NEUROVENOUS TISSUES IN CEPHALOPODS

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(*Received* 7 *July* 1969)

[Plates 64 to 71]

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The juxta-ganglionic tissues of cephalopods consist of tubes containing columns of cells and nerve fibres. They arise in or near ganglia and pass to endings in the walls of veins or the organ of the anterior chamber of the eye. The latter is a system of vascular papillae presumably regulating the composition of the anterior chamber fluid. The strand of subpedunculate tissue, which joins the anterior chamber organ to the optic lobe, may provide a visual feedback for the regulation of intra-ocular pressure and the growth of the lens. The system is similar in those cephalopods whose anterior chamber is nearly closed (octopods, *Sepia* and *Loligo*) and in those where it is widely open to the sea, *Spirula* and the oegopsids. In the stalk-eyed cranchiid *Bathothauma* the subpedunculate strand accompanies the optic tract to the brain and then returns along the stalk to the (open) anterior chamber.

The sub-buccal tissue and neurovenous tissue of the vena cava resemble each other, and their fibres end on the walls of veins. They are well developed in *Octopus* and *Eledone* and especially so in the pelagic argonautids. They are less extensive in *Sepia* and *Loligo*.

It is suggested that all the juxta-ganglionic tissues may be concerned with the regulation of the quantity and composition of body fluids by some modification of more usual nervous activities. The granules they contain suggest neurosecretion, but they may regulate by the operation of ionic pumps.

1. Introduction

Alexandrowicz (1964) has recently called attention to a new member of the enigmatic tissues that connect the nervous system with the venous system in cephalopods. Although there are some differences among these tissues they seem to form a single set (figure 1). By looking at them as a group we may find some clues to the intriguing problem of their function.

They all consist of irregular strands of cells and nerve fibres, forming columns. The strands arise from the outer surfaces of central or peripheral ganglia. They end in relation to the lining of a cavity, such as a vein or the anterior chamber of the eye. The nerve fibres innervate no

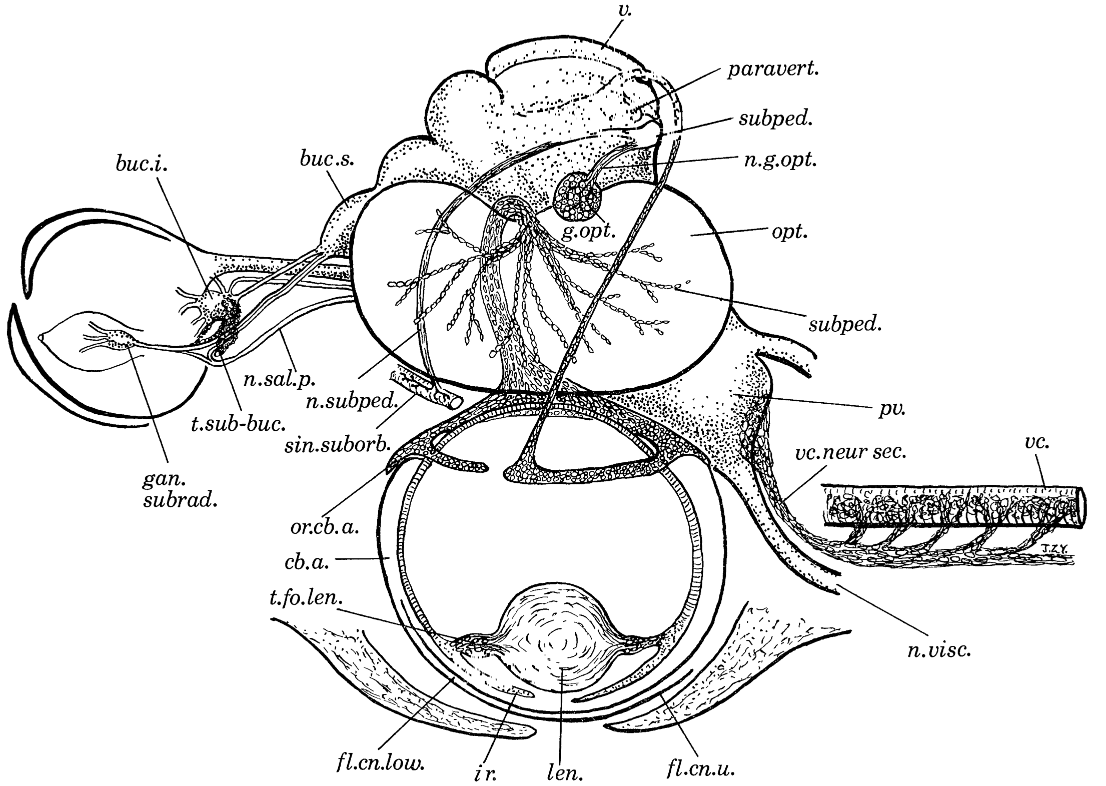


Figure 1. Diagram of the various neurovenous organs of an octopus. (All figures are of *Octopus vulgaris* Lamarck, unless otherwise stated.)

Description of plate 64

Figure 2. T.S. of the brain of a young animal, showing masses of subpedunculate tissue in the hila of the optic lobes (Bouin, haematoxylin).

Figure 3. L.S. showing strands of subpedunculate tissue (Cajal).

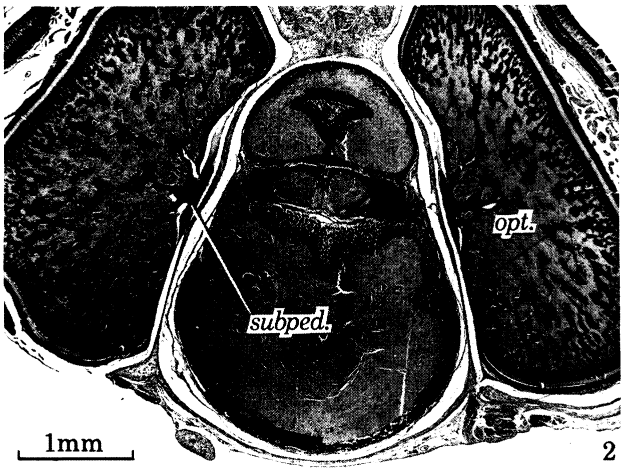
Figure 4. T.S. of a young animal showing the strand of subpedunculate tissue running down below the optic tract, spreading out beneath the orbit and coming into relation with the anterior chamber of the eye (Bouin, haematoxylin).

Figure 5. T.S. of the optic tract showing large venous spaces in the optic lobe, joining to form the optic lobe vein (Cajal).

Figure 6. *Argonauta argo* L. Sagittal section of orbit showing the orbital jelly containing the various venous channels and the subpedunculate strands (not labelled) (Cajal).

Figure 8. T.S. to show pharyngo-ophthalmic veins, subpedunculate nerves and intra-cranial muscles (Cajal).

Figure 9. T.S. of the ending of the subpedunculate nerve in relation to the opening of the pharyngo-ophthalmic vein to the suborbital sinus (Cajal).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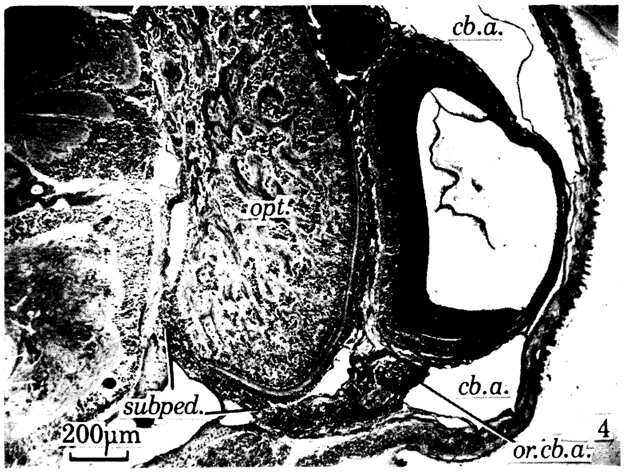
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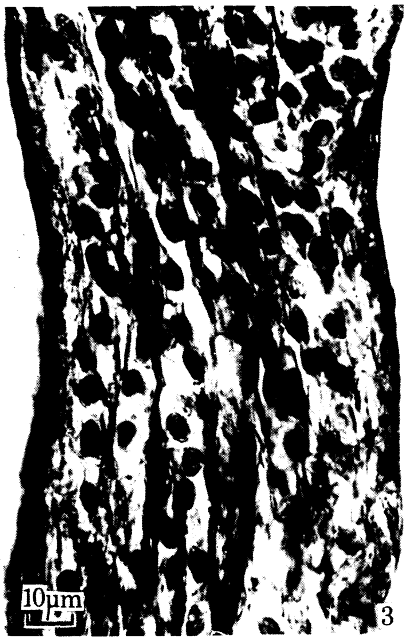
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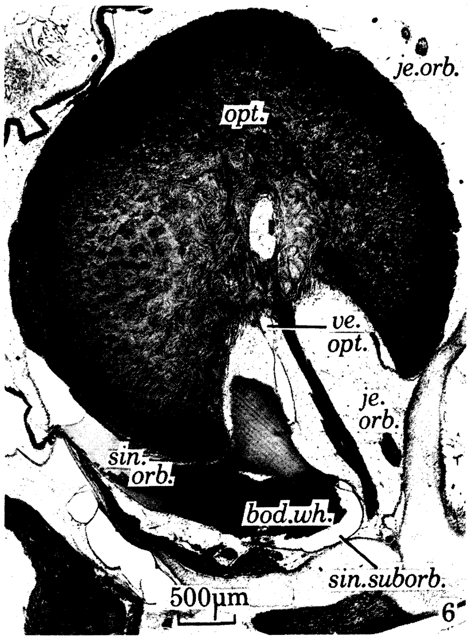
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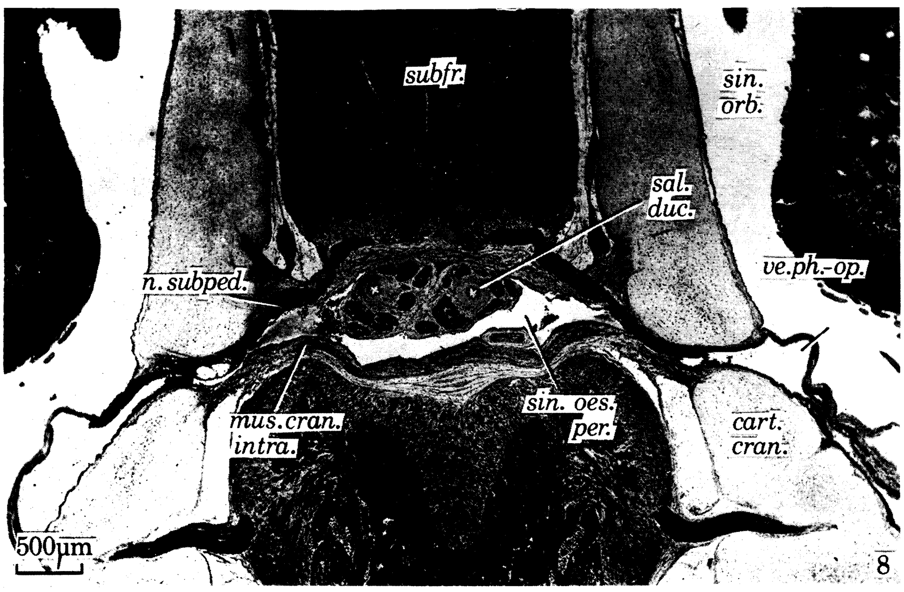
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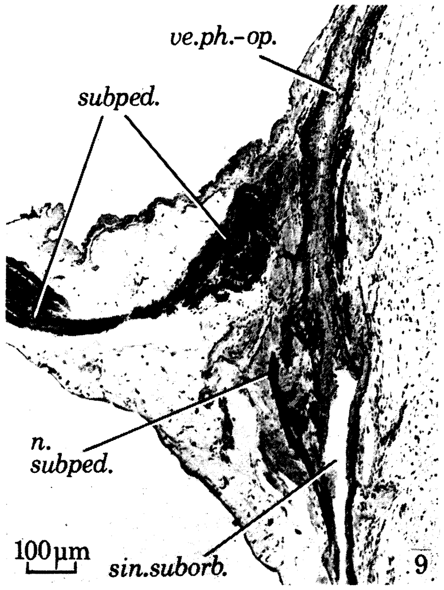
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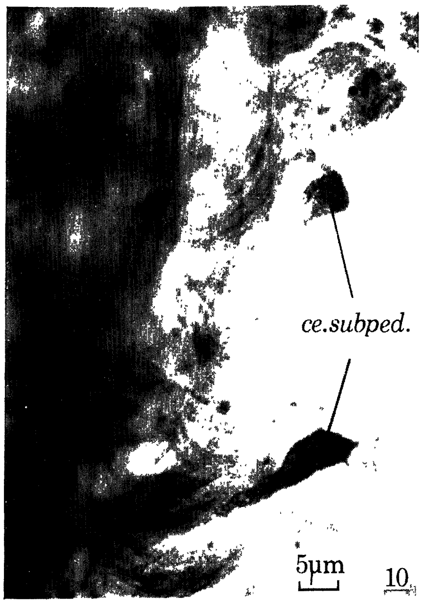
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muscles and although it cannot be excluded that they include afferents, it seems likely that they are secretors, but whether for chemical signalling, for regulating the composition of a fluid or for some other function is uncertain.

2. Methods

The neurovenous tissues have been studied in numerous series of paraffin and celloidin sections, mainly after fixation in formalin and staining with a modified Cajal method (Stephens 1970). The main part of the study has been made with *Octopus vulgaris* Lamarck and *Eledone moschata* Lamarck and *E. cirrosa* Lamarck, with some investigation of other species.

3. Subpedunculate tissue

This is a conspicuous system associated with the optic lobe and anterior chamber of the eye (Thore 1936; Boycott & Young 1956). Strands of highly basophil nuclei, in tubes lying in rows, arise among the tissues at the centre of the optic lobe (figure 2, plate 64) form a broad cord beneath the optic tract and because of this position the organ was called 'corpus subpedunculatum' by Thore (1936) who discovered it. It swells out to make a considerable mass of tissue in the floor of the orbit (figure 4, plate 64). The regular arrangement of the nuclei in rows is here lost and the tubes become irregular and radiate out beneath the orbital sinus.

After passing beneath the orbit the subpedunculate tissue reaches the back of the eye, and joins the anterior chamber organ (p. 314).

4. The venous drainage of the nervous system

The position and significance of the subpedunculate tissue can only be understood in relation to the special arrangements by which the venous system of the brain and optic lobes is protected from pressure changes in the main haemocoelomic spaces (Young 1970). Where the veins draining the nervous tissue open into the main haemocoelomic spaces they are protected by sphincter-like valves. The drainage of the optic lobes occurs partly outwards over the surface into a diffuse orbital sinus, partly inwards into a set of optic lobe veins, which join forming a single vein (figure 5, plate 64). This leaves the lobe medially and runs downwards to open into a suborbital sinus, which opens via an ophthalmic vein into the vena cava. The subpedunculate tissue lies in the medial wall of the optic lobe vein (figure 5). The orbital sinus also opens into the suborbital sinus and here there is a complicated system of valves which control the outlets of the white bodies (Boycott & Young 1956). These are very thin-walled sacks of haemopoietic tissue, lying in the orbit, but communicating only with the suborbital sinus.

These arrangements are especially easy to study in *Argonauta argo* L. (figures 6, plate 64, and 7). In this animal it can be seen that the 'orbit' is not a simple venous sinus, as it appears at first sight in *Octopus*, but is largely filled with jelly, similar to that surrounding the brain within the cranium (figure 6). Embedded in this jelly are three sets of channels: (1) the orbital sinus,

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Description of plate 65

Figures 10 to 12. Cells of the subpedunculate tissue (Cajal).

Figure 13. Electronmicrograph of T.S. subpedunculate tissue. Fixed OsO_4. (Preparation by Professor E. G. Gray.) The arrows show fibres that are presumably processes of the subpedunculate cells.

into which vessels drain from the back of the eye and the whole surface of the optic lobe, (2) the optic lobe vein, draining the centre of the lobe by the system of branching channels shown in figure 5, (3) the white bodies. All three sets of spaces open into the suborbital sinus, close together, at openings guarded by complicated sphincters.

The arrangement in *Argonauta* is shown in figure 7. This diagram is a new version of the one shown by Boycott & Young (1956). At that time it was not realized that the retina and optic lobes drain into an orbital sinus and that the white bodies are distinct and open separately into the suborbital sinus. The two sets of spaces and the optic lobe vein can be seen in figure 6. The condition in *Octopus* is essentially similar but much less jelly is present, so that the orbital sinus

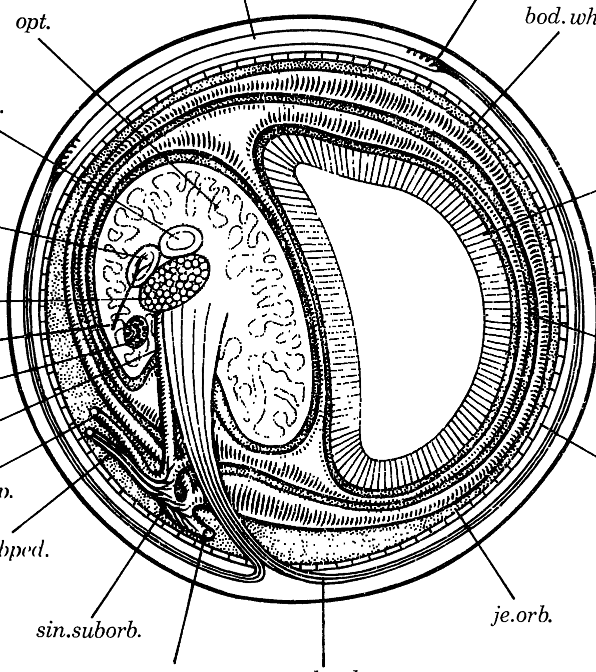


FIGURE 7. Diagram of the relations of the various venous spaces in the orbit as seen in *Argonauta argo* L.

DESCRIPTION OF PLATE 66

FIGURE 14. T.S. Subpedunculate strand after injection of Indian ink in sea water (formalin, haematoxylin and eosin).

FIGURE 15. Detail of specimen injected as figure 14.

FIGURE 16. Terminal portion of injected subpedunculate tissue as figure 14.

FIGURE 17. *Argonauta argo* L. Subpedunculate tissue, including venule (Cajal).

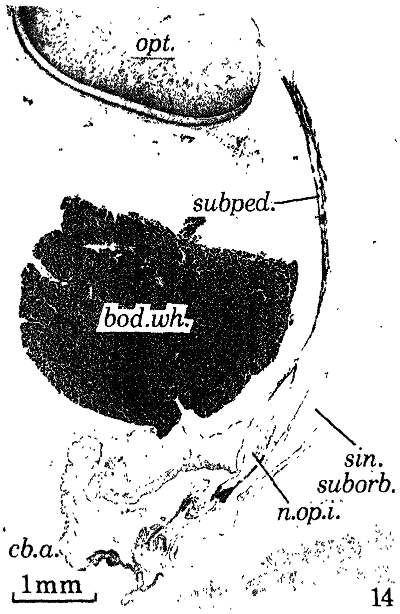
FIGURE 18. T.S. Eye to show upper and lower corneal folds, allowing a potential passage from the sea to the anterior chamber (Bouin, haematoxylin and eosin).

FIGURE 19. *Argonauta argo* L. T.S. Eye to show corneal folds, anterior chamber and its organ (Cajal).

FIGURE 20. T.S. to show strand of subpedunculate tissue extending from the optic lobe to the anterior chamber organ (formalin, haematoxylin and eosin).

FIGURE 21. Sagittal section of back of anterior chamber of the eye of a young animal, showing the mass of subpedunculate tissue beneath the anterior chamber organ (Bouin, haematoxylin and eosin).

FIGURES 22 to 24. T.S. anterior chamber organ (formalin, haematoxylin and eosin).



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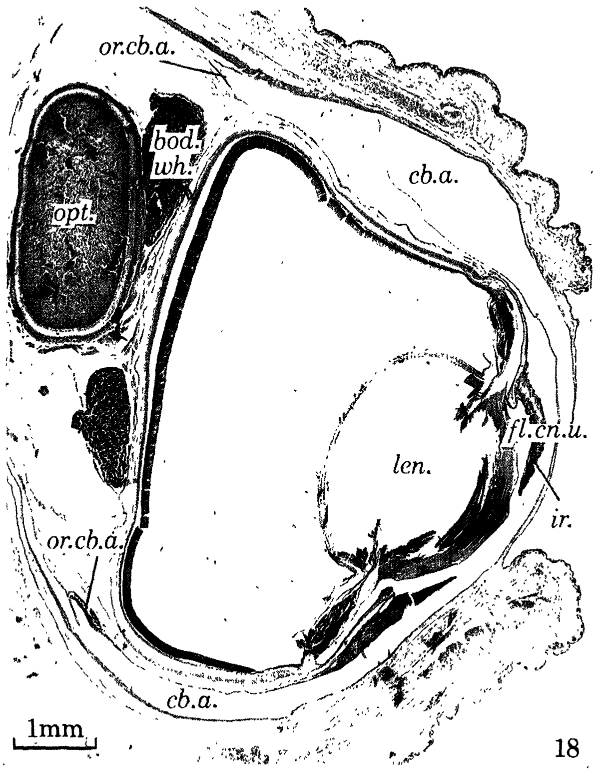

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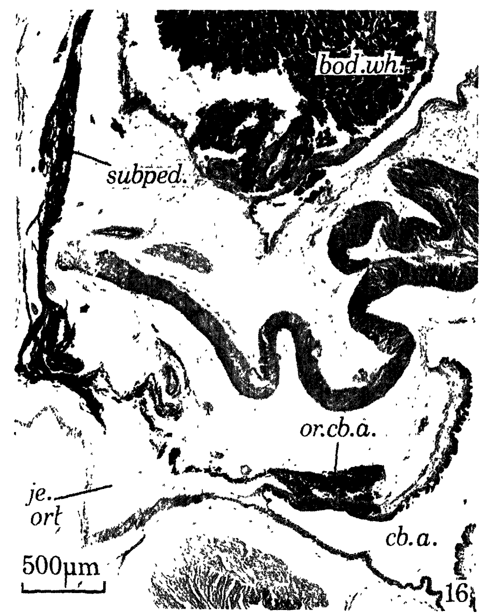

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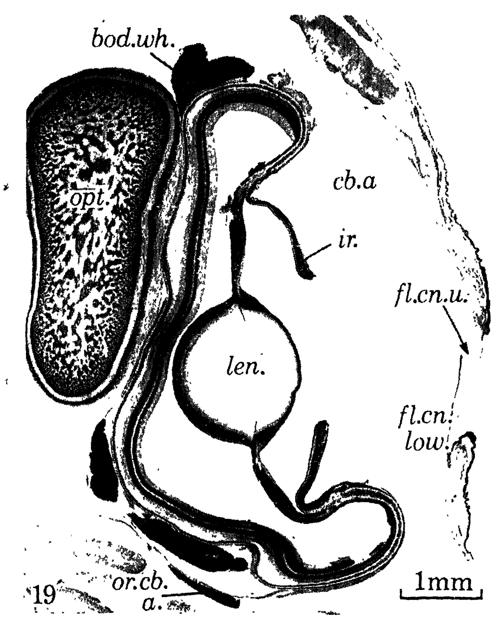

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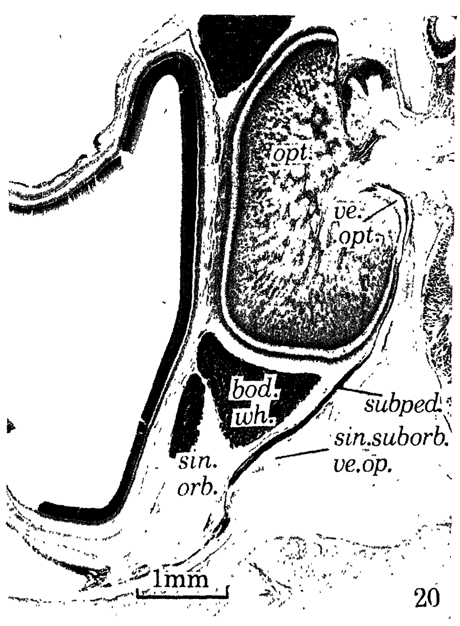

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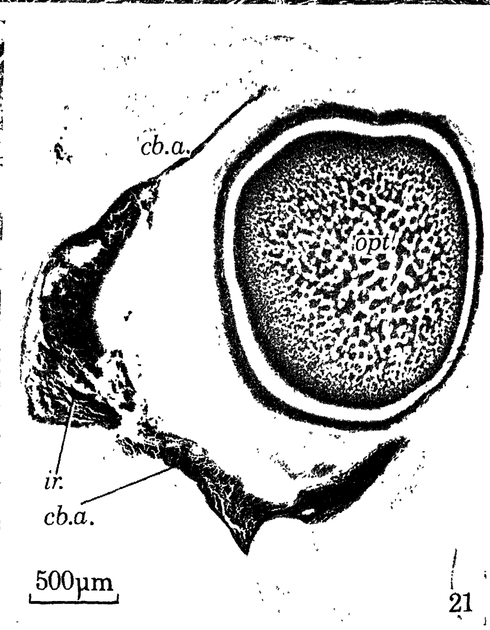

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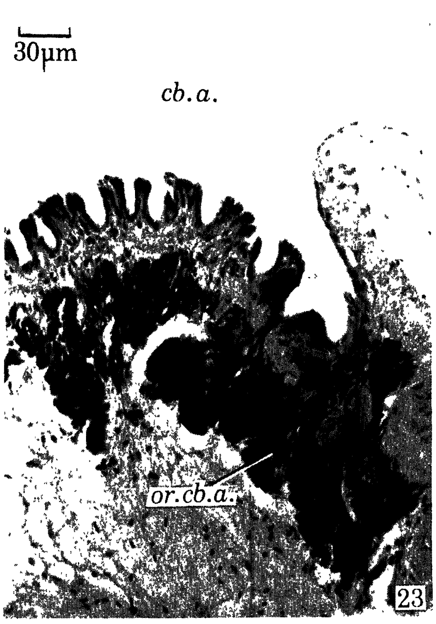
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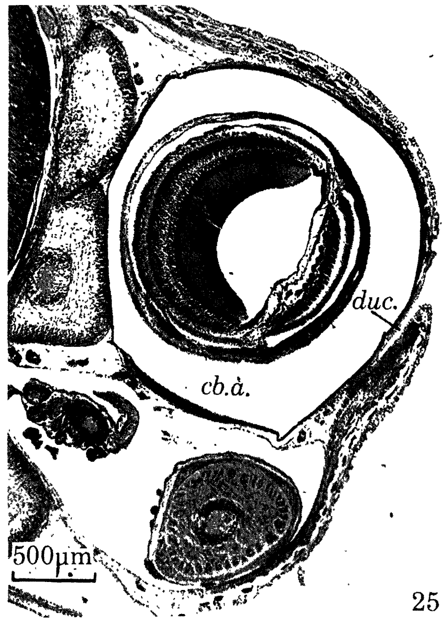
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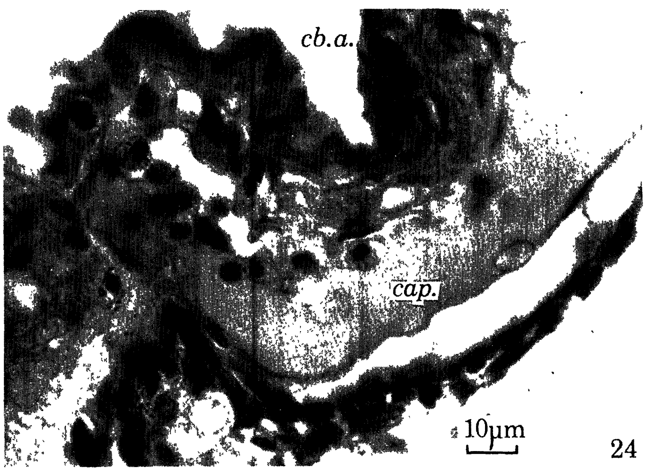
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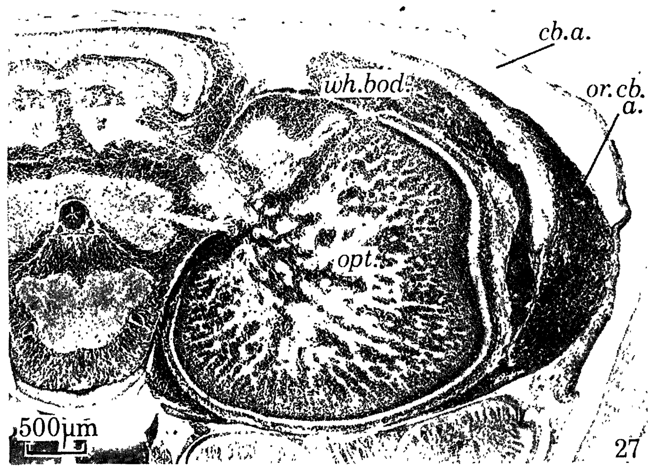
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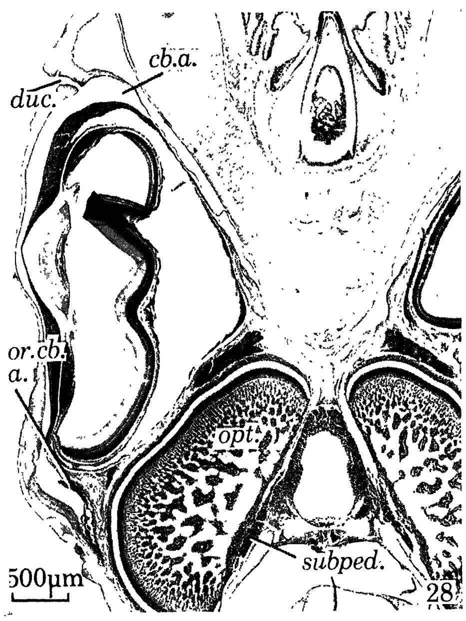
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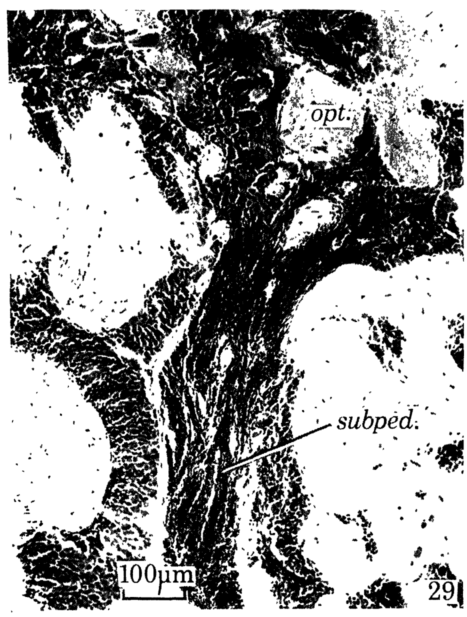
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and white bodies seem to occupy almost the whole space. The 'jelly-space' can however be found beneath the surface of the anterior chamber and separately injected (Young 1970).

The sphincters of the venous channels of the orbit are innervated by a very curious nerve, called the subpedunculate nerve by Thore (1939). It remains uncertain whether there is more than a relationship of position between the subpedunculate nerve and subpedunculate tissue (see below). The nerve is found only in octopods. It arises in the lateral postero-dorsal part of the dorsal basal lobe, immediately below the back of the vertical lobe (figure 1). The nerve to the optic gland also arises in this region and these are the only two peripheral nerves that reach directly to the supraoesophageal lobes (other than those from the lips). The optic gland is concerned with the regulation of the maturation of the gonads (Boycott & Young 1956; Wells & Wells 1959). The only obvious connexion this has with venous drainage of the optic lobe is that light is also important in the control of the development of the gonads (Richard 1967).

The subpedunculate nerves run forward and downward through the supraoesophageal mass to pass in front of the anterior basal lobe and turn laterally, leaving the cranium with the pharyngo-ophthalmic vein (figure 8, plate 64). This large vessel runs between the peri-oesophageal sinus and the suborbital sinus. It receives the veins of the supra- and suboesophageal lobes (Young 1970). These are guarded by sphincters, which probably receive nerve fibres from the subpedunculate nerve. The nerve probably also innervates the large intracranial muscle that joins the cartilage of the two sides at this level (figure 8). The function of this and the other intracranial muscles is not known but they may come into play in regulation of intracranial pressure, perhaps during the passage of food through the oesophagus. The main part of the nerve runs with the pharyngo-ophthalmic vein. It spreads out as an elaborate terminal plexus in the muscular tissue around the common meeting place of the orbital sinus, optic lobe vein, white bodies, pharyngo-ophthalmic vein and suborbital sinus. This is probably the place at which the venous drainage of the whole central nervous system is regulated. Degeneration experiments show that the subpedunculate nerve contains both afferent and efferent fibres (Boycott & Young 1956). The motor fibres end among the muscle fibres of the sphincters and the afferents probably form the plexus in the thick wall surrounding the lumen of the vein (figure 9, plate 64). As this figure shows, the subpedunculate tissue lies very close to this sphincter system, but it is not clear whether it has any functional relation to it.

5. Structure of the subpedunculate tissue

The tubes are probably formed of collagen and some of the nuclei of the tissue are fibroblasts, flattened along the walls of the tubes. The characteristic nuclei of the tissue however are spherical and densely basophilic.

