuses. It is possible that degeneration is continually present in these lobes because the fibres ending there originate as neurosensory cells in the suckers, whose margins are often torn away under natural conditions. However other evidence suggests that the primary receptor cells make synapse within the ganglia in the arms (Graziadei 1962). The significance of these masses of axoplasm therefore remains doubtful.

Whatever may be the explanation for these structures, they give to the neuropil of the median inferior frontal lobe an appearance distinct from that of the median superior frontal lobe. Both have interweaving bundles of afferent fibres but in the median inferior frontal lobe there are fewer distinct islands of synaptic neuropil. Presumably the contacts between the cells of the lobe and the incoming fibres are made in the interstices of the web of the latter. Indeed, in places there are structures that may be synaptic terminals along the major bundles (figure 44, plate 16).

(c) *Afferent fibres of the median inferior frontal lobe*

The median inferior frontal lobe receives its afferents mainly through the lateral inferior frontals, together with some through the posterior buccal lobes. Presumably fibres of all the three types that reach the lateral lobes continue into the median inferior frontal lobe. It is not known whether the fibres that reach the median lobe have already given off collaterals in the lateral lobes. There is no evidence that cells of the lateral lobes send fibres to the median one. Some fibres enter the median lobe from the posterior buccal lobes, at the sides (figure 23, plate 14) and presumably these are afferents from the lips and perhaps other sources.

It would be useful to know how widely single incoming bundles spread through the median inferior frontal lobe. Unfortunately, the prevalence of irregular masses of axoplasm, even in normal octopuses, makes the tracing of degeneration very hazardous.

Following a small cut in the lobe, granules presumed to be degeneration products have been seen both lateral and medial to the cut and on the opposite side. Some bundles can be seen crossing in the normal neuropil (figure 42, plate 16). A wide degree of interchange of influences is probably a main function of the lobe.

(*d*) *Efferent fibres of the median inferior frontal lobe*

These all run to the subfrontal lobes (see p. 60). It has been suspected that some pass to the lateral superior frontals, but these are now considered to arise in the lateral inferior frontal lobes.

7. Subfrontal lobes

(*a*) *Position, relations and effects of removal*

These can be considered as approximately cylinders, with thick walls of numerous cells. The cylinders run vertically from the median inferior frontal above to the posterior buccal lobes below (figure 1 and figure 42, plate 16). The lateral inferior frontals lie on either side, but are not connected with the subfrontals. The two subfrontals are joined together dorsally in the hilum of the median inferior frontal lobe. More ventrally their median walls are in contact with each other.

The lobes cannot be removed without damage to other structures. The evidence of Wells (1959*a*) shows that octopuses deprived of all cells of subfrontal type cannot learn not to draw in objects touched.

(*b*) *Cell layers and neuropil of subfrontal lobes*

The lobes have very thick layers of densely packed cells (figure 17, plate 13, and figure 45, plate 16). At intervals lie larger cells, usually close to the neuropil. There are estimated to be some 7000000 cells with nuclei less than 5 μm, but only 75000 with nuclei greater than 5 μm in diameter, in the two subfrontal lobes together. Most of the larger cells are only slightly greater than 5 μm. There are, however, a very few much larger cells, with nuclei up to 20 μm in diameter. There are probably not more than 10000 of them greater than 6 μm, perhaps considerably fewer. These very large cells have not been seen satisfactorily with Golgi stains, but presumably constitute the output channel of the lobes. A trunk of one of them, with its branches, is seen in figure 46, p. 62. It resembles the trunks of the large output cells of the vertical lobe (Young 1964).

Fibres from the small cells of the subfrontal all end within the lobe. Shortly after the main trunks of the small cells have entered the neuropil, they usually carry a marked swelling (but not always). These swellings sometimes contain a clear vacuole (figure 46, and figure 47, plate 16). Short lateral twigs may be given off from the swelling or near by, but the trunks do not carry many dendritic collaterals (at least of a size within the limits of resolution with light microscopy). These swellings on the fibres lie in the region of ending of the incoming fibres of the inferior frontal to subfrontal tract. Beyond the swellings the trunks of the small cells continue for various distances towards the centre of the lobe. Some seem to end in the inner part of the outer neuropil region, with or without a terminal knob. Others continue onwards and are lost in a tangle of fibres that forms the central neuropil (figure 45, plate 16). It is hard to follow them all the way to their terminations. Those that have been followed end in rather simple terminal bifurcations, with some swelling along their course (figure 46). This may well be the fate of the majority or all of them. Of course, fibres, with long, more tortuous trunks, would be less likely to appear sufficiently clearly for identification in the tangle, and it cannot be excluded that they exist.

The neuropil of the subfrontal lobe also contains glial cells with numerous fine beaded branches (figure 51, plate 16). These stretch out for considerable distances in all directions and they may extend into the cell layers. It is often difficult to distinguish between glia fibres and the axons of the small neurons.

A further component of the lobe is the branching system of trabeculae of connective tissue. These form a supporting skeleton all round the lobe in the outer region of the neuropil. Branches extend into the central neuropil and out to the cell layers. The major arteries run in this skeleton.

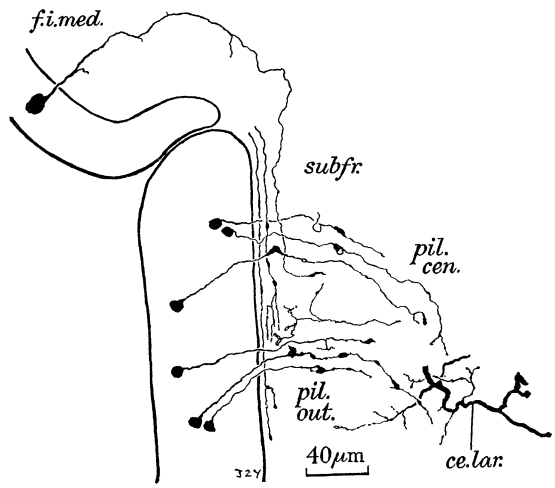


FIGURE 46. Drawing of cells in sagittal section of part of median inferior frontal and subfrontal lobes after Golgi staining.

(c) *Afferent pathways to the subfrontal lobe*

(1) *Median inferior frontal to subfrontal tract*

The incoming fibres of the median inferior frontal to subfrontal tract run as a series of bundles in the outer part of the neuropil, exactly as do the fibres of the superior frontal to vertical tract (figure 46, and figures 48 to 50, plate 16). They end here as very fine varicose fibres, showing some branching. These fibres thus cross the trunks of the cells of the lobe and presumably bear the same synaptic relations to them as are found in the vertical lobe (Gray & Young 1964). These fibres degenerate after injury to the median inferior frontal lobe. After a few days the position of the bundles is occupied by a number of cells, which are presumably amoebocytes and/or proliferated glia cells (figure 52, plate 17).

(2) *Buccal to subfrontal tract*

The second input to the lobe is provided by fibres entering from below. They pass through the posterior buccal lobes but are presumed not to arise there, but from some more distant source. They have been seen degenerating after lesions in which the posterior buccal lobes had been damaged (figures 53, 54, plate 17). Fine ramifications that are presumably the ends of these fibres have been seen with the Golgi method (figure 46). Some of these fibres come from the buccal tract (figure 55, plate 17), running beneath the superior and posterior buccal lobes (p. 54). Others may come from the labial nerves, and perhaps still others from the arms. Fibres can be seen leaving the buccal tract (figure 55, plate 17) and entering the neuropil of the lower part of the subfrontal where it joins the posterior buccal lobe.

(*d*) *Efferent fibres of the subfrontal lobes*

The larger cells of the lobe send fibres downwards and it is presumed that they end in the neuropil of the posterior buccal lobes. Unfortunately the details of these endings have not been seen in Golgi preparations, and this leaves a serious gap in knowledge of the organization of the whole system.

8. Embryological development of the inferior frontal system

Sections of unhatched embryos 2 mm long show the inferior frontal system as a single mass of neuropil surrounded by cell layers (figure 56, plate 17). Moreover, this is broadly continuous with the superior buccal in front and the subvertical behind. The separate lobes have hardly begun to differentiate. A single main ganglion on each side represents the future posterior buccal and lateral inferior frontal lobes (figure 57, plate 17). This ganglion communicates with the anterior suboesophageal mass below. Dorsally, the two lobes are joined by a commissure, which will become the median inferior frontal lobe. The subfrontals appear only as slight indentations of the medial walls of the lobes.

The only freshly hatched specimens available were of *O. briareus*, which eliminate the planktonic phase by hatching in an advanced condition (Messenger 1963). The differentiation has proceeded much further but is still incomplete (figure 58, plate 17). The posterior buccal and lateral inferior frontal lobes are now distinct. The median inferior frontal is still little more than a commissure joining the two lateral inferior frontal lobes. The subfrontal lobes appear as diverticulae of the medial walls of the posterior buccal lobes.

A newly settled specimen of *O. vulgaris*, weighing 0·32 g, showed the lobes as incomplete miniatures of the adult condition (figure 59, plate 17). It is still possible to see that all the four lobes are derivatives of one original one. The subfrontal, in particular, appears as the modified medial wall.

9. The functional connexions of the inferior frontal system

The use of degeneration methods and Golgi staining has made it possible to understand the design of the inferior frontal system much more satisfactorily than before. Four new facts of especial importance are: (1) that there are distinct lateral inferior frontal and posterior buccal lobes, (2) that the median inferior frontal lobe fibres project only to the subfrontal, (3) that the subfrontal fibres project to the posterior buccal, (4) that the subfrontal receives a second input from below. These facts, together with those about the cell types, neuropils and tracts, allow us to define many features of the functional connectivity.

In the lateral inferior frontal lobes the bundles of incoming fibres interweave and the cells are therefore presumably stimulated by suitable *combinations* of inputs. Such responses might be either unconditional or learned. Many of the cells here are quite large and their axons reach to parts of the sub- and supra-oesophageal masses and to the optic lobes. In the lateral inferior frontal lobes signals from the lips indicating food are probably made to increase the tendency of the arms to take objects. The corresponding visual centres (lateral superior frontal lobes) certainly have the function of increasing the tendency to attack a moving object. Since the tactile system is heavily biased towards taking objects towards the mouth this type of function is less important than in the visual system. It may be that one of the most significant functions of the lateral inferior frontal lobes is to pass on signals indicating food to the visual learning system via the large tracts that run to the optic and lateral superior frontal lobes.

After passing through the lateral inferior frontal lobes the input fibres continue to interweave and stimulate the uniform population of small cells of the median inferior frontal lobe. The axons of these cells all end in the subfrontals; none passes outside the inferior frontal system. The great interweaving in the neuropil surely signifies that this is a system for responding to combinations of inputs. It seems very likely that such activities are part of the tactile learning system. Wells showed that after injury to this region transfer of learning between arms did not occur (Wells 1959*a*). A reasonable hypothesis is that the lobe serves as an essential part of the classifying system and for 'reading-in' to the memory, but does not itself contain the tactile memory record.

The output from the median inferior frontal passes down the medial face of the system but only reaches the posterior buccals after passing through the subfrontal tissue. Here its fibres meet the immense numbers of tiny cells whose axons do not leave the lobe. This is the most interesting and obscure part of the system. Wells (1959*a*) showed that some of these small cells must be present if an octopus is to learn *not* to draw in objects that it has touched. The provision of opportunity for a large number of possible combinations is evidently a feature of the plan. The considerable interweaving of the fibres entering the subfrontals and the great number of cells it contains suggest this. However, the incoming fibres do not form very extensive terminal ramifications and many of the trunks of the subfrontal cells show no branching at all (with the light microscope).

The second input from below is the other key feature. It has been suggested that the similar fibres of the vertical lobe system signal pain (trauma) (Young 1963*b*). The result would then be that the circuit re-inforces the tendency to draw in the object touched *unless* pain intervenes.

The whole system thus receives input from several types of afferents from the periphery, and also receives descending fibres from the vertical lobe system. The chemotactile fibres from the arms are the specific input, carrying signals that represent the particular characteristics of the objects touched. The other inputs are perhaps all from receptors that signal the effective results of actions for the homeostasis of the animal (Young 1963*b*). These bundles of fibres that we suppose to signal the results of action all enter the centre of the posterior buccal lobes. Here their first function may be (1) to establish connexions that allow the appropriate actions of drawing in objects or rejecting them. Accordingly the posterior buccal lobes have large cells and a neuropil like that of the lower motor centres. These afferent fibres presumably have, however, to perform the further functions of (2) increasing or decreasing the exploratory tendency, and (3) establishing a record in the memory that particular combinations of signals from the arms indicate objects that are to be taken or avoided (see Young 1963*b*). It is suggested that for these latter purposes the fibres carrying signals of results continue into the remainder of the inferior frontal system, where they are appropriately mixed with the fibres bringing the specific chemo-tactile signals.

Presumably somewhere in the system there are cells that have two possible outputs, one increasing and the other decreasing the tendency to draw in objects (Young 1963*b*). Alteration in the probability of the use of these channels would be the change that constitutes an enduring record in the memory. It is reasonable to locate this change in the neuropil of the posterior buccal lobes. The large cells of this lobe may be the ones with two possible outputs, perhaps controlled by the small cells that accompany them.

Unfortunately, we cannot yet locate the cells that are sensitive to particular patterns of input from the arms. They may lie in the inferior frontal system or possibly in the anterior suboesophageal mass. Wells (1961) has suggested that the significant feature may be the firing frequencies produced by stimulation of the margins of the suckers. The prominence of numerous interweaving pathways shows that spatial summation is likely to be relevant.

10. Origin of the tactile learning system

Embryology shows that the learning system develops out of the feeding system, as it has presumably done in phylogeny. The cerebral cord was probably originally simply the pathway by which impulses passed in both directions between the feeding system and the locomotor and other mechanisms. Some possibility of modification of actions according to circumstances must be present in any animal where, for example, pain signals can promote retreat, which involves inhibiting the advance mechanism. It is an interesting hypothesis that the small cells that accompany the large ones in some centres are connected with this inhibition. The learning mechanism may thus have originated by development of means for prolonging the inhibition of one of two alternative pathways (Young 1963*b*).

In support of such a theory of the origin of the learning mechanism, some facts are now available. The small cells of the lobes that were shown by Wells (1959*a*) to be essential for tactile learning, are continuous with the inner layers of small cells that accompany the larger ones of the posterior buccal lobes. During ontogeny these centres essential for learning arise by special development of small neurons whose axons end within the system (those of the median inferior frontal) or even within one lobe (subfrontals). This is evidence that numerous small cells are essential for establishing the record of particular combinations of input activities. In particular, the tactile learning system is concerned with establishing records in the memory that *prevent* the drawing in of objects having a particular quality (Wells & Wells 1956). This suggests that lowering of the probability of use of one pathway may be the mechanism of this type of learning.

11. Similarity of tactile and visual learning systems

The visual and tactile learning systems have exactly similar components and they develop in the same way. The circulation of specific impulses is identical in the two systems. The impulses enter at the sides and pass dorsally and then medially. As they pass they make synapse with cells whose axons remain within the system. These proceed to the output centre either direct (e.g. from lateral superior frontal to subvertical) or after a further synapse (e.g. in the median superior frontal) down what is essentially the medial face of the system (e.g. the vertical lobe). The smallest cells of all occur here, with axons that do not leave the lobe.

In the visual system it is certain that the actual memory record is not wholly dependent upon the vertical lobe. Discrimination between objects simultaneously presented may be quite effective without it (Muntz, Sutherland & Young 1962). The record is presumably preserved in the optic lobes, which indeed can be regarded as lateral outgrowths of the supraoesophageal mass.

Aberrations of learned performance, however, certainly occur after a removal of either the vertical or median superior frontal lobe. We may therefore conclude that this upper circuit is concerned with what may be called 'reading-in' to the memory or 'reading-out' from it. This may well apply to the upper parts of the corresponding lobes of the inferior frontal system, whereas the actual memory record is established in the lowest part of the subfrontal, where it meets the posterior buccal and large and small cells are mixed. These relatively few cells may prove to be very suitable subjects for revealing the mechanism of the memory.

The material for this and the preceding paper was collected at the Zoological Station at Naples and I am most grateful to Dr Dohrn and his staff for their assistance. I am also indebted to Mr B. Boycott and Mr M. J. Wells for reading the MSS and to Mrs M. Nixon and Mr V. Barber for their valuable help in preparing the papers and to Mrs J. I. Astafiev for help with the illustrations. Miss P. Stephens was responsible for the histological preparations and Mr J. Armstrong and Miss T. Hogan for the photography.

The work was supported in part by the Air Force Office of Scientific Research OAR, through the European Office of Aerospace Research, United States Air Force.

References

Boycott, B. B. & Young, J. Z. 1965 The brain of *Octopus vulgaris*. (In preparation.)

Gray, E. G. & Young, J. Z. 1964 Electron microscopy of synaptic structure of *Octopus* brain. *J. Cell. Biol.* **21**, 87–103.

Graziadei, P. 1962 Receptors in the suckers of *Octopus*. *Nature, Lond.*, **195**, 57–59.

Messenger, J. B. 1963 Behaviour of young *Octopus briareus* Robson. *Nature, Lond.*, **197**, 1186–1187.

Muntz, W. R. A., Sutherland, N. S. & Young, J. Z. 1962 Simultaneous shape discrimination in *Octopus* after removal of the vertical lobe. *J. Exp. Biol.* **39**, 557–566.

Thore, S. 1939 Beiträge zur Kenntnis der vergleichenden Anatomie des zentralen Nervensystems der dibranchiaten Cephalopoden. *Pubbl. Staz. zool. Napoli*, **17**, 313–506.

Uexküll, J. von 1895 Physiologische Untersuchungen an Eledone moschata. IV. Zur Analyse der Functionen des Centralnervensystems. *Z. Biol.* **31**, 584–609.

Wells, M. J. 1959*a* A touch learning centre in *Octopus*. *J. Exp. Biol.* **36**, 590–612.

Wells, M. J. 1959*b* Functional evidence for neurone fields representing the individual arms within the central nervous system of *Octopus*. *J. Exp. Biol.* **36**, 501–511.

Wells, M. J. 1961 Centres for tactile and visual learning in the brain of *Octopus*. *J. Exp. Biol.* **38**, 811–826.

Wells, M. J. & Wells, J. 1956 Tactile discrimination and the behaviour of blind *Octopus*. *Pubbl. Staz. zool. Napoli*, **28**, 94–126.

Wells, M. J. & Wells, J. 1957 The effect of lesions to the vertical and optic lobes on tactile discrimination in *Octopus*. *J. Exp. Biol.* **34**, 378–393.

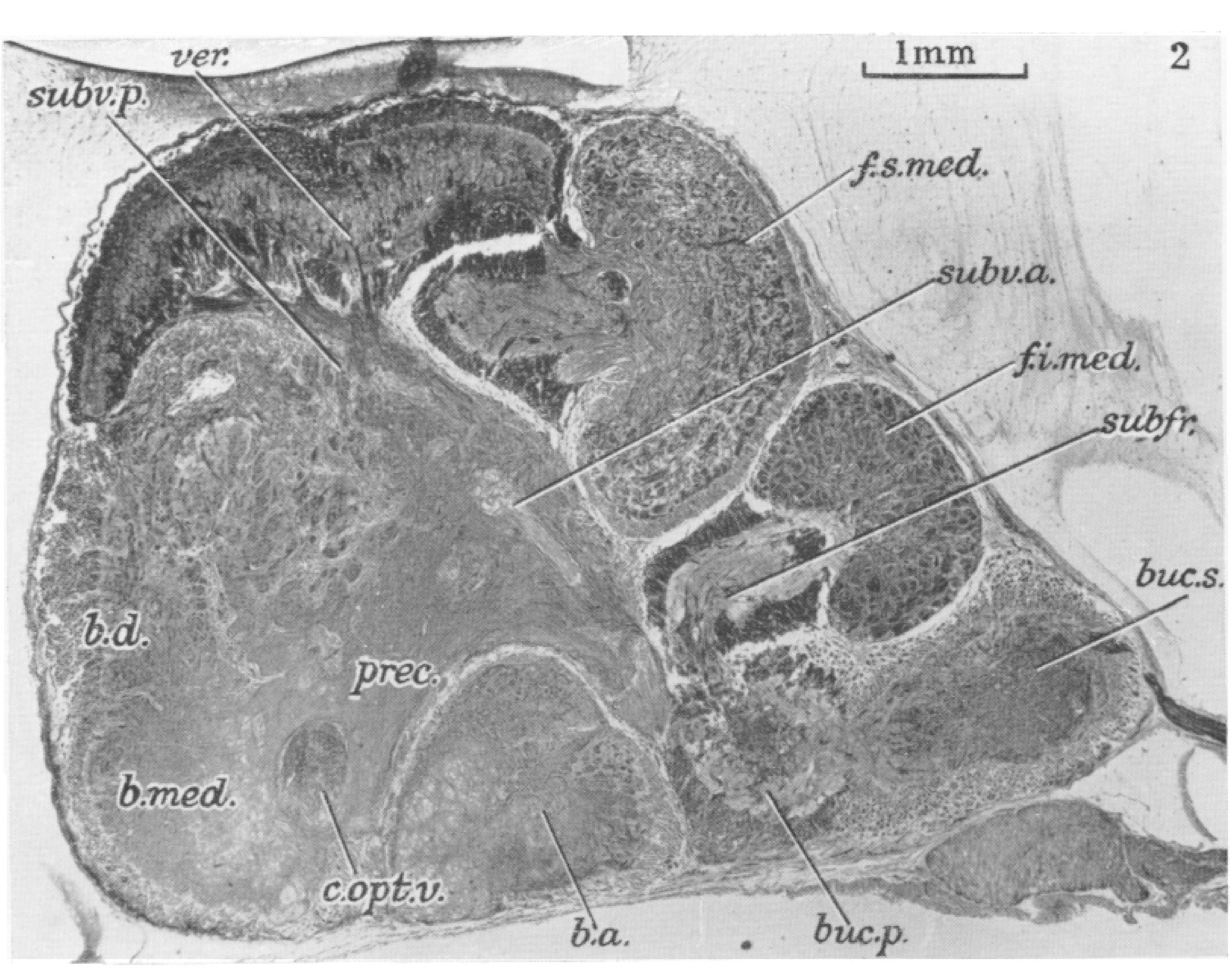
Young, J. Z. 1939 Fused neurons and synaptic contacts in the giant nerve fibres of cephalopods. *Phil. Trans.* B, **229**, 465–503.

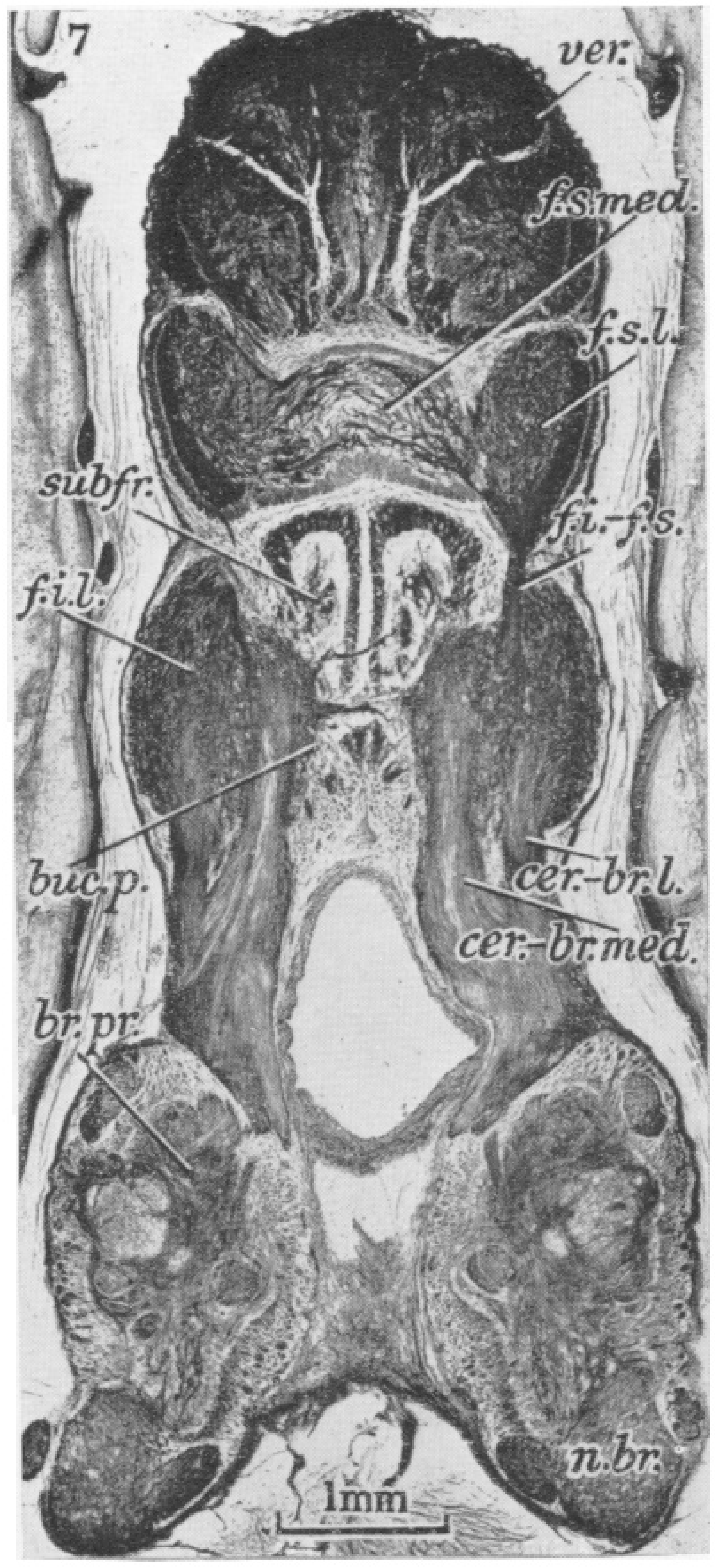
Young, J. Z. 1963 *a* The number and sizes of nerve cells in *Octopus*. *Proc. Zool. Soc. Lond.* **140**, 229–254.

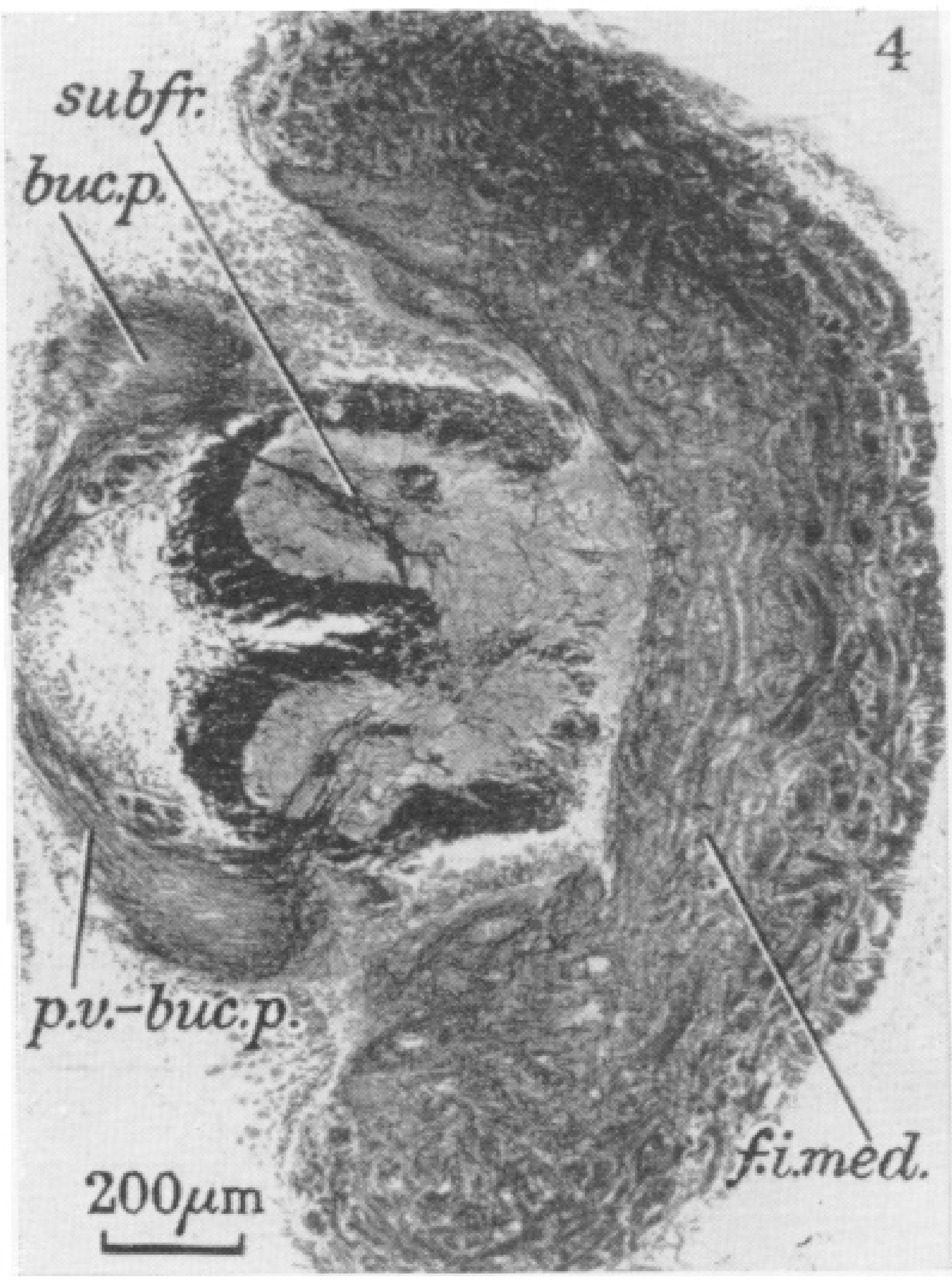
Young, J. Z. 1963 *b* Some essentials of neural memory systems. Paired centres that regulate and address the signals of the results of action. *Nature, Lond.*, **198**, 626–630.

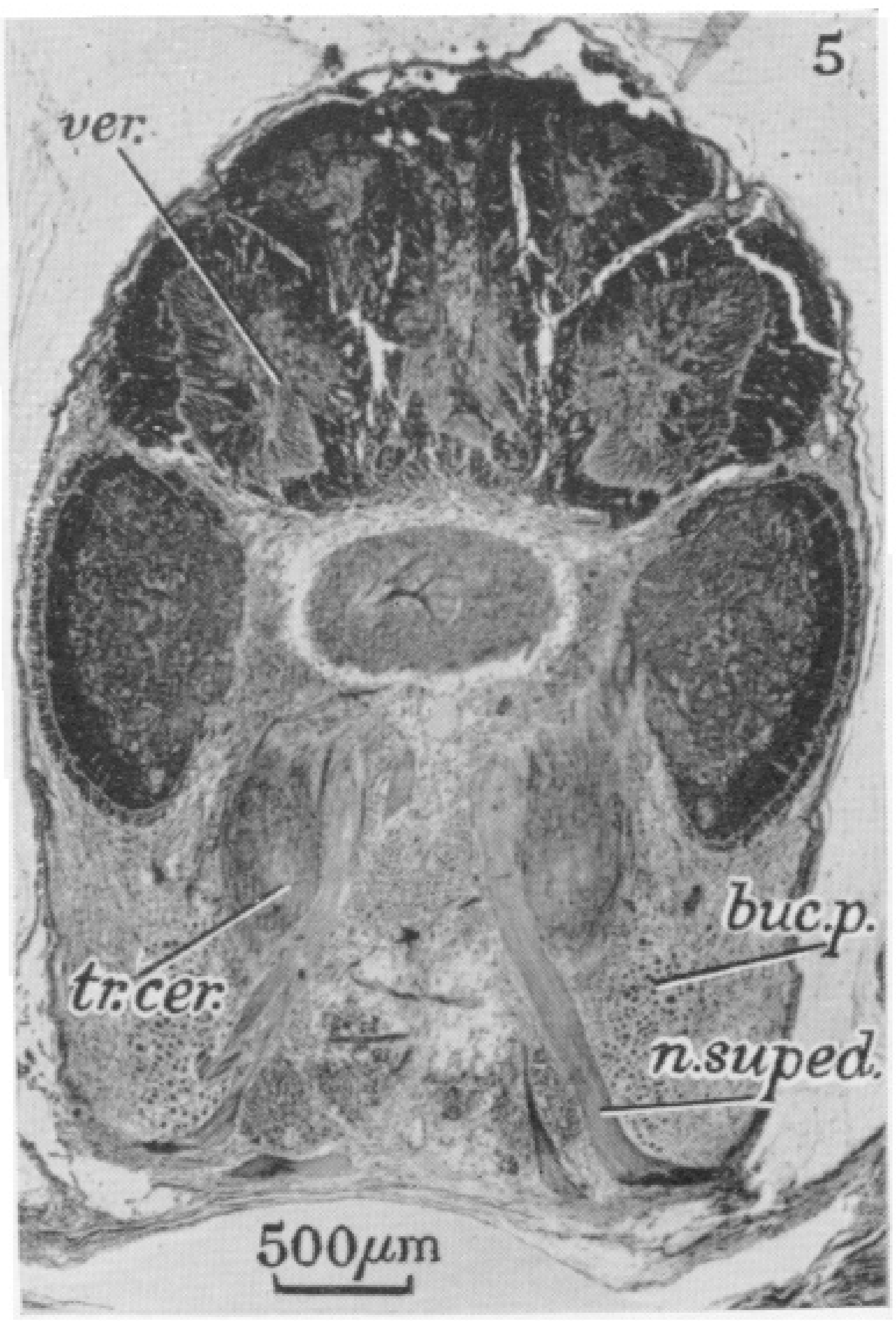
Young, J. Z. 1964 Paired centres for the control of attack by *Octopus*. *Proc. Roy. Soc.* B, **159**, 565–588.

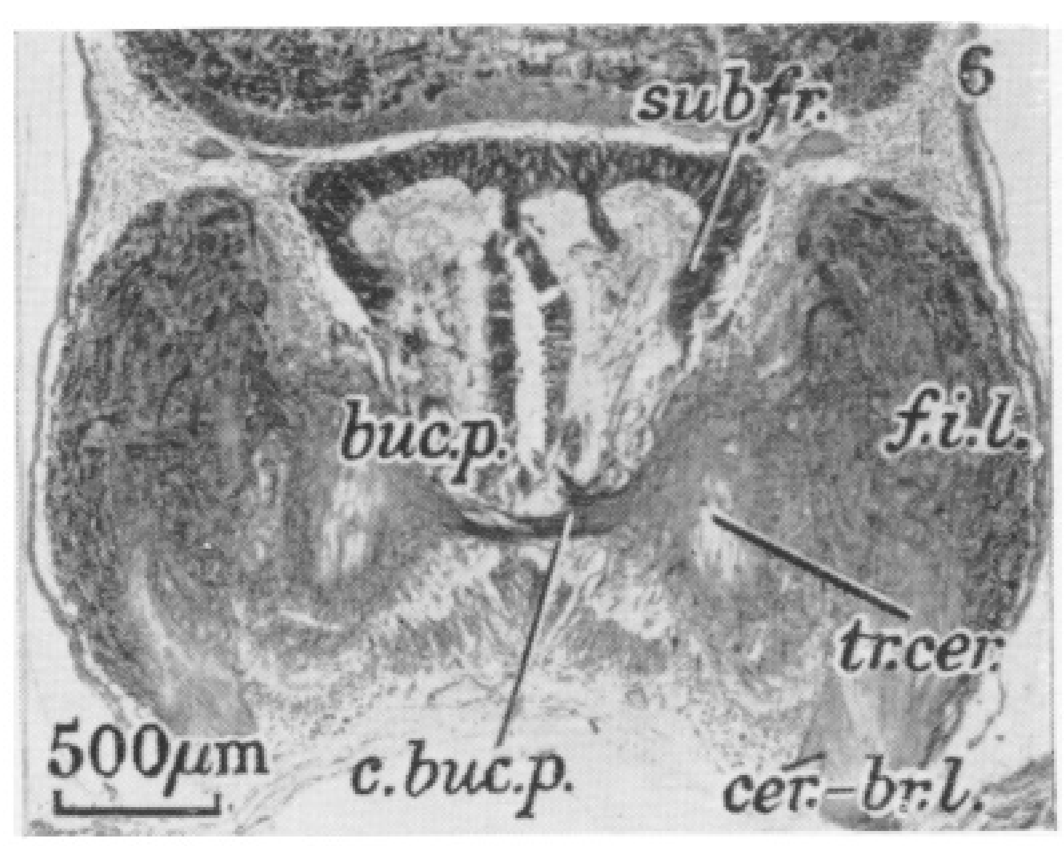
Young, J. Z. 1965 The buccal nervous system of *Octopus*. *Phil. Trans.* B, **249**, 27–44.

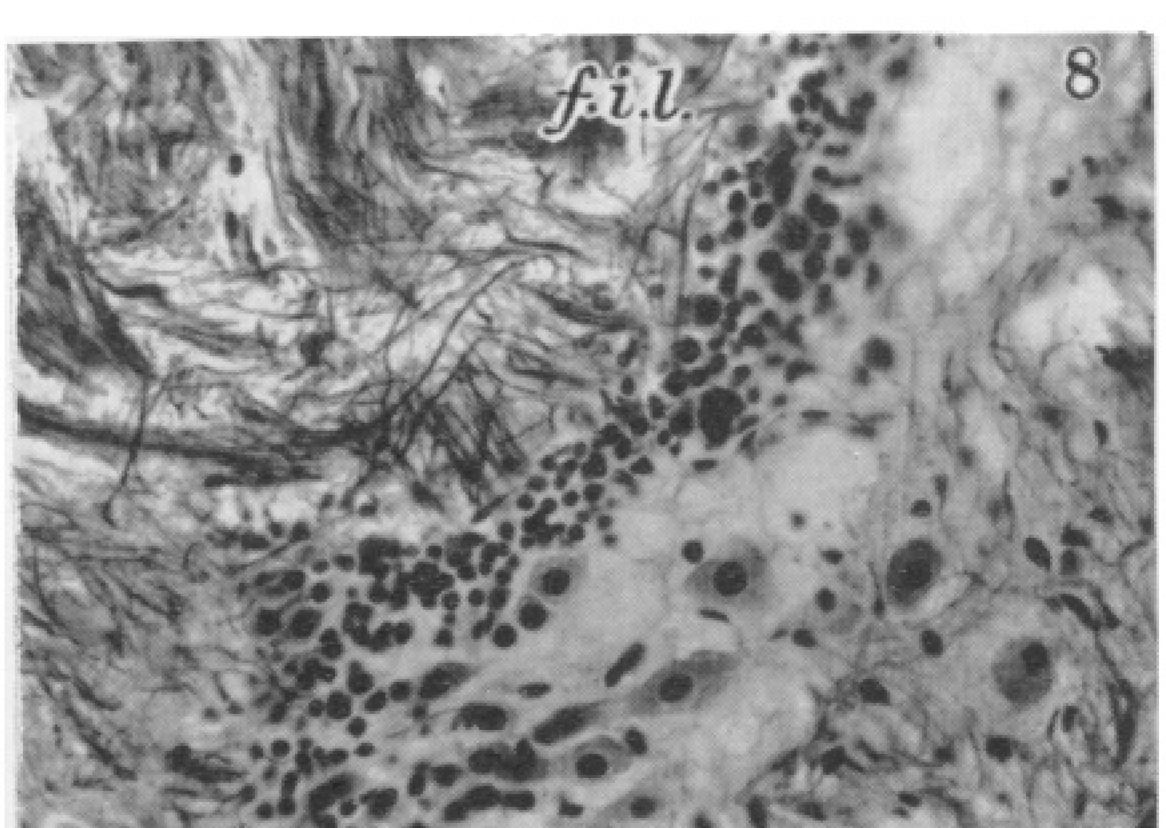

2
1mm
ver.
subv.p.
f.s.med.
subv.a.
f.i.med.
subfr.
buc.s.
b.d.
prec.
b.med.
c.opt.v.
b.a.
buc.p.

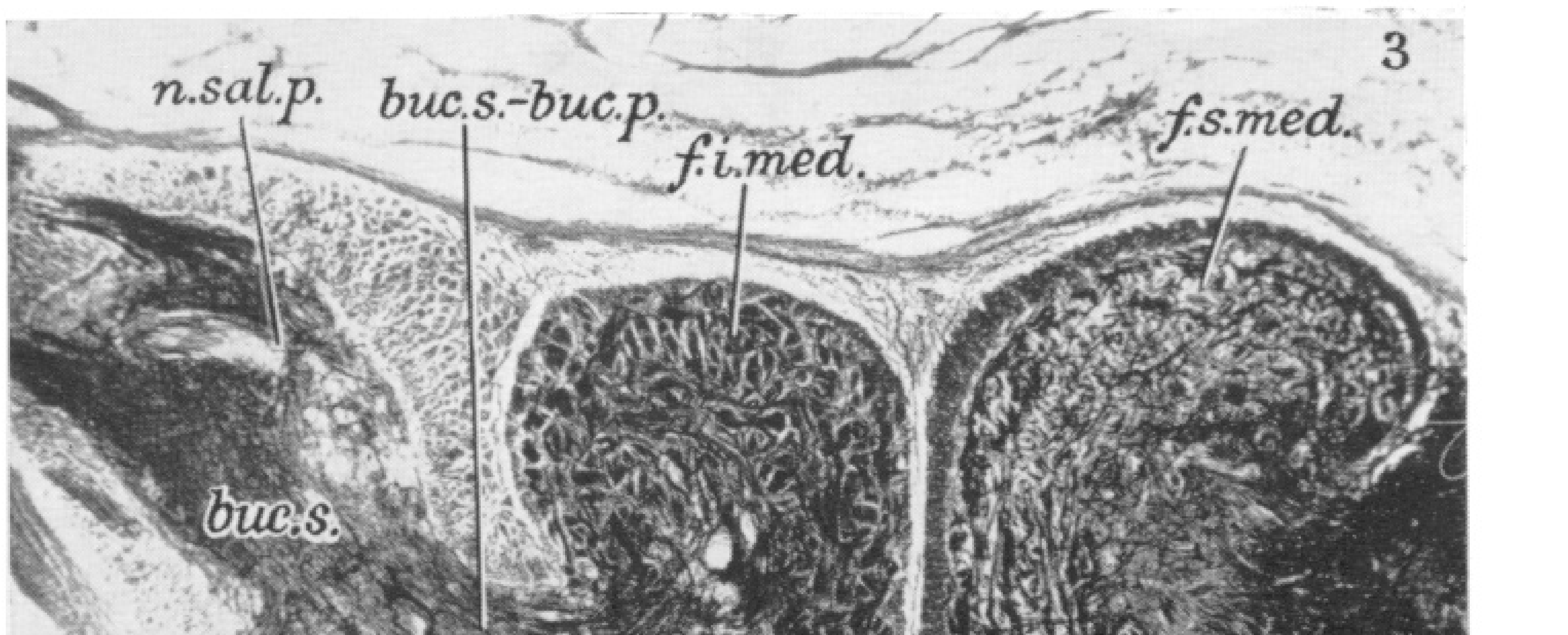

7
ver.
f.s.med.
f.s.l.
subfr.
f.i.-f.s.
f.i.l.
buc.p.
cer.-br.l.
cer.-br.med.
br.pr.
n.br.
1mm