Description of plate 67

Figures 23, 24. T.S. anterior chamber organ (formalin, haematoxylin and eosin).

Figure 25. *Sepia officinalis* L. T.S. young animal to show external opening of channel from the sea to the anterior chamber (Bouin, Masson).

Figure 26. *Sepia officinalis* L. T.S. duct near internal opening of the channel seen in figure 25.

Figure 27. *Sepia officinalis* L. T.S. showing subpedunculate tissue forming a large mass at the back of the anterior chamber (as figure 25).

Figure 28. *Loligo peallii* Lesueur. H.S. young animal showing channel from the outside to the anterior chamber. Also anterior chamber organ (Bouin, haematoxylin and eosin).

Figure 29. *Loligo peallii* Lesueur. Origin of subpedunculate tissue in optic lobe (as figure 28).

The shape of the cells associated with these nuclei has not been fully determined. In their usual position in the tubes their cytoplasm does not show with silver stains. However, at a point immediately below the optic tract the strand of tissue turns sharply ventrally. Here the contents sometimes stain deeply and with certain planes of section the tubes appear to be open as if the cells and fibres within them were emptying into the orbital sinus. This is presumably an artefact of sectioning but it enables us to see that the contents of the tubes are fibres that are sometimes argentophilic and resemble nerve fibres. Moreover, the cells can sometimes be seen to have a fibre attached (figures 11 to 13, plate 65). The interpretation of these tubes is difficult. The cells where they originate in the optic lobes are apparently elongated and fusiform (figure 32, plate 68). One interpretation is that the tubes contain rows of cells moving outwards from the optic lobes (or, of course, it might be inwards). Electronmicrographs prepared by Professor E. G. Gray confirm that the cells carry processes that extend along the strand (arrows in figure 13). Each bundle of subpedunculate cells is enclosed in a sheath containing several layers of cells resembling the Schwann cells of the peripheral nerves. Outside these again are intercellular channels and collagen. The cytoplasm of the subpedunculate cells themselves resembles that of immature nerve cells, with many free ribosomes and some tubules and filaments.

6. Injection of channels in the subpedunculate strands

A suspension of Indian ink in sea water injected into the strand in the floor of the orbit runs up to the optic lobe and down nearly to the anterior chamber (figure 14, plate 66). Within the main strand the injected material runs in channels between the tubes that contain nuclei, rather than within them (figure 15, plate 66). Towards the periphery it does not reach to the final ramifications of the subpedunculate tissue in the anterior chamber organ (figures 14 and 16, plate 66). This does not of course prove that the channels do not reach them, only that they were not filled at the injection pressures used. The channels within the main strands are seen to be constricted at intervals (in *Argonauta*) as if by contraction of their lining cells (figure 17).

7. Anterior chamber organ

The anterior chamber of the eye of octopods is separated from the sea by transparent overlapping upper and lower 'corneal flaps'. These are not fused (figures 18 and 19, plate 66) and if the pressure within was lowered sea water could enter. Nevertheless, the anterior chamber fluid is regulated to a composition distinct from that of sea water (Robertson 1953; Amoore, Rogers & Young 1959). The anterior chamber organ is a ring of specialized epithelium of the back of the chamber (figures 20 and 21, plate 66). Immediately behind it lies a corresponding

Description of plate 68

Figure 30. *Loligo peallii* Lesueur. T.S. of a young animal showing mass of subpedunculate tissue at the back of the anterior chamber (Bouin, haematoxylin and eosin).

Figure 31. *Loligo peallii* Lesueur. T.S. optic lobe of a young individual, showing strands of subpedunculate tissue (Bouin, haematoxylin and eosin).

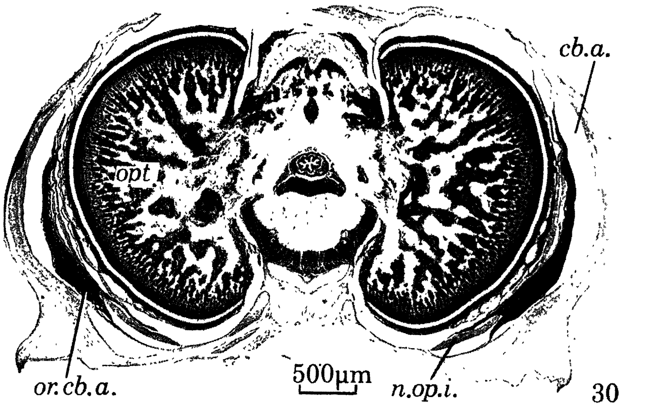
Figure 32. Same as figure 31, showing strands reaching nearly to the surface of the lobe.

Figure 33. *Spirula spirula* (L.) T.S. eye, showing anterior chamber widely open to the sea (Cajal).

Figure 34. *Spirula spirula* (L.) Anterior chamber organ (Cajal).

Figure 35. *Bathothauma lyromma* Chun. T.S. eye showing open anterior chamber and its organ (Cajal).

Figures 36 to 38. *Bathothauma lyromma* Chun. T.S. eye-stalk at various levels to show the course of the subpedunculate strand (Cajal).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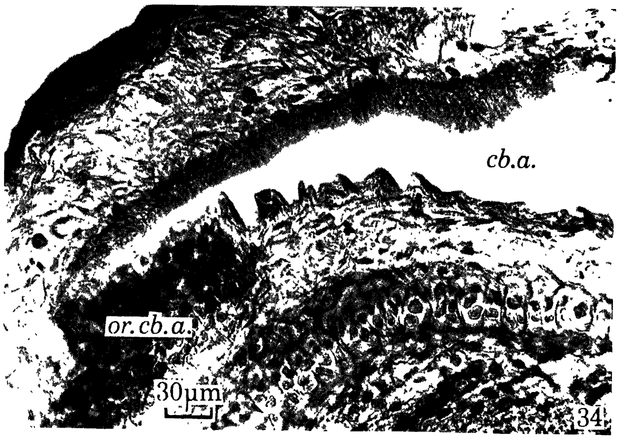
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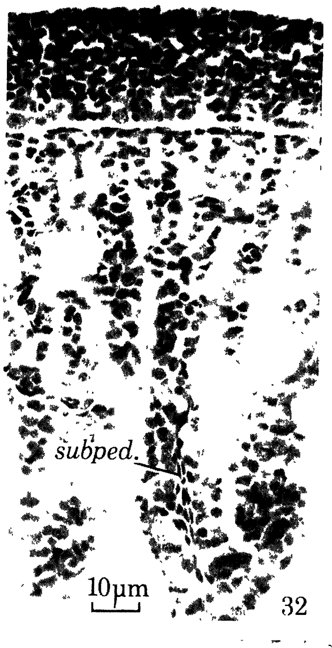
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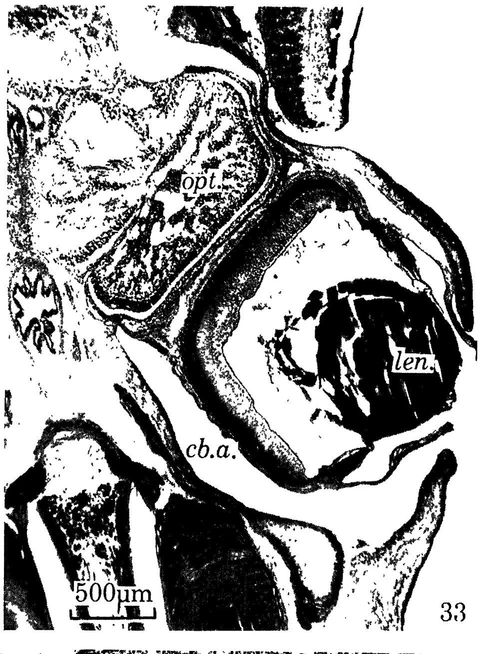
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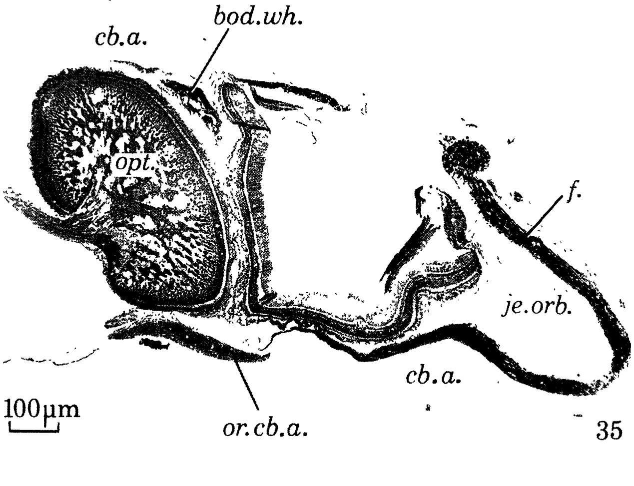
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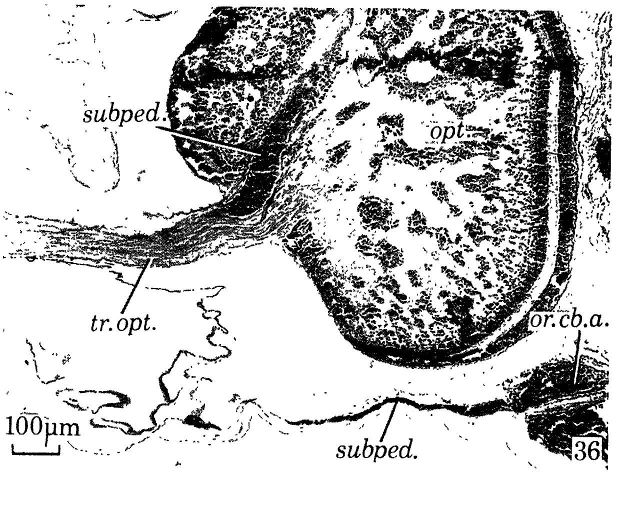
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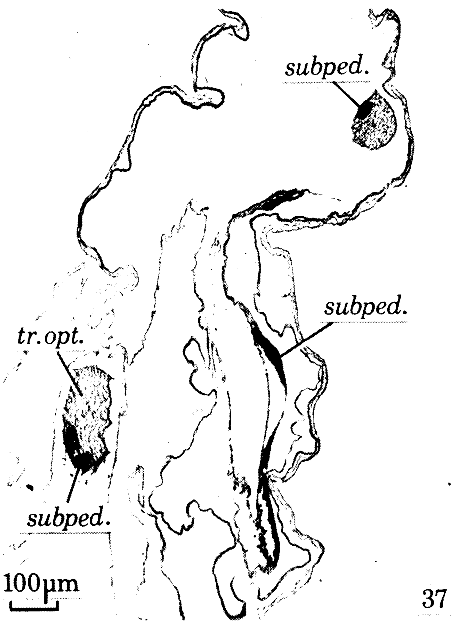
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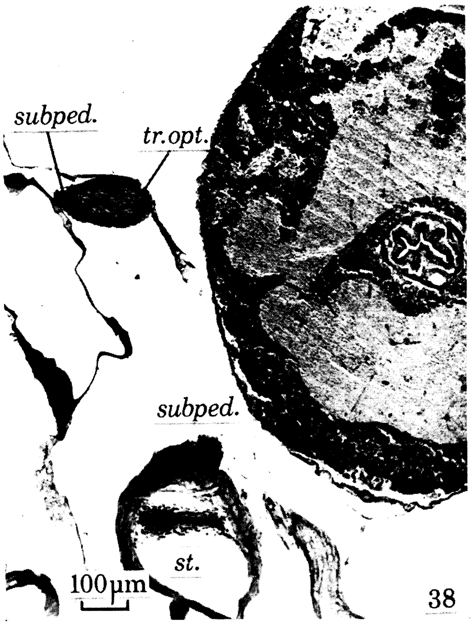
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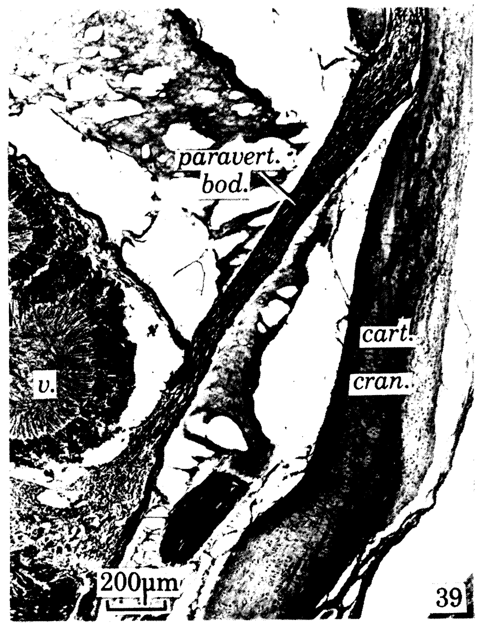
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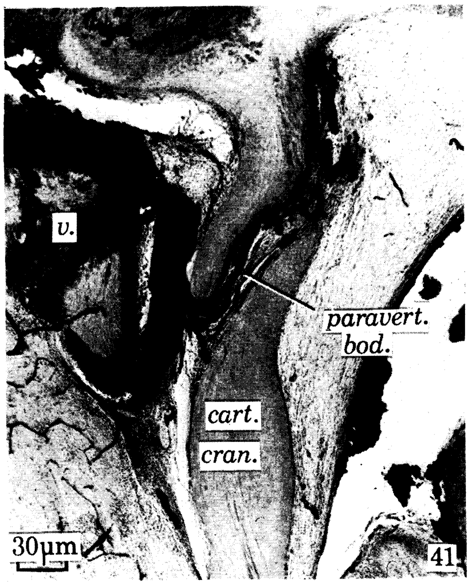
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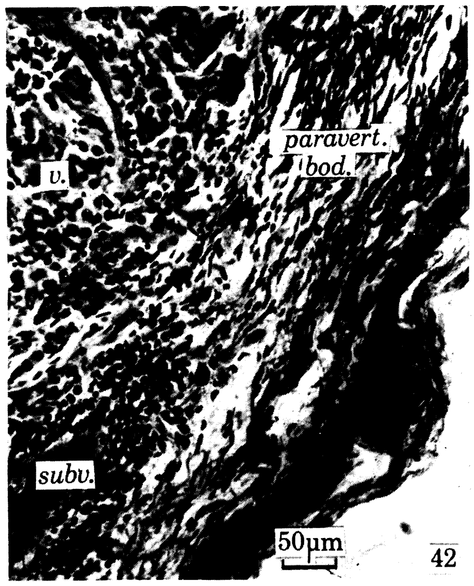
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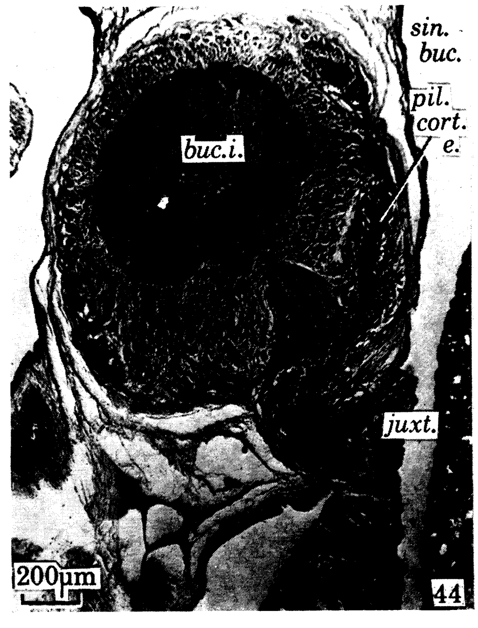
10μm
43b


sin.
buc.
pil.
cort.
e.
buc.i.
juxt.
200μm
44

ring of subpedunculate tissue, thicker ventrally than dorsally. The paravertical tissue also joins this ring dorsally (p. 316).

The specialized epithelium is raised into a number of papillae (figures 22 to 24, plates 66 and 67). These do not appear to be secretory, but there are sometimes signs of a channel within each of them. The surface of the cells is often raised into folds of various shapes. There is a very rich supply of capillaries below the epithelium (figure 24). These often contain amoebocytes, which have been seen as if penetrating between the cells of the epithelium. The subpedunculate tissue forms masses of cells lying outside some but not all parts of the epithelium of the anterior chamber organ (figure 23 and 23*a*). Most of the tissue lies outside the layer of capillaries, but at intervals strands of subpedunculate cells pass around and between the vessels to lie against or between the epithelial cells (figure 23).

8. The anterior chamber organ in various cephalopods

The arrangements of the anterior chamber differ so fundamentally in different cephalopods that they are sometimes made the basis of the classification of modern groups into 'myopsids' and 'oegopsids'. Yet all those investigated have a fundamentally similar anterior chamber organ, backed by subpedunculate tissue. In *Sepia* the anterior chamber is almost more completely separated from the sea than in *Octopus*, communication being only by a narrow ciliated duct at the front of the eye (figures 25 and 26, plate 67). There is a massive ring of subpedunculate tissue at the back of the anterior chamber (figure 27, plate 67), which is very deep and sometimes called the 'orbit' (e.g. Tompsett 1939).

Loligo is also classed as 'myopsid' but the channel to the sea is shorter and wider than in *Sepia* (figure 28, plate 67). The subpedunculate tissue arises in the optic lobe and forms a ring in the usual way (figures 29 and 30, plates 67 and 68). Within the lobe the strands can be followed along the veins almost to the plexiform zone (figures 31 and 32, plate 68).

In the 'oegopsid' decapods, including *Spirula*, the anterior chamber is still more widely open to the sea but nevertheless there is a large anterior chamber organ backed by strands of subpedunculate tissue (figures 33 and 34, plate 68).

In the stalk-eyed *Bathothauma* the anterior chamber is enlarged around the enigmatic so-called 'light organ' (figure 35, plate 68). There is a well-marked anterior chamber organ, with strands of subpedunculate tissue, protruding into the chamber. The organ is connected with the optic lobe by a strand of cells running a very long course to the base of the eye stalk. The strand leaves the optic lobe and runs with the optic tract all the way back to the brain (figures 36

Description of plate 69

Figures 37 and 38. *Bathothauma lyromma* Chun. T.S. eye-stalk at various levels to show the course of the subpedunculate strand (Cajal).

Figure 39. T.S. paravertical tissue (Cajal).

Figure 40. *Sepia officinalis* L. T.S. paravertical tissue (Cajal).

Figure 41. T.S. paravertical strand after injection of Indian ink. The veins in the cerebral membrane are filled and communicate with vessels in the paravertical strand extending into the orbit (formalin, haematoxylin and eosin).

Figure 42. T.S. showing origin of paravertical strand at the junction of the vertical and subvertical lobes (Cajal).

Figures 43*a* and *b*. T.S. and L.S. of paravertical strand (Cajal).

Figure 44. T.S. inferior buccal ganglion, showing extra-cortical neuropil and origin of sub-buccal juxta-ganglionic tissue (Cajal).

to 38, plates 68 and 69). Here it passes round just in front of the statocyst and then out again all along the optic stalk to the anterior chamber organ. This is the pathway that would be followed in an animal without stalked eyes. Presumably no new morphogenetic processes have been developed to allow a short cut. Whatever migration of cells or other activities go on in the tissue are evidently not interfered with by this great lengthening of the course.

9. Paravertical tissue

The anterior chamber organ is connected with the brain by another route (figure 1). Below the vertical lobes at the sides is the paravertical tissue (figure 39, plate 69), a characteristic member of the set of neurovenous tissues (Boycott & Young 1956). Its small cells lie outside the main cell layers of the vertical lobes, away from the main neuropil. They are irregular and interspersed at their origin with a few nerve fibres, but there is little 'extra-cortical neuropil'. A strand of cells proceeds upwards from this region, enters the orbit and runs forwards in its medial wall to join the anterior chamber organ (figure 1). Paravertical tissue of the same type is found also in *Sepia* and *Loligo* (figure 40, plate 69).

The paravertical strands are accompanied by several arteries and veins (figure 41, plate 69). Each strand is surrounded by a thick connective tissue sheath, which joins the cerebral membrane (figure 42, plate 69). The nuclei of the paravertical cells are mostly long and thin, not resembling those of the nearby neurons either of the vertical, dorsal basal or subpedunculate lobes (figure 43*a* and *b*, plate 69).

The detailed relationship of these cells to the vertical lobe (or other neighbouring part of the brain) remains uncertain. The strands of subpedunculate and paravertical tissue seem to be partly nervous, but they do not originate from the central neuropil as other nerve fibres do. The rows of nuclei in the tubes suggest that these are cells travelling along them to be discharged at the tips. No nerve fibres have actually been seen in the paravertical tissue except near its origin. In this it differs markedly from the neurovenous tissue of the vena cava.

10. Juxta-ganglionic tissue

The 'juxta-ganglionic tissue' of Bogoraze & Cazal (1944) lies below the inferior buccal ganglion; similar tissue, even more abundant, has since been recognized by Alexandrowicz in the wall of the vena cava and called by him 'neurosecretory system of the vena cava'. The name

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Description of plate 70

Figure 45. T.S. buccal ganglion and sub-buccal juxta-ganglionic tissue (Cajal).

Figure 46. T.S. inferior buccal ganglion and sub-buccal tissue to show the nerve fibres arising from the neuropil of the ganglion (Cajal).

Figure 47. Sub-buccal tissue near the inferior buccal ganglion, showing the mixture of nerve cells and fibres (Cajal).

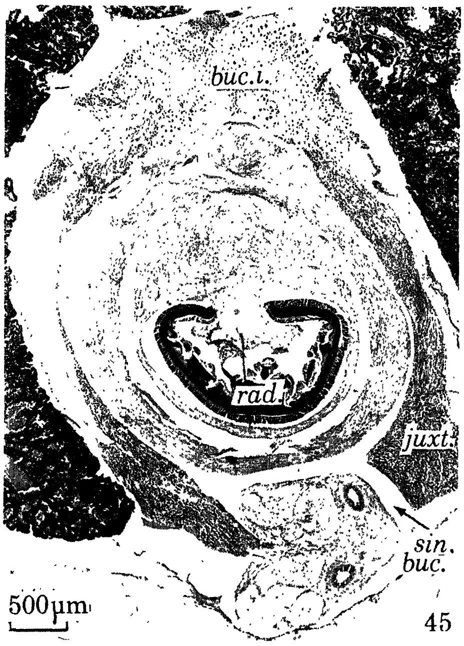
Figure 48. Sub-buccal tissue showing nerve cells, their processes and knob endings.

Figure 49. T.S. sub-buccal tissue to show nerve fibres and cells close to the lumen of the buccal venous sinus (Cajal).

Figure 50. As figure 49. Detail of a portion of the epithelium showing deposit of silver grains. The nerve fibres end very close to the lumen (Cajal).

Figure 51. H.S. showing nerves emerging from the inferior buccal ganglion surrounded by sub-buccal tissue (Cajal).

Figure 52. *Argonauta argo* L. T.S. inferior buccal ganglion showing juxta-ganglionic tissue extending upwards to the oesophagus (Cajal).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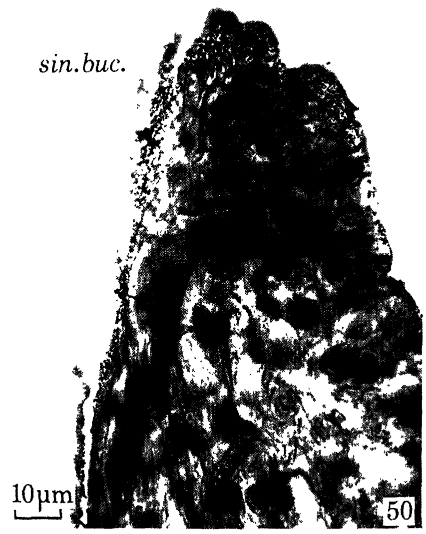
500µm
45


10µm
48a


sin.buc.
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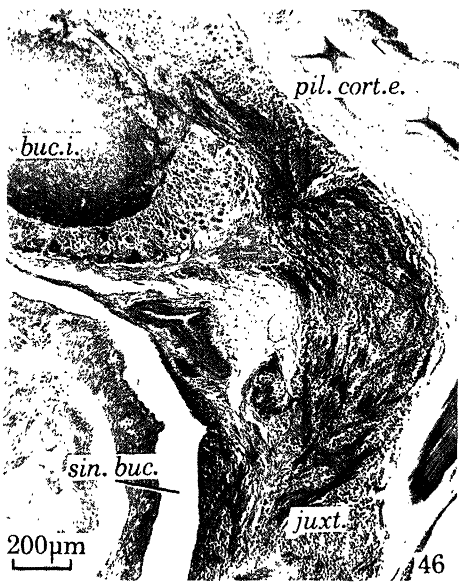
pil. cort.e.
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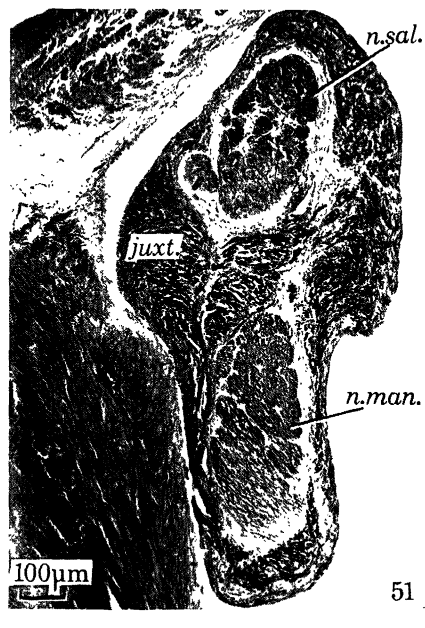
200µm
46


10µm
48b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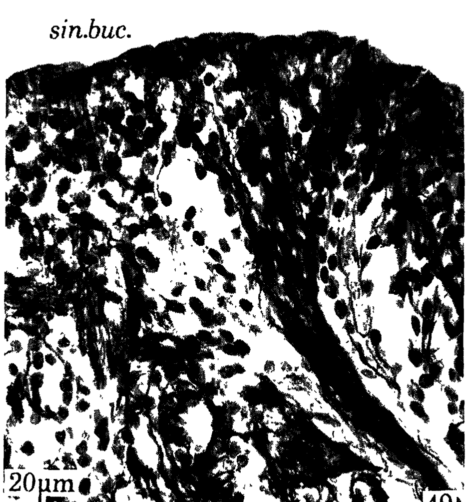
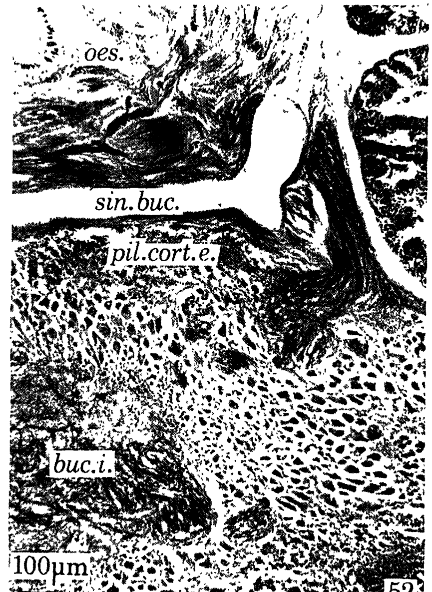
n.man.
100µm
51


50µm
47


sin.buc.
20µm
49


oes.
sin.buc.
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buc.i.
100µm
52


buc.i.
pil.cort.e.
sin.buc.
500μm
54


buc.i.
pil.cort.e.
100μm
sin.buc.
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oes
juxt.
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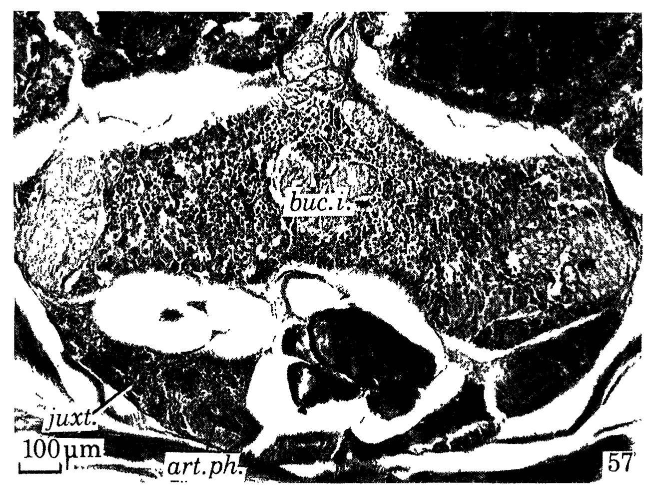
buc.s.
sin.buc.
buc.i.
juxt.
100μm
53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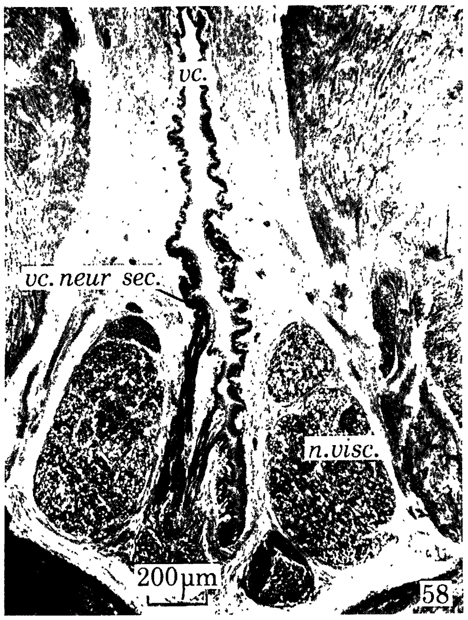
57


vc.
vc. neur sec.
n.visc.
200μm
58


vc.
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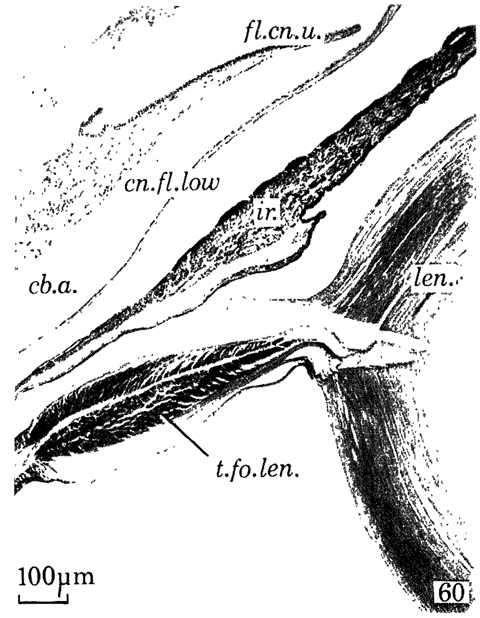
59


fl.cn.u.
cn.fl.low
ir.
cb.a.
len.
t.fo.len.
100μm
60

juxtaganglionic is appropriate to both these tissues. The 'extracortical neuropil' of Thore (1936) is the part of each system around the ganglia. We shall call all this tissue either 'juxtaganglionic' or 'neurovenous', the part related to the inferior buccal ganglion will then be called sub-buccal tissue and that in the vena cava 'neurovenous tissue of the vena cava' (NSV).

The sub-buccal tissue arises from the inferior buccal ganglion and the neurosecretory system of the vena cava from the palliovisceral ganglion. In both situations the juxta-ganglionic tissue springs from a characteristic 'extra-cortical neuropil', consisting of groups of small neurons around a centre of fibrous neuropil (figure 44, plate 69). Strands composed of neurons and nerve fibres run for several millimetres with the nerves that proceed downwards from the inferior buccal ganglion (figure 45, plate 70). Indeed in places the neurovenous tissue is wrapped completely round the nerve trunks (figure 51, plate 70).

The strands contain irregular bundles of nerve fibres, some at least springing from the neuropil of the inferior buccal ganglion (figure 46, plate 70). The strands are different from peripheral nerves in the irregularity of their fibres and the occurrence of nerve cells scattered along them (figure 47, plate 70). On the other hand, they are not similar to the usual neuropil or cell layers of the ganglia. Occasionally it can be seen that the nerve cells are unipolar, but then give off two branches (figure 48*a* and *b*, plate 70). No tubes precisely similar to those of the subpedunculate tissue were seen in the sub-buccal tissue of *Octopus*, but they occur in argonautids (see below) and have been seen by Alexandrowicz (1964, 1965) in the similar neurovenous tissue of the vena cava. The sub-buccal tissue ends in close association with the wall of the venous sinus that surrounds the buccal mass (figures 49 to 51, plate 70). Nerve fibres in many places line the actual wall of the vein. In other places there are traces of a very thin epithelium of flattened cells. The tissue that terminates the neurovenous strands consists of an irregular tangle of very fine nerve fibres, including some terminal swellings (figures 48*a* and *b*, 50, plate 70). Occasionally there are larger irregular masses of axoplasm. Thus these terminal fibres come into close contact with the contents of the sinus. This is the arrangement as shown by electron-microscopy in this tissue (Barber 1967) and also in the neurovenous tissue of the vena cava (Martin 1968). No actual openings of the tubes have been seen, but it is possible that neuroplasm is actually extruded into the vein. Small masses of argentophil material are characteristic of the epithelium, here as in the subpedunculate tissue. The whole surface of the tissue is often covered with granules after silver staining (figure 50).

Description of plate 71

Figure 53. *Tremoctopus violaceus* delle Chiaje. Sagittal section, showing the inferior buccal ganglion surrounded by juxta-ganglionic tissue. There is none around the other ganglia shown (Cajal).