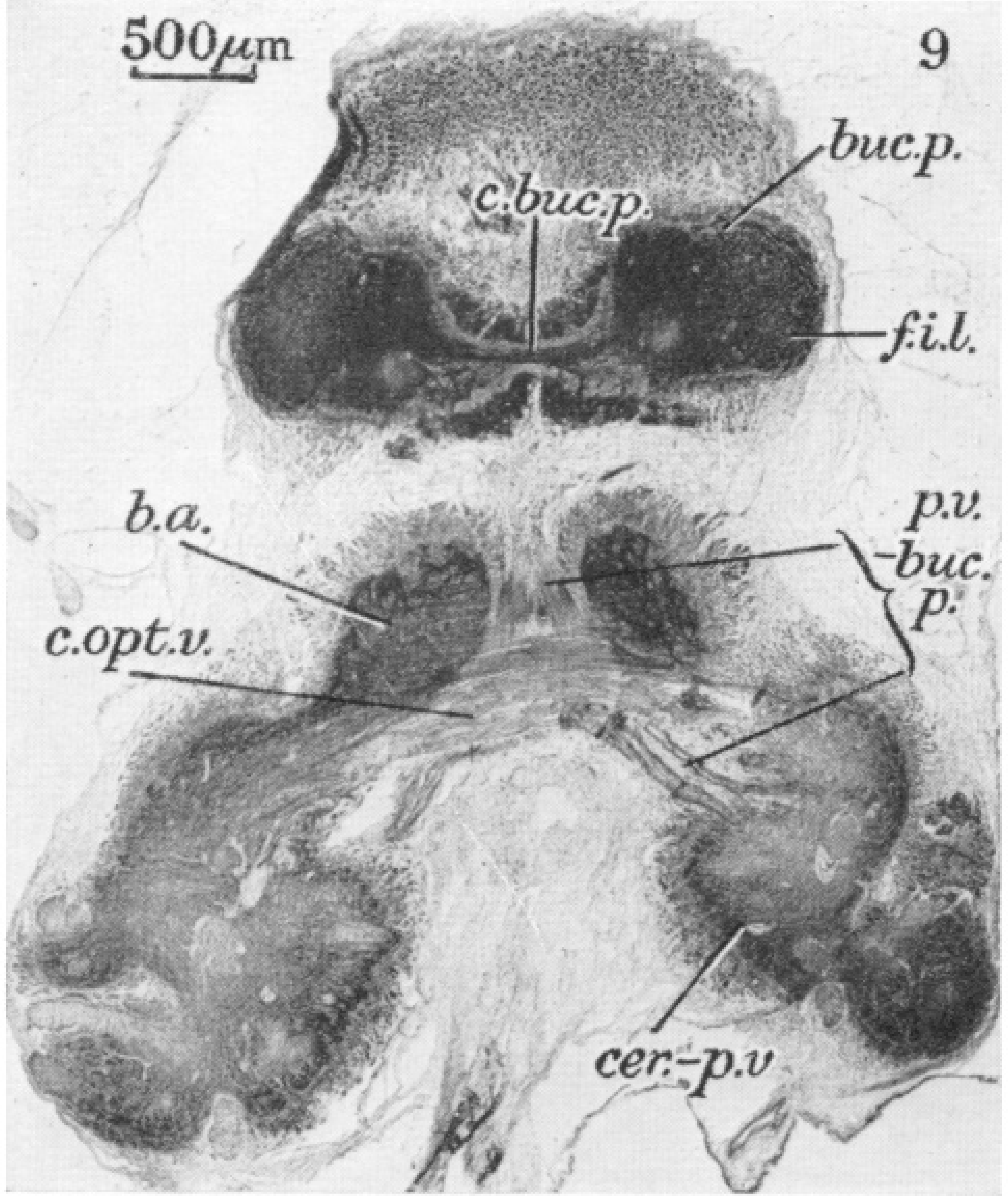

4
subfr.
buc.p.
p.v.-buc.p.
f.i.med.
200μm

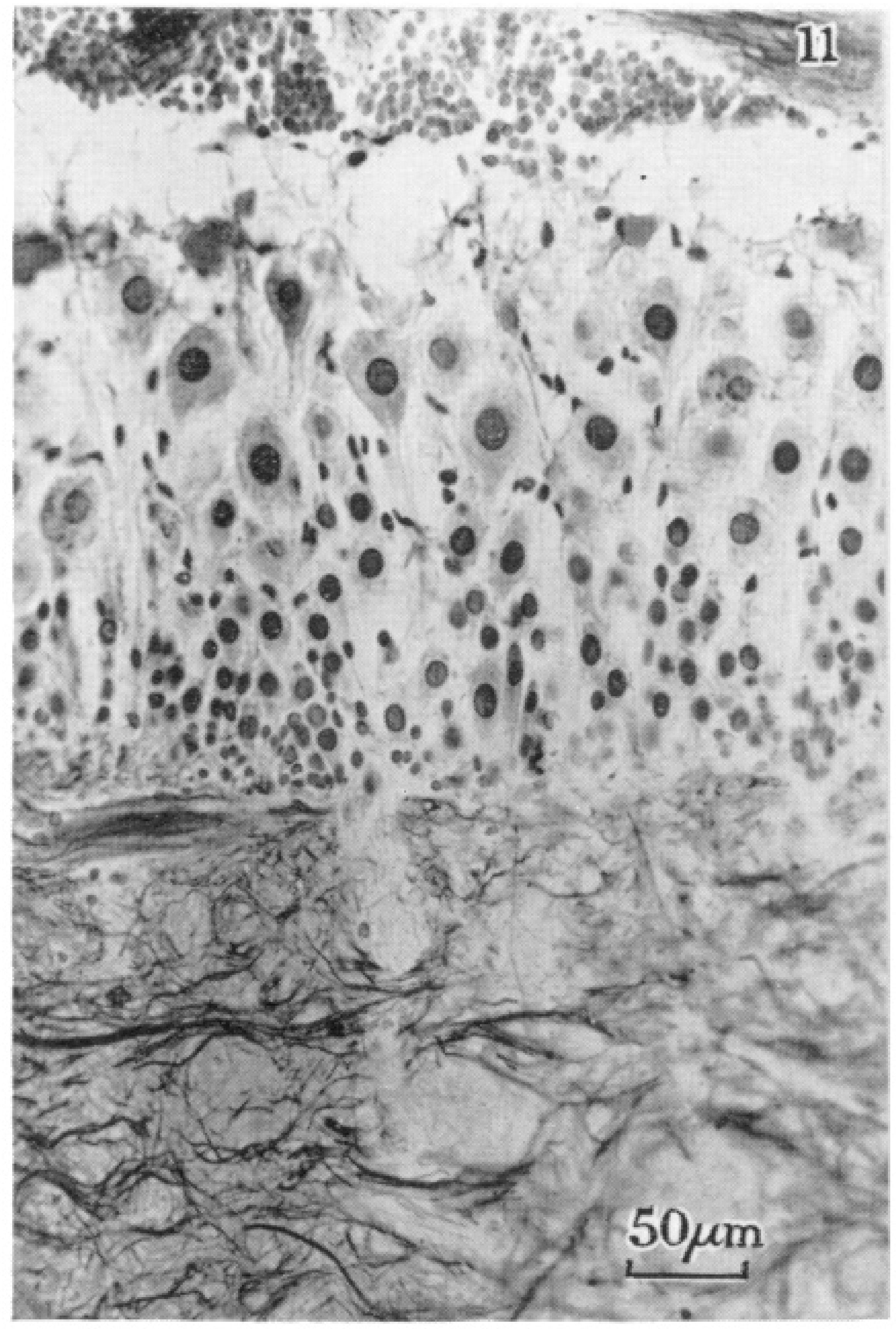

5
ver.
tr.cer.
buc.p.
n.suped.
500μm

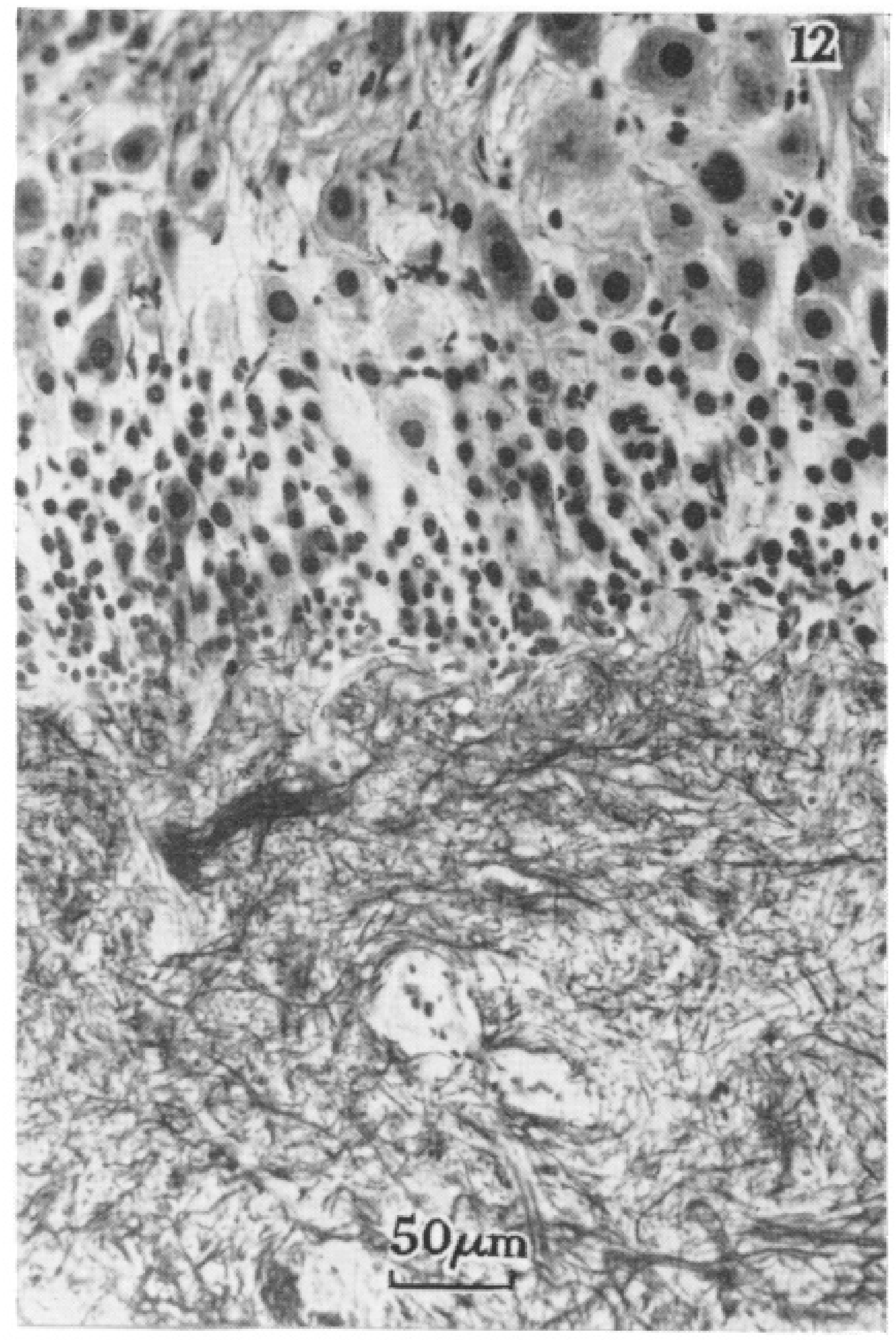

6
subfr.
buc.p.
f.i.l.
tr.cer.
500μm
c.buc.p.
cer.-br.l.

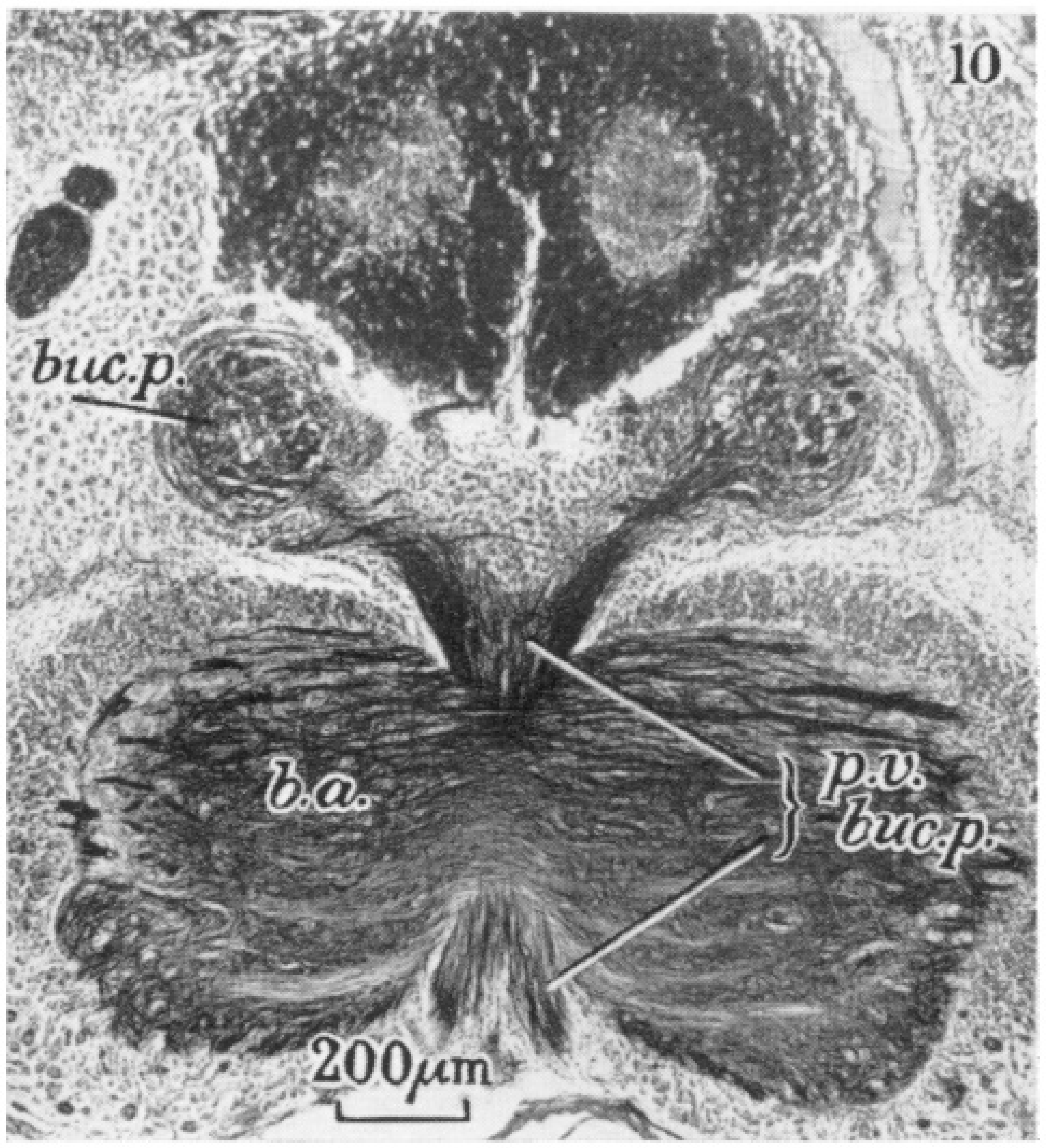

8
f.i.l.
buc.p.
50μm


3
n.sal.p.
buc.s.-buc.p.
f.i.med.
f.s.med.
buc.s.
cer.-br.
200μm
buc.p.
tr.cer.