Figure 54. *Ocythöe tuberculata* Rafinesque. T.S. inferior buccal ganglion, showing the sheath of juxta-ganglionic tissue (Cajal).

Figure 55. *Ocythöe tuberculata* Rafinesque. As figure 54, showing the extra-cortical neuropil in relation to the lining of the buccal venous sinus.

Figure 56. *Tremoctopus violaceus* delle Chiaje. Juxta-ganglionic tissue near the inferior buccal ganglion, showing the rows of cells (Cajal).

Figure 57. *Loligo vulgaris* Lamarck. T.S. front of inferior buccal ganglion, showing the small amount of sub-buccal tissue (Cajal).

Figure 58. T.S. vena cava showing the visceral nerves and neurovenous trunks, sending numerous branches to the lining of the vessel (Cajal).

Figure 59. T.S. vena cava, showing plexus of nerve fibres beneath the lining epithelium (Cajal).

Figure 60. T.S. of the eye of a young octopus showing the corneal folds, anterior chamber, iris and lens-forming tissue (Bouin, haematoxylin and eosin).

It may be significant that the sub-buccal tissues are very highly developed in the pelagic Argonautidae, where the subpedunculate system is also large (p. 312).† The inferior buccal ganglia of these animals are surrounded by quite a thick sheath of rows of small highly basophilic nuclei (figures 52 and 53, plates 70 and 71). Many of these rows run only for a short distance and end as a layer of neuropil close to the lining of the vein near the ganglion (figures 54 and 55, plate 71). Here indeed we have a ganglion turned inside-out, with cells towards the centre and neuropil outside. Where the rows of cells originate in the ganglion they are not very unlike cell layers elsewhere in the nervous system (e.g. in the vertical lobes). But instead of emitting fibres that conduct, the cells themselves seem to move down the tubes, apparently with their fibres.

In all the argonautids many of the strands pass *upwards* from the inferior buccal ganglion. They line the sinus around the anterior salivary glands and penetrate along some of the veins into the muscles of the oesophagus (figure 56, plate 71). These strands resemble those of the subpedunculate tissue more than does the sub-buccal tissue of *Octopus*. It is not clear why these pelagic animals have the tissue so well developed. The neurovenous tissue arising from the visceral lobe is also very extensive in these animals.

In contrast there is little sub-buccal tissue in *Sepia* and in *Loligo* it consists only of a few strands at the lower front end of the inferior buccal ganglion (figure 57, plate 71).

11. Neurovenous tissue of the vena cava

Alexandrowicz (1965) has been so convinced that in the vena cava of *Octopus* some chemical signalling is involved that he has named the tissues he has found 'neurosecretory system of the vena cava (NSV)'. It shows all the typical features. It arises from the outer side of the pallio-visceral ganglion, where indeed Thore (1939) first described the 'extra-cortical neuropil'. Alexandrowicz (1964, 1965) has given a very thorough description of the course of the tissue. It consists of very numerous small nerve fibres and columns of cells (figure 58, plate 71). From the main NSV trunks numerous branches proceed to the lining of the vena cava and its tributaries. Here the fibres end close to the lumen, exactly as do the endings of the sub-buccal tissue (figure 59, plate 71). The precise relation of the cells and fibres in this tissue have not been determined. The cells are very numerous (Alexandrowicz estimated 2 000 000 in *Eledone*). Some of the fibres run forwards and perhaps they are axons of cells of the tissue. Material staining with paraldehyde fuchsin was found here in oegopsid squids (Martin 1966) and in *Eledone* but not in *Sepia* (Alexandrowicz 1965).

Electron-microscopy has shown that the terminal axons come very close to the lumen, from which they are separated in places only by a basement membrane (Martin 1968). The endothelial cell layer is not continuous. The terminal axons are packed with membrane bound granules of 80 to 200 nm diameter, electron opaque after glutaraldehyde and lead staining. There are also some rather larger and less dense granules and still others with a dense core. A few smaller structures (30 to 50 nm) resemble synaptic vesicles, but no undoubted synapses have been described in this tissue.

† The three forms of pelagic octopod, *Argonauta*, *Tremoctopus* and *Ocythöe* are often referred each to a separate family. They certainly show many differences (e.g. only *Argonauta* has a shell) but also many similarities—for instance in the sub-buccal tissue.

12. Discussion

The various tissues here described are shown diagrammatically in figure 1. They all have it in common that they arise from or around nerve centres and pass to the periphery. Of course it is not known that this is the direction in which they proceed either in development or adult functioning. They all contain columns of small cells whose deeply basophilic nuclei perhaps suggest that they may be uncommitted cells. The form of these cells is little known but some of them have branches and resemble neurons. No synapses have been described in the tissues. Nerve fibres are abundant in the sub-buccal tissue and NSV tissue but are probably absent from the subpedunculate and paravertical tissues, except near the central nervous system. This suggests that these tissues related to the anterior chamber of the eye are different from those related to the veins, but morphologically the rows of cells are similar.

Alexandrowicz (1964) believes that 'the function of the neuropile layer consists in liberating some hormone into the blood passing through the vena cava'. There are indeed indications for a secretory activity for all these tissues, and few for any other! But if the various tissues described are really similar and if their product is a chemical *messenger* it is curious that it should be produced in so many places, including the anterior chamber of the eye, and under control of such diverse higher and lower nerve centres. The wide dispersal of the system suggests that its actions are not specific to the sites where it occurs.

It is possible that the neurovenous tissues are concerned somehow with regulation of the volume, composition and disposition of body fluids. This must be an important function in animals that have large open venous sinuses and no fixed skeleton. It becomes especially important if they vary their depth and use the secretion of fluids of special composition as a means of flotation (Denton 1961). There may be a similar explanation for the connexion with the eye and orbit. It has been suggested that the afferent fibres in the subpedunculate nerves signal that the pressure in the orbit is excessive, as for example if the arms try to drag the animal through a crevice that is too narrow (Boycott & Young 1956). This may well be too restricted an interpretation. It may be that the whole system is concerned with signalling changes in depth and making the appropriate adjustments.

The adjustment of the composition of the fluid in the anterior chamber is obviously important when this space can be closed off from the sea, as in octopods, *Sepia* and *Loligo*. Indeed in *Octopus* its composition is known to differ from that of sea water (Robertson 1953; Amoore *et al.* 1959). It is more surprising to find a well developed anterior chamber organ in the oegopsid squids and *Spirula*, where the contents are in open communication with sea water.

Presumably the fluid in the anterior chamber has some influence upon the lens-forming tissue, whose outer surface it bathes (figure 60, plate 71). The refractive index of the various parts of the lens is continuously adjusted during growth so that the lens remains remarkably achromatic at all sizes (Pumphrey 1961). It is not known how this adjustment is achieved, but it is possible that deposition of the fibres of the outer segment of the lens is regulated by a visual feedback through the subpedunculate tissue, which originates in the optic lobe. This would not explain the contribution from the paravertical strand. It would be interesting to study the growth of the lens in animals where the circuit was broken by blinding or other operations.

The significance of the nervous connexions of the other juxta-ganglionic tissues remains completely obscure. The NSV tissue arises from the palliovisceral lobe close to regions that are held to contain vasomotor centres (Mislin 1950). But the inferior buccal ganglion, which gives rise to the sub-buccal tissue, is otherwise concerned wholly with the mechanism of feeding. What signals does it send to the 'extra-cortical neuropil' around it? The presence of vesicles of various types in the NSV tissue certainly suggests a secretory function, but it cannot be excluded that all these tissues regulate fluid contents in some other way, possibly by subtraction rather than addition of components. A possible clue to the function of the NSV tissue was that the vesicles were no longer electron dense in an octopus subjected to severe dehydration stress (Martin 1968). This would agree with the emptying of the cells of the neurosecretory tissue of other molluscs as a result of osmotic or thermal stressing (Lubet & Pujol 1963; Lever & Joose 1961), but does not tell us what part such tissue plays in homeostasis. The fact that all these tissues are nervous derivatives suggests that they operate by some variant of nervous activity. The most obvious suggestion is that the granules seen in the endings produce material that is passed outwards. But there is no direct evidence of any such secretion. The surface of the endings is covered with a well-marked basement membrane and the whole system might be concerned with transport of ions in either direction. The fact that it consists of an enormous number of very small fibres suggests that a surface phenomenon is involved.

Much of the material for this study has been collected at the Naples Zoological Station, over many years. I am deeply grateful to the Director Dr P. Dohrn, the Commissario Straordinario, Professor M. Pantaleo, and to all the staff of the Station for their help.

The work has only been possible because of the numerous excellent sections prepared by Miss P. Stephens, to whom I am most deeply indebted. Also to Mr J. Armstrong and Miss T. Hogan for assistance with photography and to Mrs M. Nixon for help in the preparation of the MS.

Work at Naples has been assisted by the Science Research Council and by the USAF Office of Aerospace Research under Grant 67-22.

Abbreviations used on figures

art.ph.	pharyngeal artery
bod.wh.	white body
buc.i.	inferior buccal ganglion
buc.s.	superior buccal lobe
cap.	capillary
cart.cran.	cranial cartilage
cb.a.	anterior chamber
ce.subped.	subpedunculate cell
duc.	duct
f.	fibre
fl.cn.low	lower corneal flap
fl.cn.u.	upper corneal flap
g.opt.	optic gland
gan. subrad.	subradular ganglion
ir.	iris
je.orb.	orbital jelly
juxt.	juxta-ganglionic tissue
len.	lens
mus.	muscle
mus.cran.intra	intracranial muscle
n.g.opt.	optic gland nerve
n.man	mandibular nerve
n.ol.	olfactory nerve
n.op.i.	inferior ophthalmic nerve
n.sal.	posterior salivary nerve
n.subped.	subpedunculate nerve
n.visc.	visceral nerve
oes.	oesophagus
ol.	olfactory lobe
opt.	optic lobe
or.cb.a.	anterior chamber organ
paravert.	paravertical tissue
paravert.bod.	paravertical body
ped.	pedal lobe
pil.cort.e.	extra cortical neuropil
pv.	palliovisceral lobe
rad.	radula
ret.	retina
sal.duc.	salivary duct
sin.buc	buccal sinus
sin.oes.per.	perioesophageal sinus
sin.orb.	orbital sinus
sin.suborb.	suborbital sinus
st.	statocyst
subfr.	subfrontal lobe
subped.	subpedunculate tissue
subv.	subvertical lobe
t.fo.len.	lens forming tissue
t.sub-buc.	sub-buccal tissue
tr.opt.	optic tract
v.	vertical lobe
vc.	vena cava
vc.neursec.	neurosecretory tissue of the vena cava
ve.op.	ophthalmic vein
ve.opt.	optic vein
ve.ph.-op.	pharyngo-ophthalmic vein

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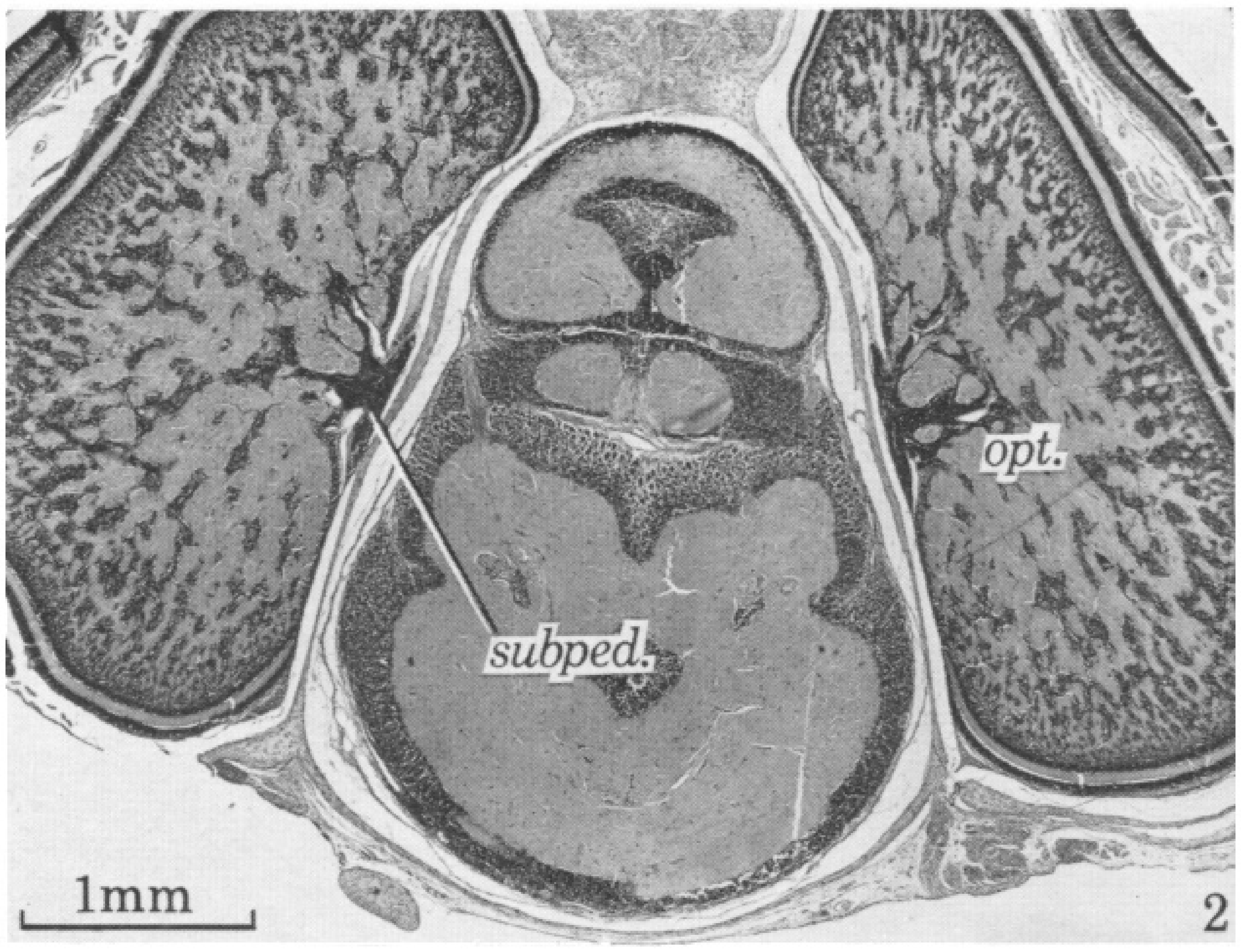
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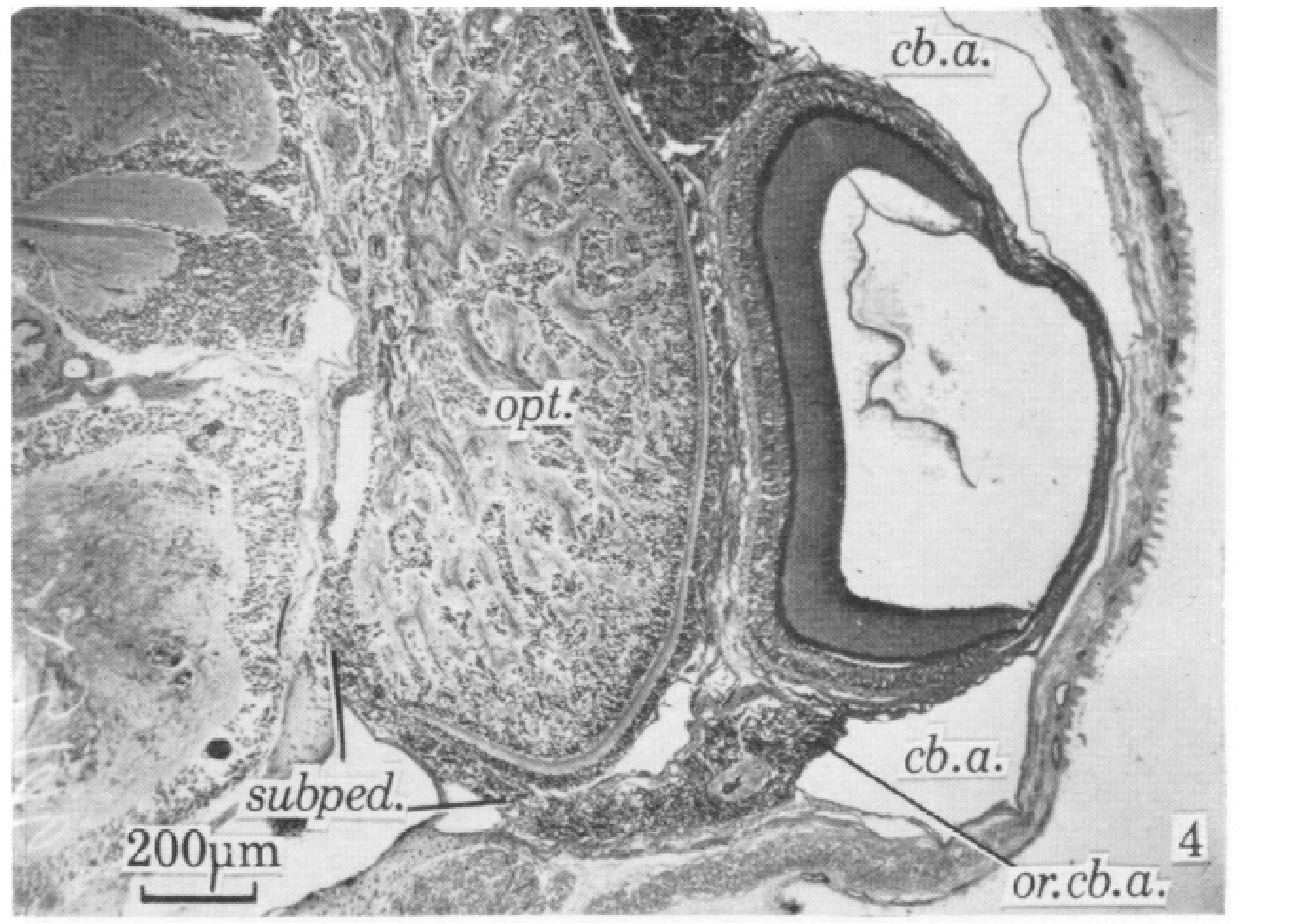
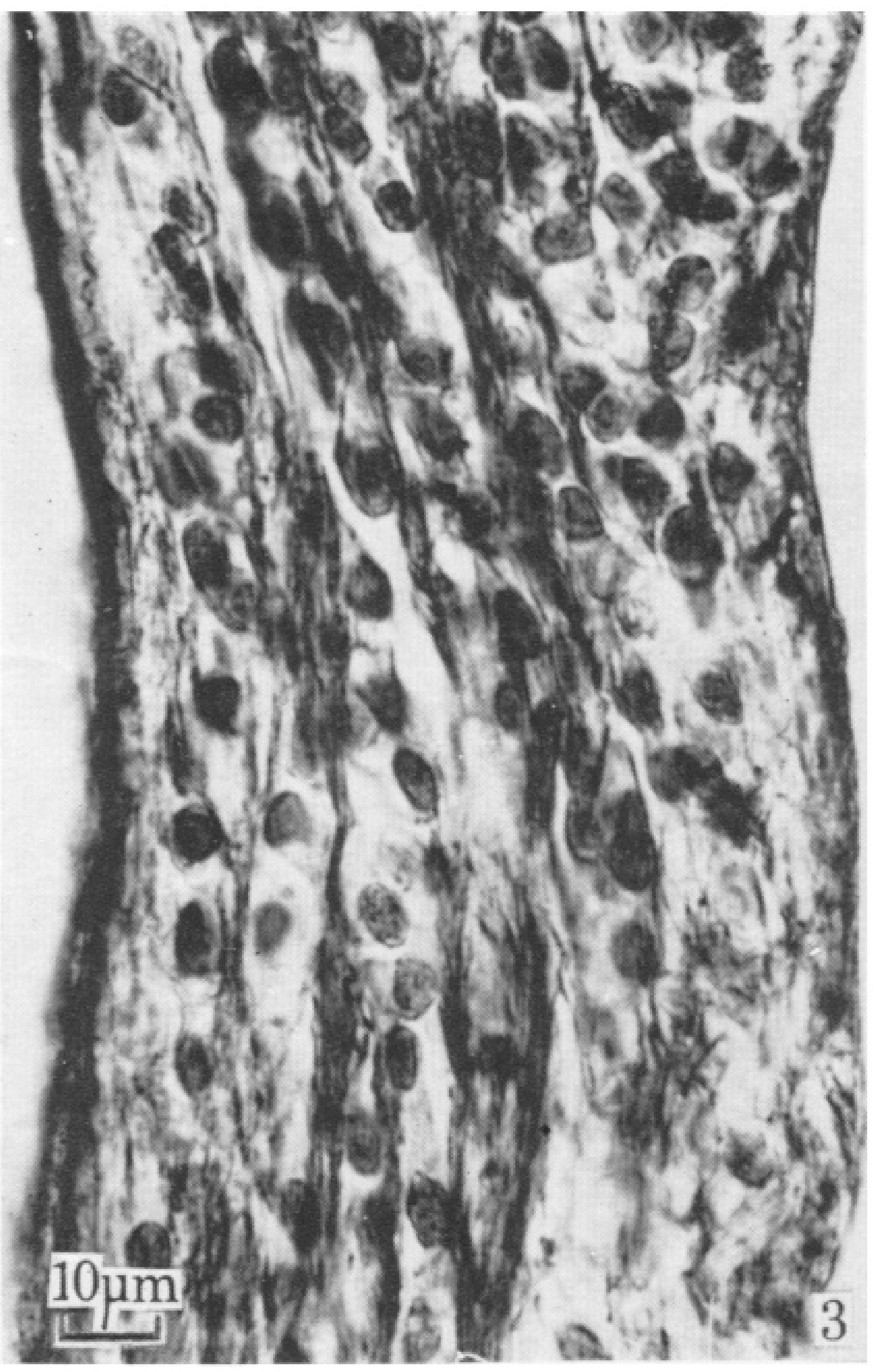
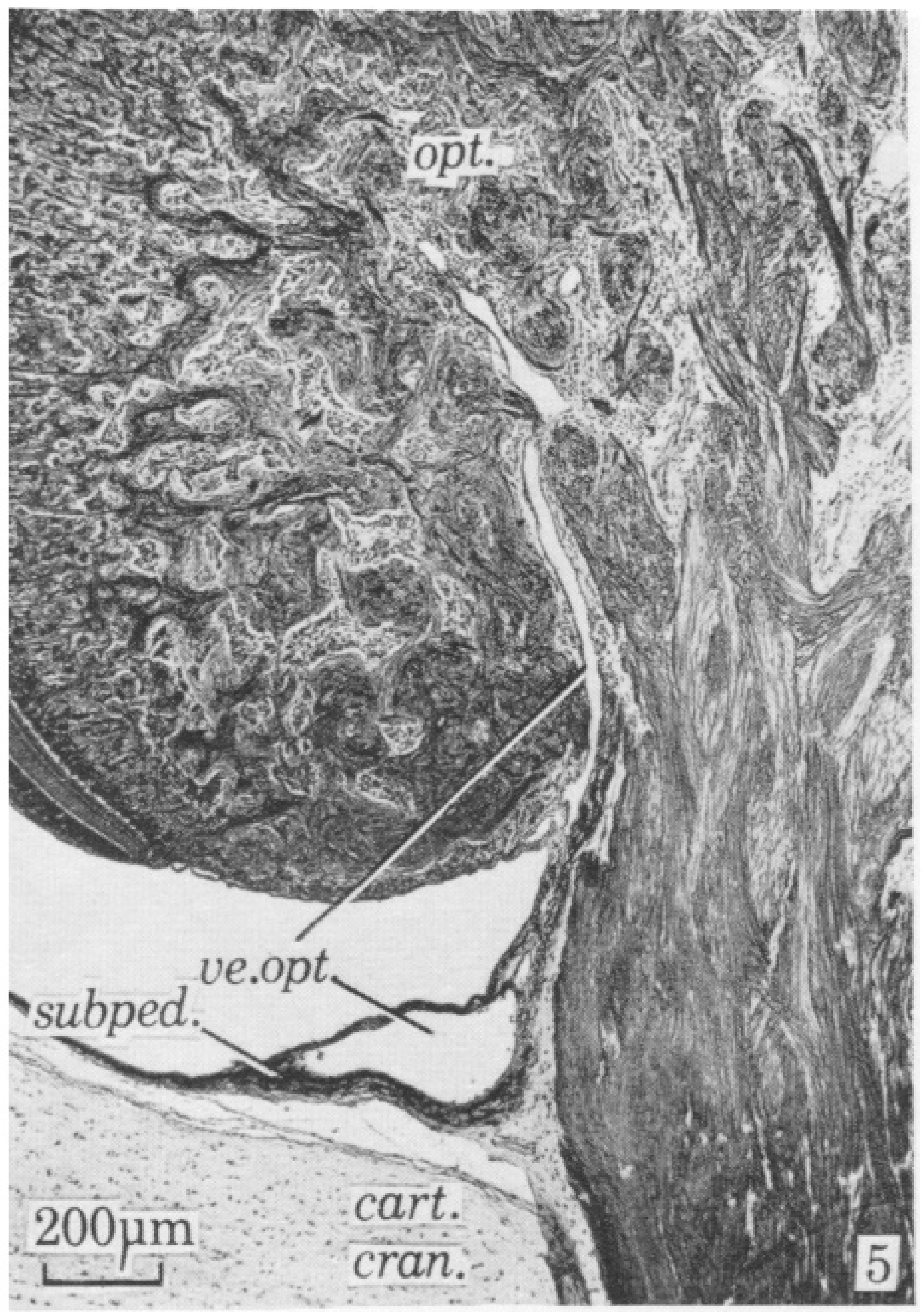
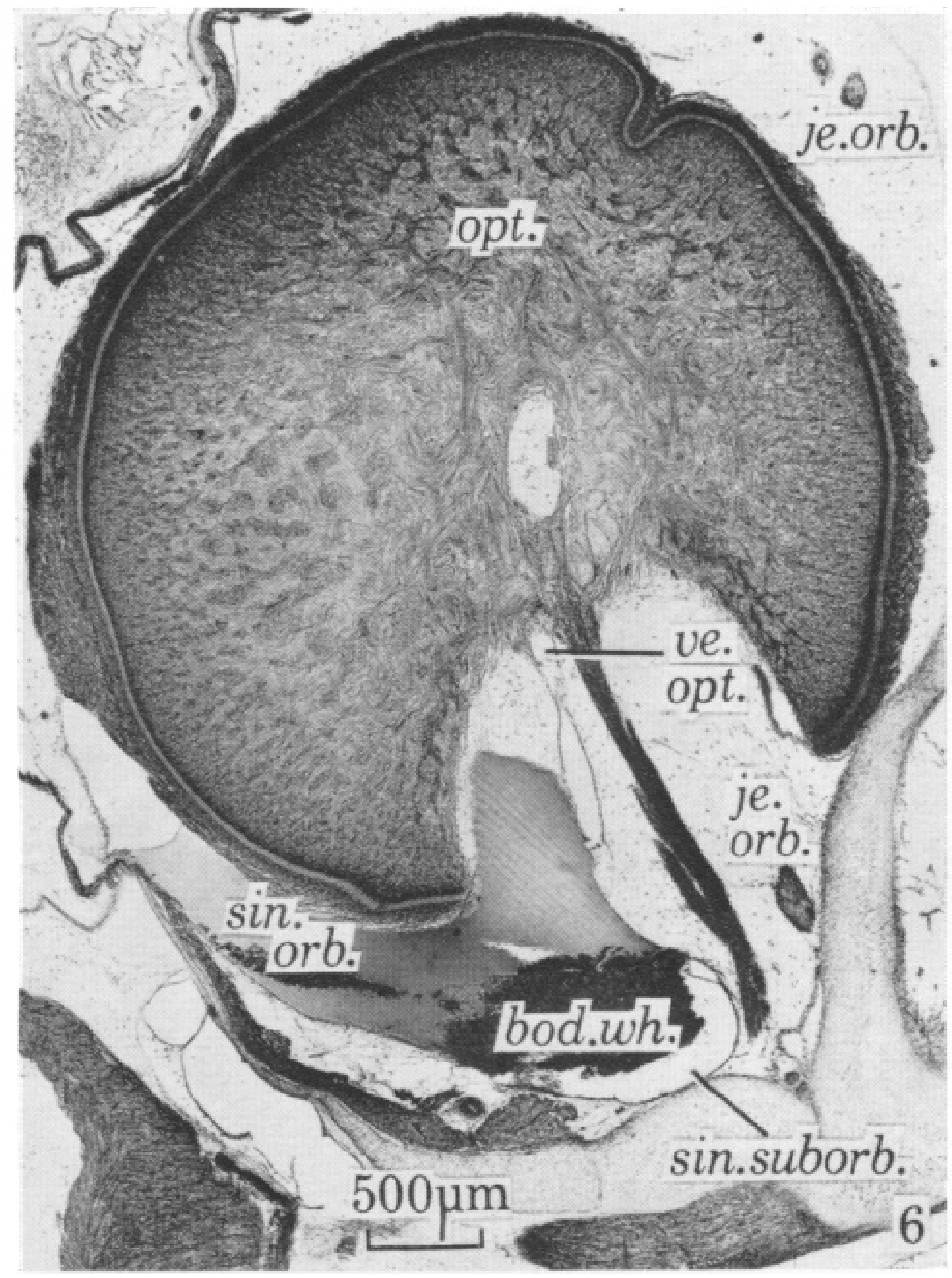
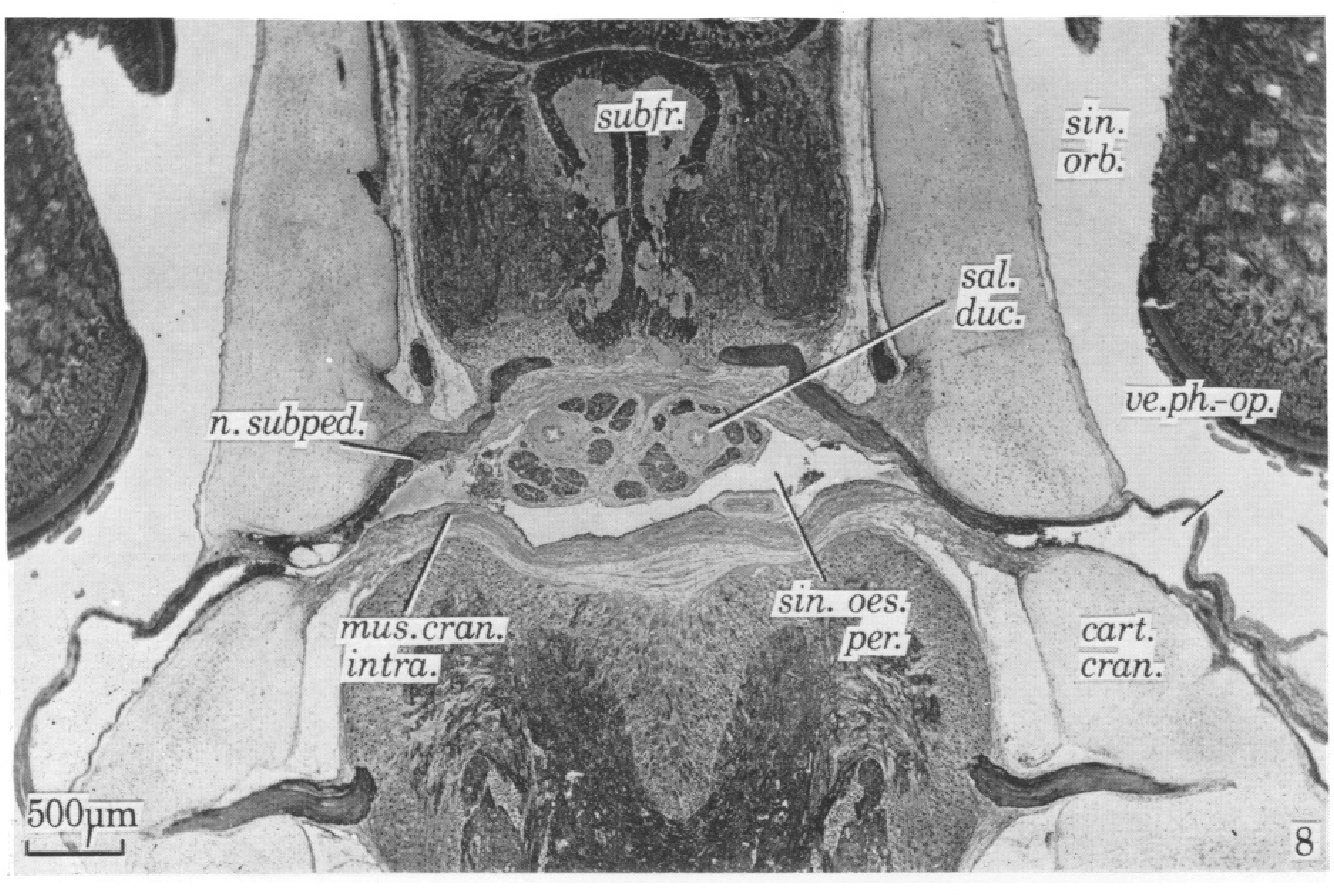
1mm
2