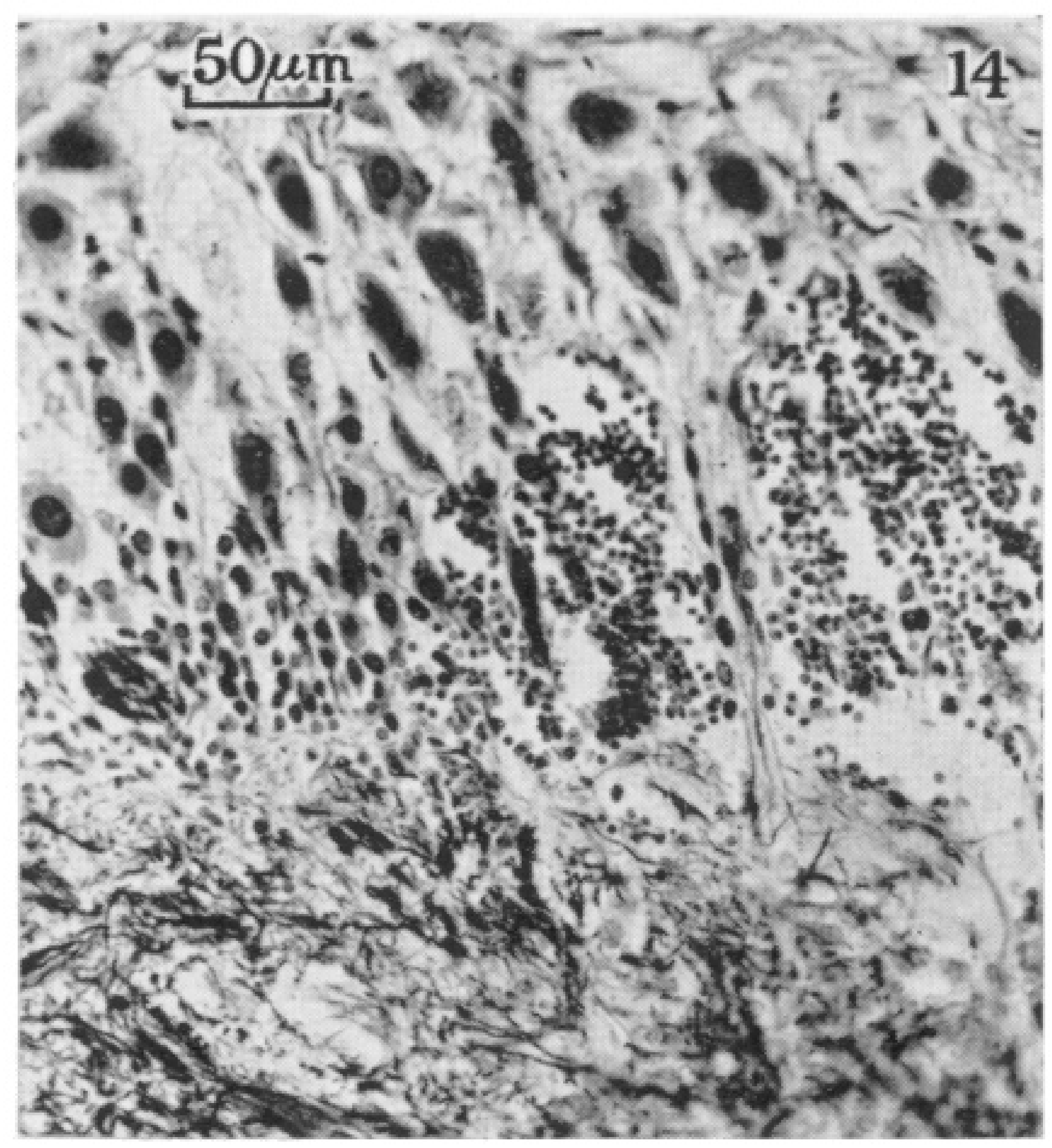

500μm
9
buc.p.
c.buc.p.
f.i.l.
b.a.
p.v.
-buc.
p.
c.opt.v.
cer.-p.v

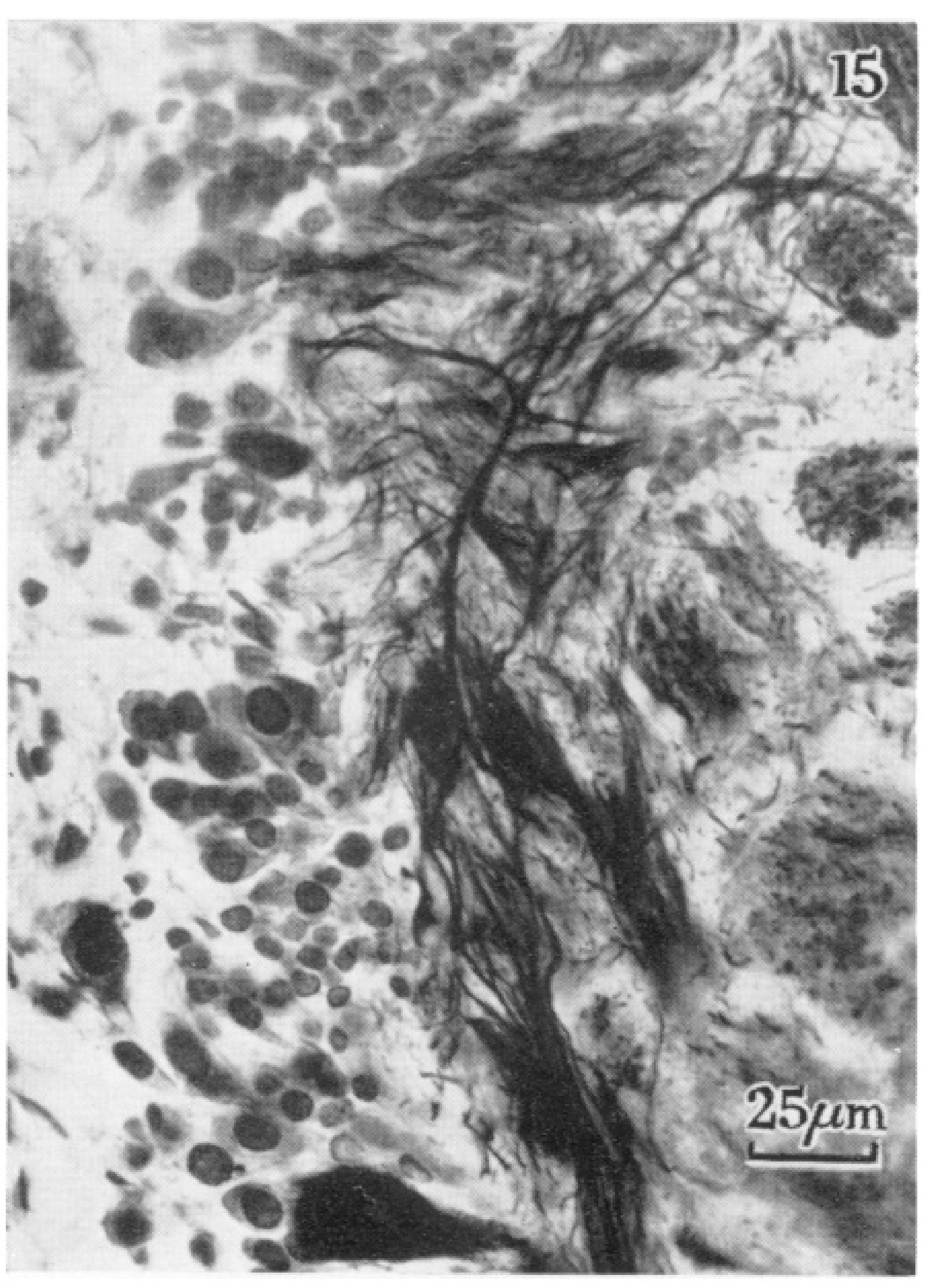

11
50μm


12
50μm

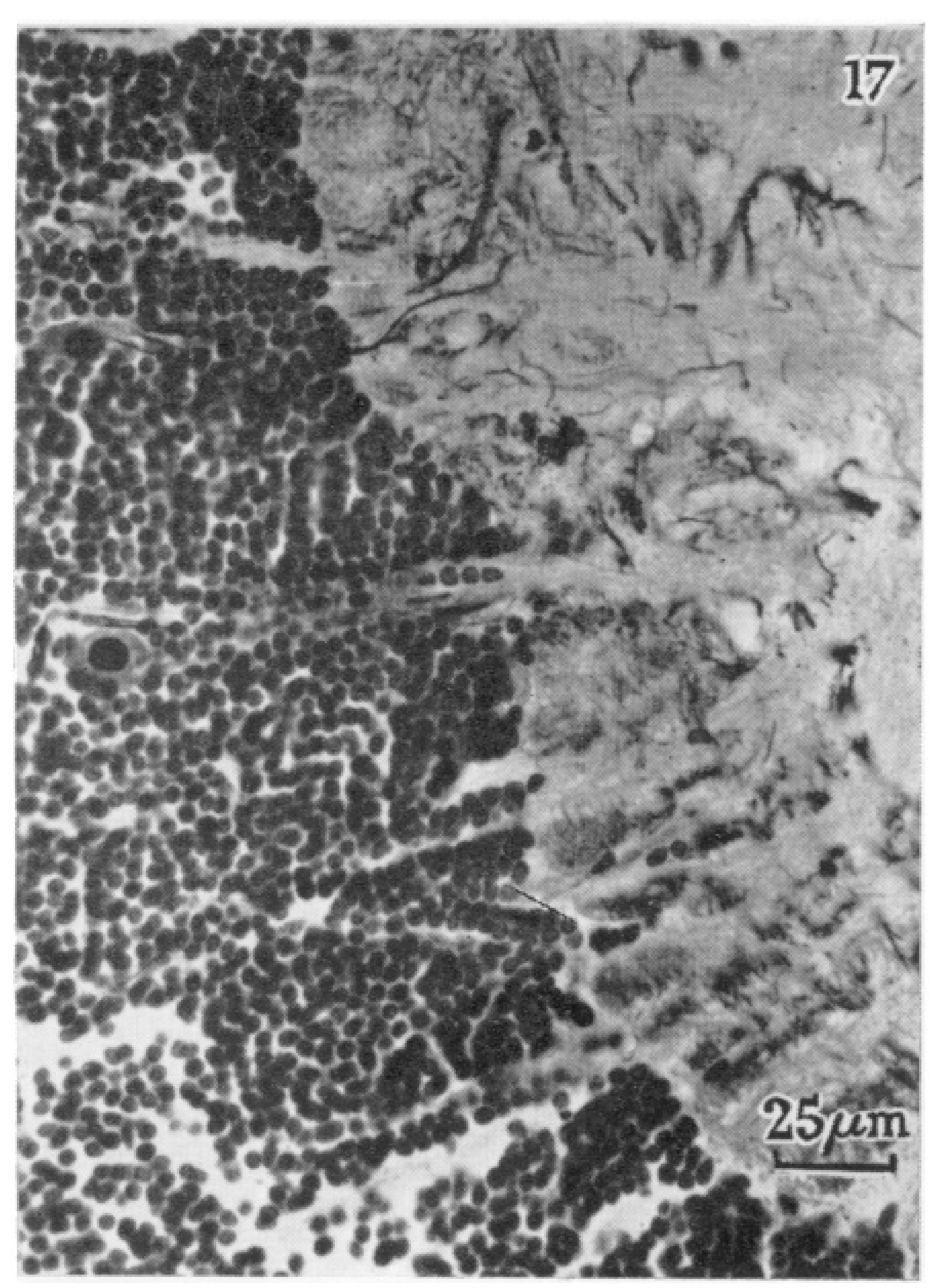

10
buc.p.
b.a.
p.v.
buc.p.
200μm

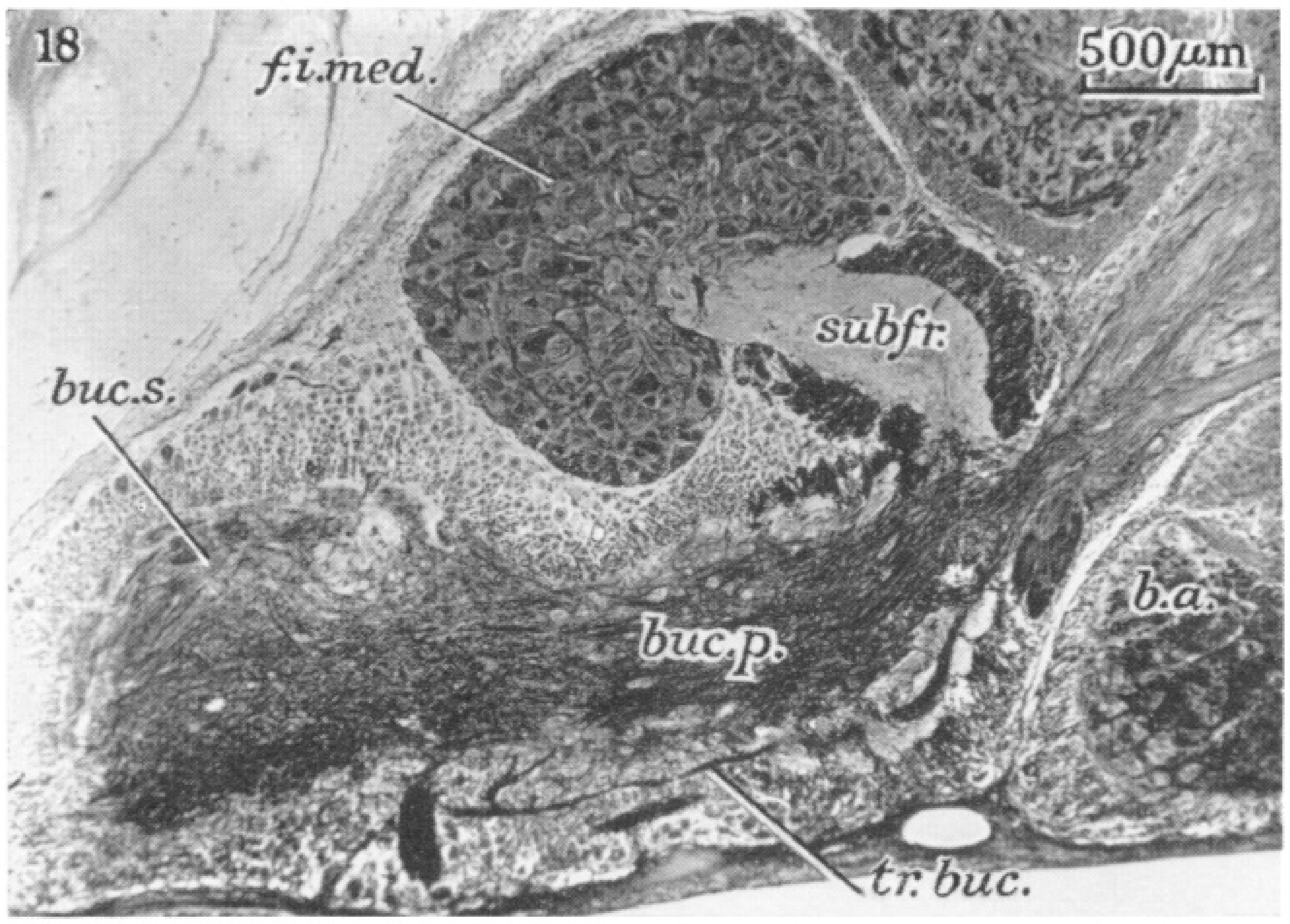

50μm
13

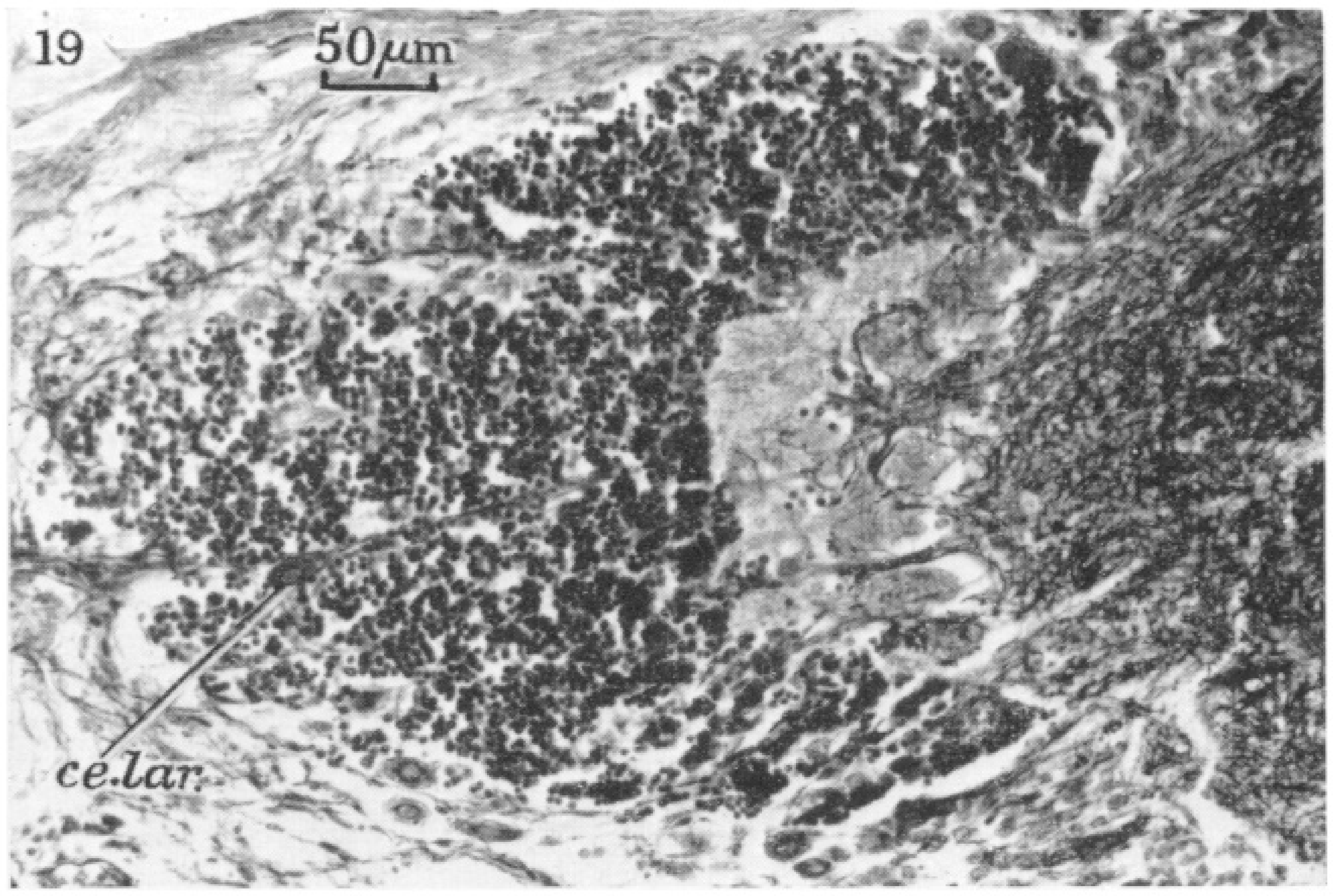

50μm
14

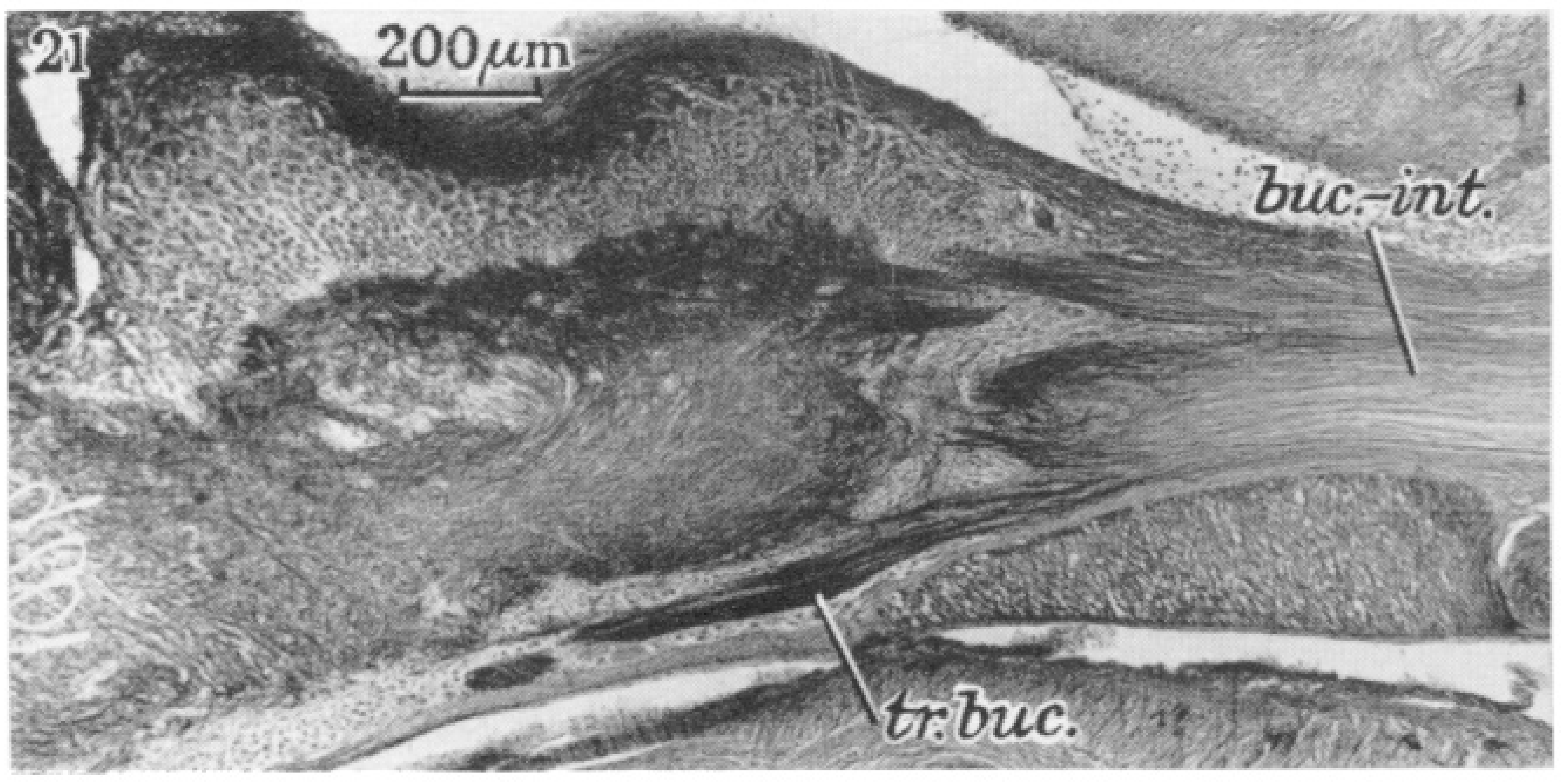

15
25μm

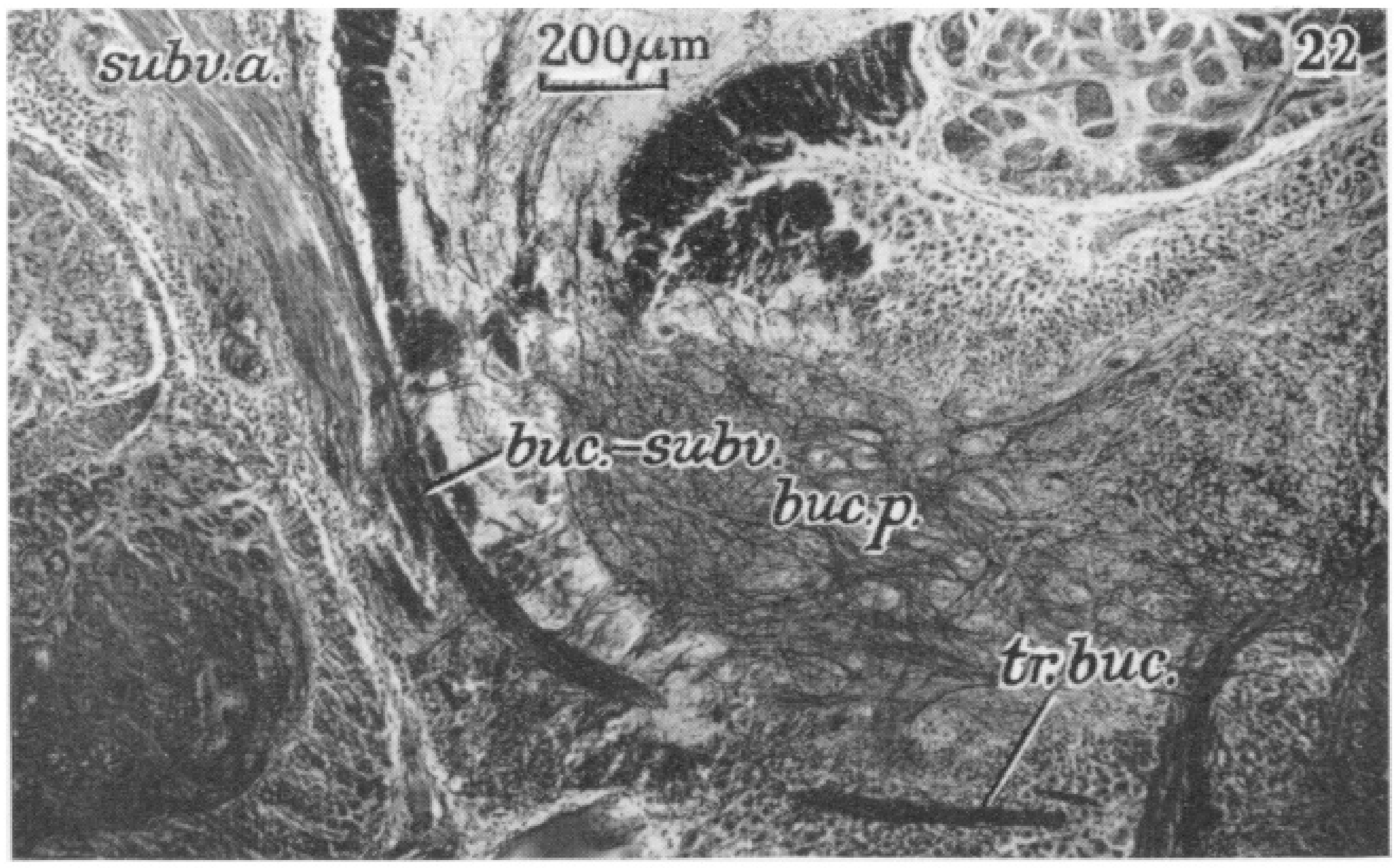

16
25μm