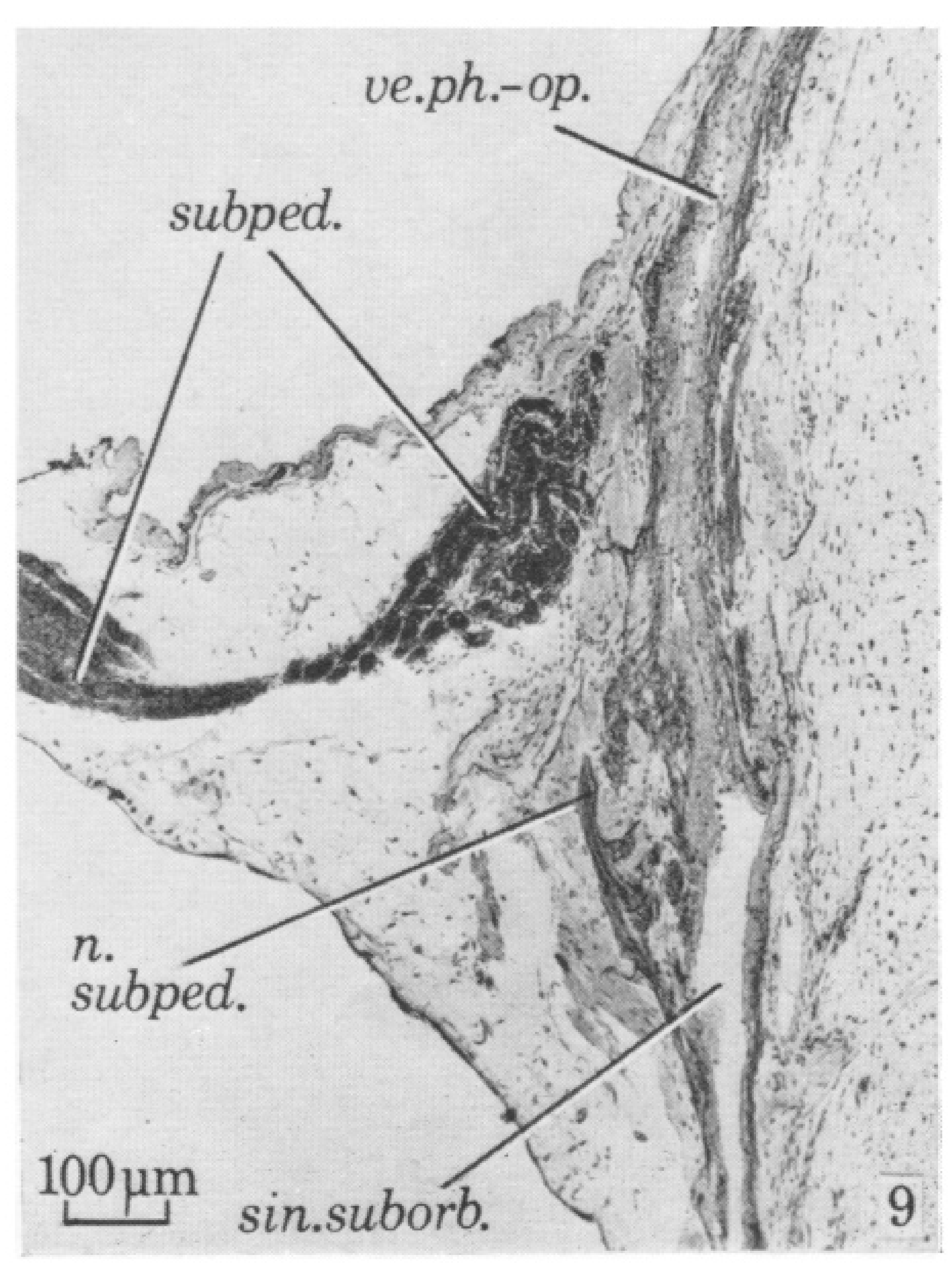

cb.a.
opt.
cb.a.
subped.
200µm
or.cb.a.
4

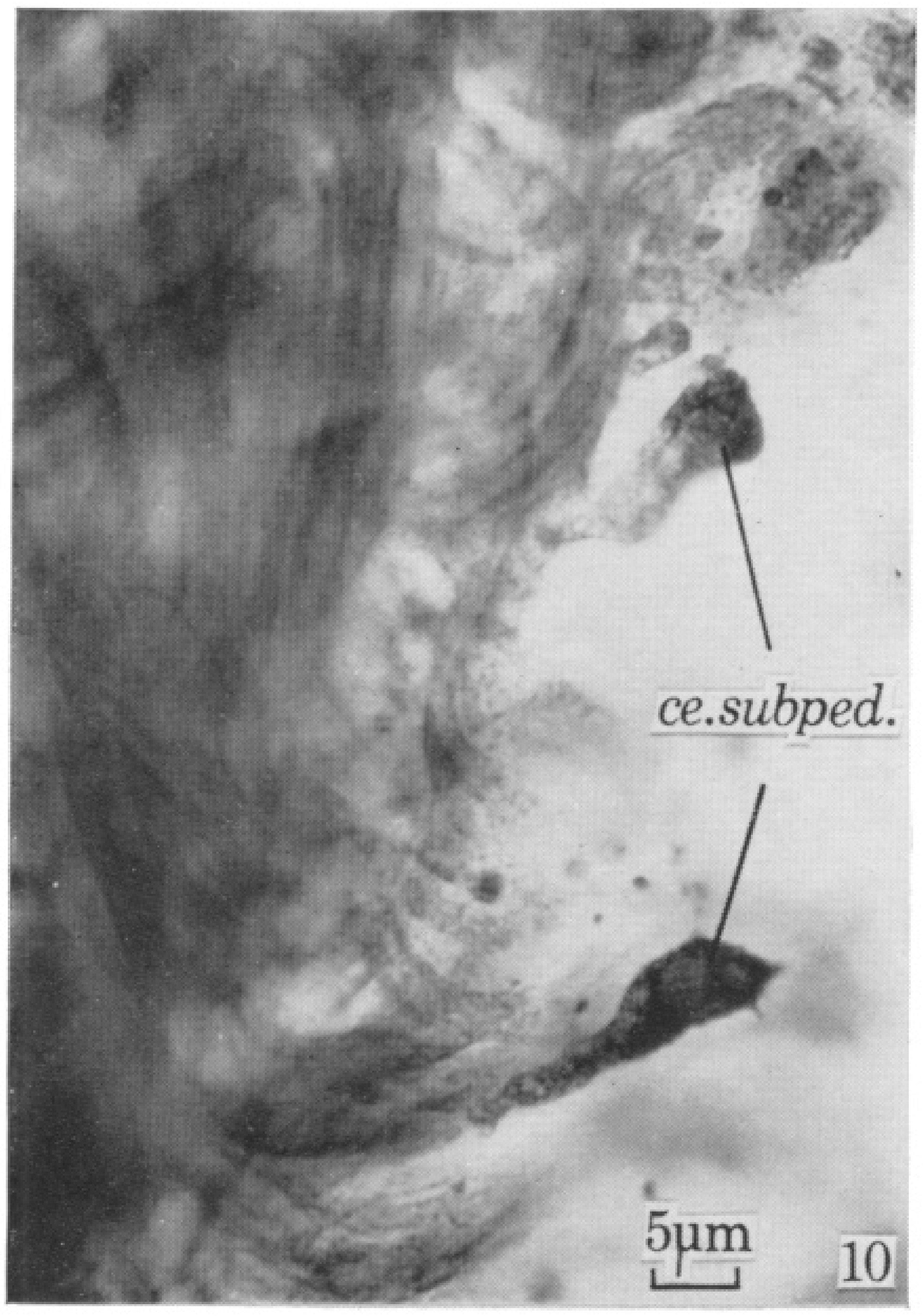

10µm
3

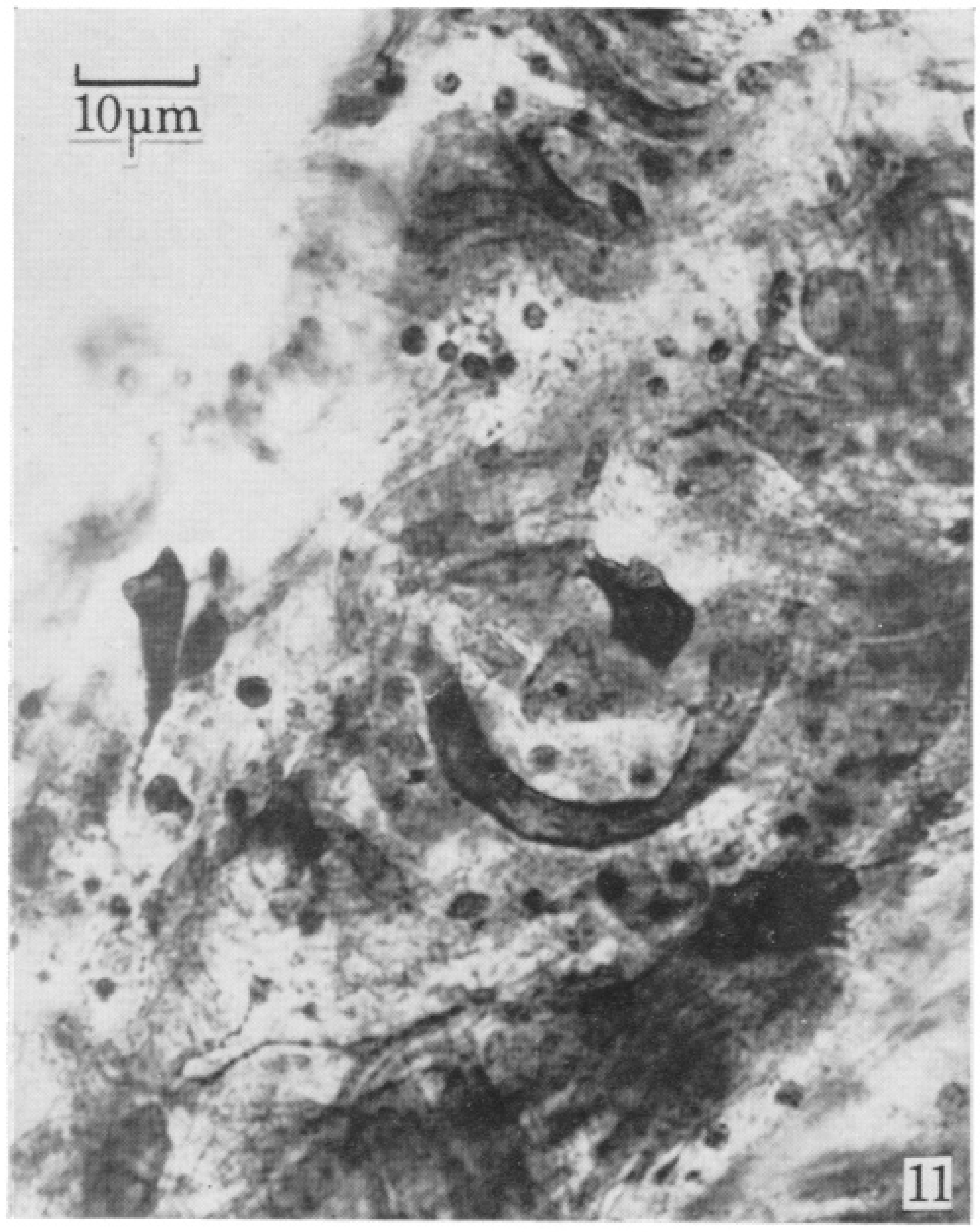

opt.
ve.opt.
subped.
200µm
cart.
cran.
5

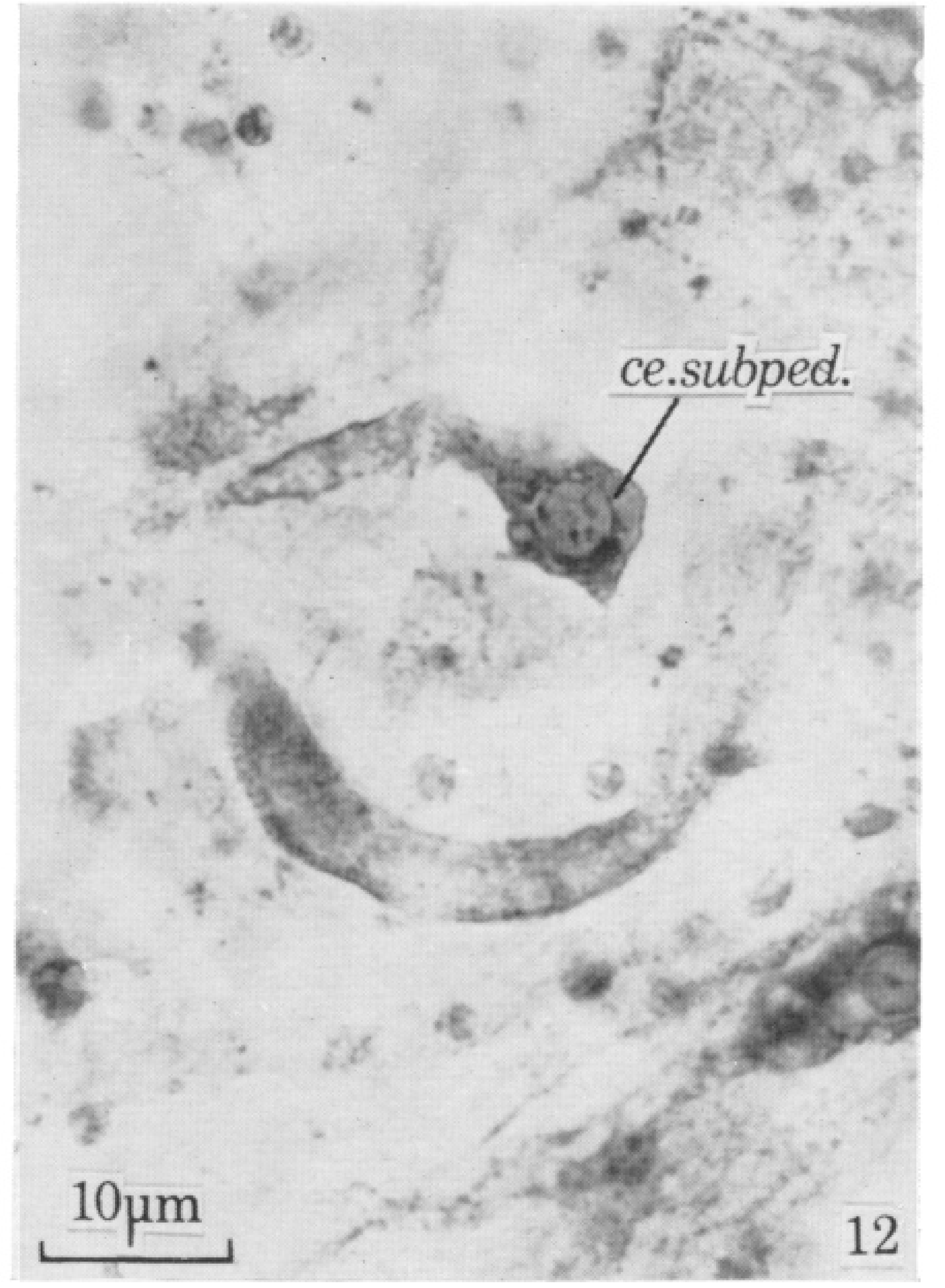

je.orb.
opt.
ve.
opt.
je.
orb.
sin.
orb.
bod.wh.
sin.suborb.
500µm
6

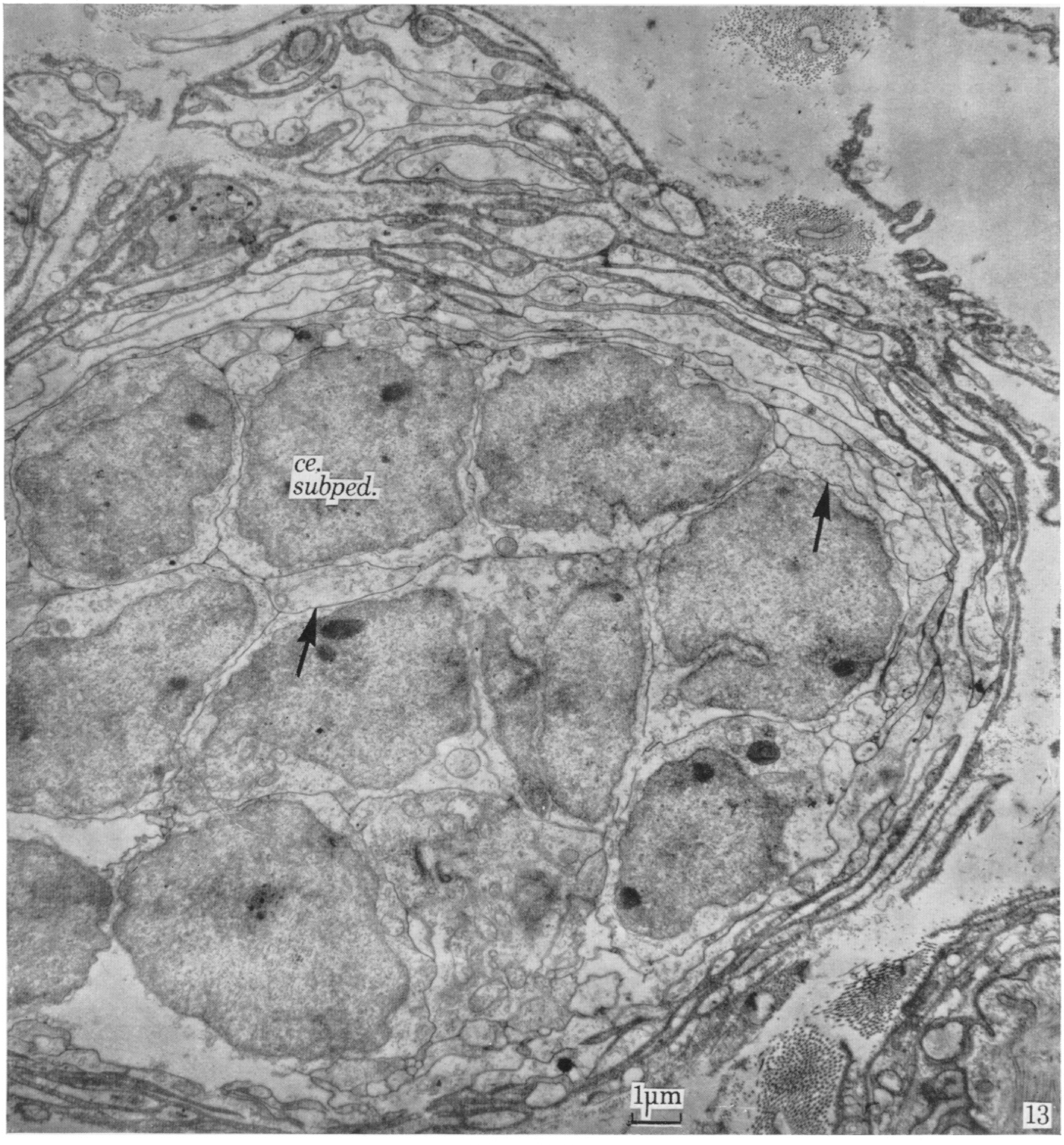

subfr.
sin.
orb.
sal.
duc.
n. subped.
ve.ph.-op.
mus.cran.
intra.
sin. oes.
per.
cart.
cran.
500µm
8