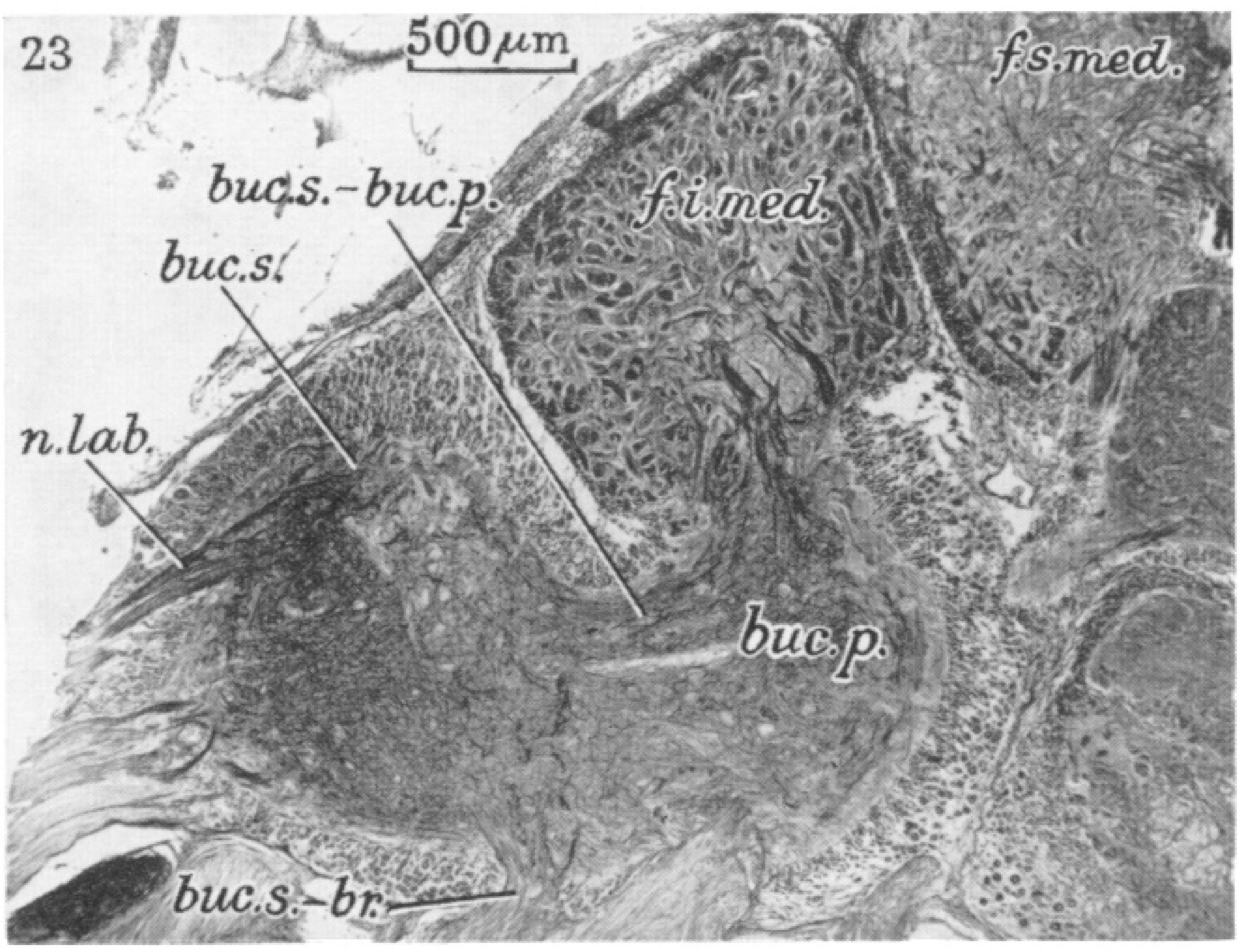

17
25μm

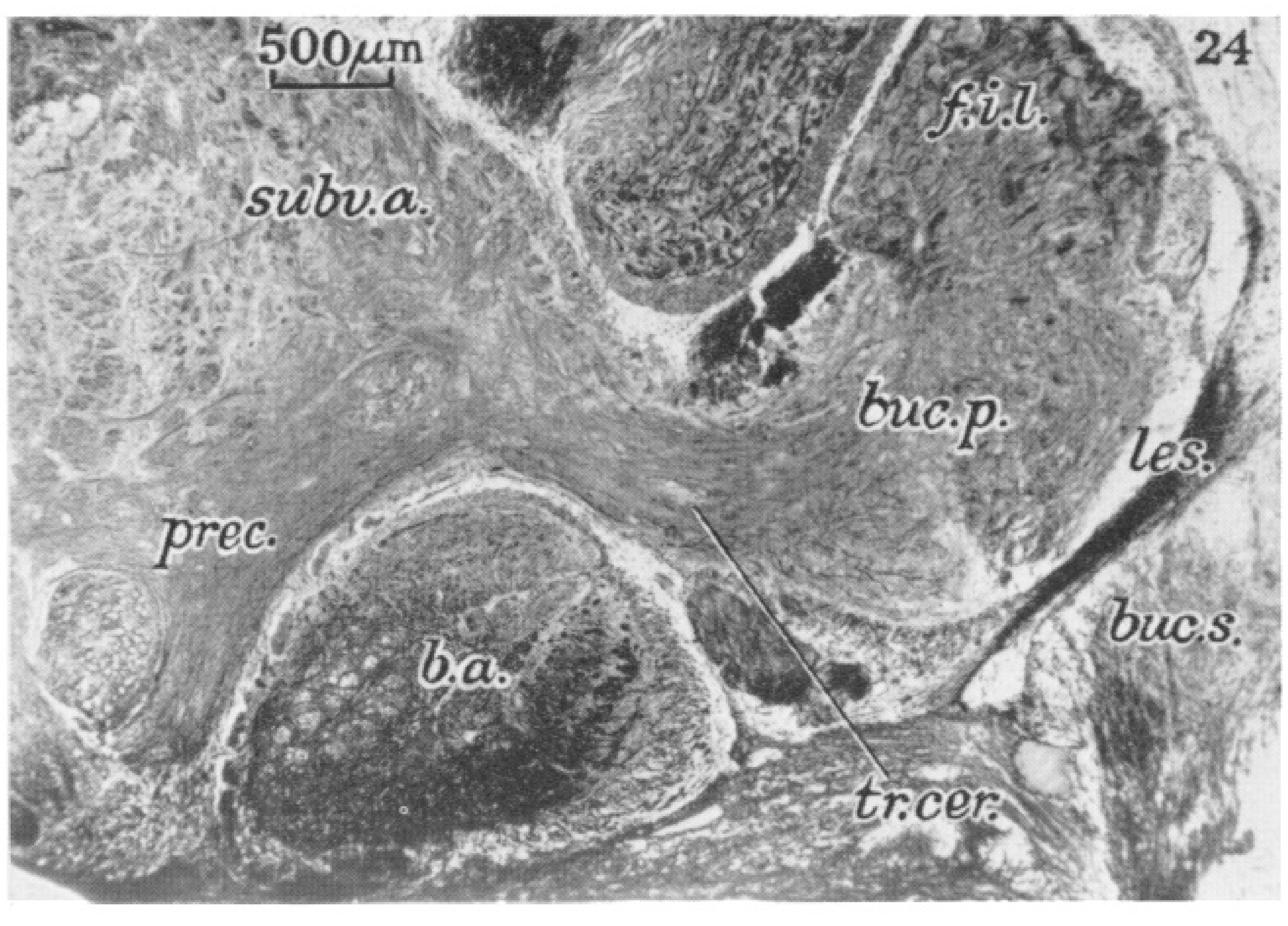

18
f.i.med.
500μm
subfr.
buc.s.
b.a.
buc.p.
tr.buc.

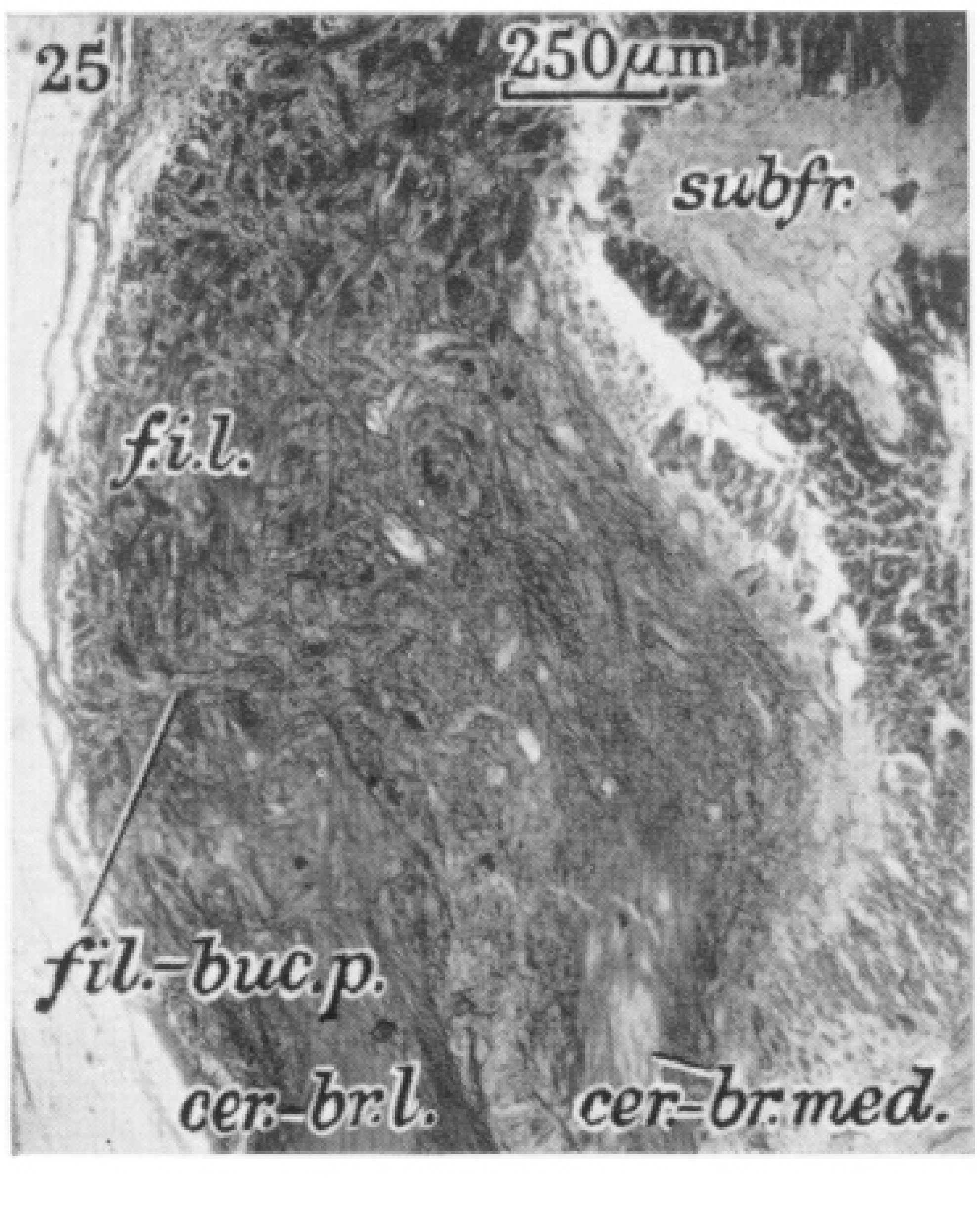

19
50μm
ce.lar.

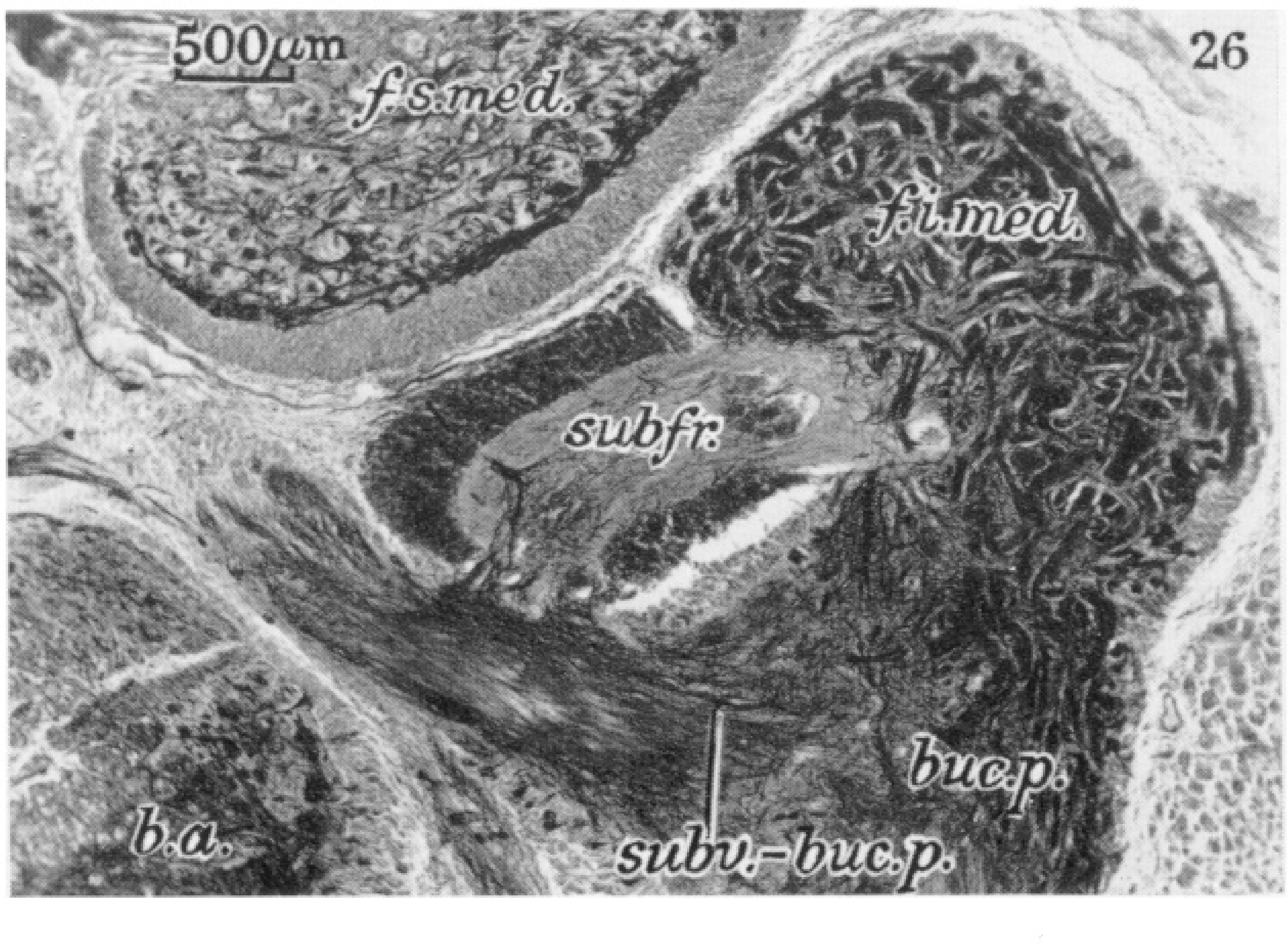

21
200μm
buc.-int.
tr.buc.

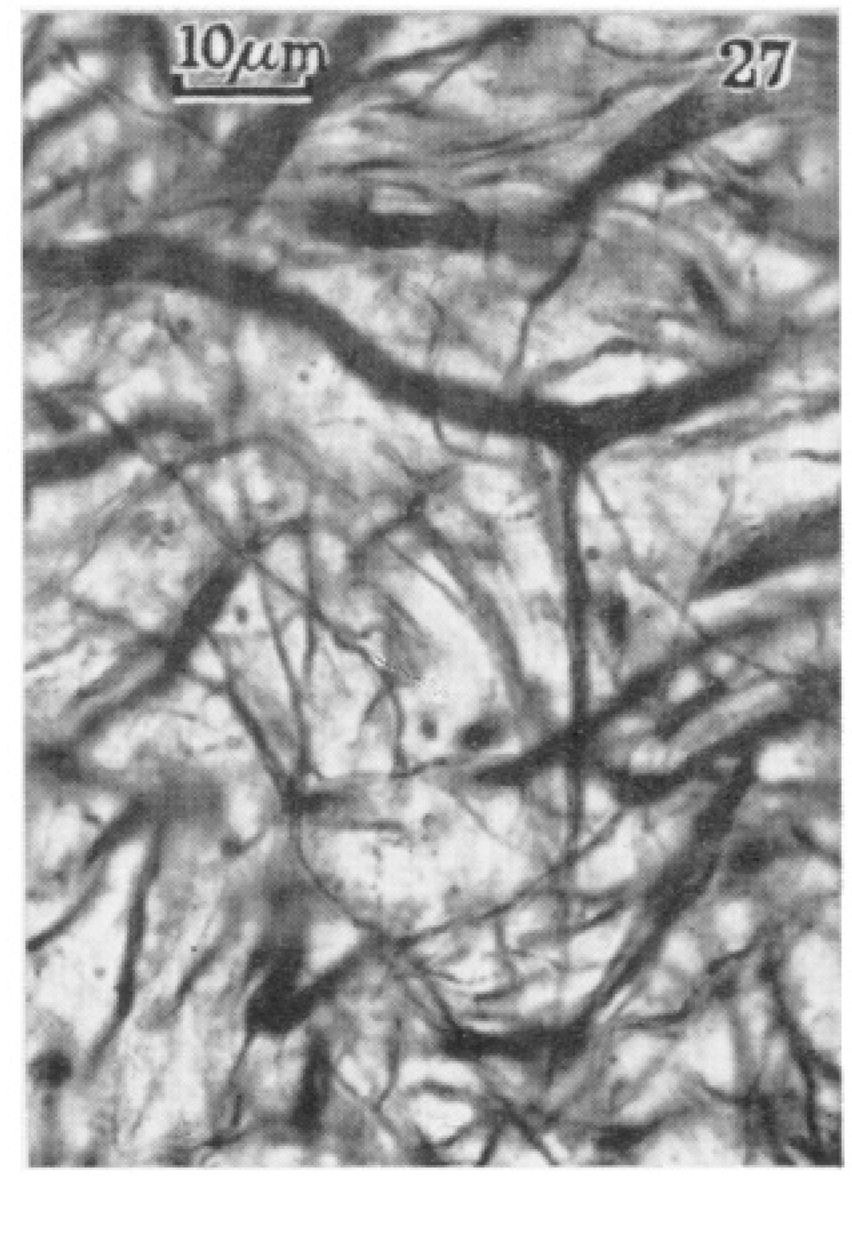

subv.a.
200μm
22
buc.-subv.
buc.p.
tr.buc.

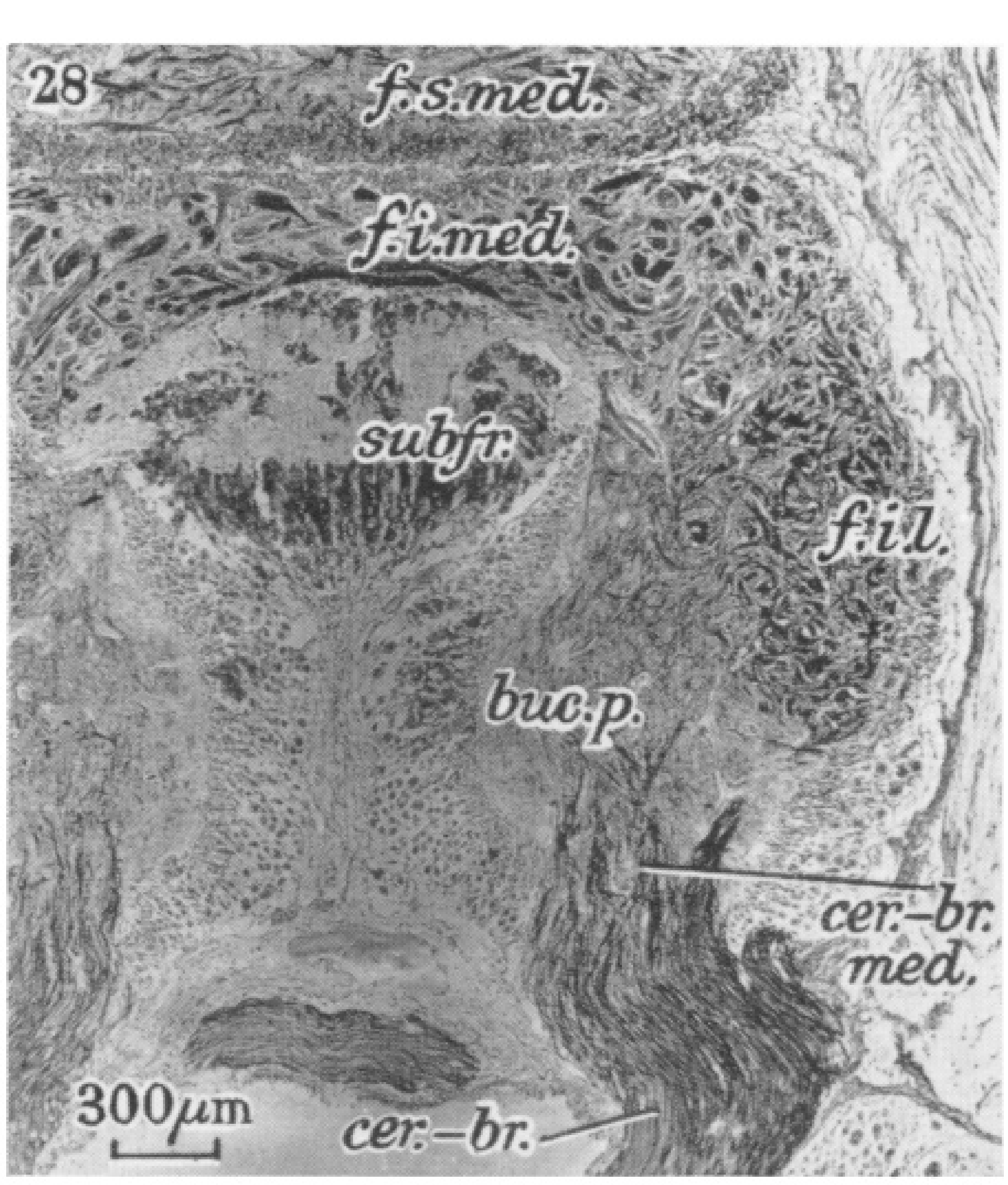

23
500μm
f.s.med.
buc.s.-buc.p.
f.i.med.
buc.s.
n.lab.
buc.p.
buc.s.-br.

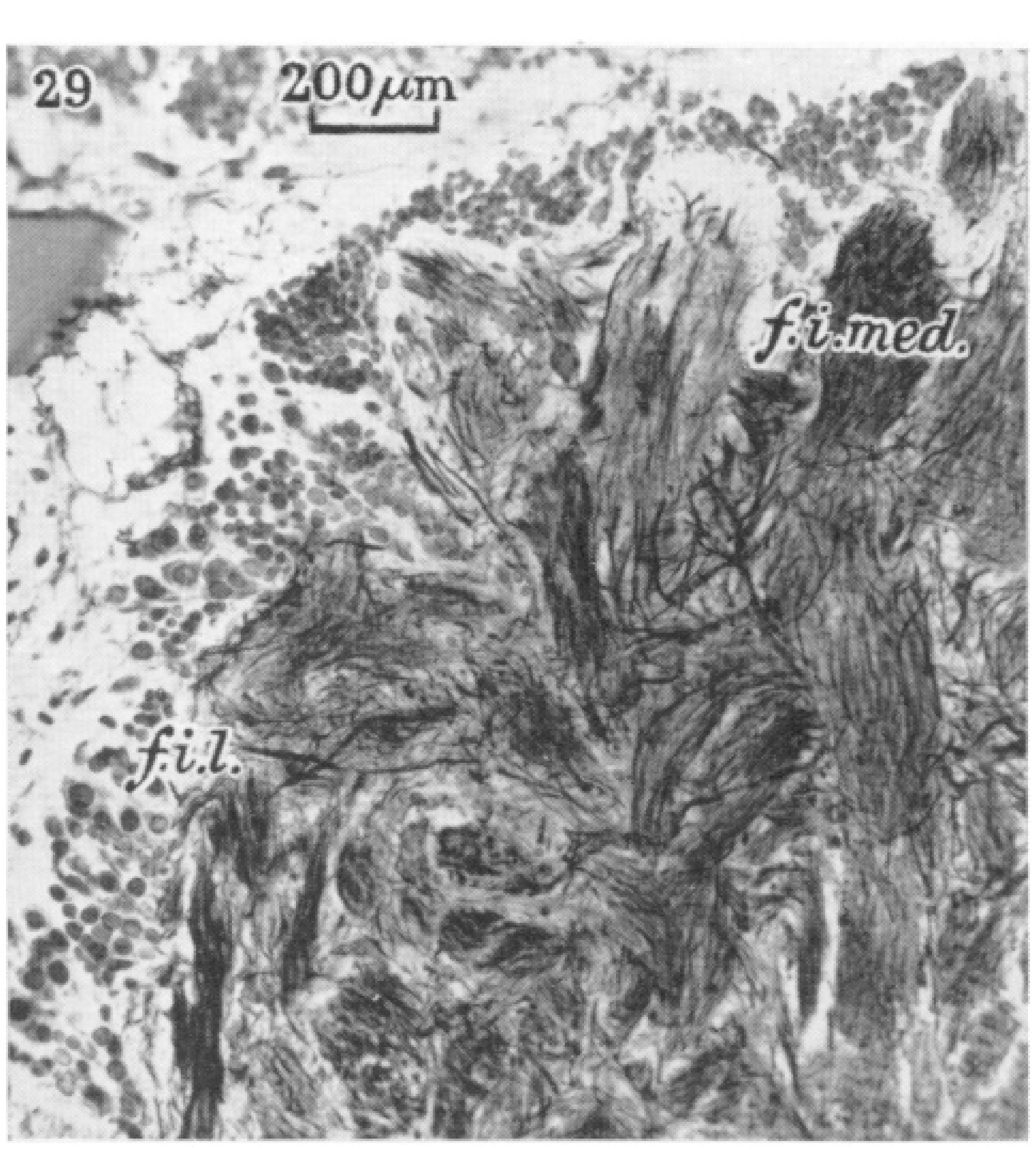

500μm
24
f.i.l.
subv.a.
buc.p.
les.
prec.
buc.s.
b.a.
tr.cer.

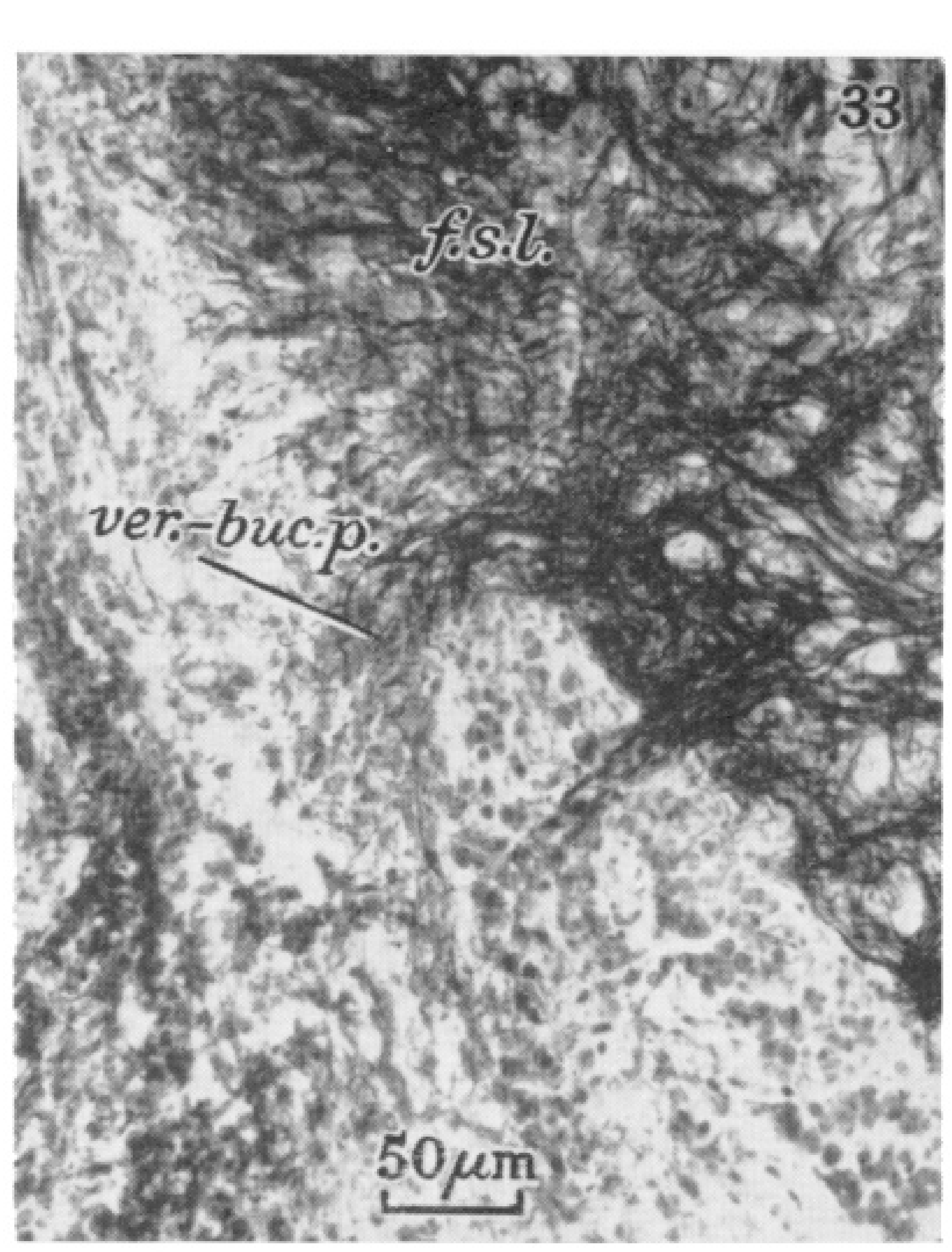

25
250μm
subfr.
f.i.l.
fil.-buc.p.
cer.-br.l.
cer.-br.med.


500μm
26
f.s.med.
f.i.med.
subfr.
buc.p.
b.a.
subv.-buc.p.

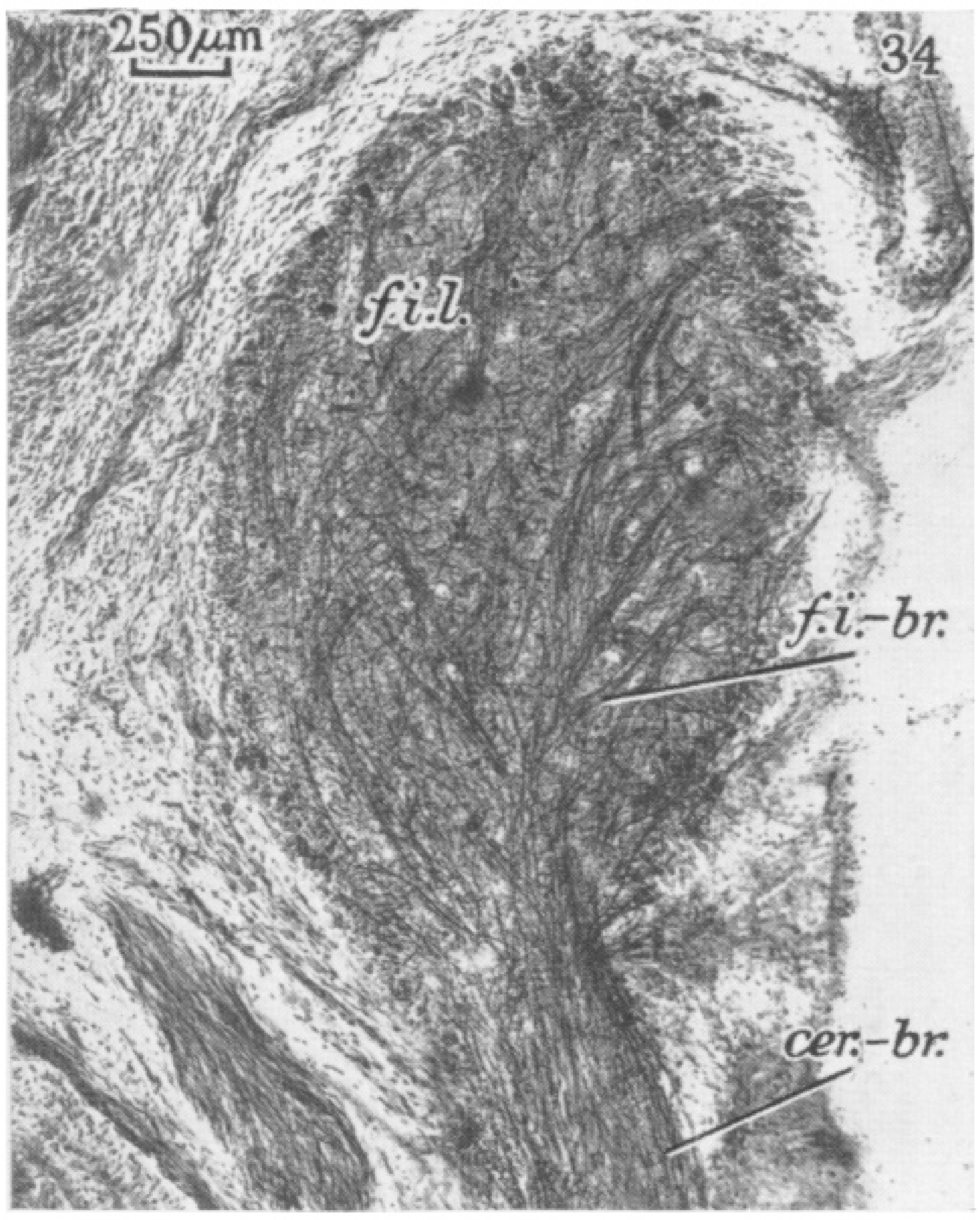

10μm
27

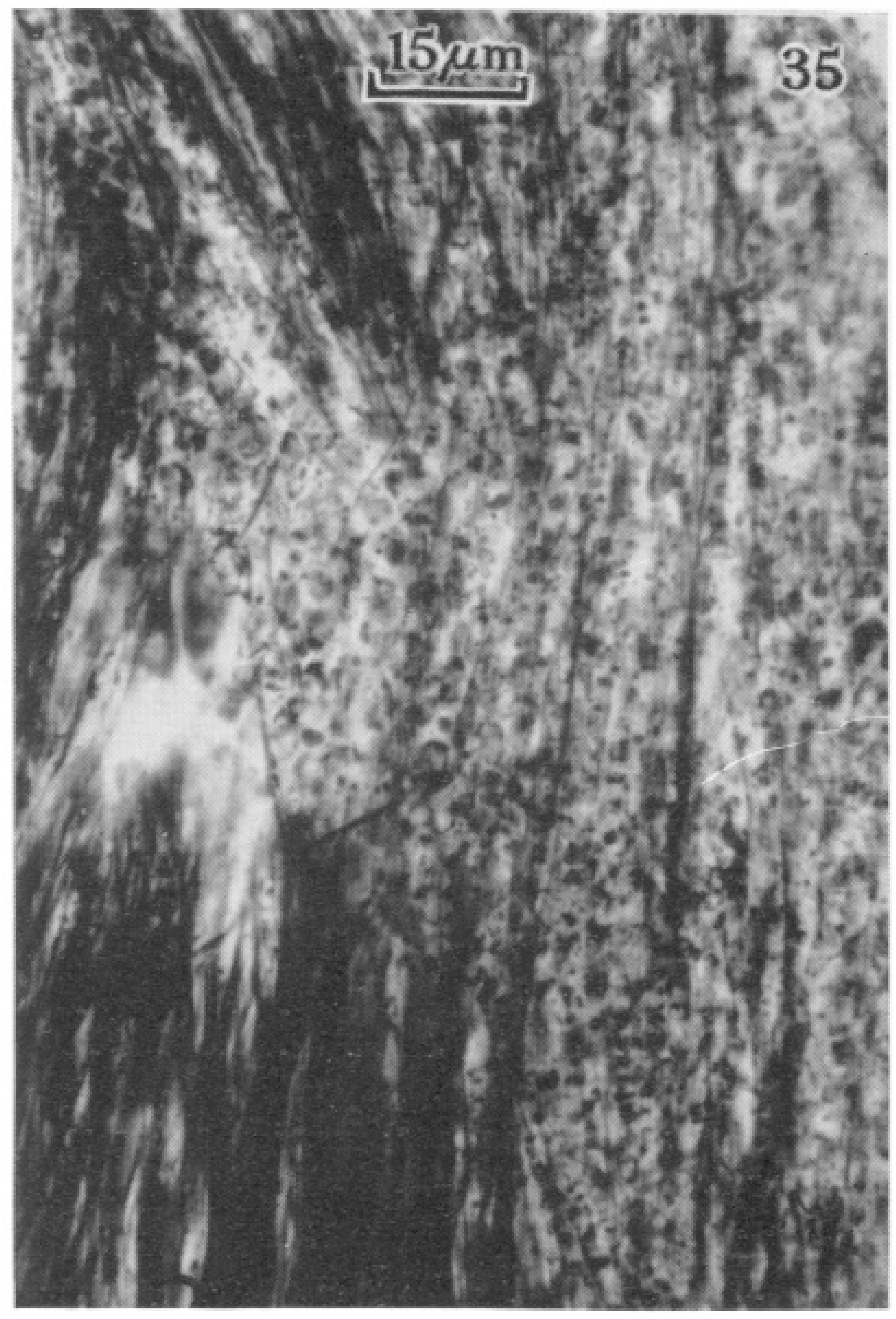

28
f.s.med.
f.i.med.
subfr.
f.i.l.
buc.p.
cer.-br.
med.
300μm
cer.-br.

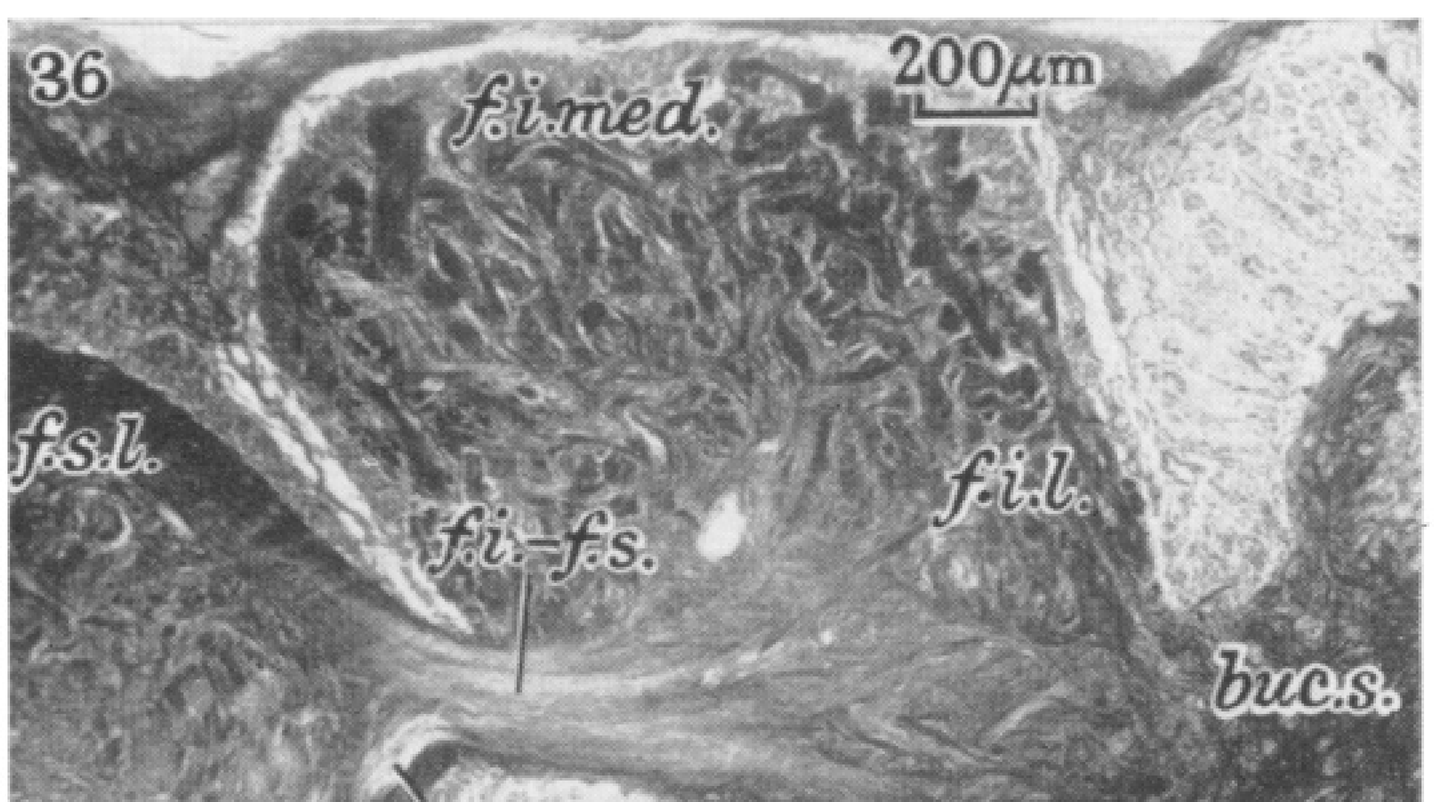

29
200μm
f.i.med.
f.i.l.