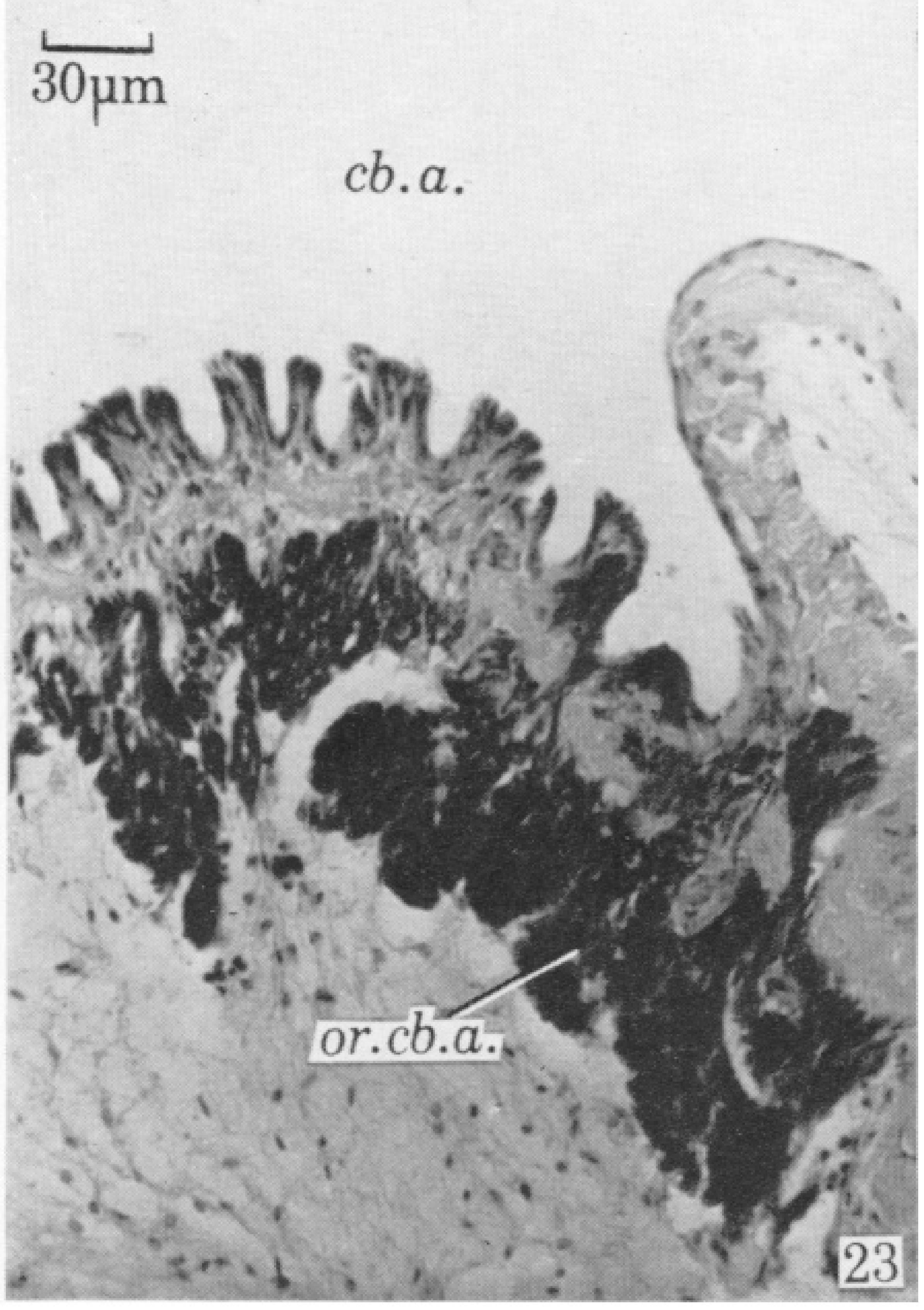

ve.ph.-op.
subped.
n.
subped.
100µm
sin.suborb.
9

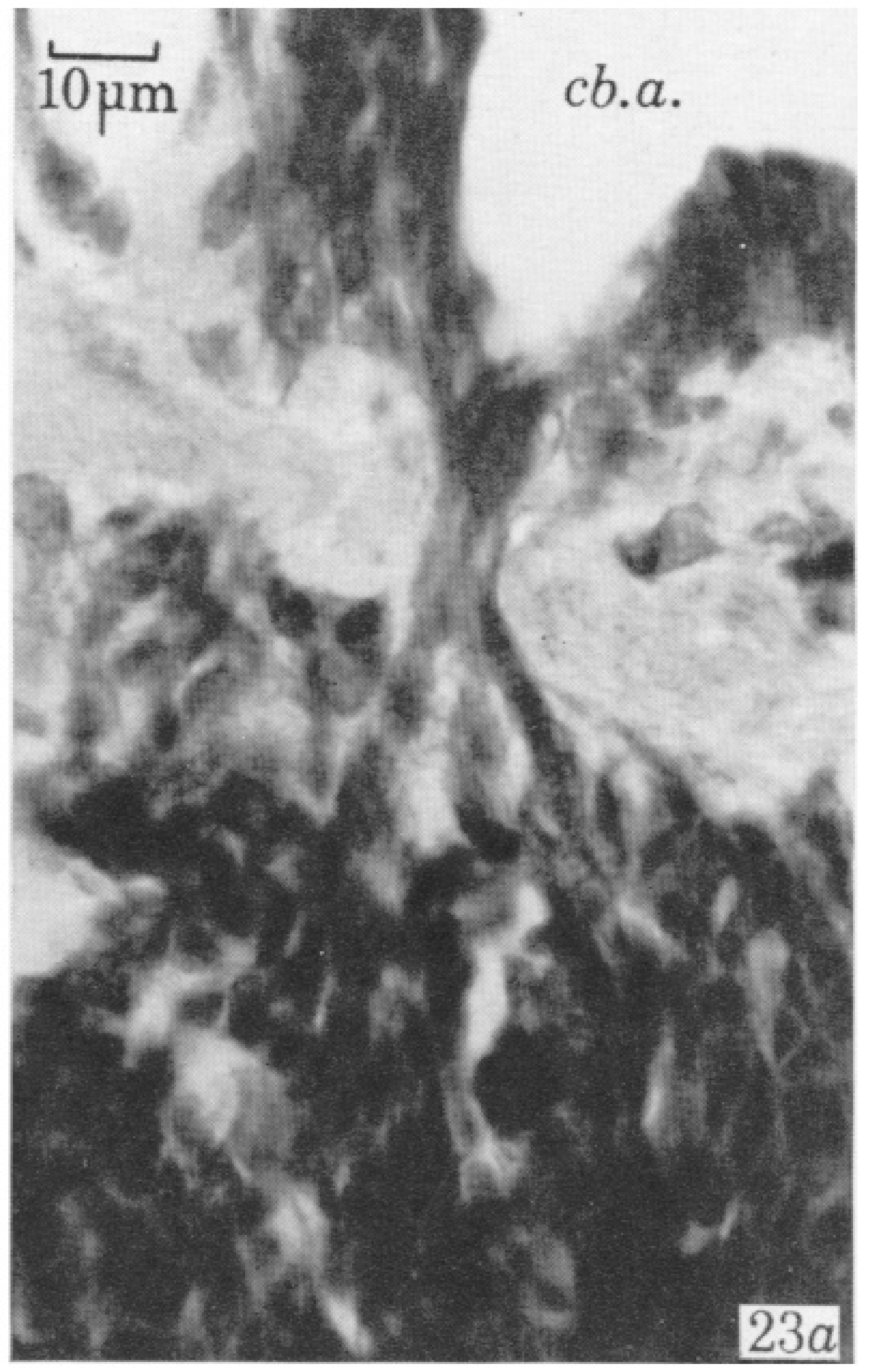

ce.subped.
5μm
10

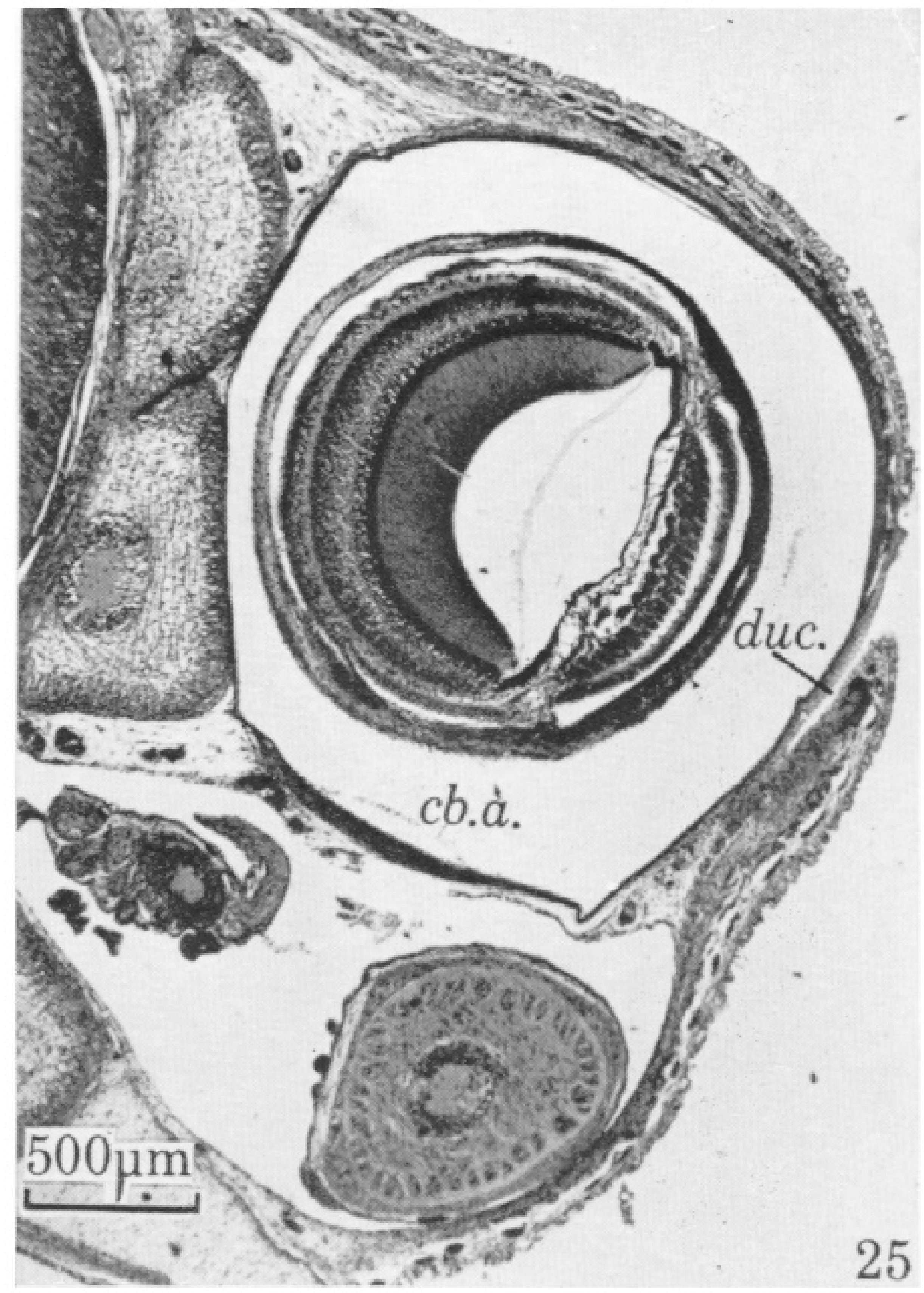

10μm
11

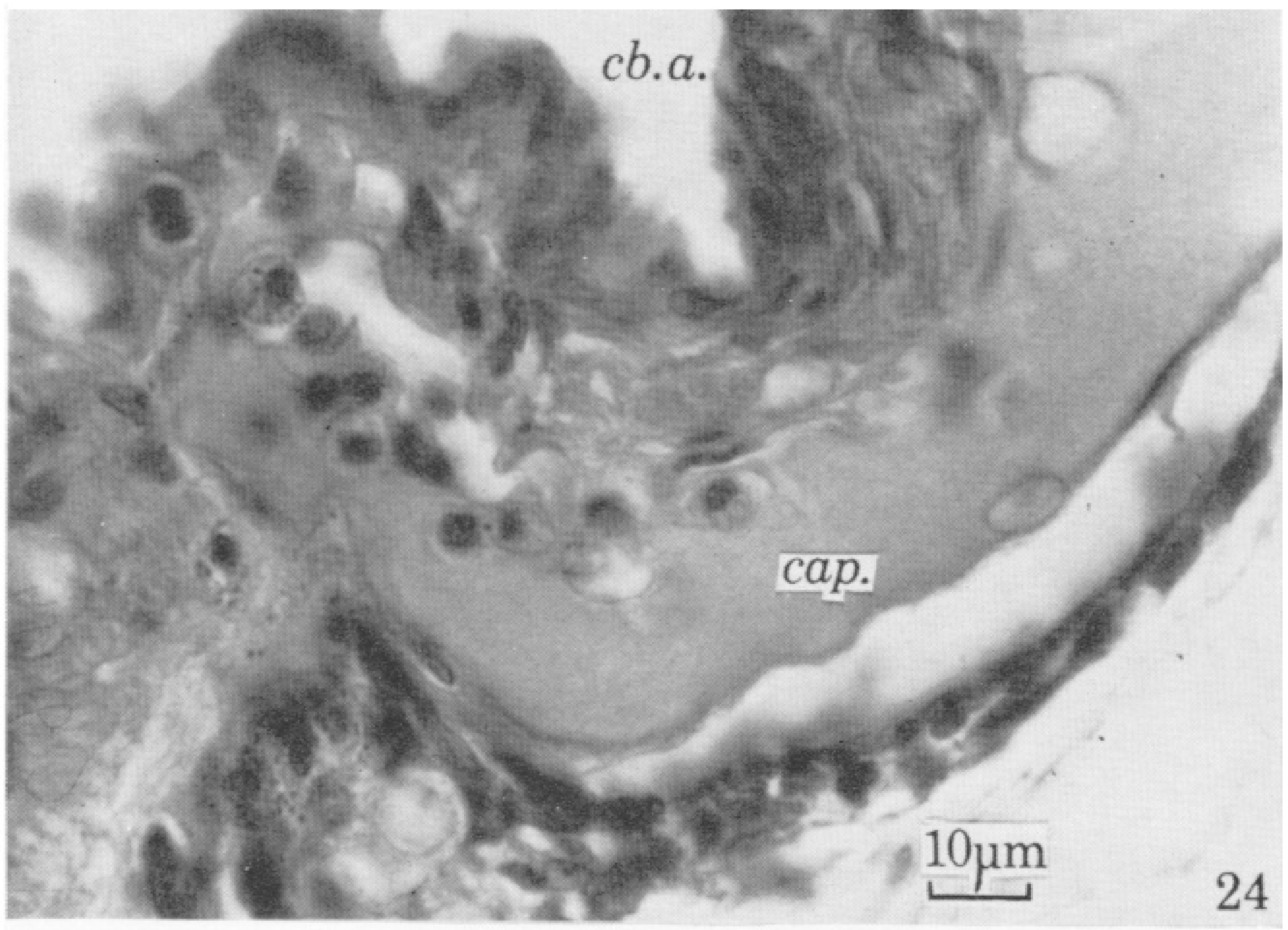

ce.subped.
10μm
12

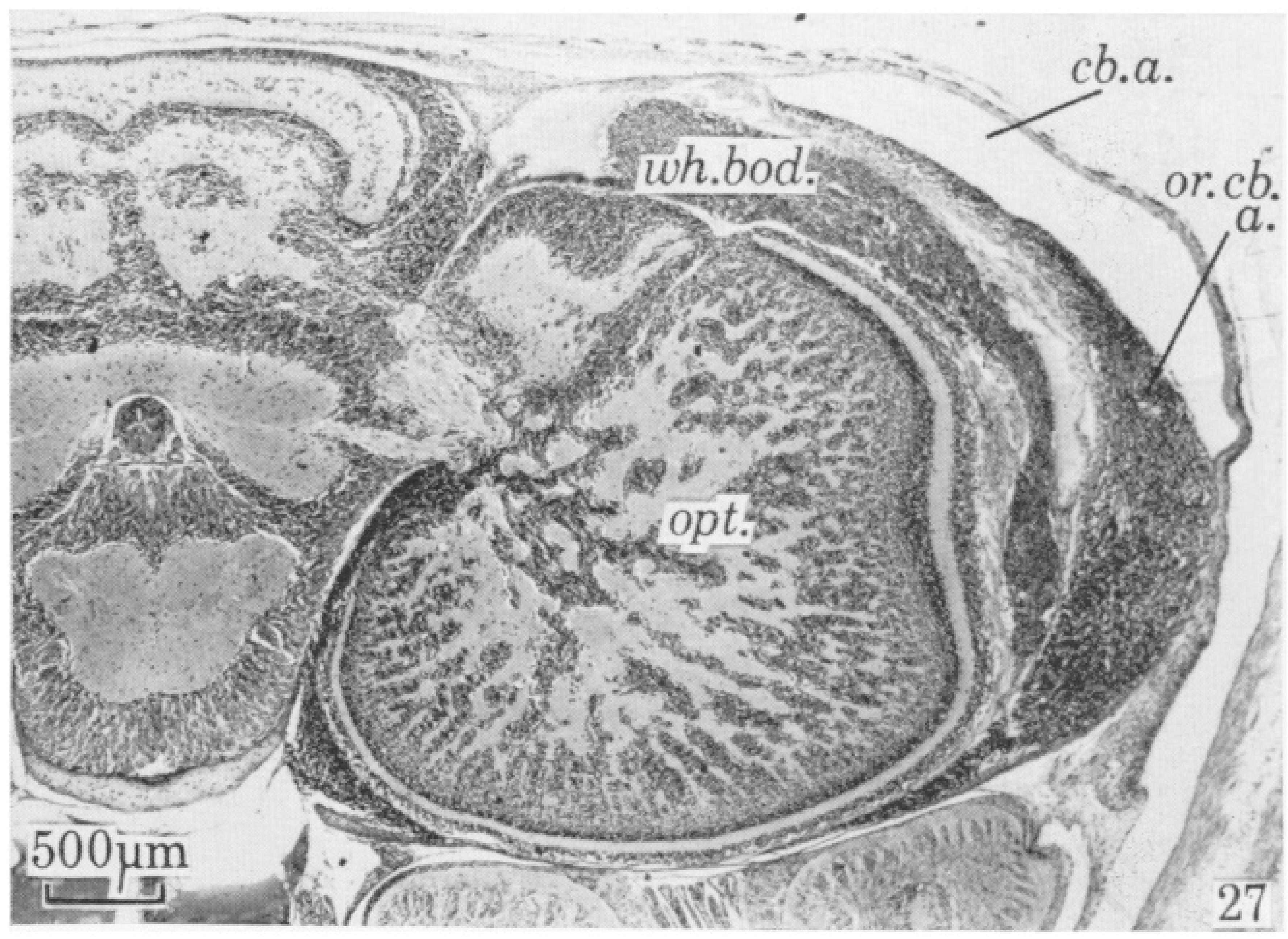

ce.
subped.
1μm
13

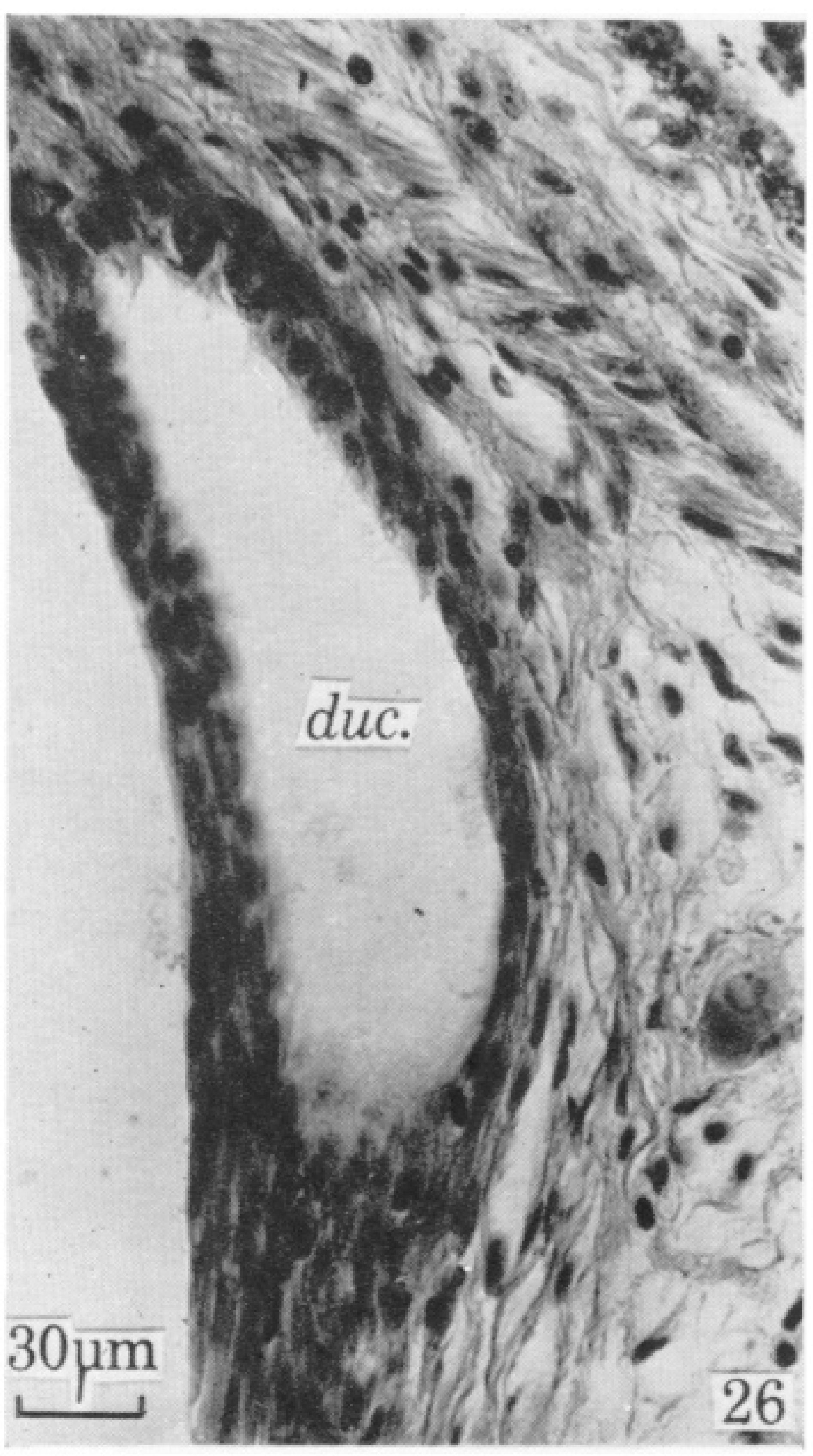

30μm
cb.a.
or.cb.a.
23

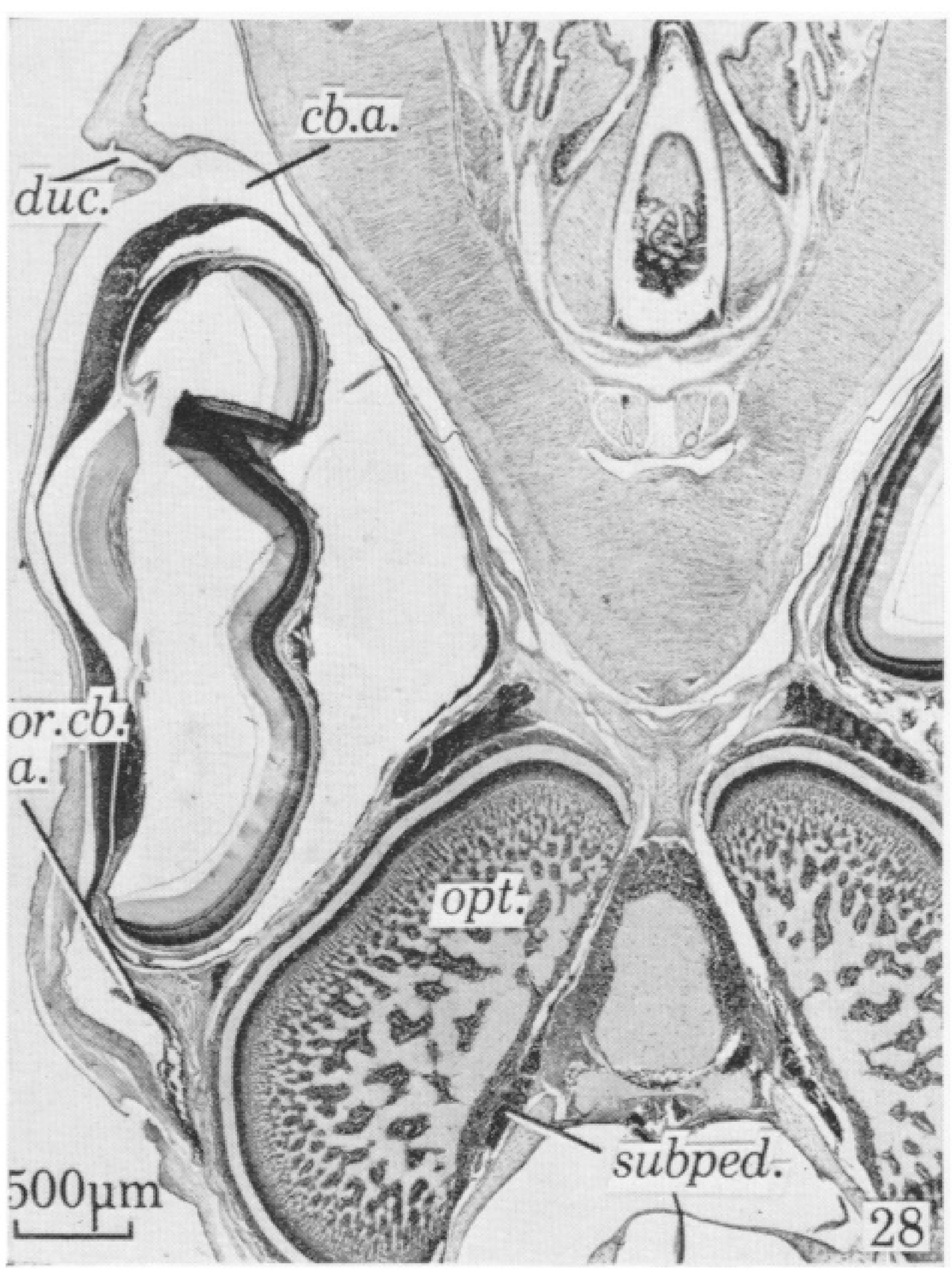

10μm
cb.a.
23a

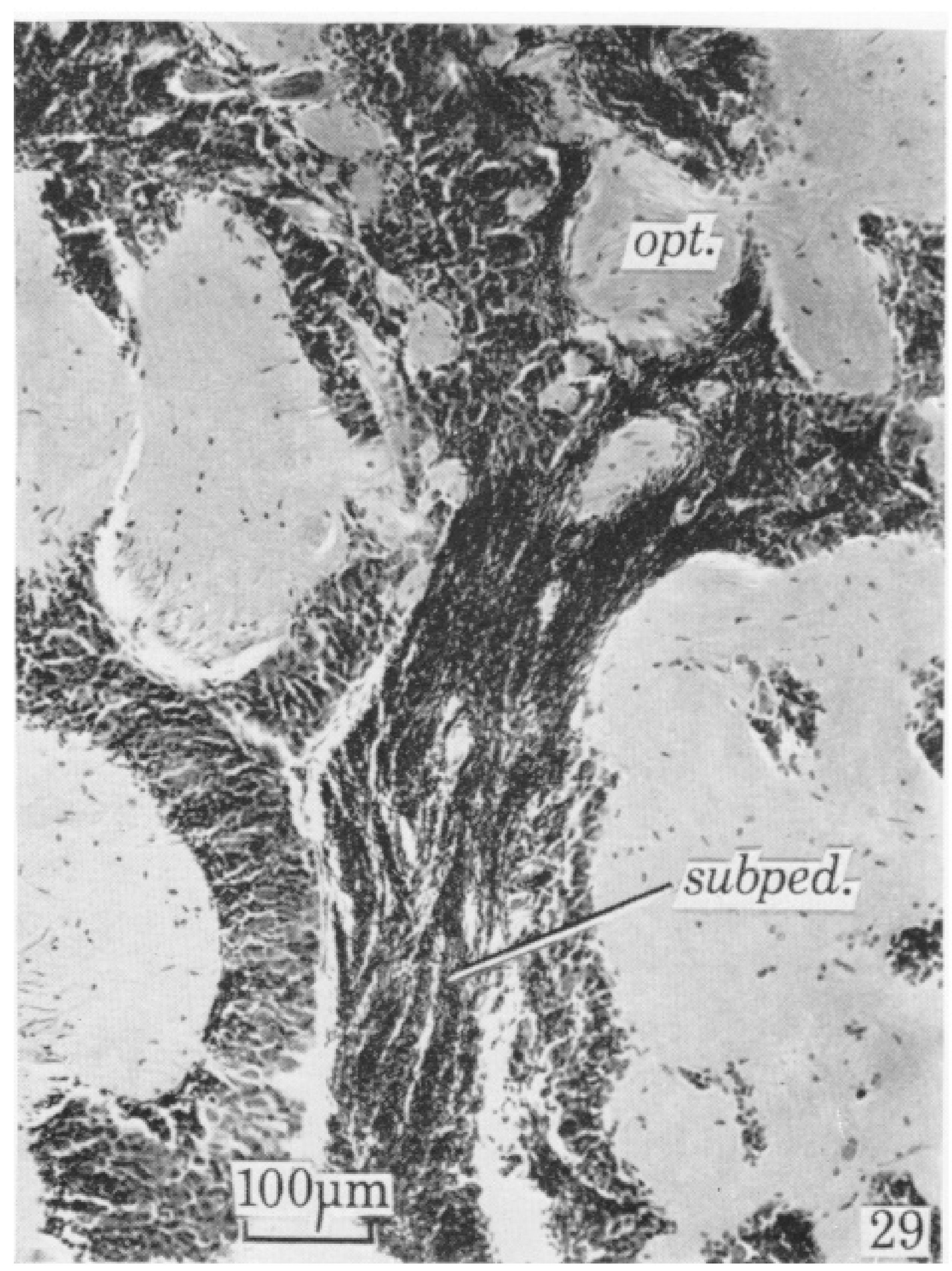

duc.
cb.a.
500μm
25

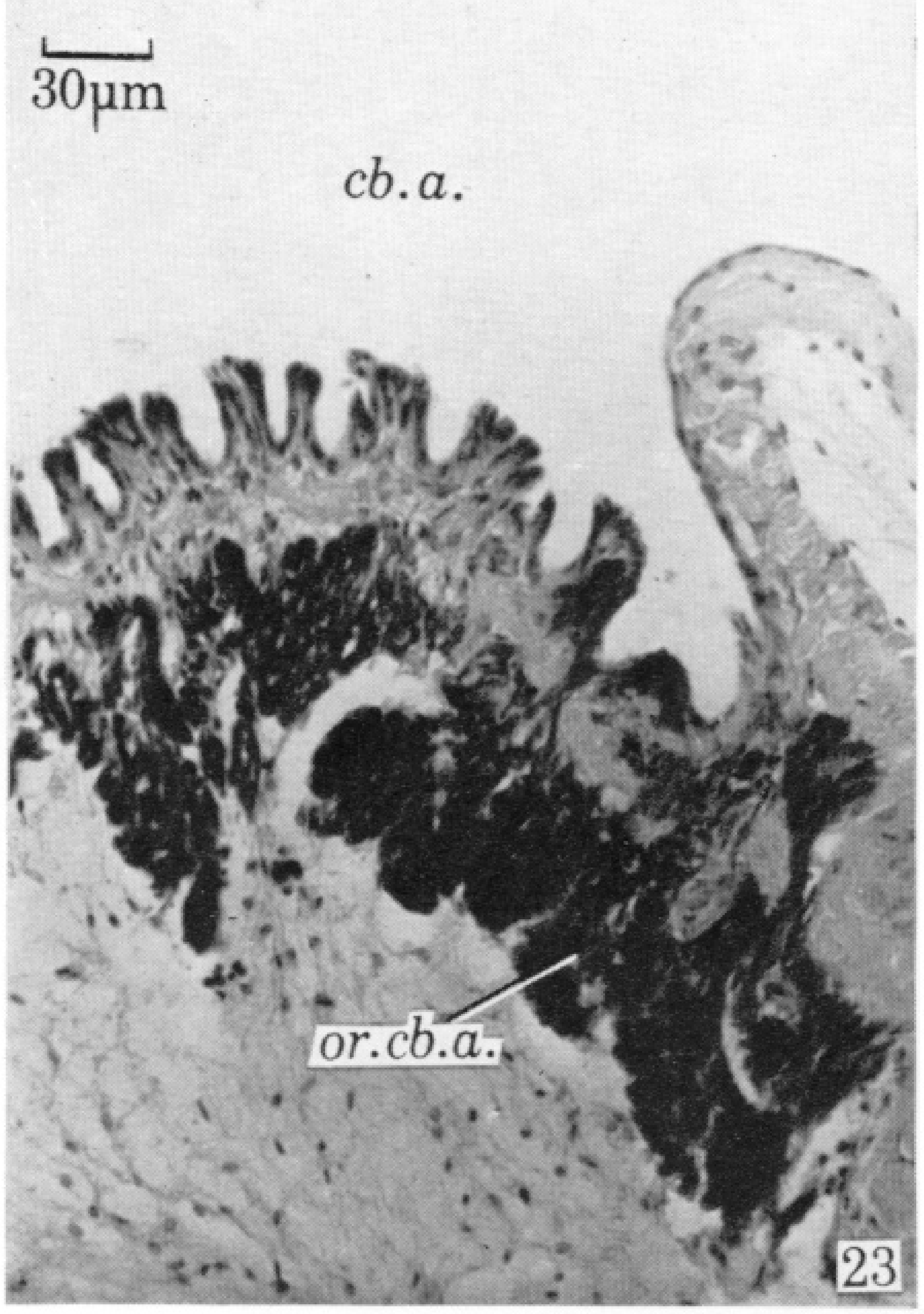

cb.a.
cap.
10μm
24


cb.a.
wh.bod.