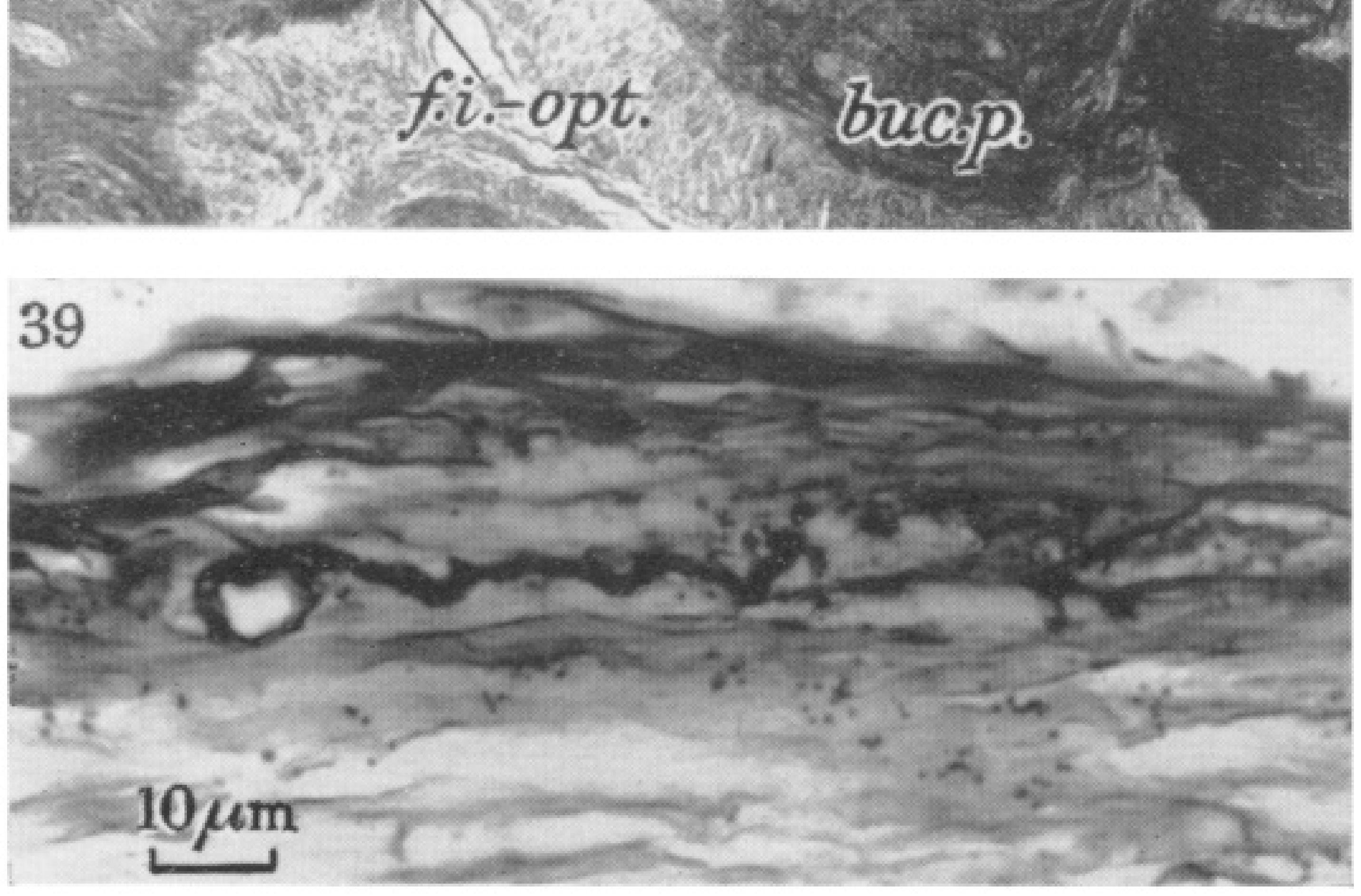

33
f.s.l.
ver.-buc.p.
50μm

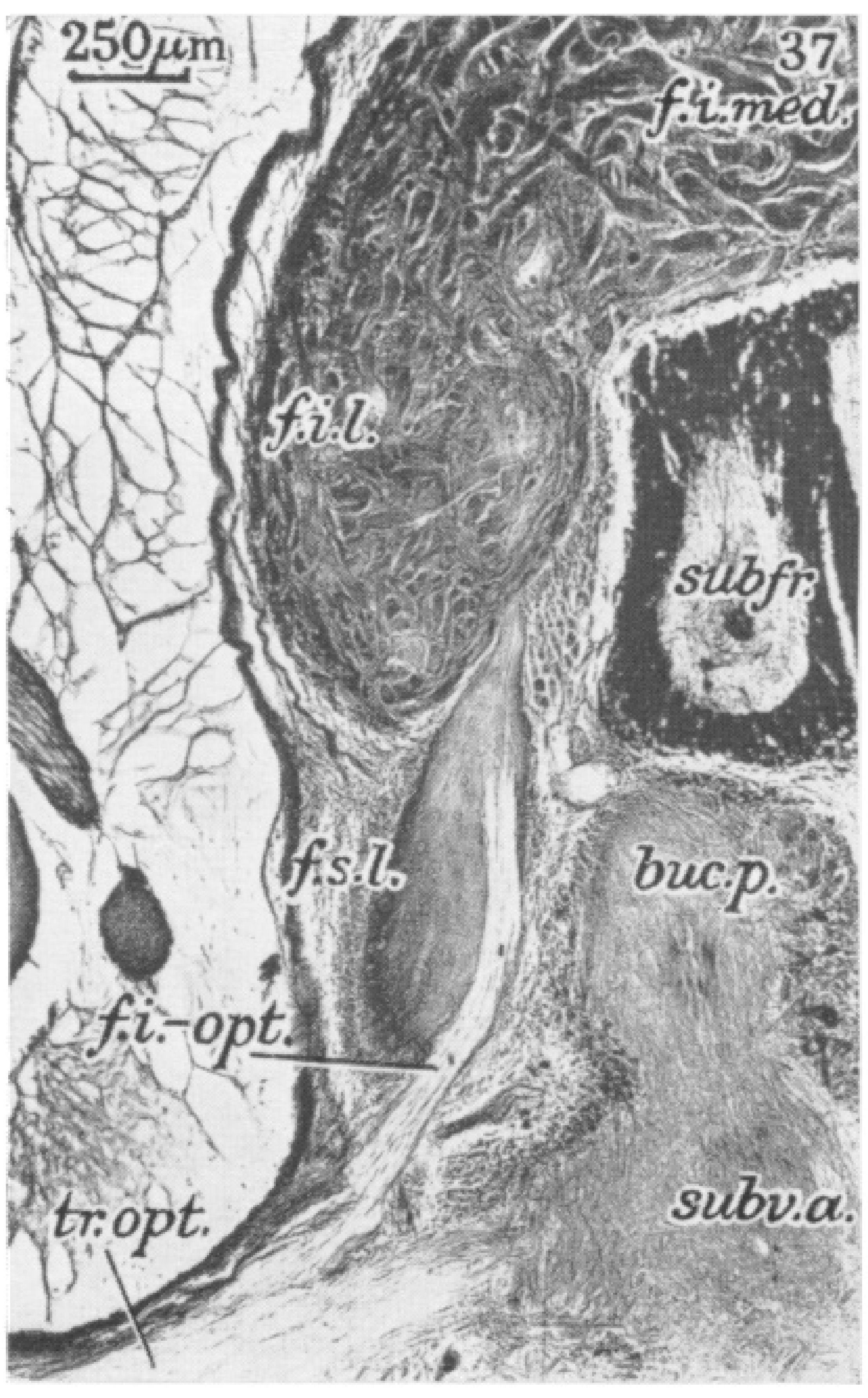

32
200μm
f.i.l.
f.i.-f.s.
buc.p.
cer.-br.

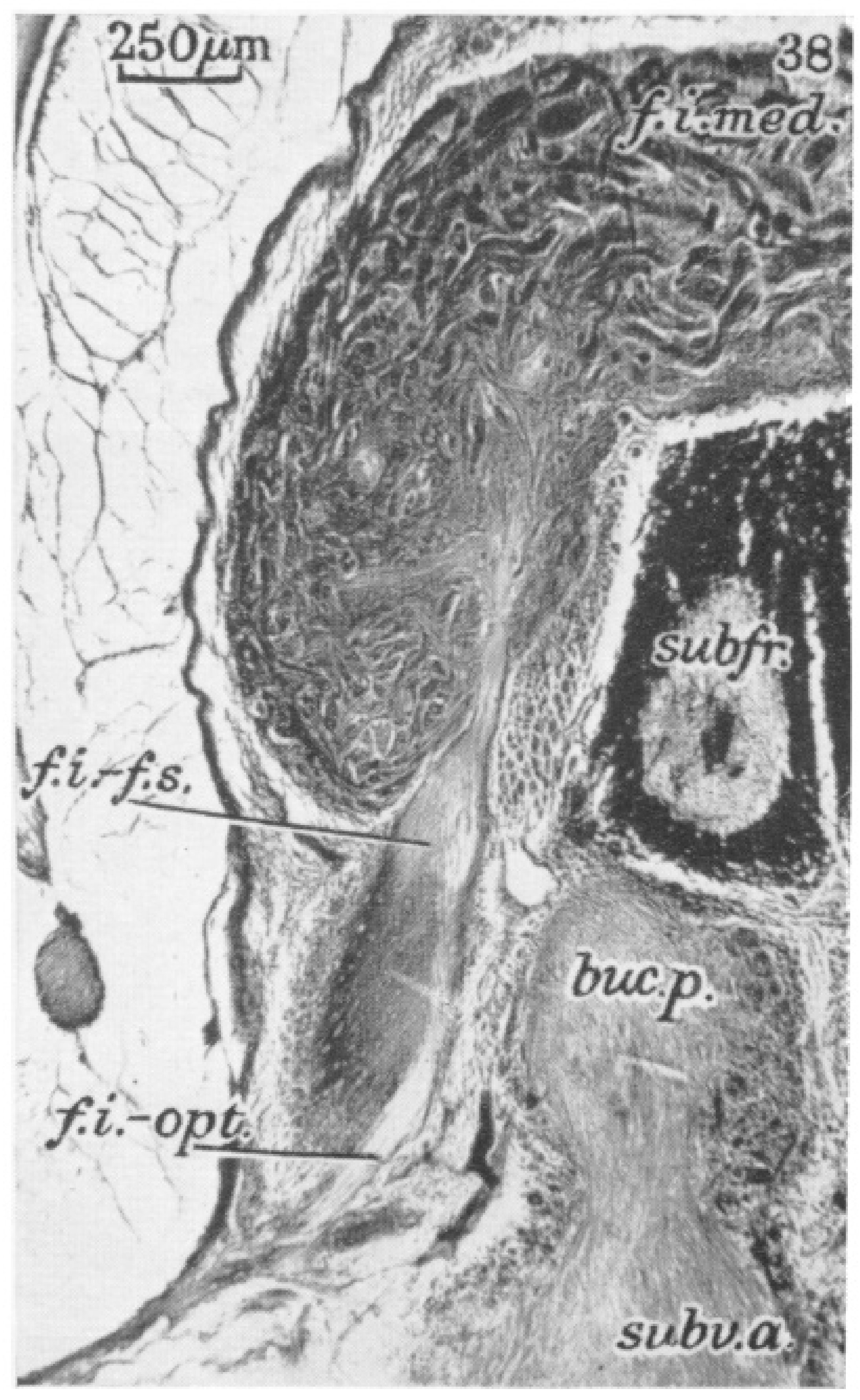

250μm
34
f.i.l.
f.i.-br.
cer.-br.

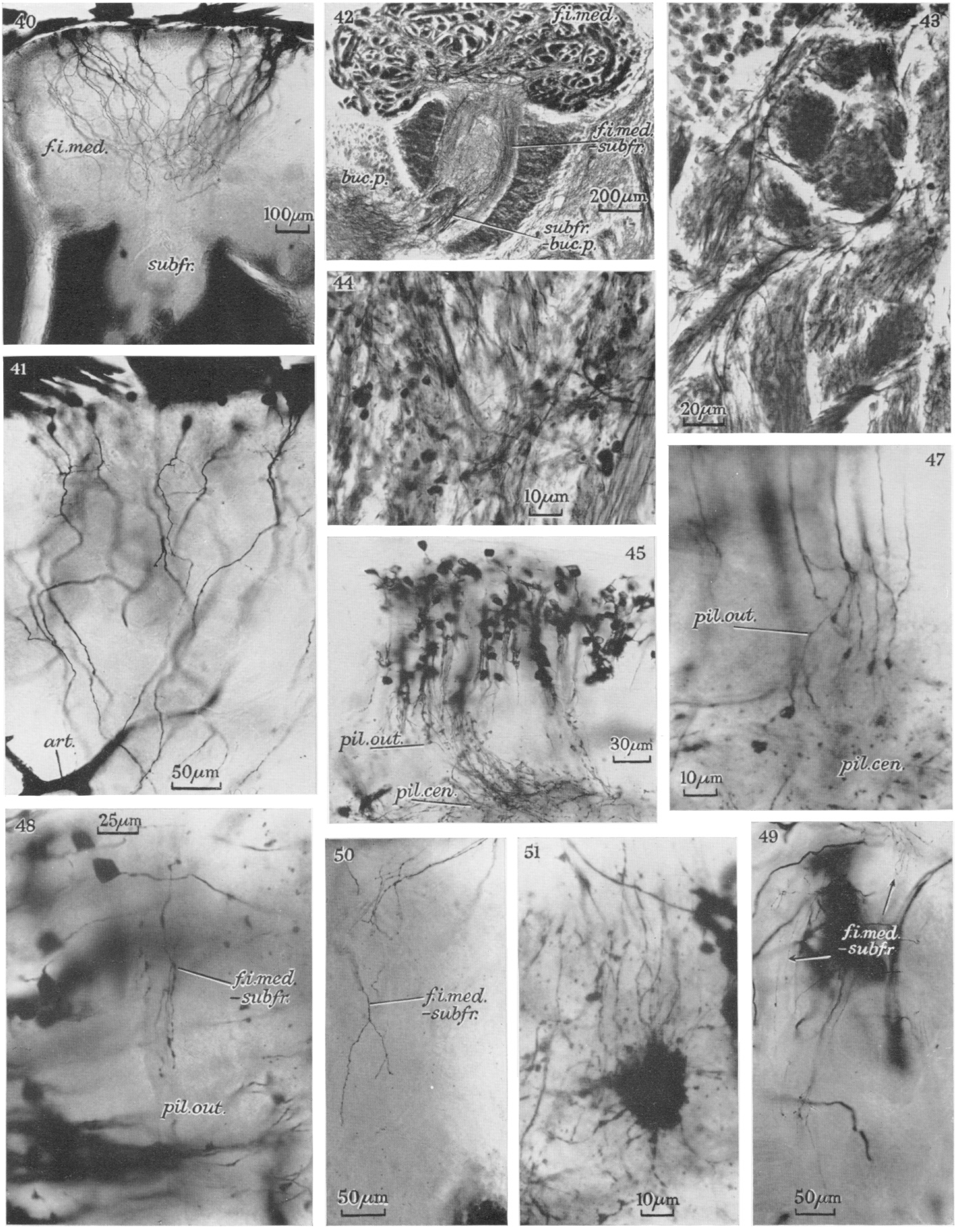

15μm
35


36
f.i.med.
200μm
f.s.l.
f.i.-f.s.
f.i.l.
buc.s.
f.i.-opt.
buc.p.

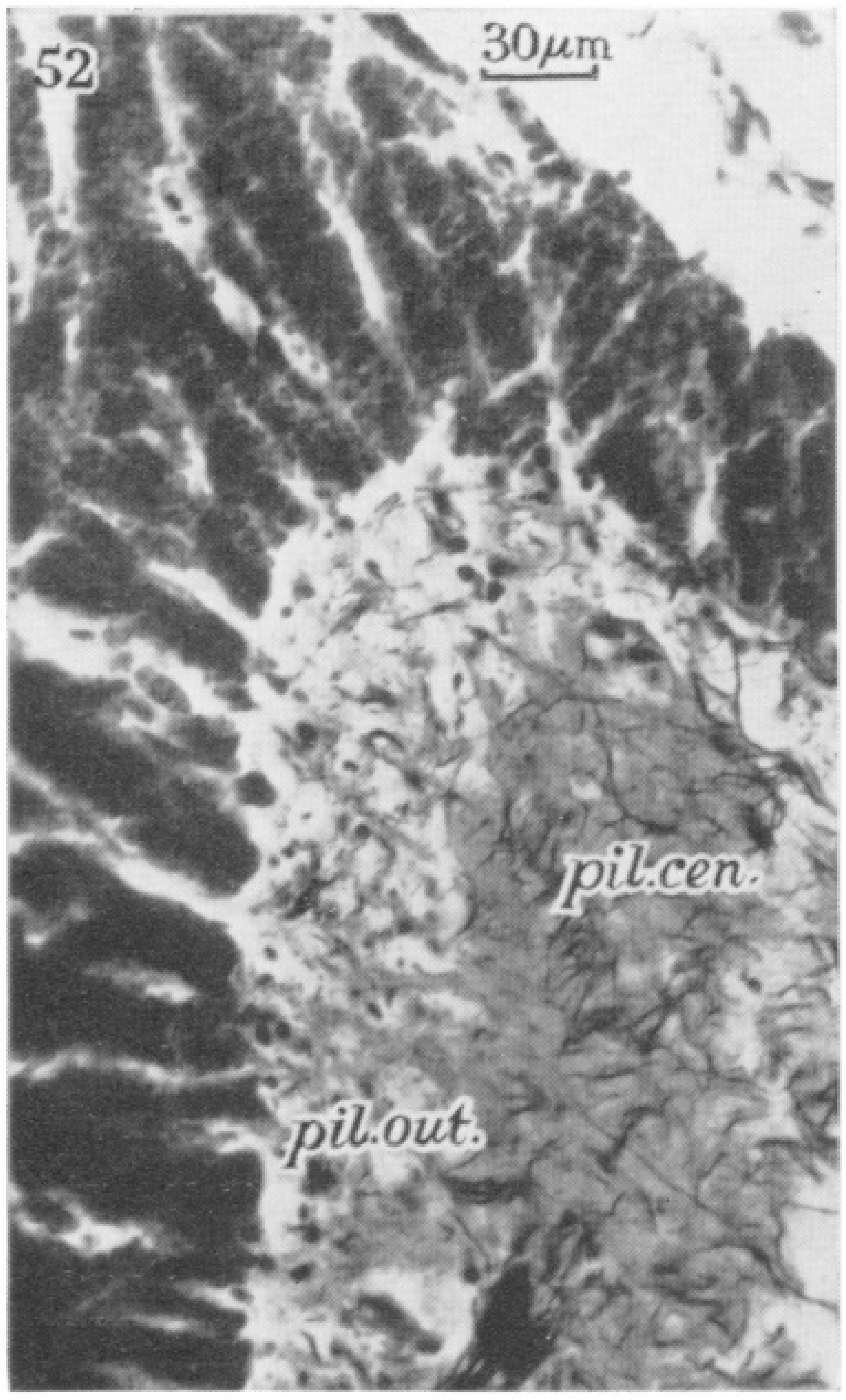

39
10μm

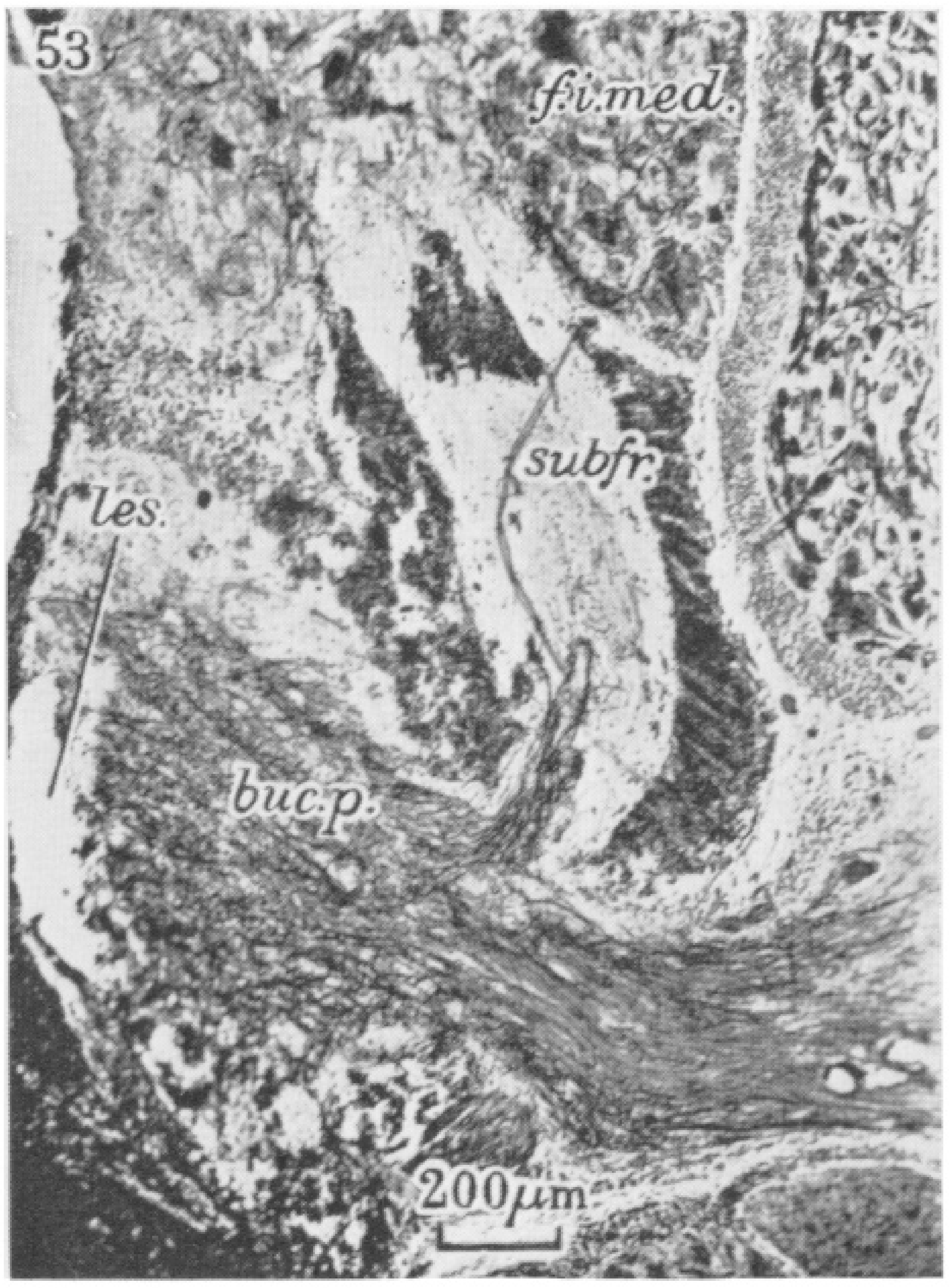

250μm
37
f.i.med.
f.i.l.
subfr.
f.s.l.
buc.p.
f.i.-opt.
tr.opt.
subv.a.

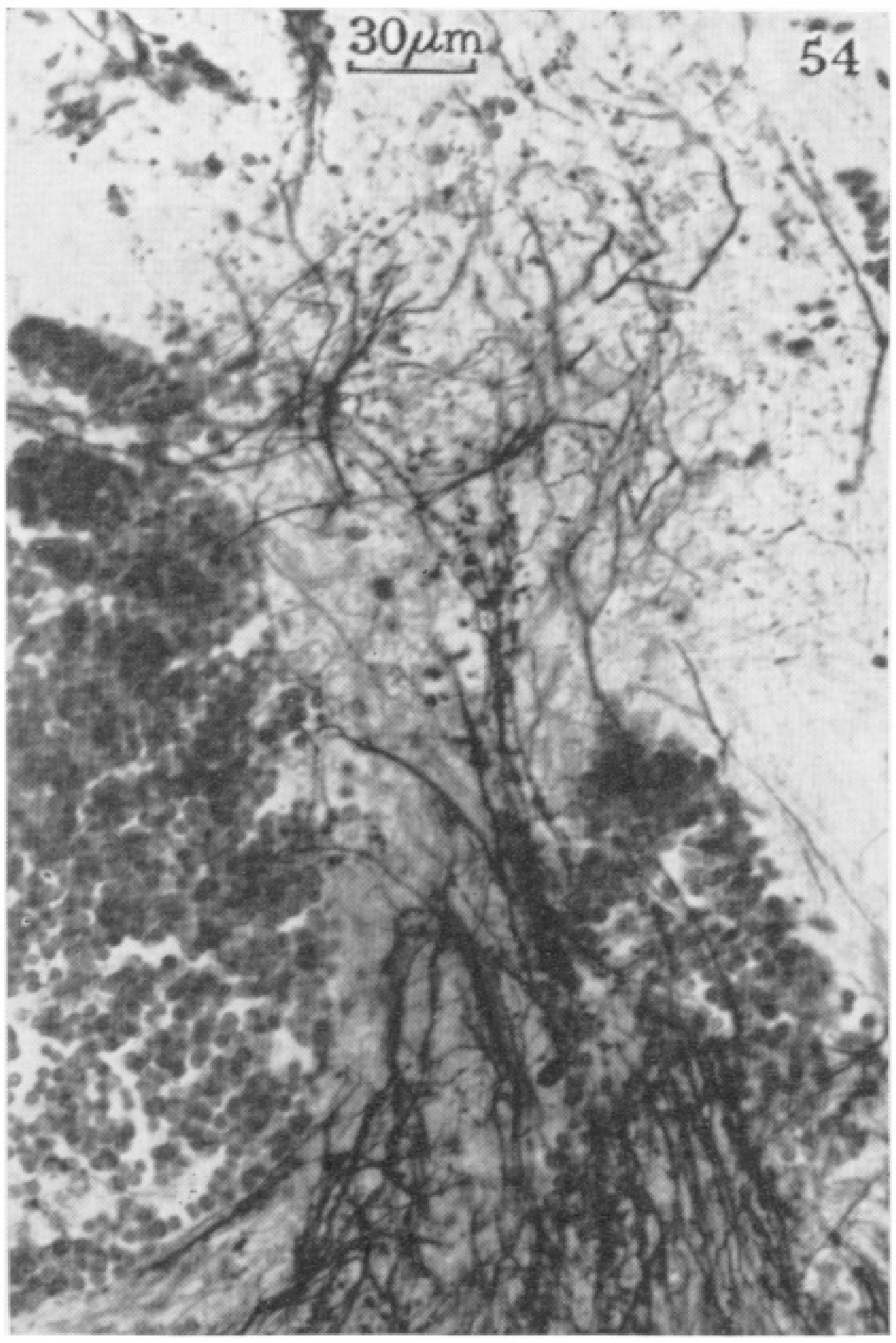

250μm
38
f.i.med.
subfr.
f.i.-f.s.
buc.p.
f.i.-opt.
subv.a.