or.cb.
a.
opt.
500μm
27

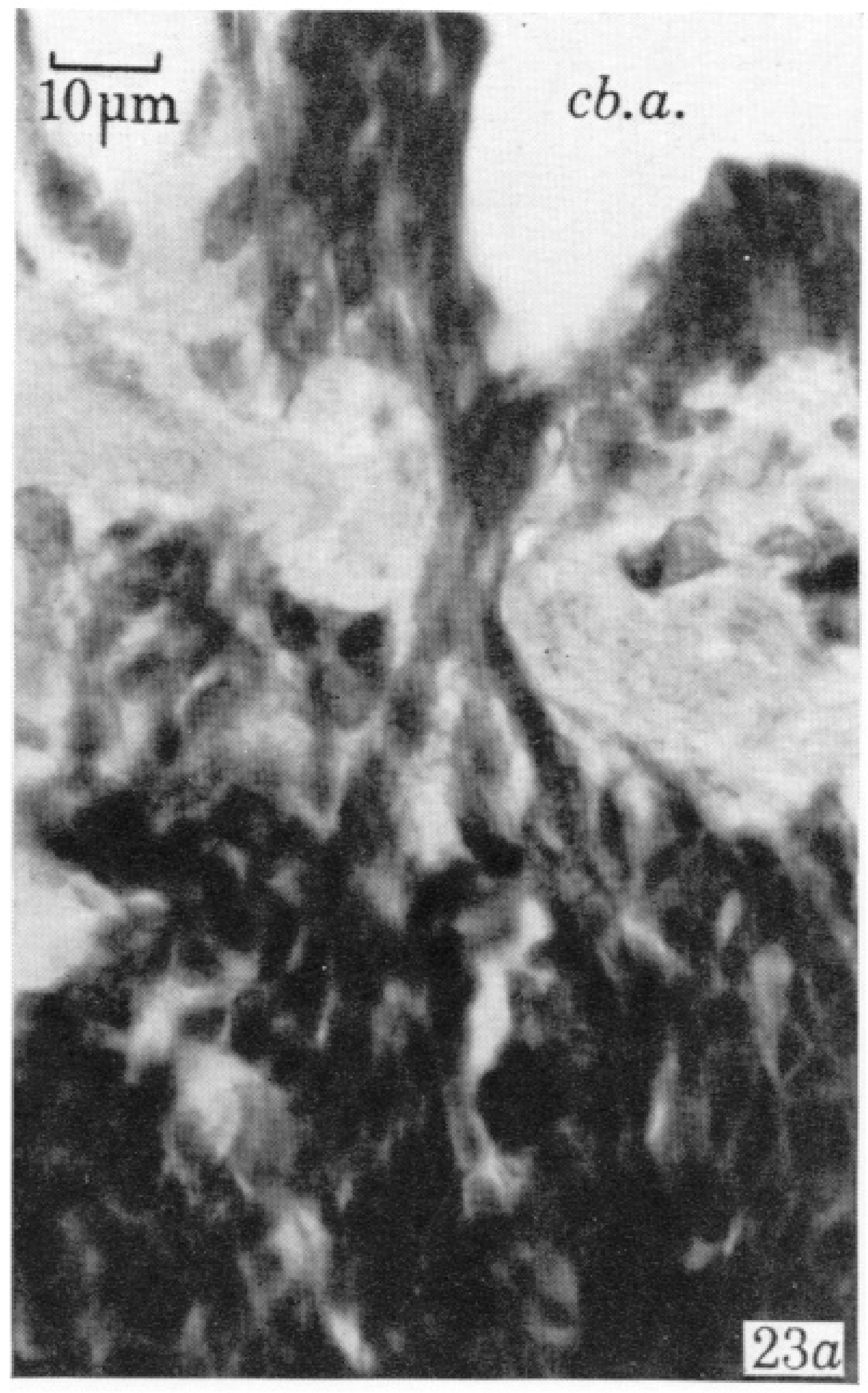

duc.
30μm
26


cb.a.
duc.
or.cb.
a.
opt.
subped.
500μm
28

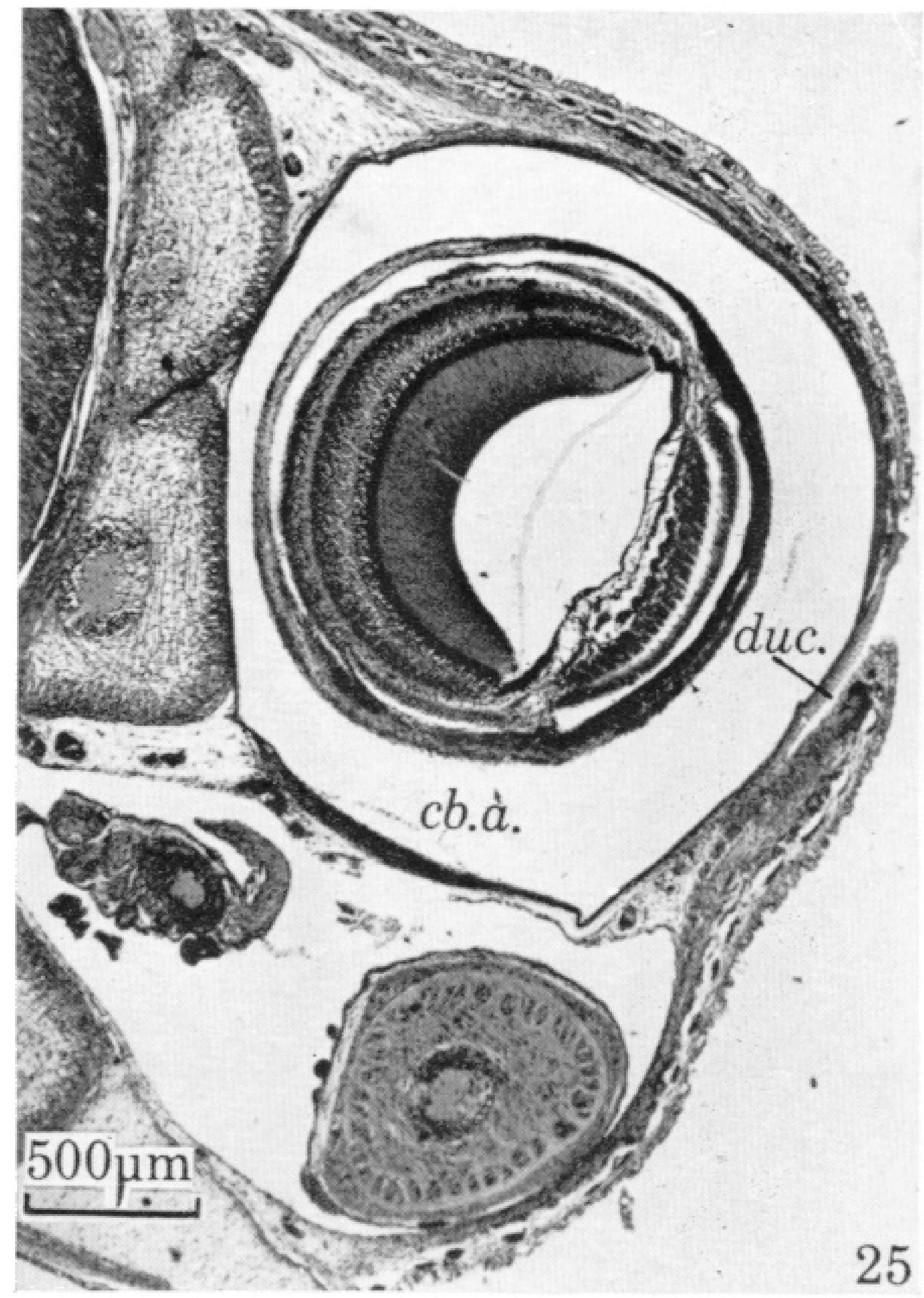

opt.
subped.
100μm
29



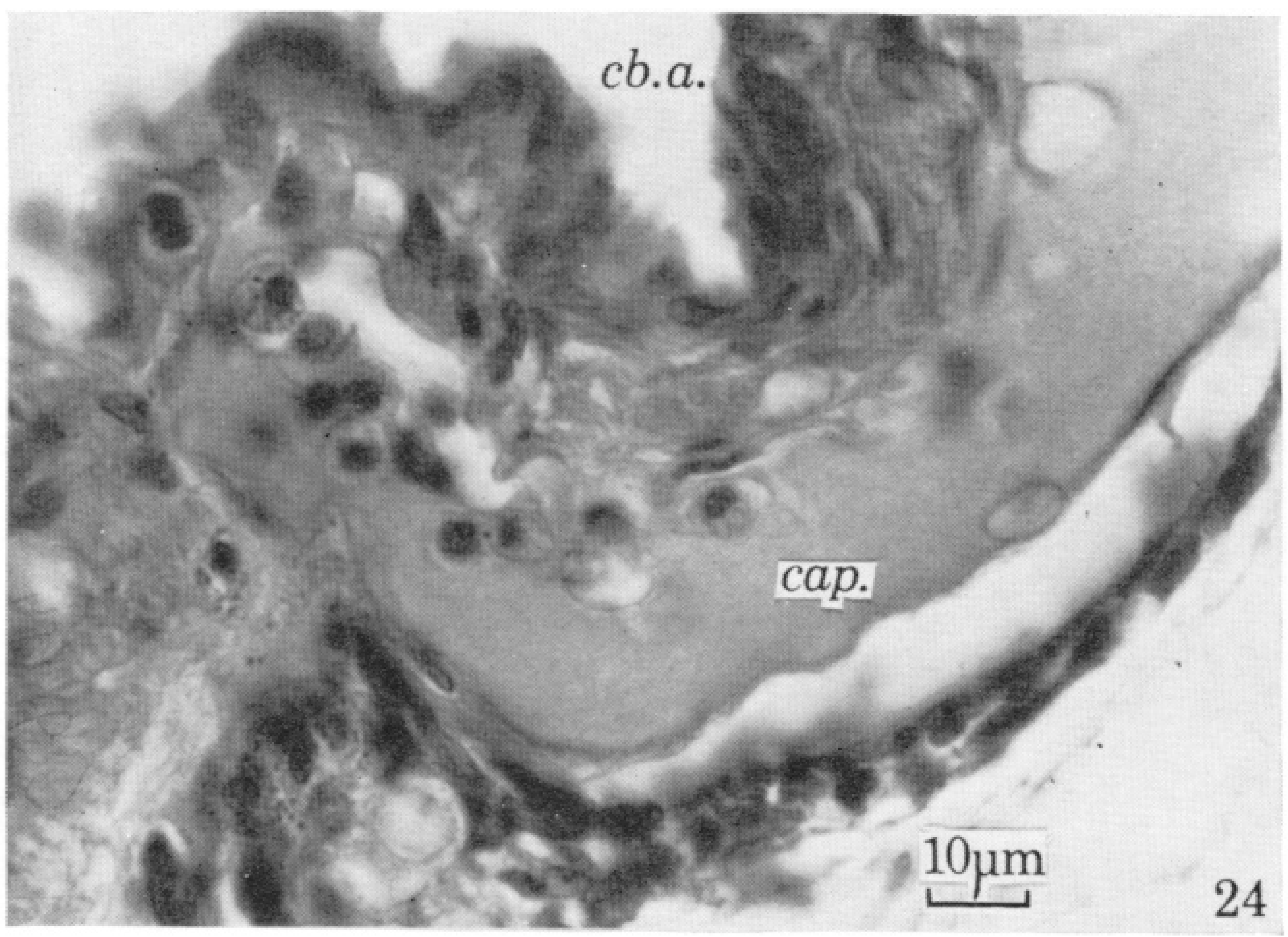
23



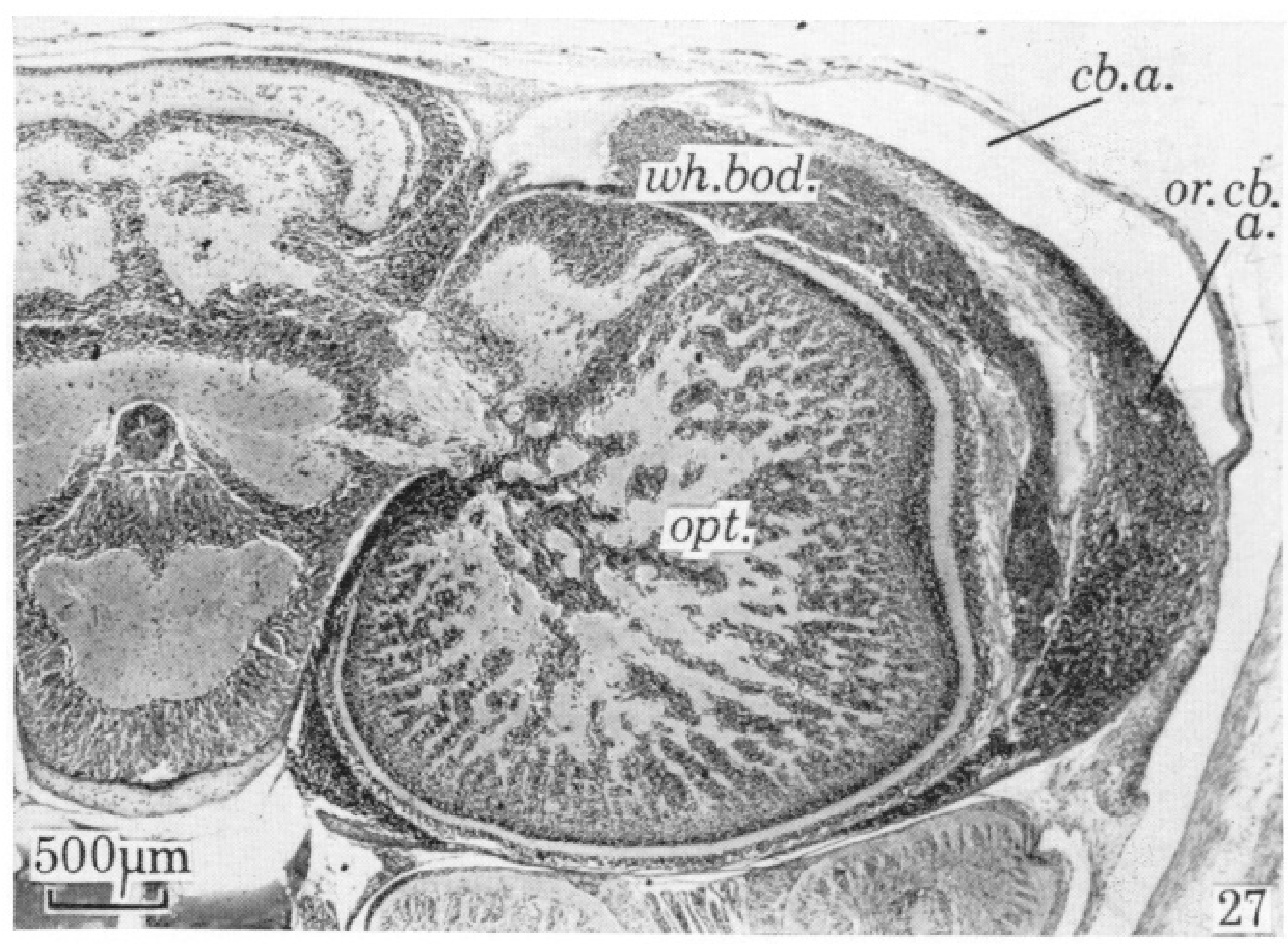
23a



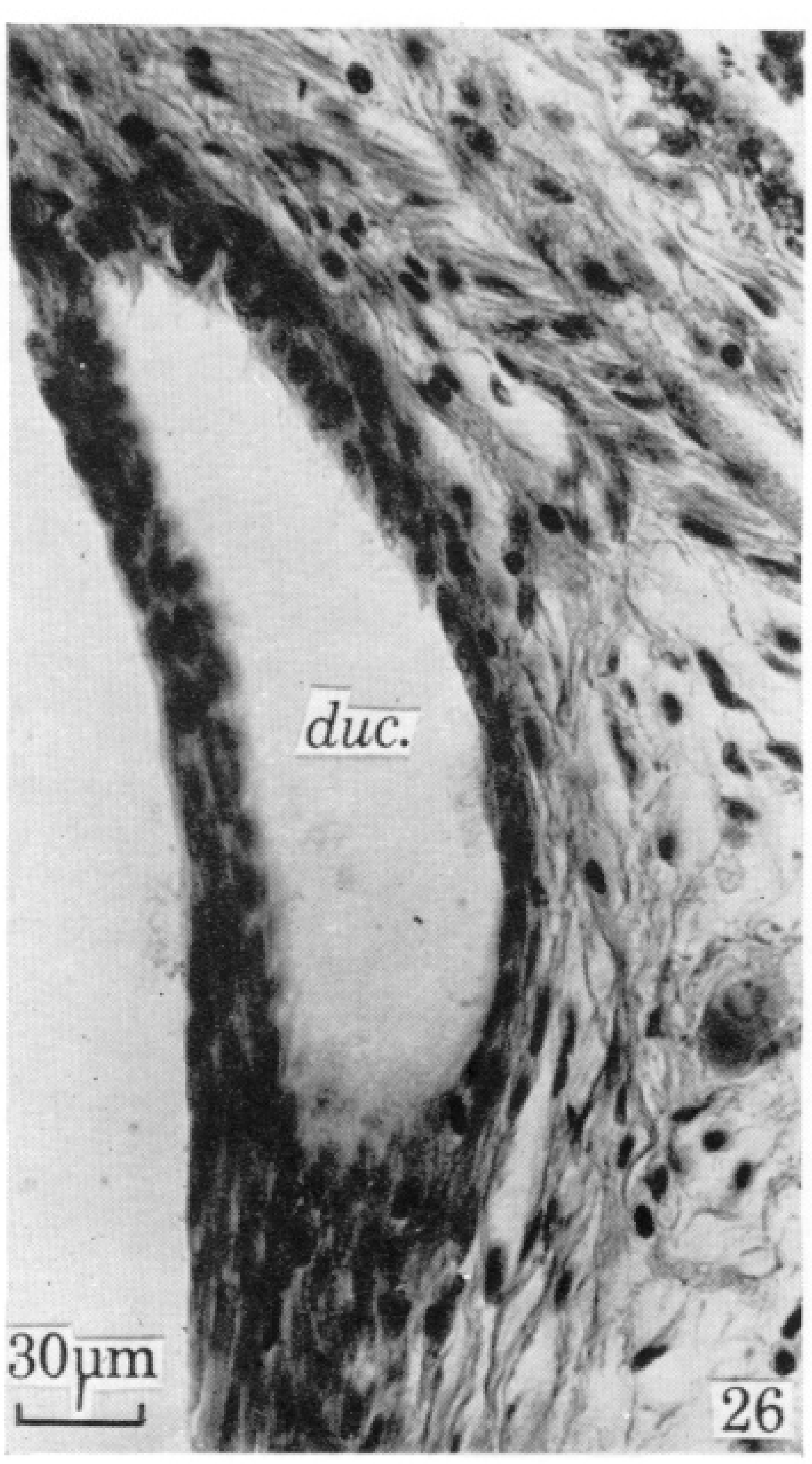
25



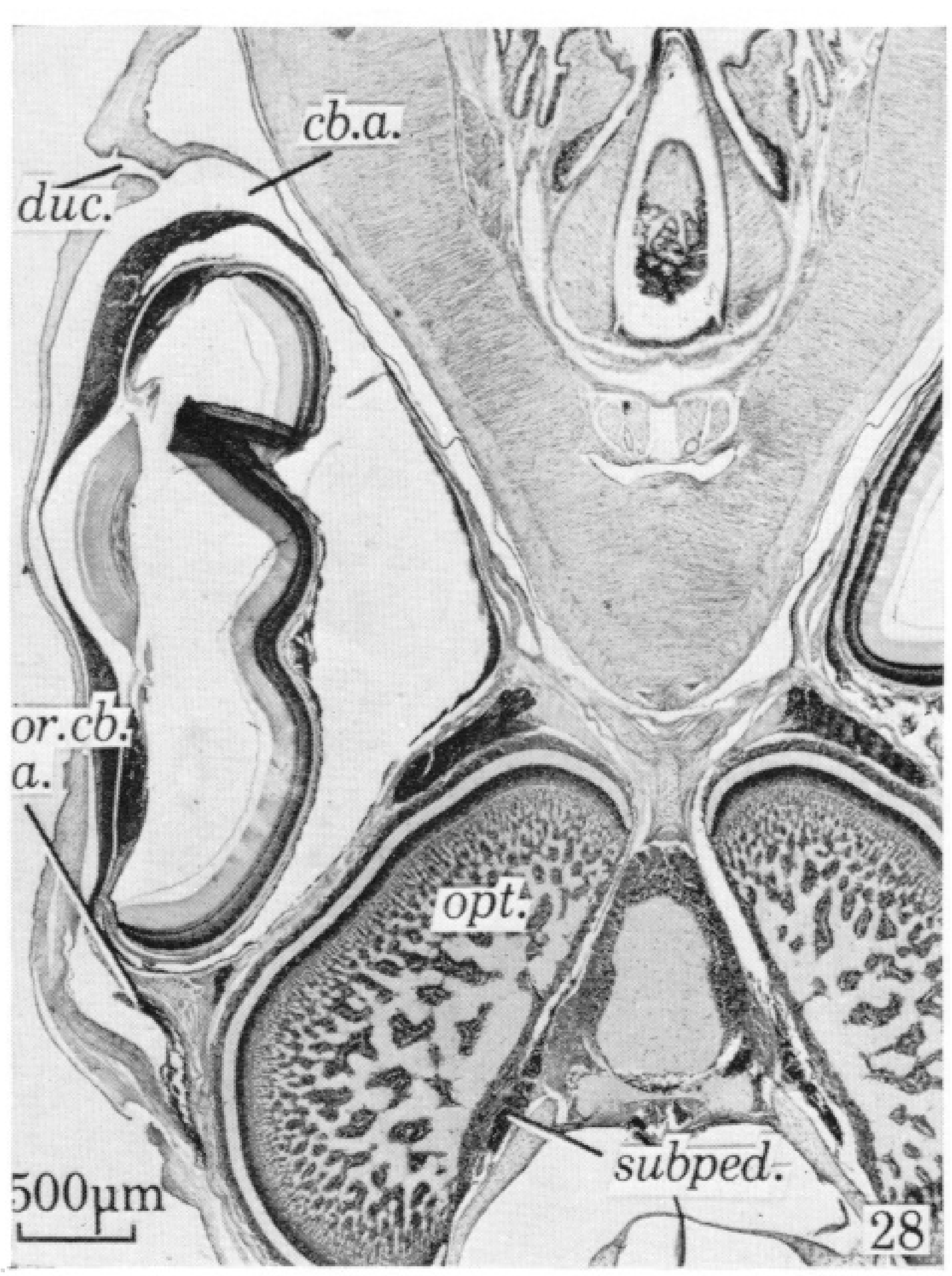
24



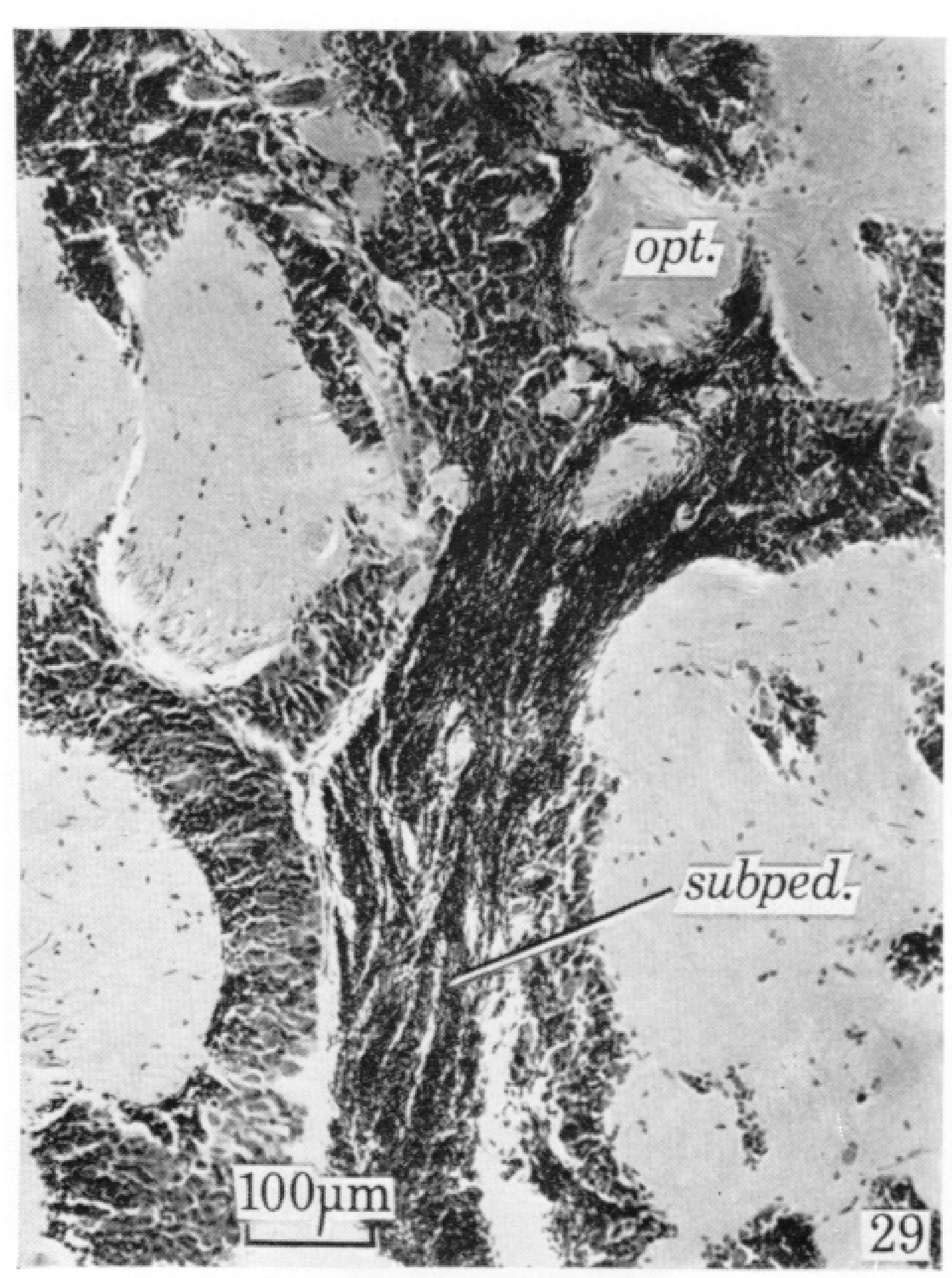
27



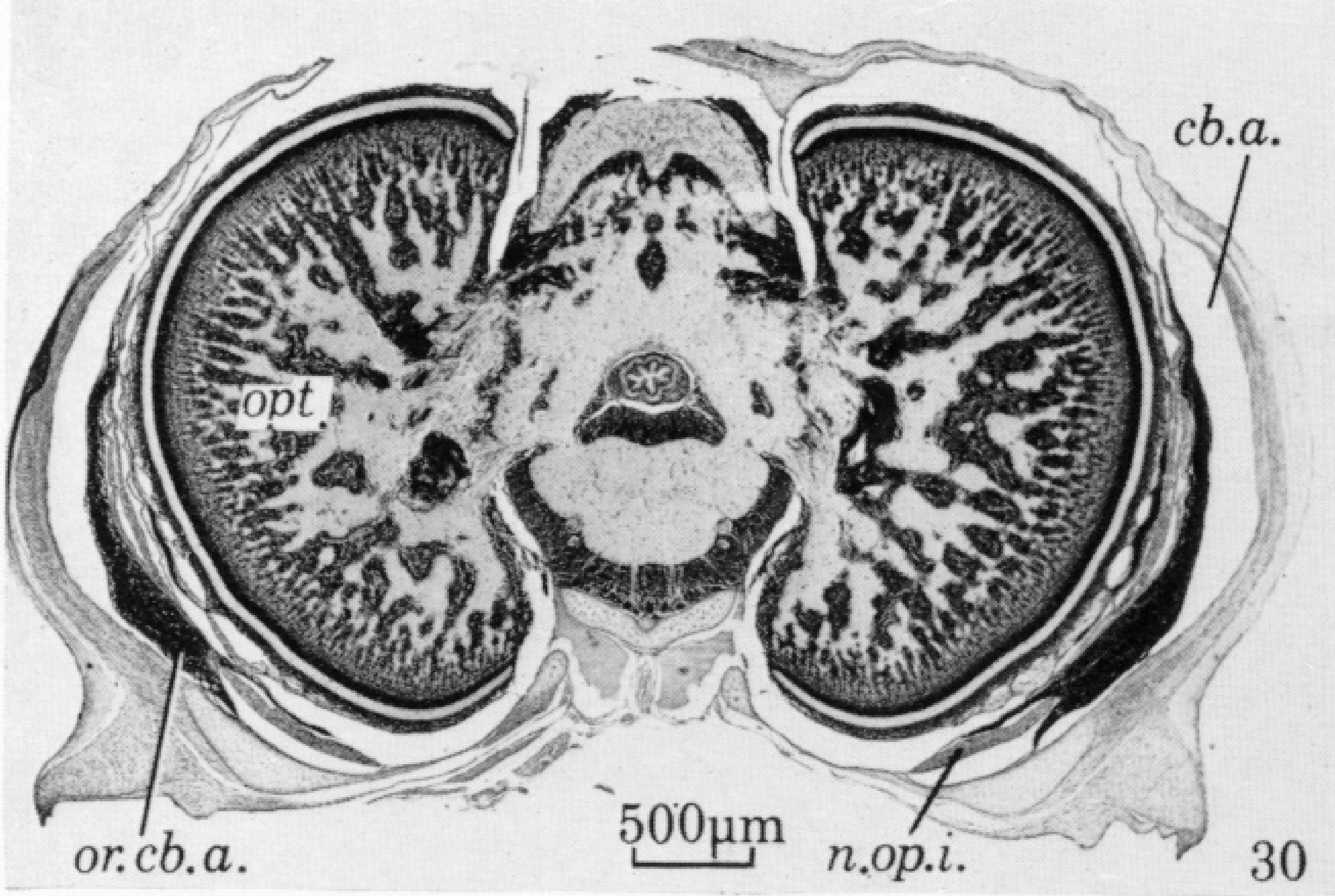
26



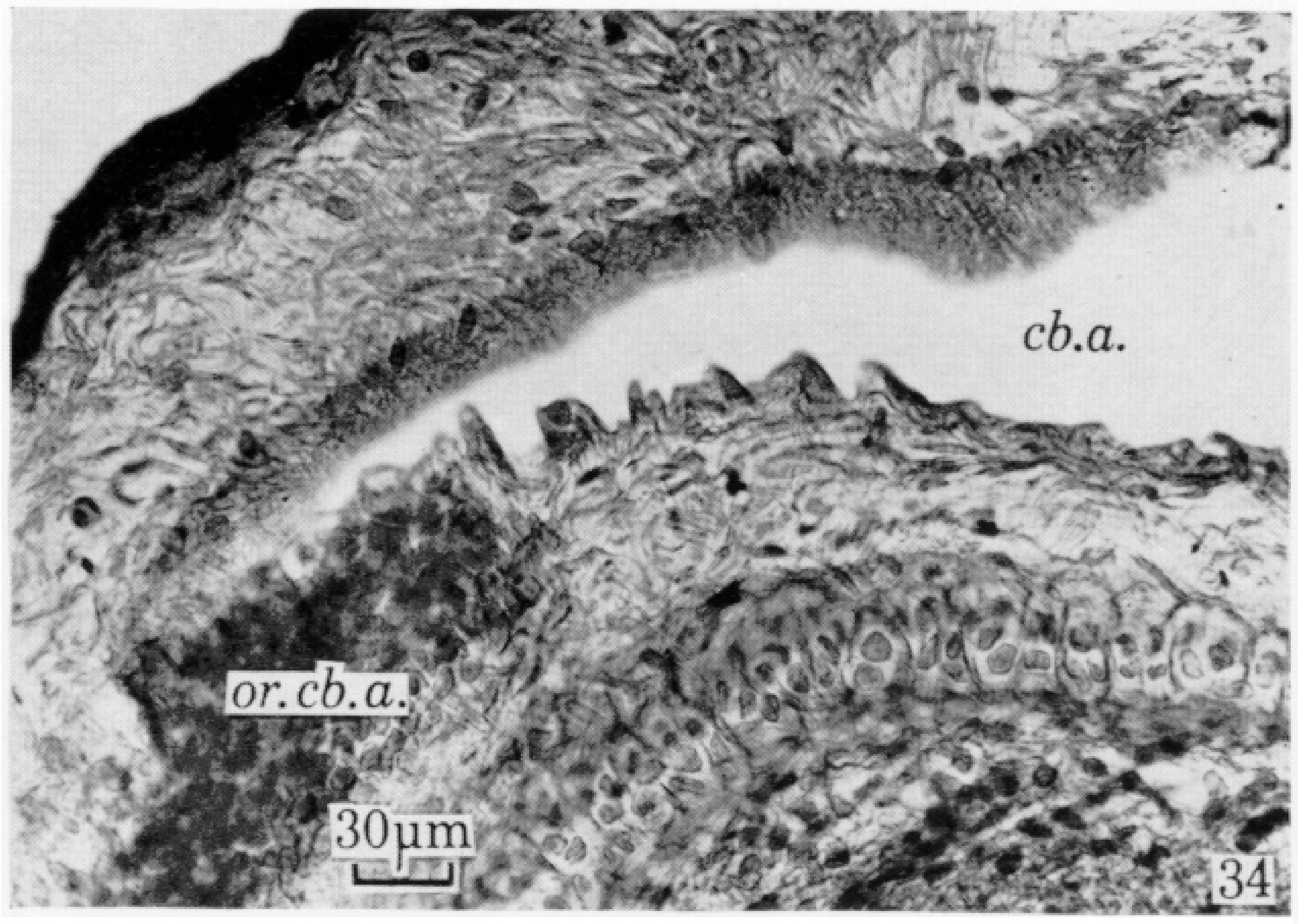
28



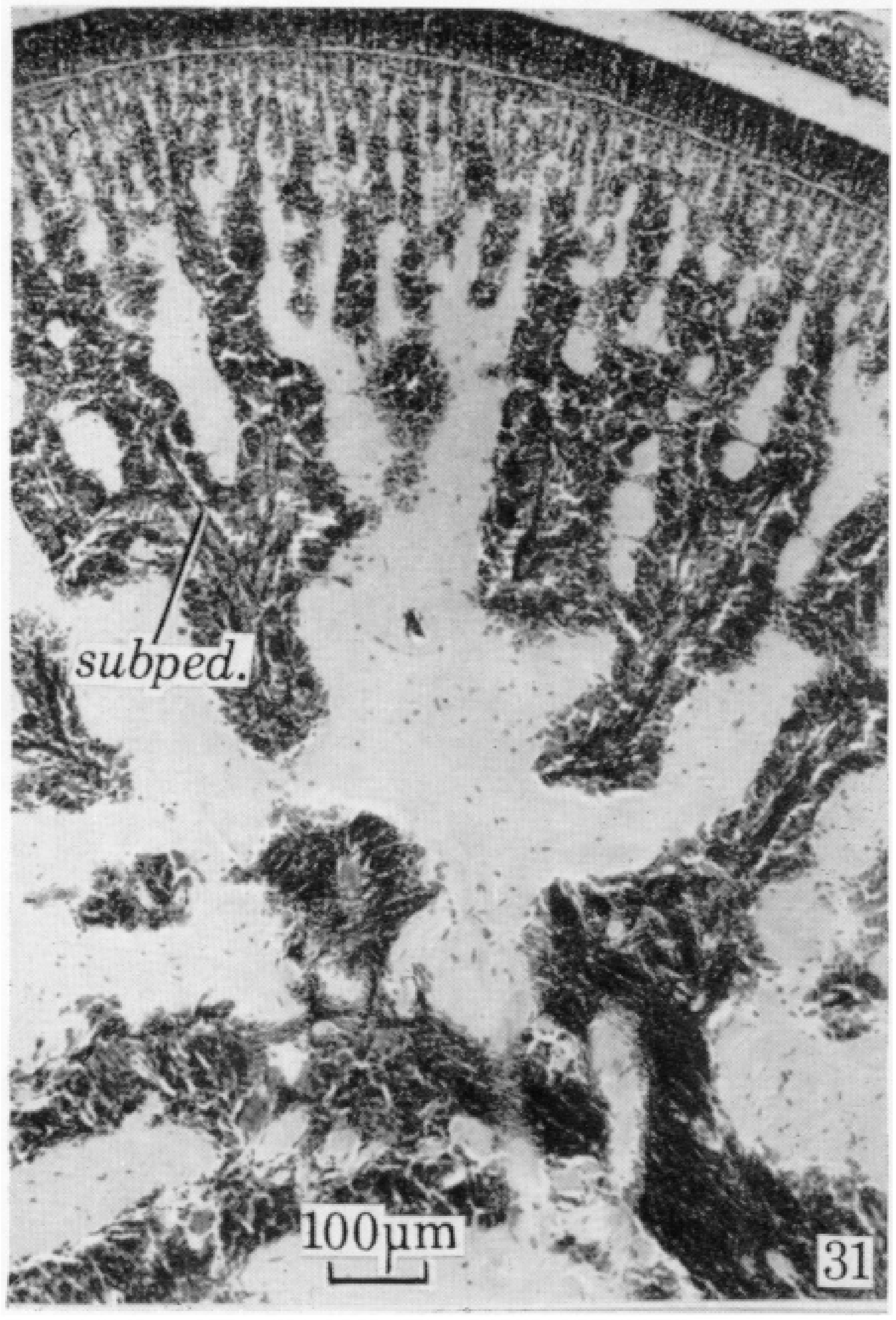
29



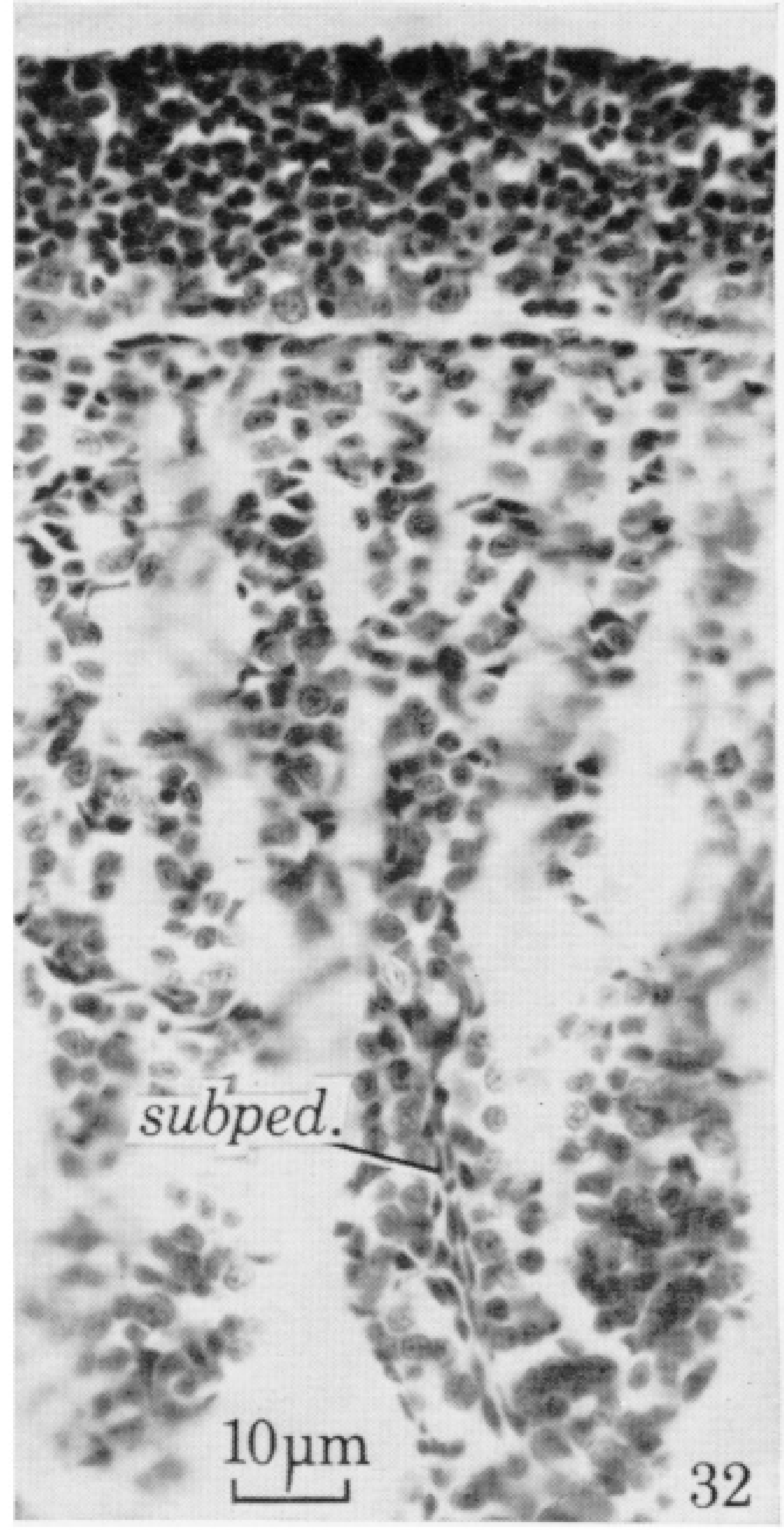
30



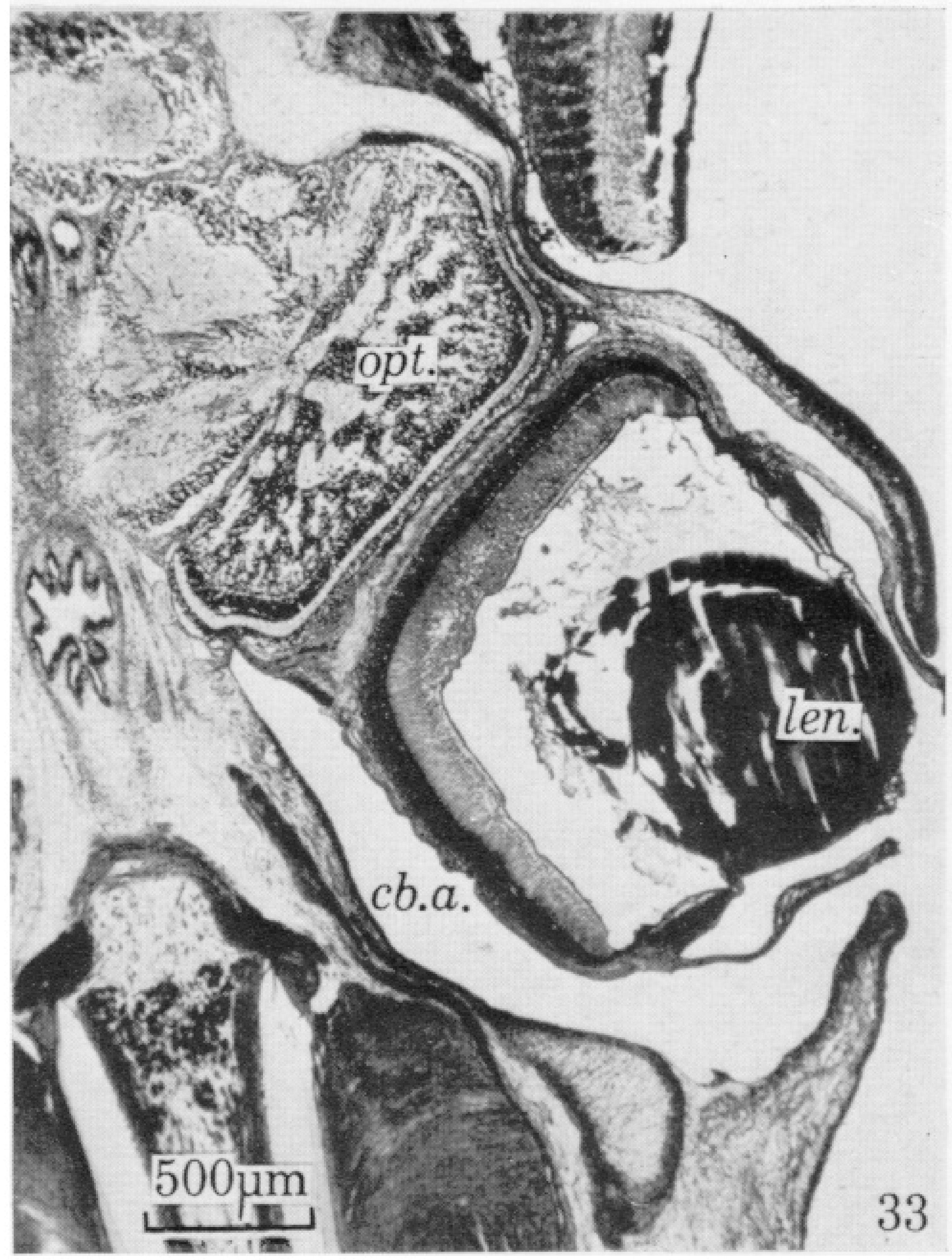
34



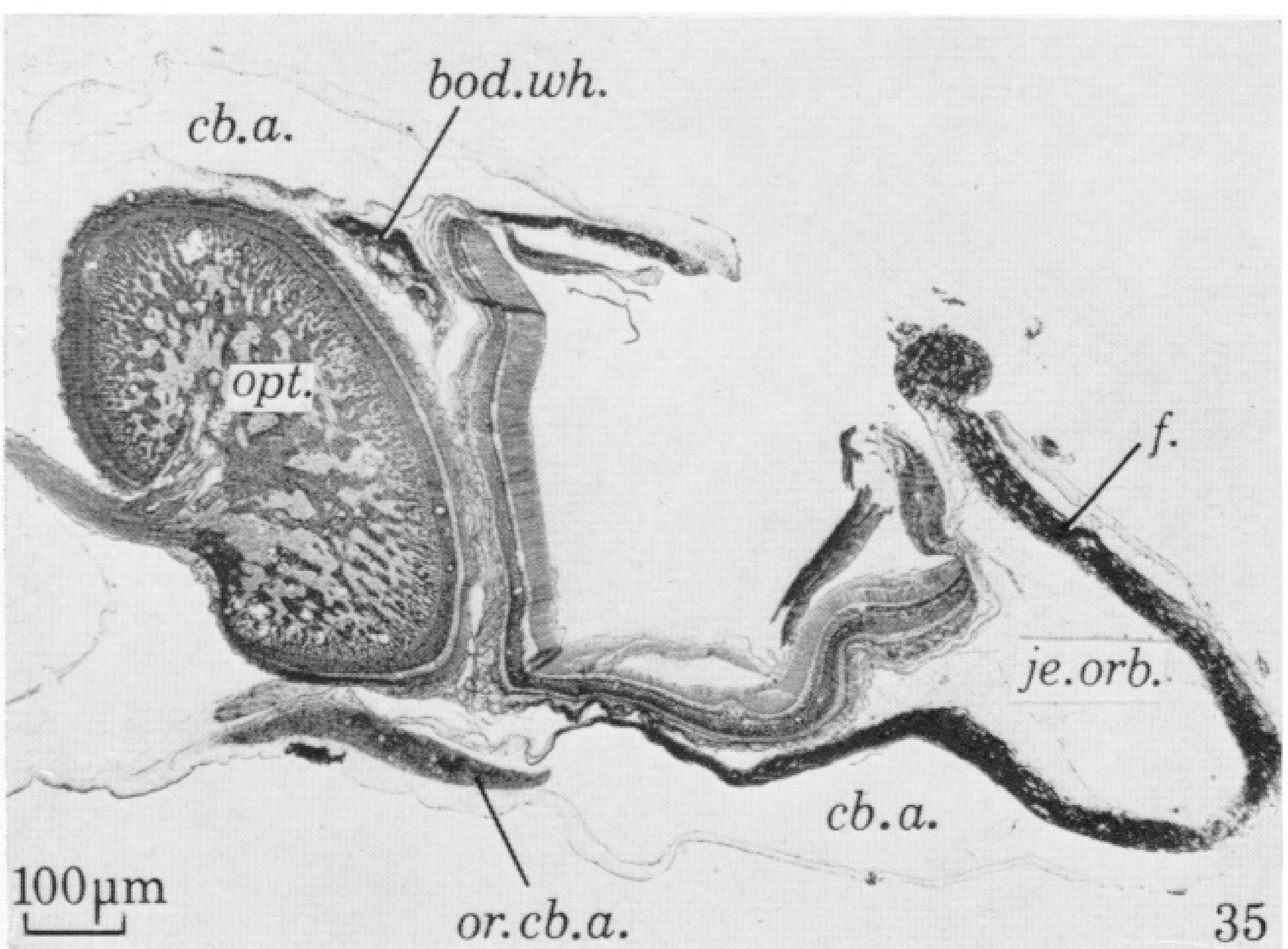
31



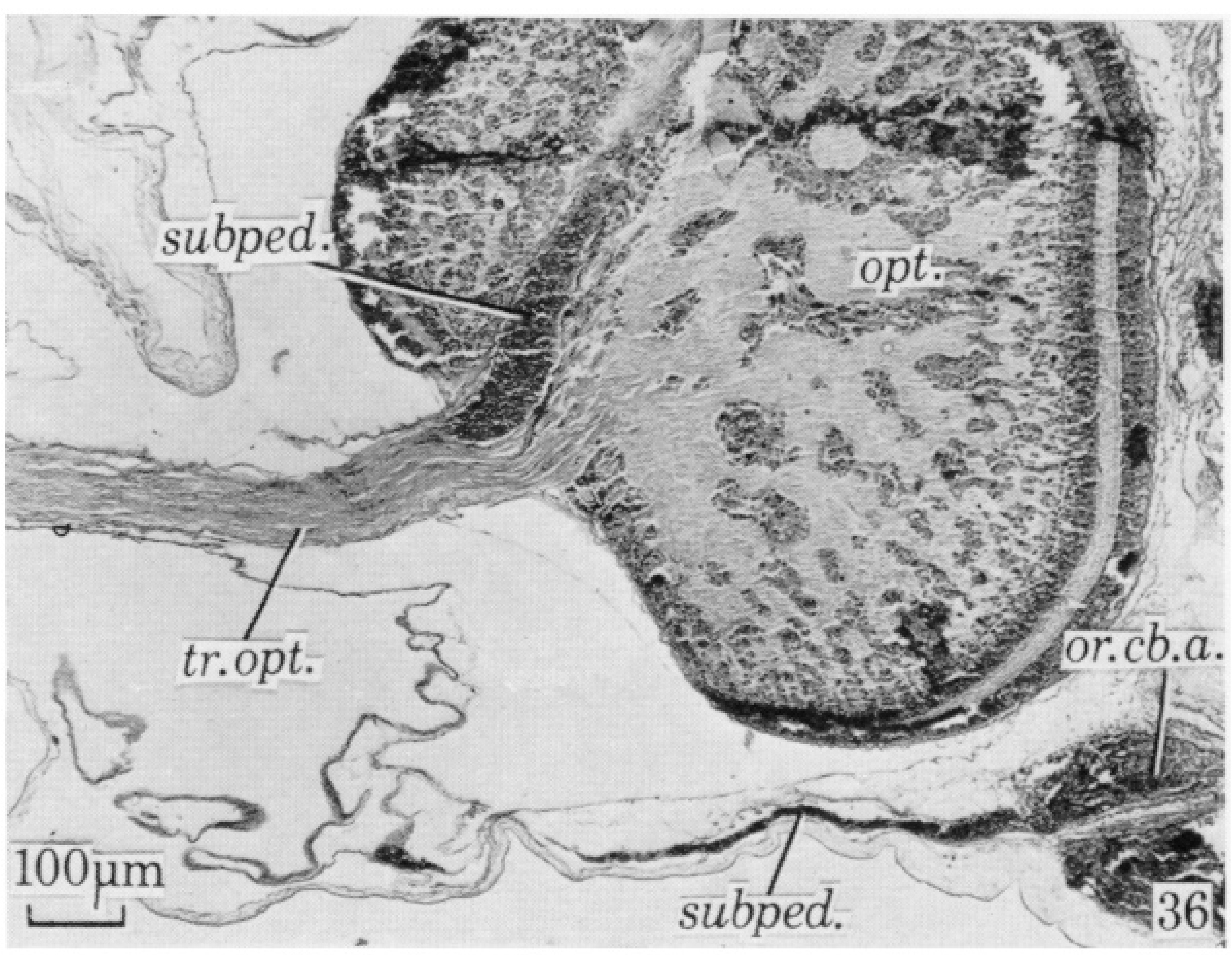
32



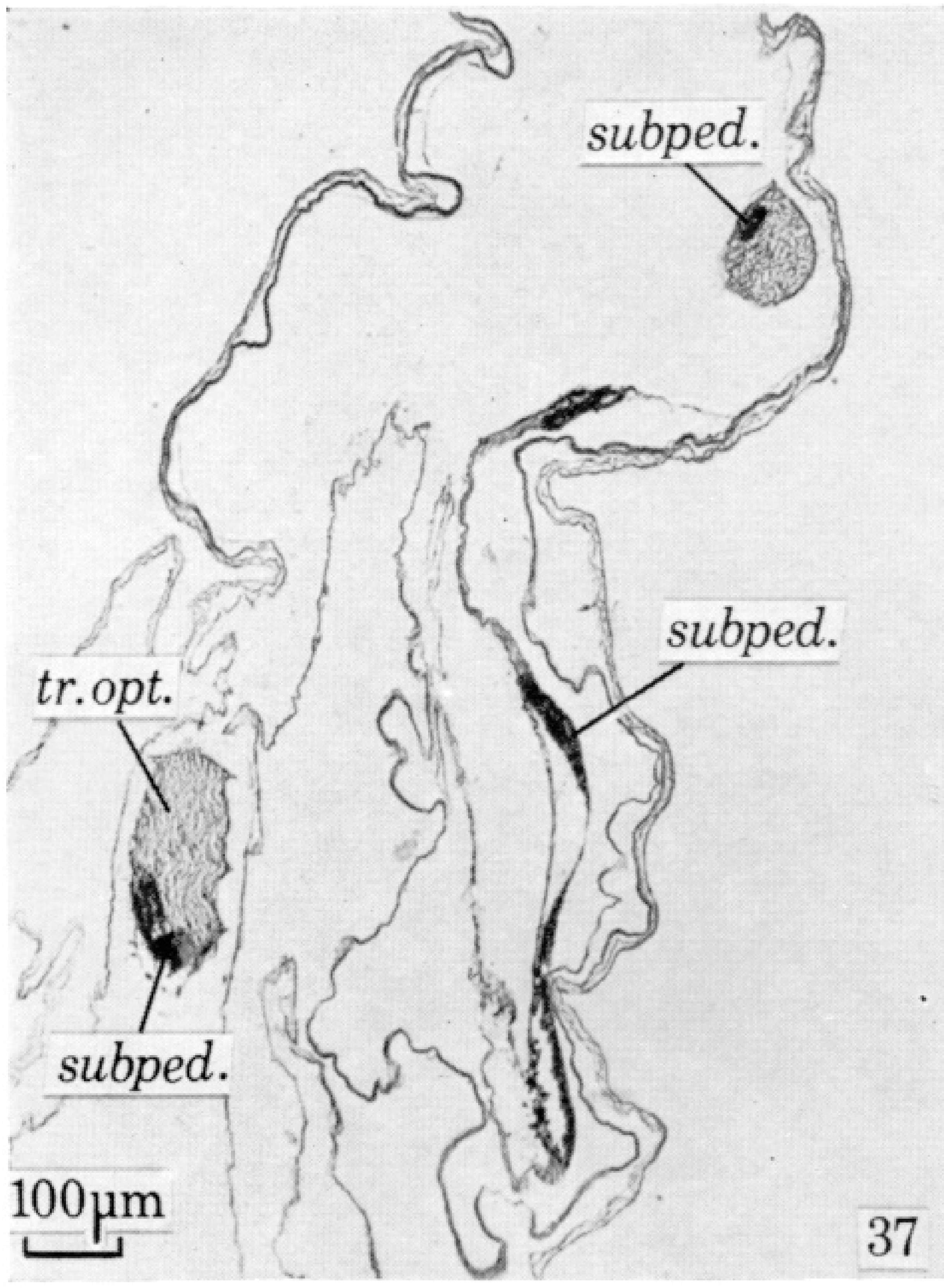
33

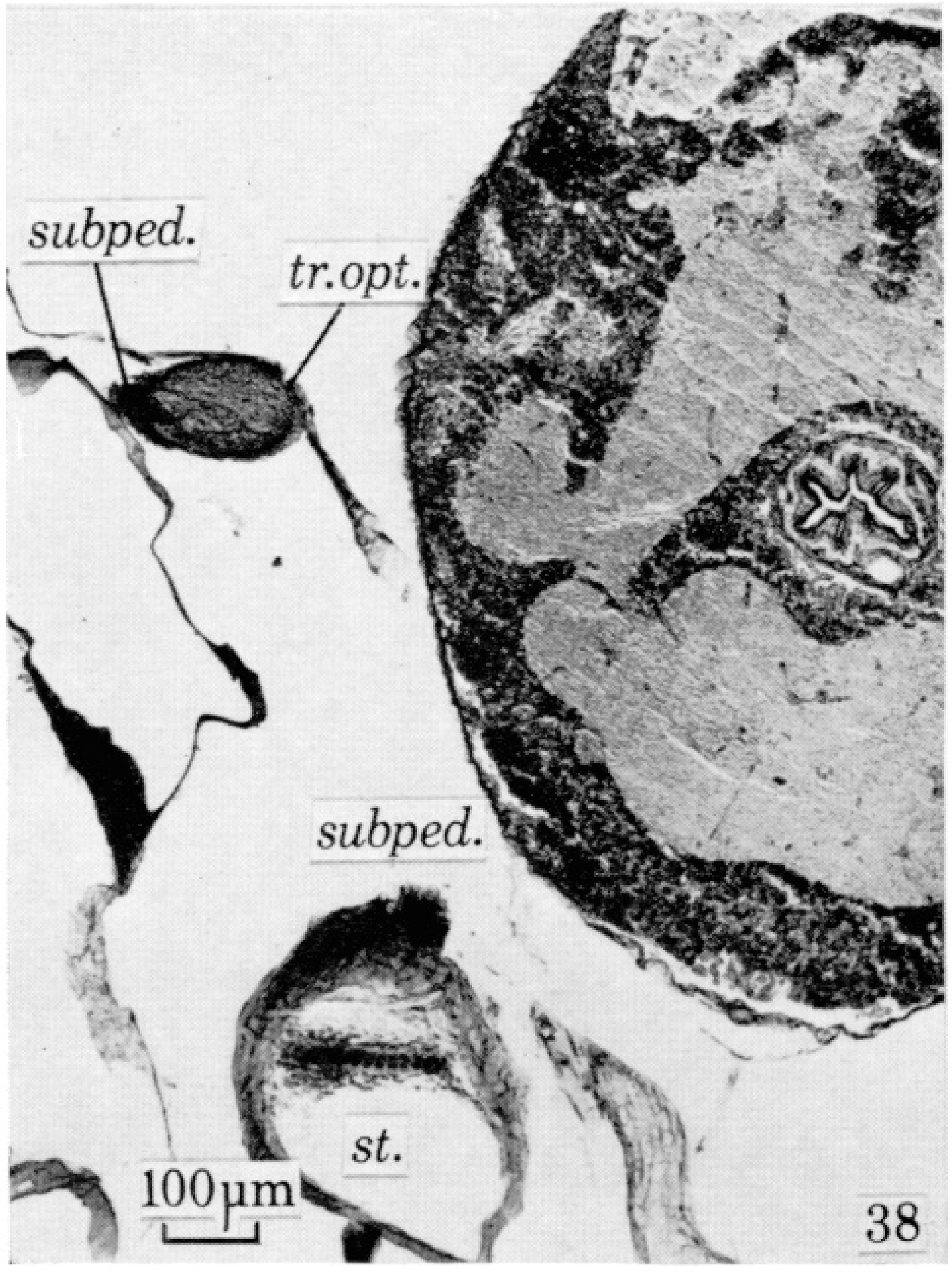


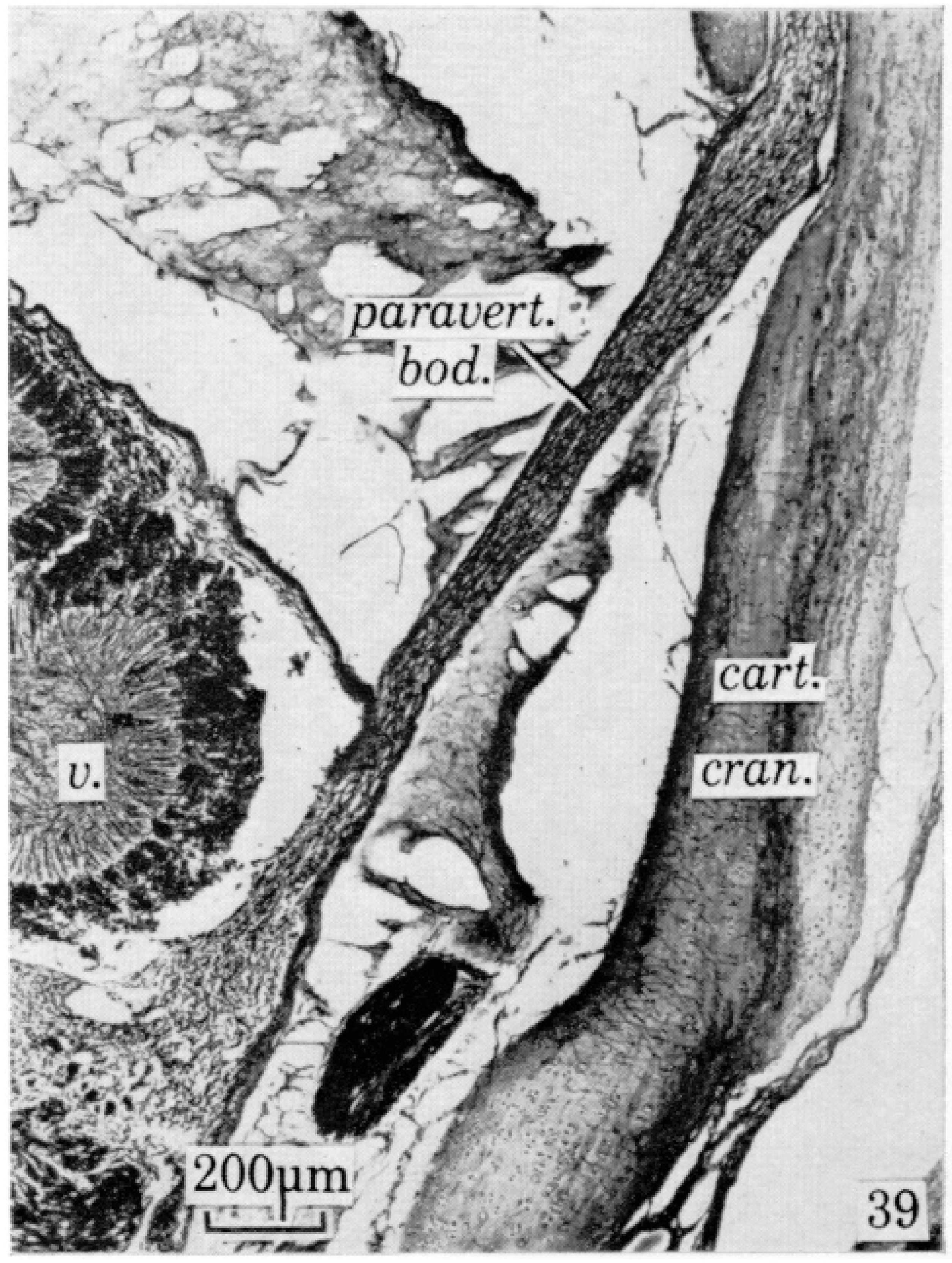
35

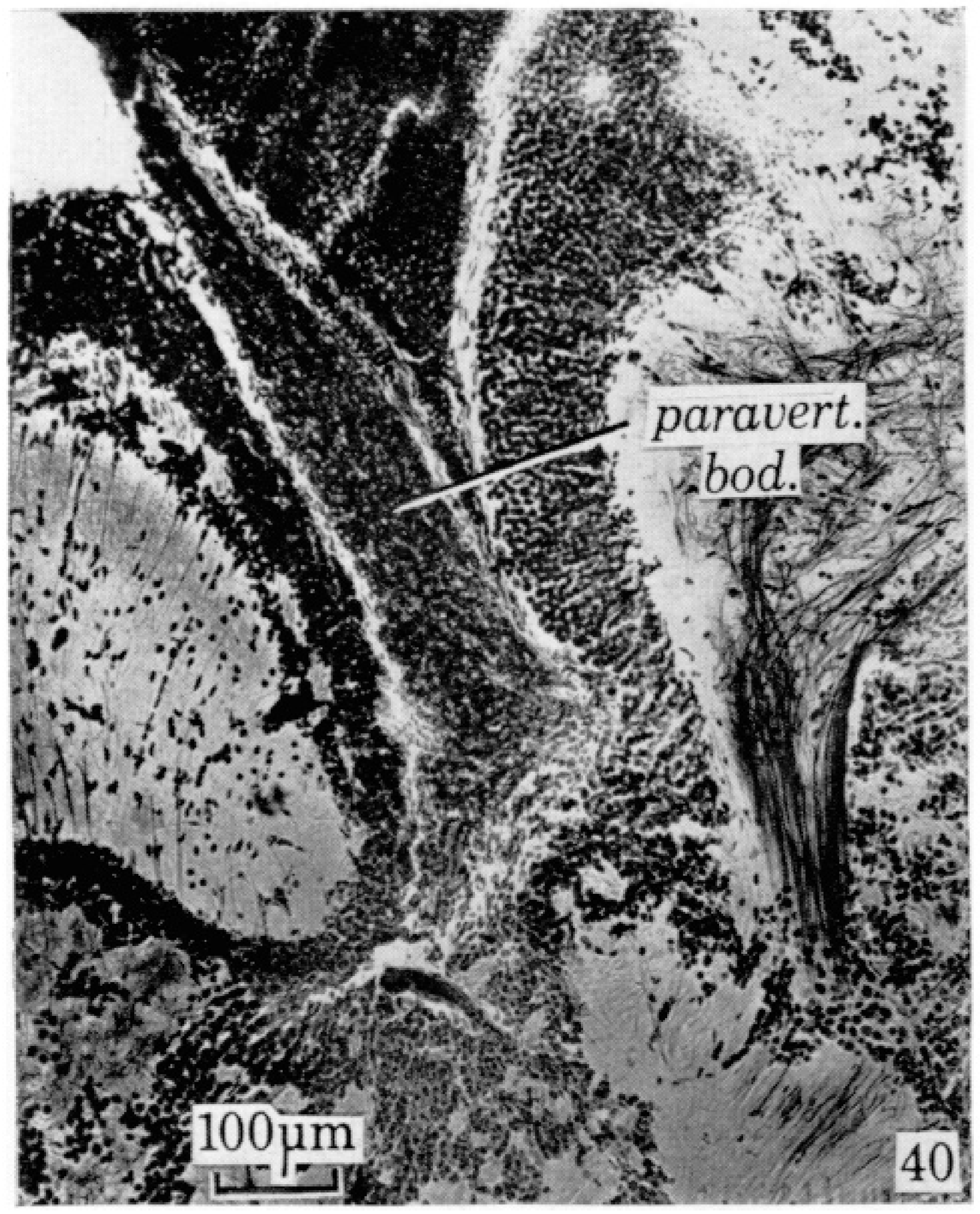


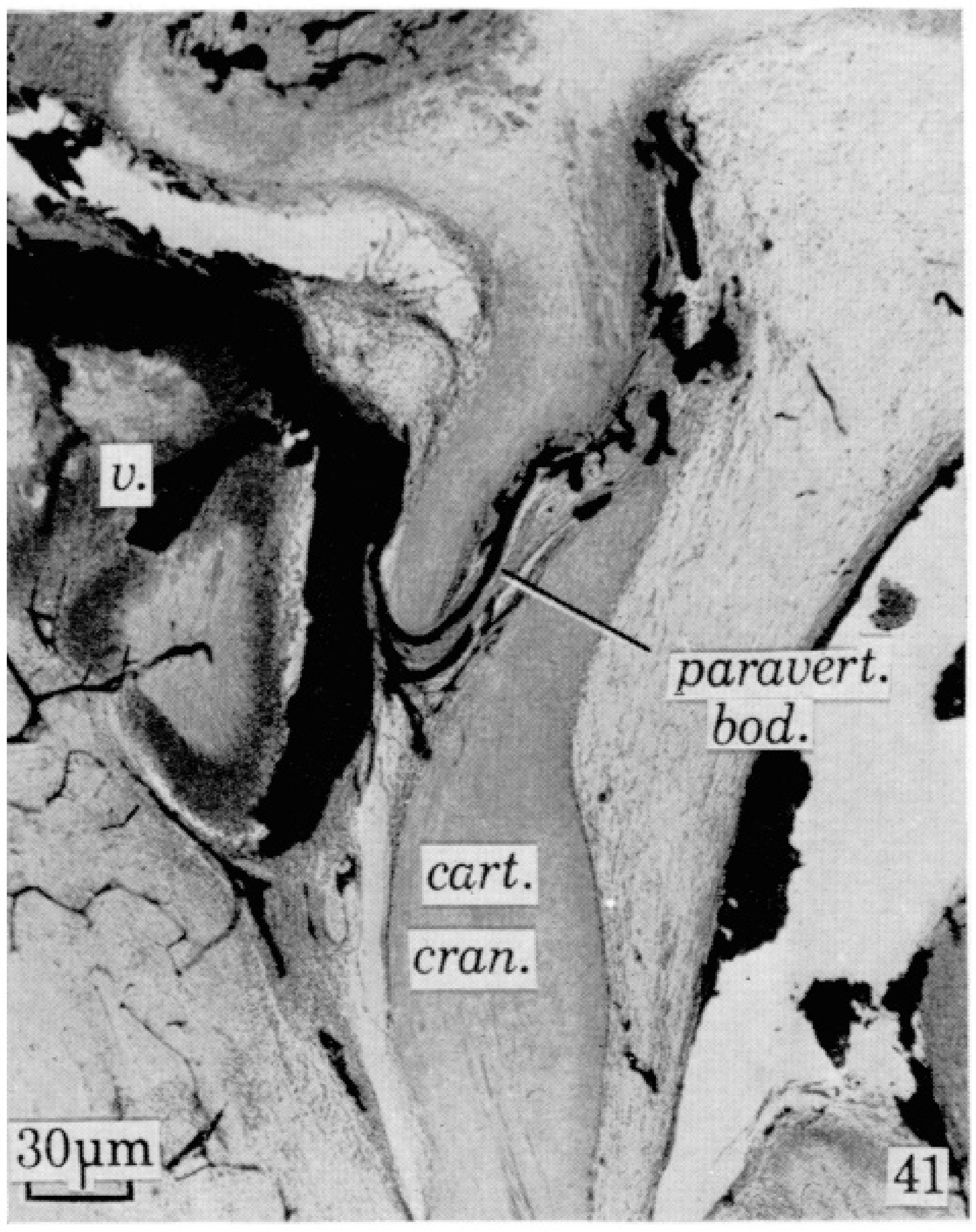
36

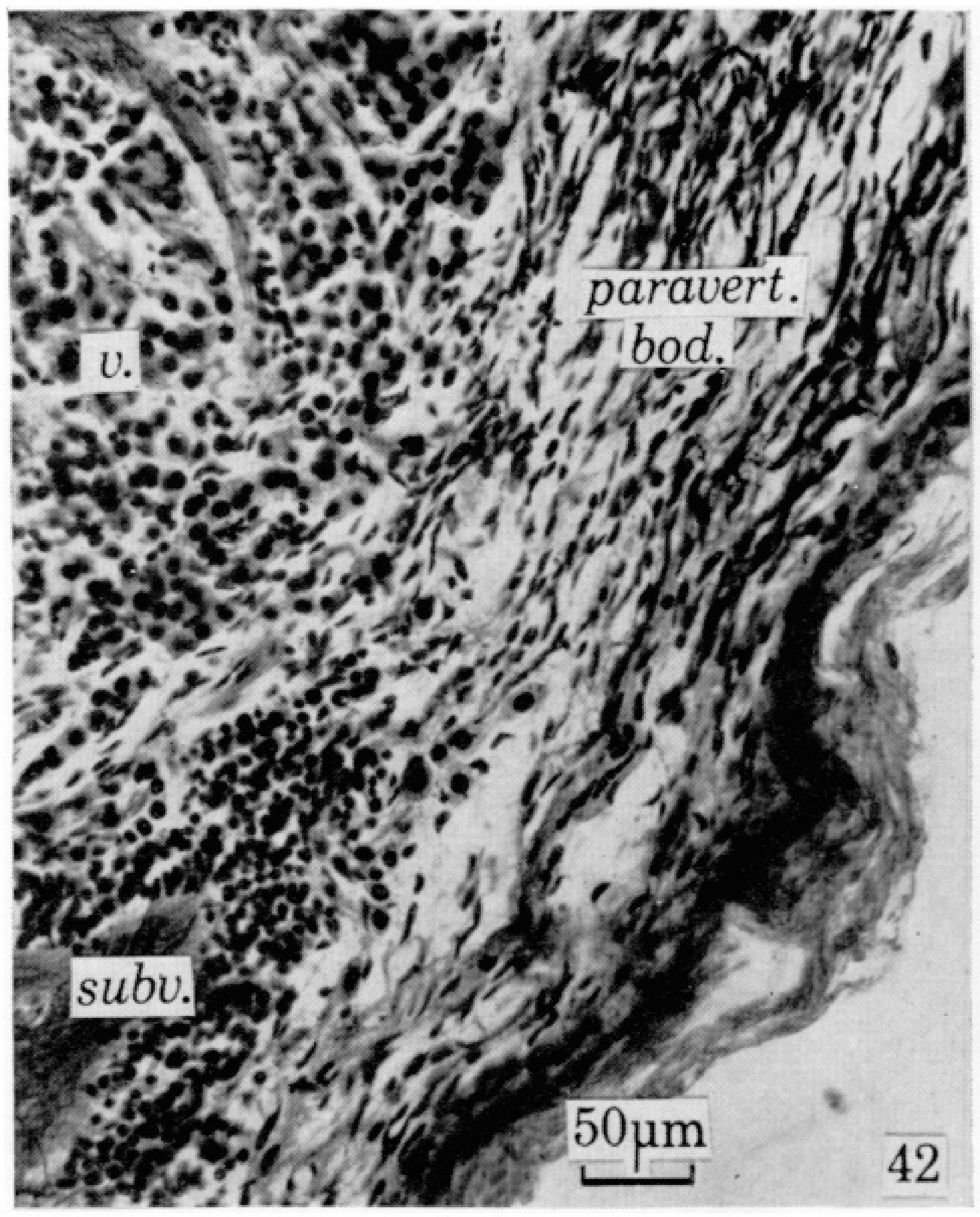

subped.
tr.opt.
subped.
subped.
100μm
37


subped.
tr.opt.
subped.
st.
100μm
38


paravert.
bod.
v.
cart.
cran.
200μm
39

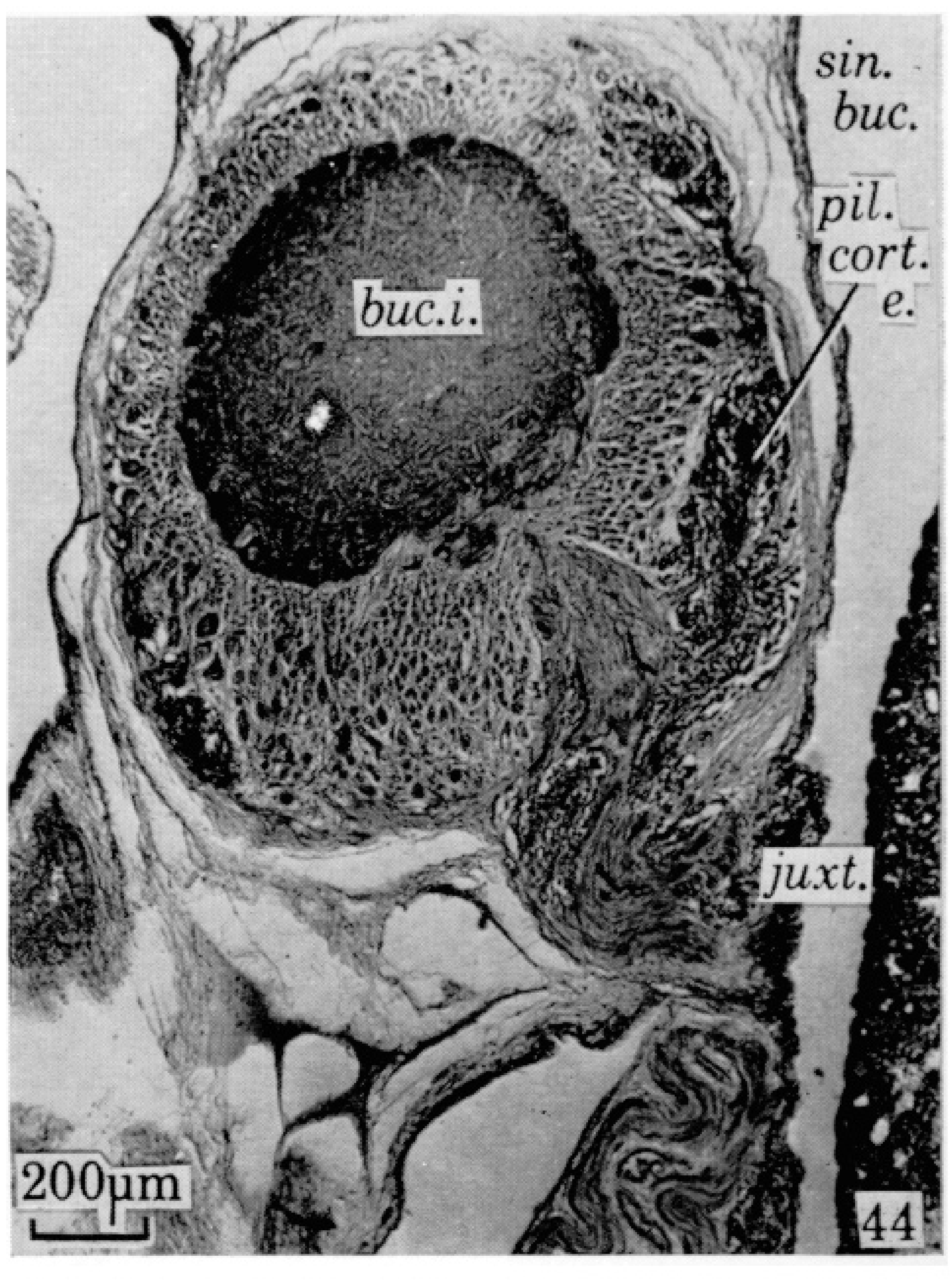