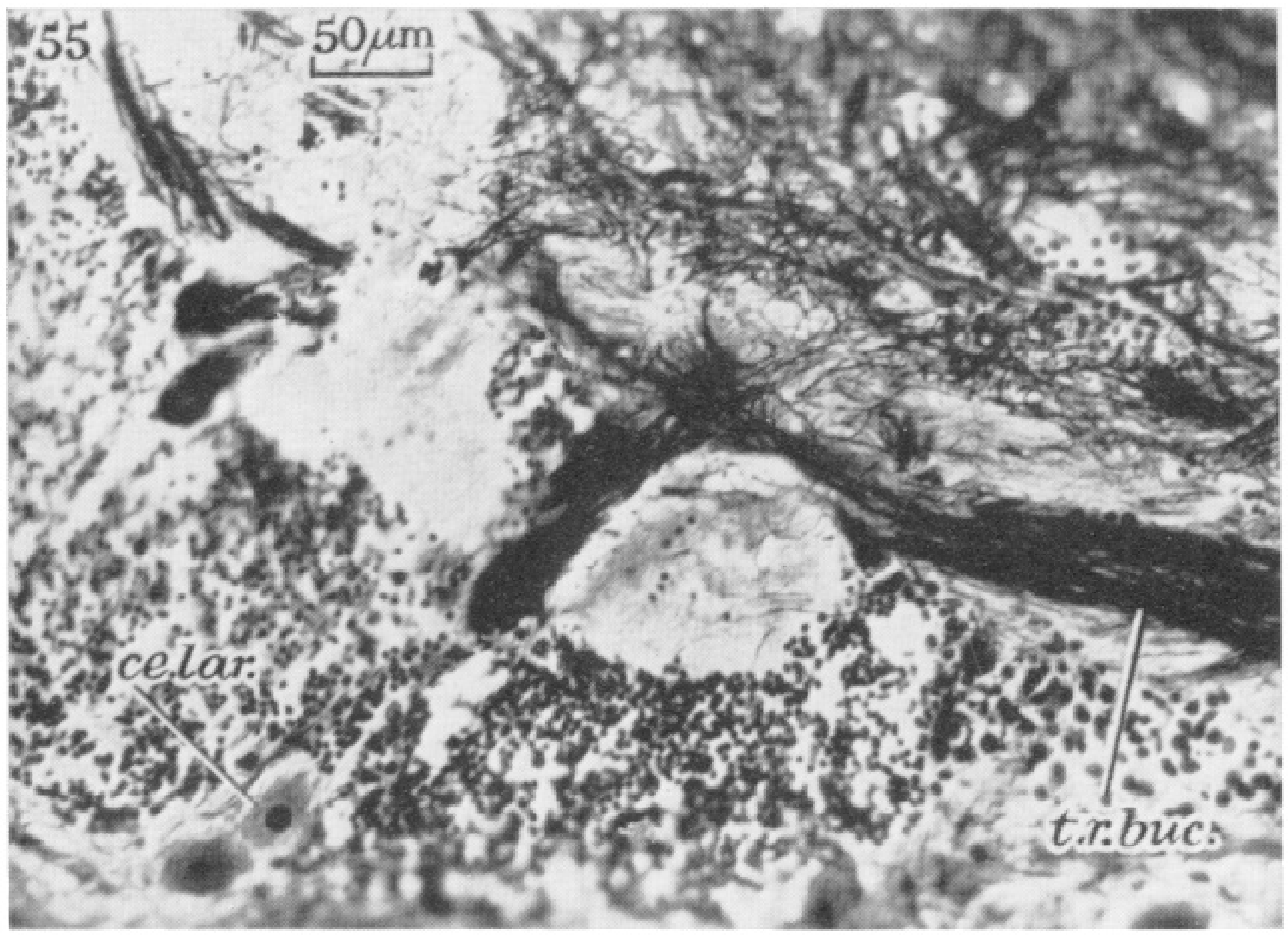


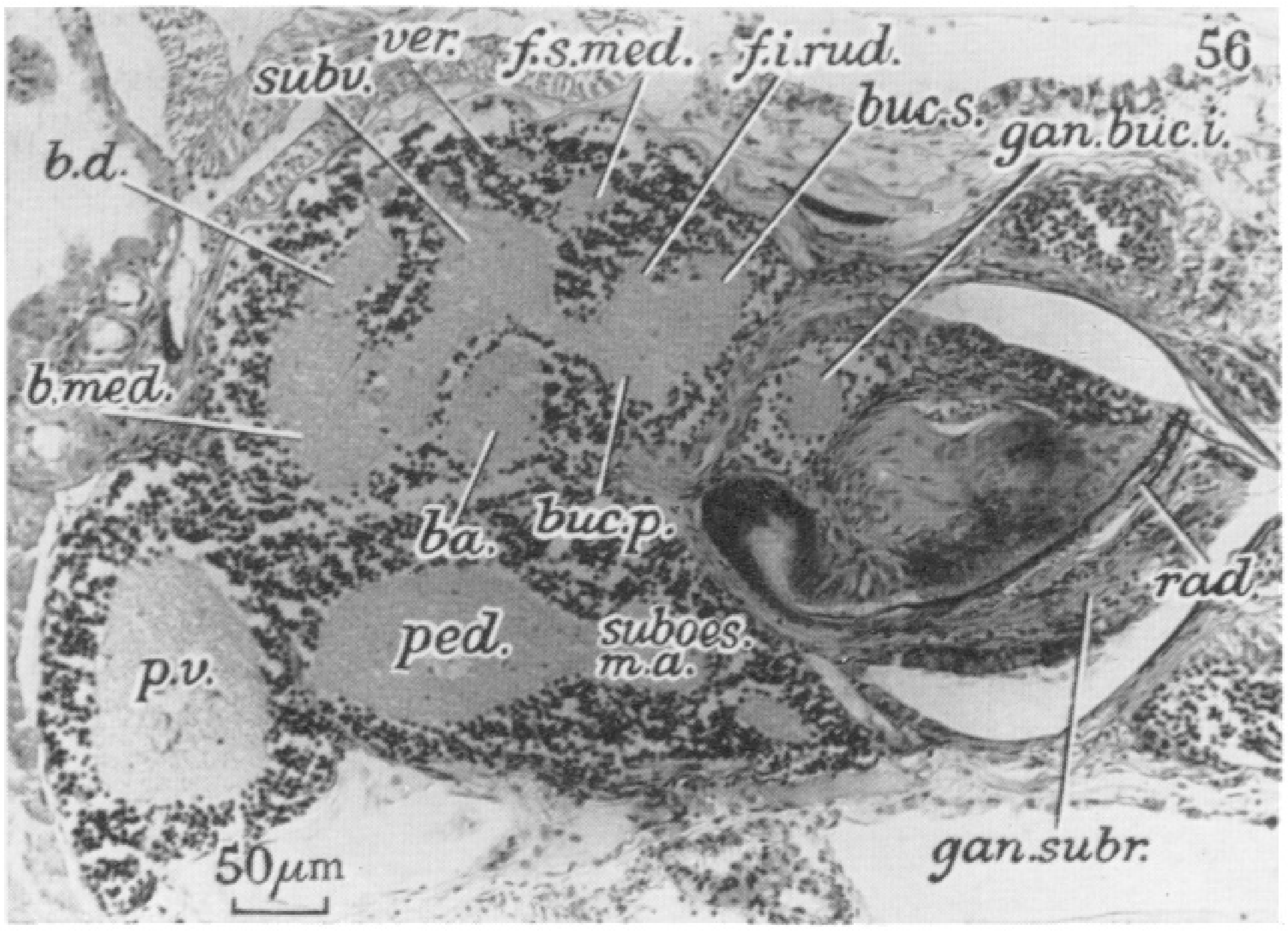
40
f.i.med.
100μm
subfr.
41
art.
50μm
42
f.i.med.
f.i.med.
-subfr.
buc.p.
200μm
subfr.
-buc.p.
43
20μm
44
10μm
45
pil.out.
30μm
pil.cen.
47
pil.out.
10μm
pil.cen.
48
25μm
f.i.med.
-subfr.
pil.out.
50
f.i.med.
-subfr.
50μm
51
10μm
49
f.i.med.
-subfr.
50μm

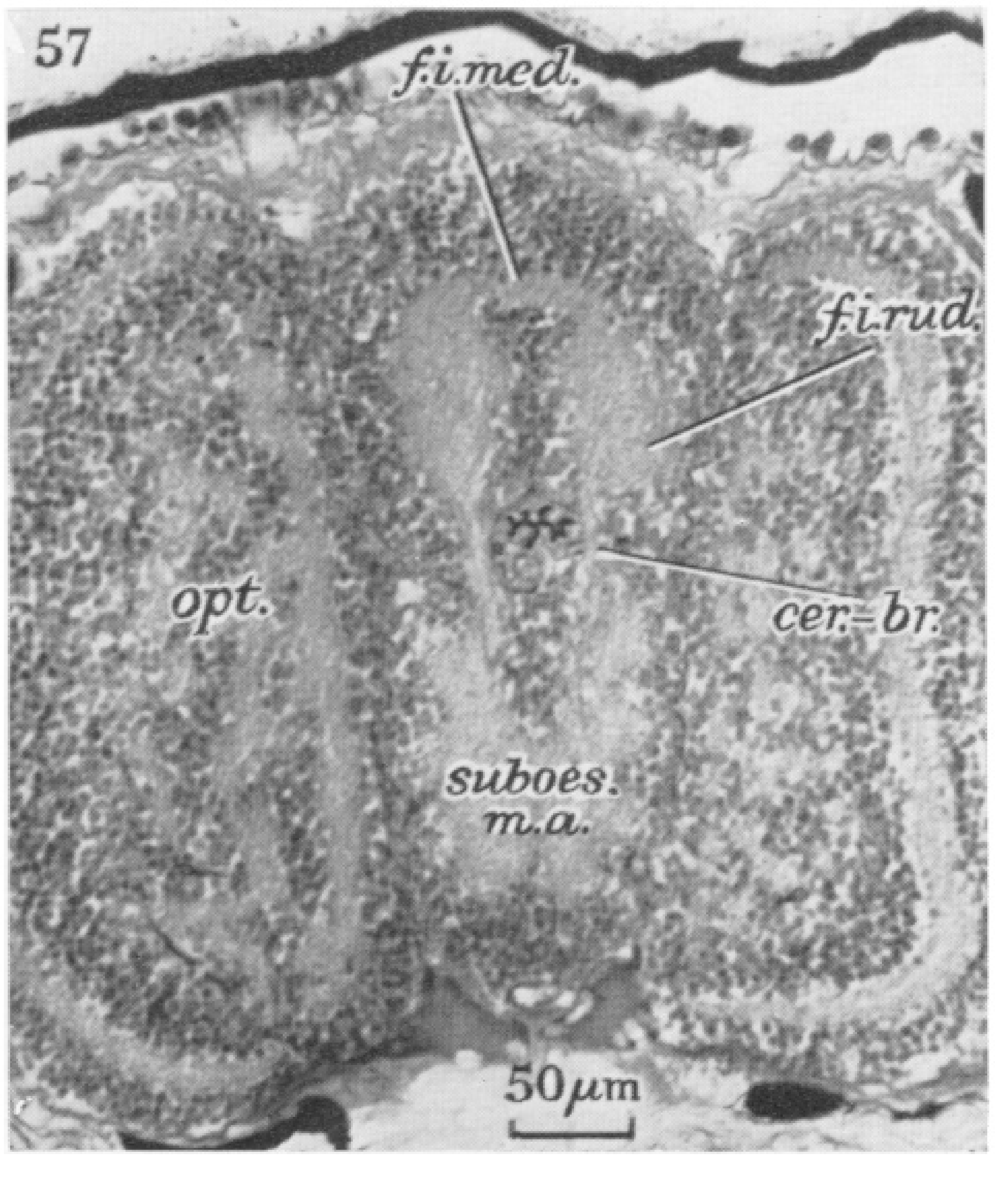

52
30μm
pil.cen.
pil.out.

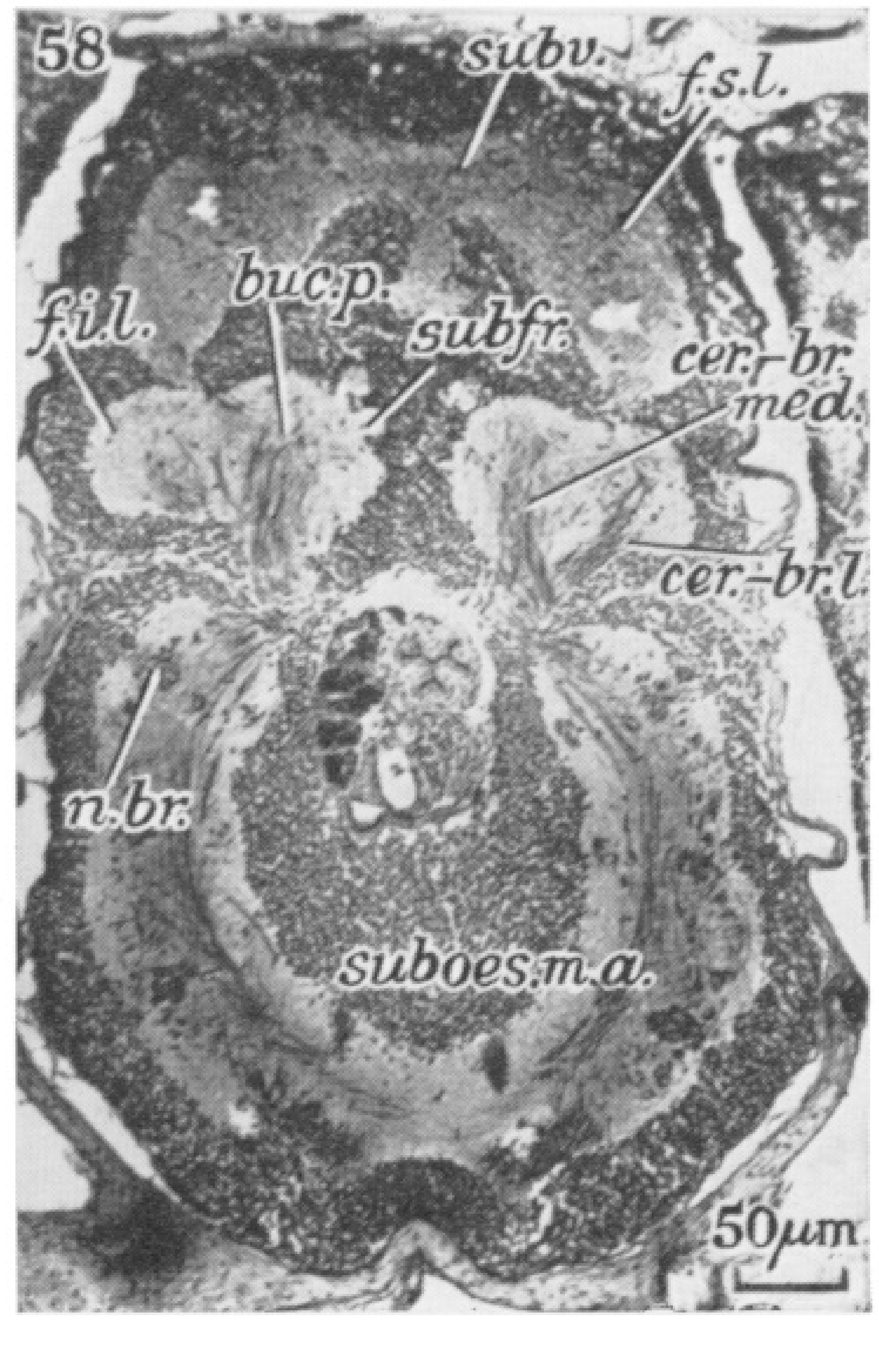

53
f.i.med.
subfr.
les.
buc.p.
200μm

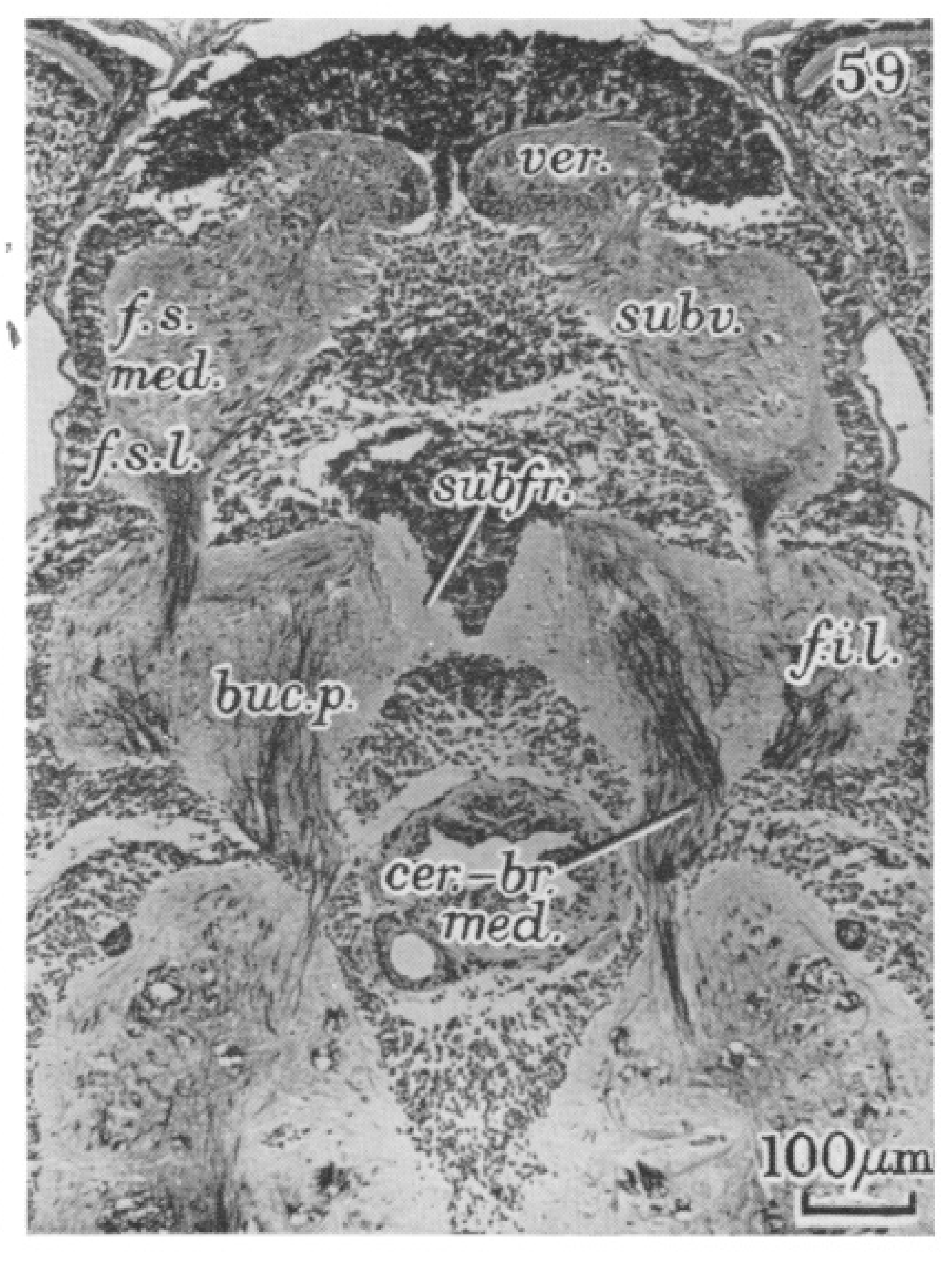

54
30μm


55
50μm
ce.lar.
t.r.buc.


56
subv.
ver.
f.s.med.
f.i.rud.
buc.s.
gan.buc.i.
b.d.
b.med.
ba.
buc.p.
rad.
p.v.
ped.
suboes.
m.a.
gan.subr.
50μm


57
f.i.med.
f.i.rud.
opt.
cer.-br.
suboes.
m.a.
50μm


58
subv.
f.s.l.
f.i.l.
buc.p.
subfr.
cer.-br.
med.
cer.-br.l.
n.br.
suboes.m.a.
50μm


59
ver.
f.s.
med.
subv.
f.s.l.
subfr.
f.i.l.
buc.p.
cer.-br.
med.
100μm