paravert.
bod.
100μm
40

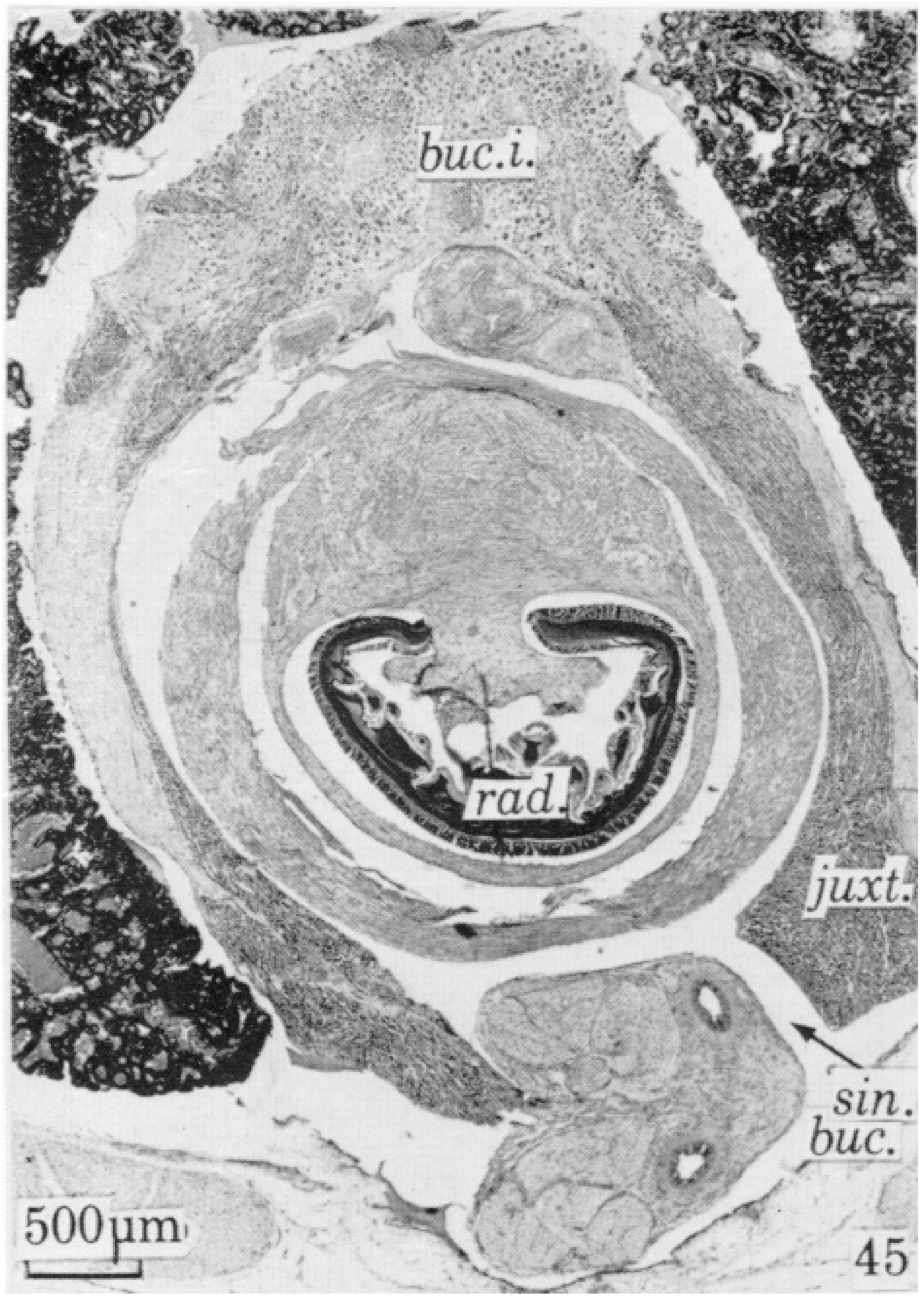

v.
paravert.
bod.
cart.
cran.
30μm
41


paravert.
bod.
v.
subv.
50μm
42

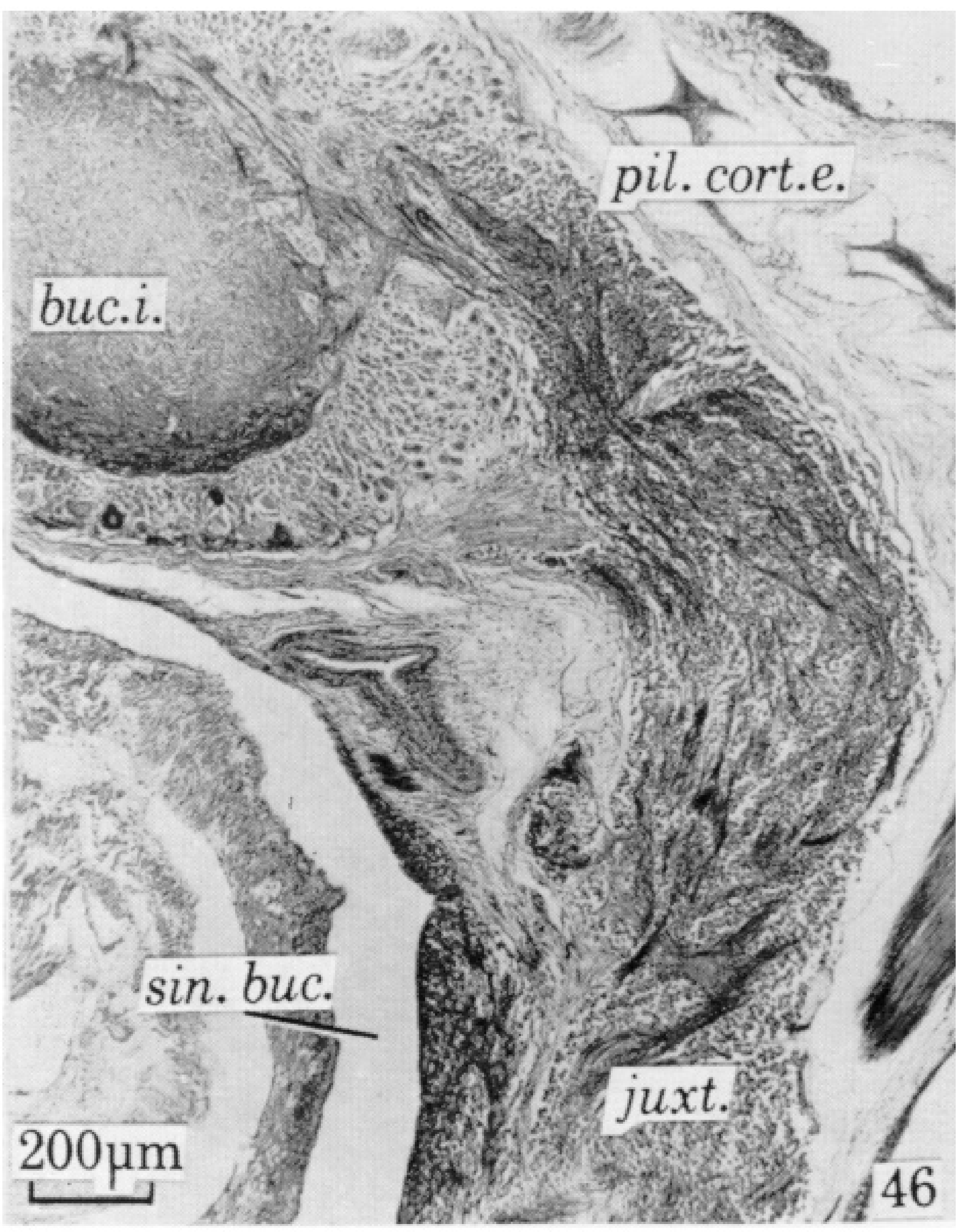

10μm
43a


10μm
43b

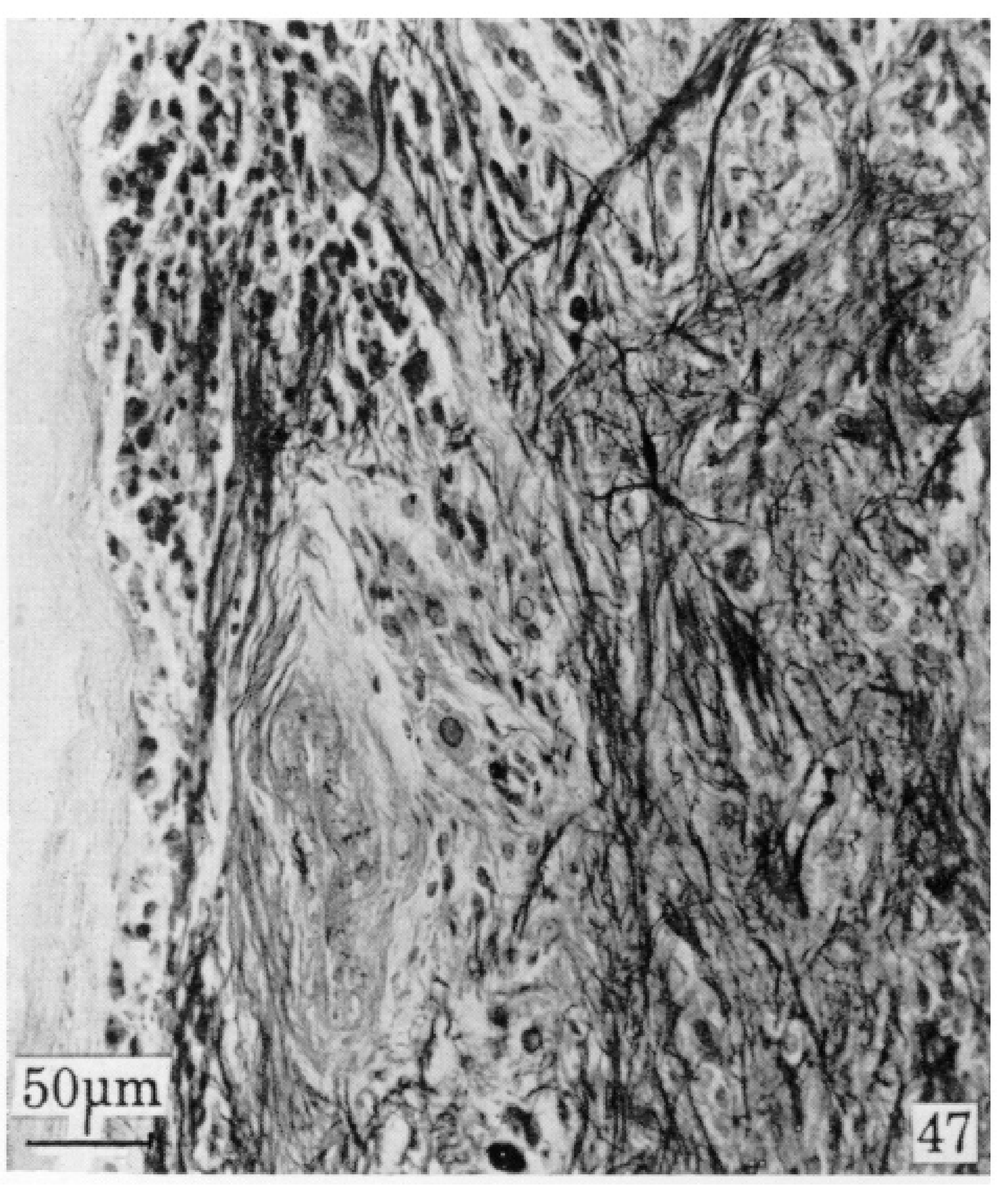

sin.
buc.
pil.
cort.
e.
buc.i.
juxt.
200μm
44



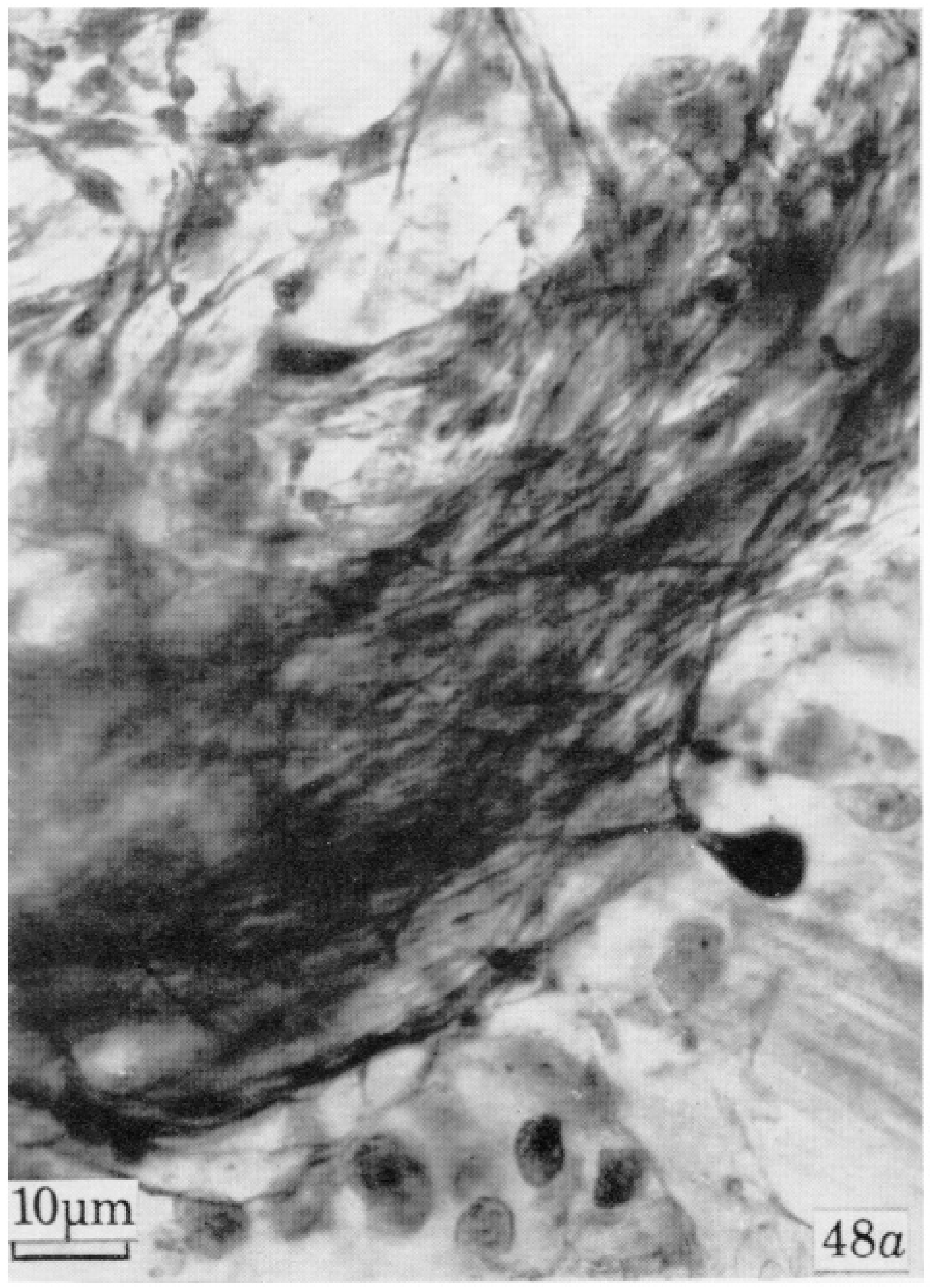
45



46



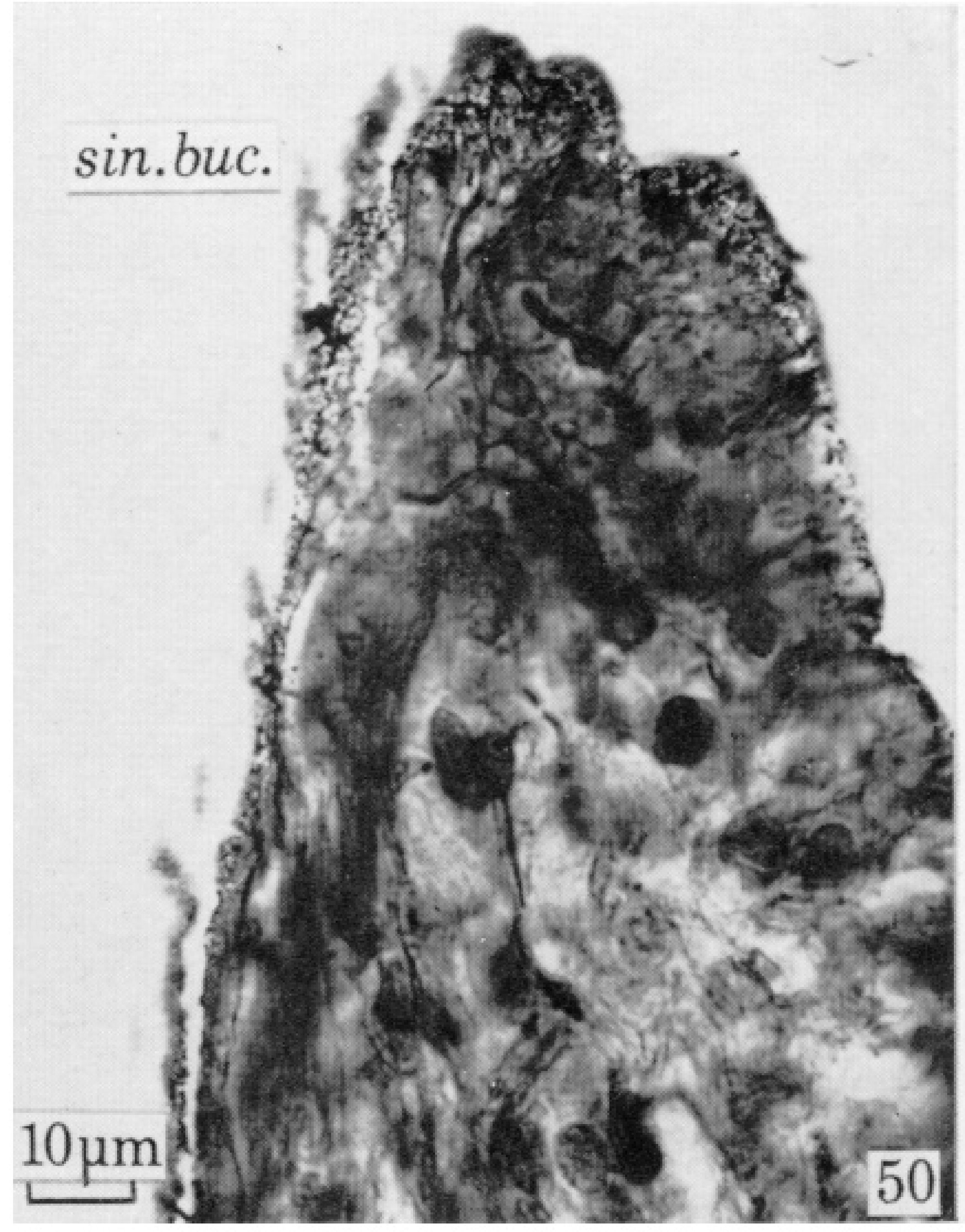
47



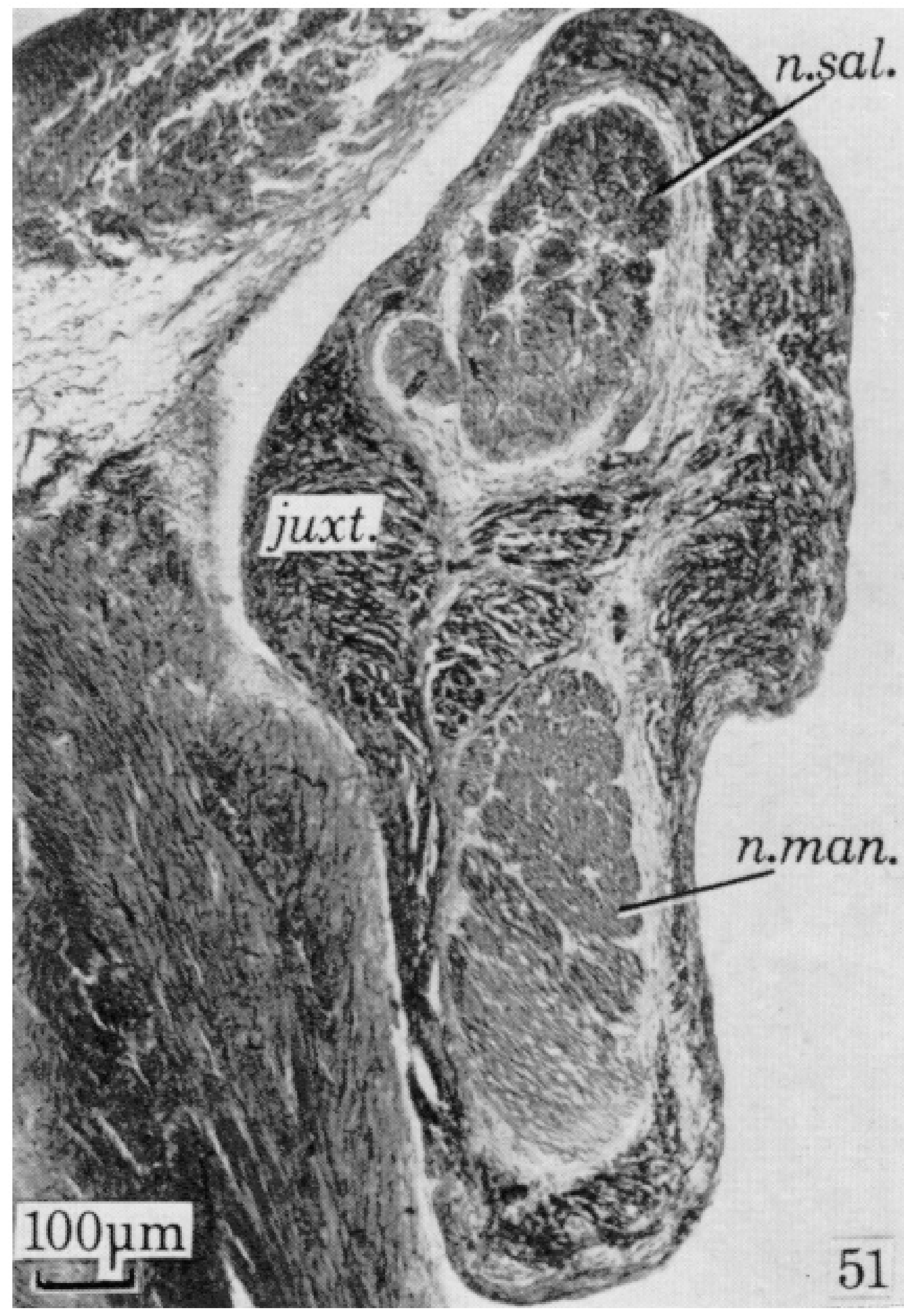
48*a*

48*b*

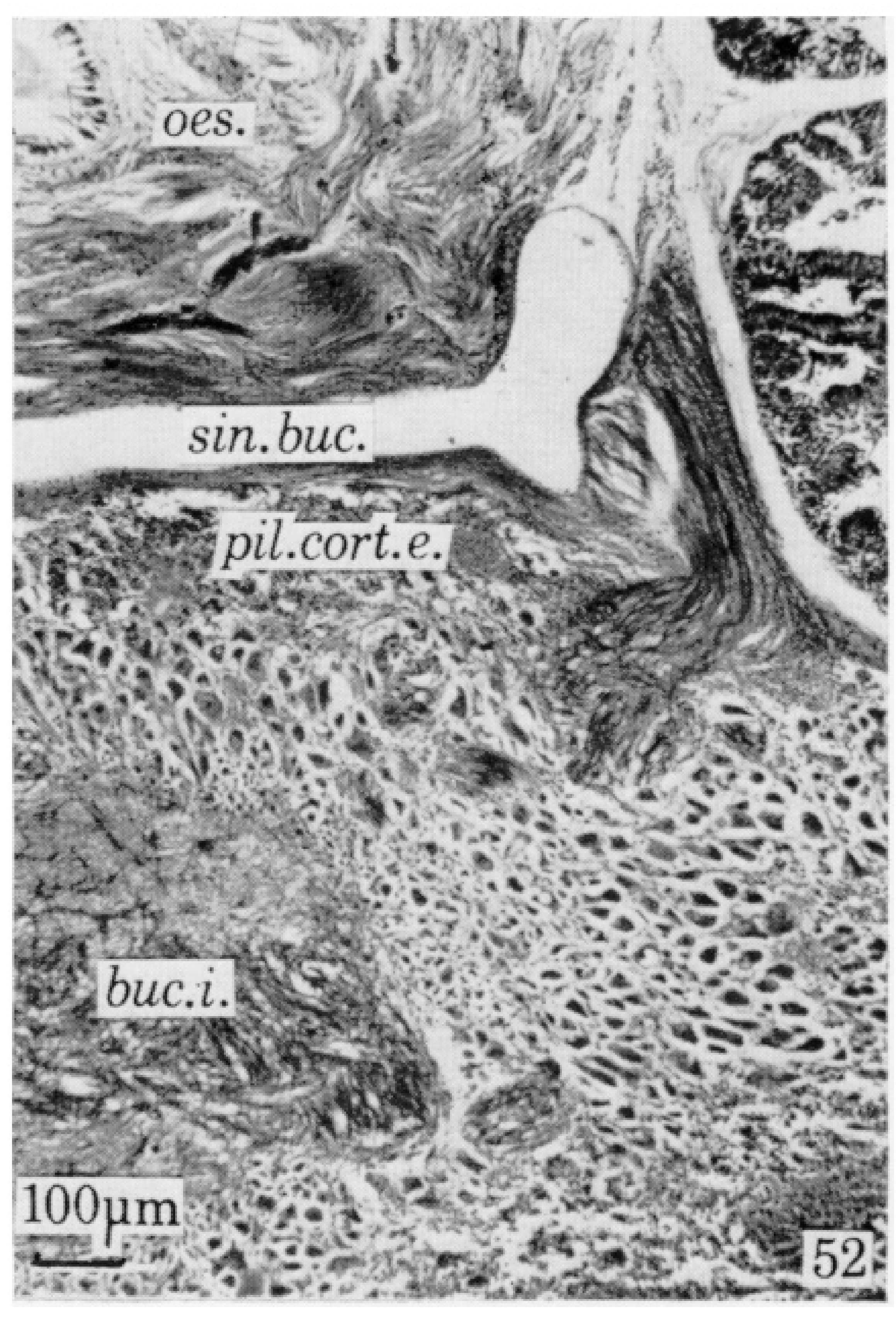
49



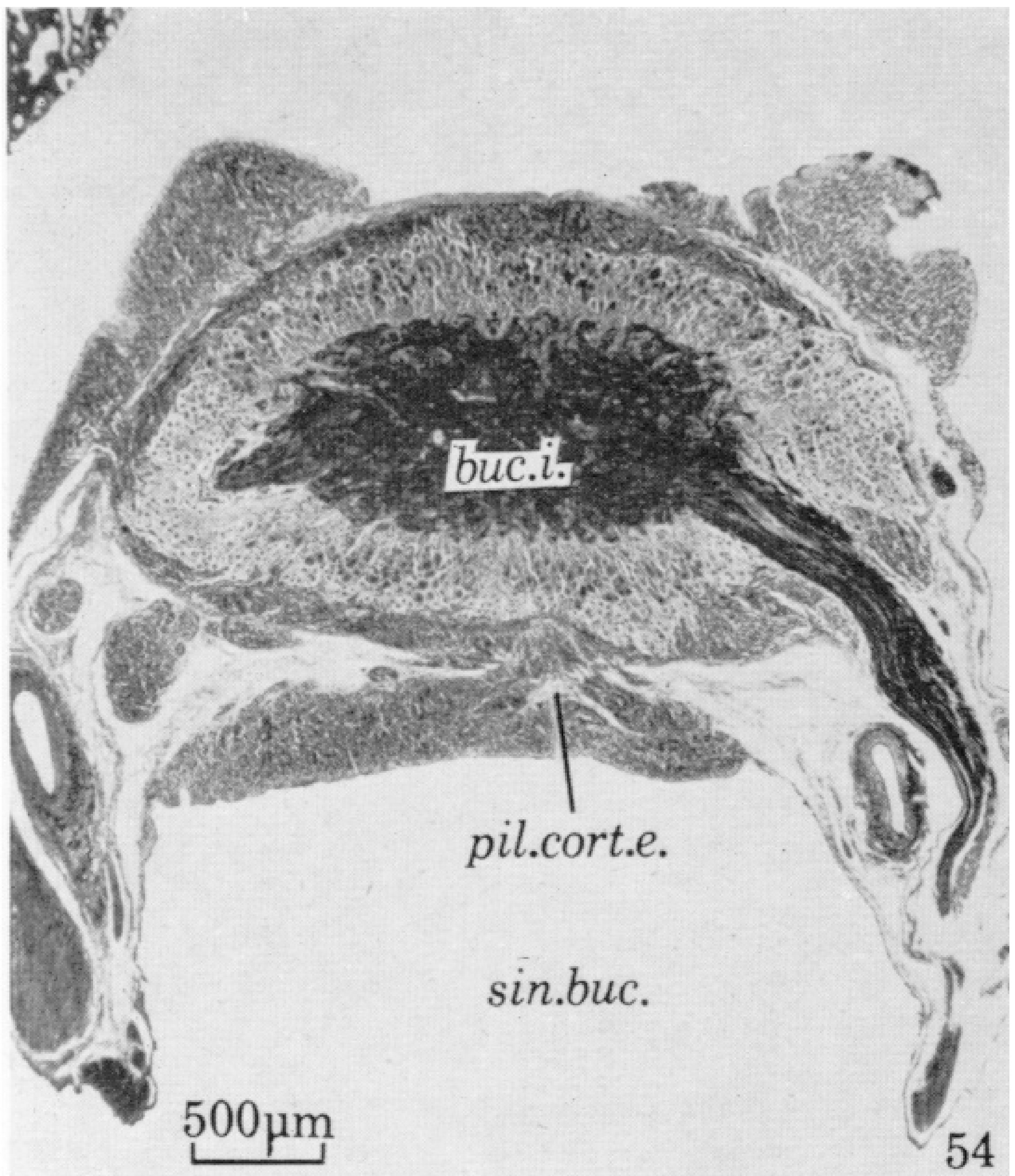
50

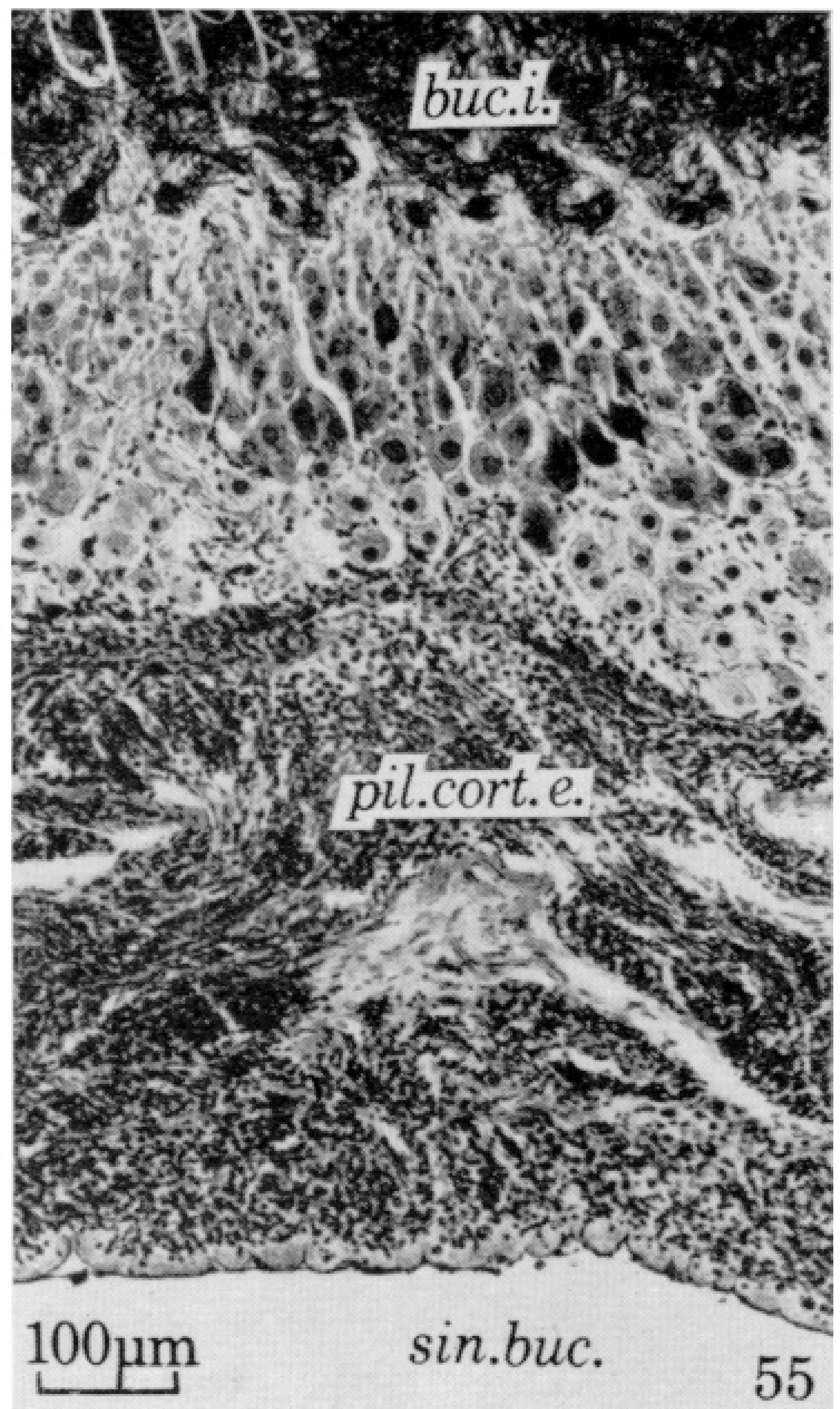


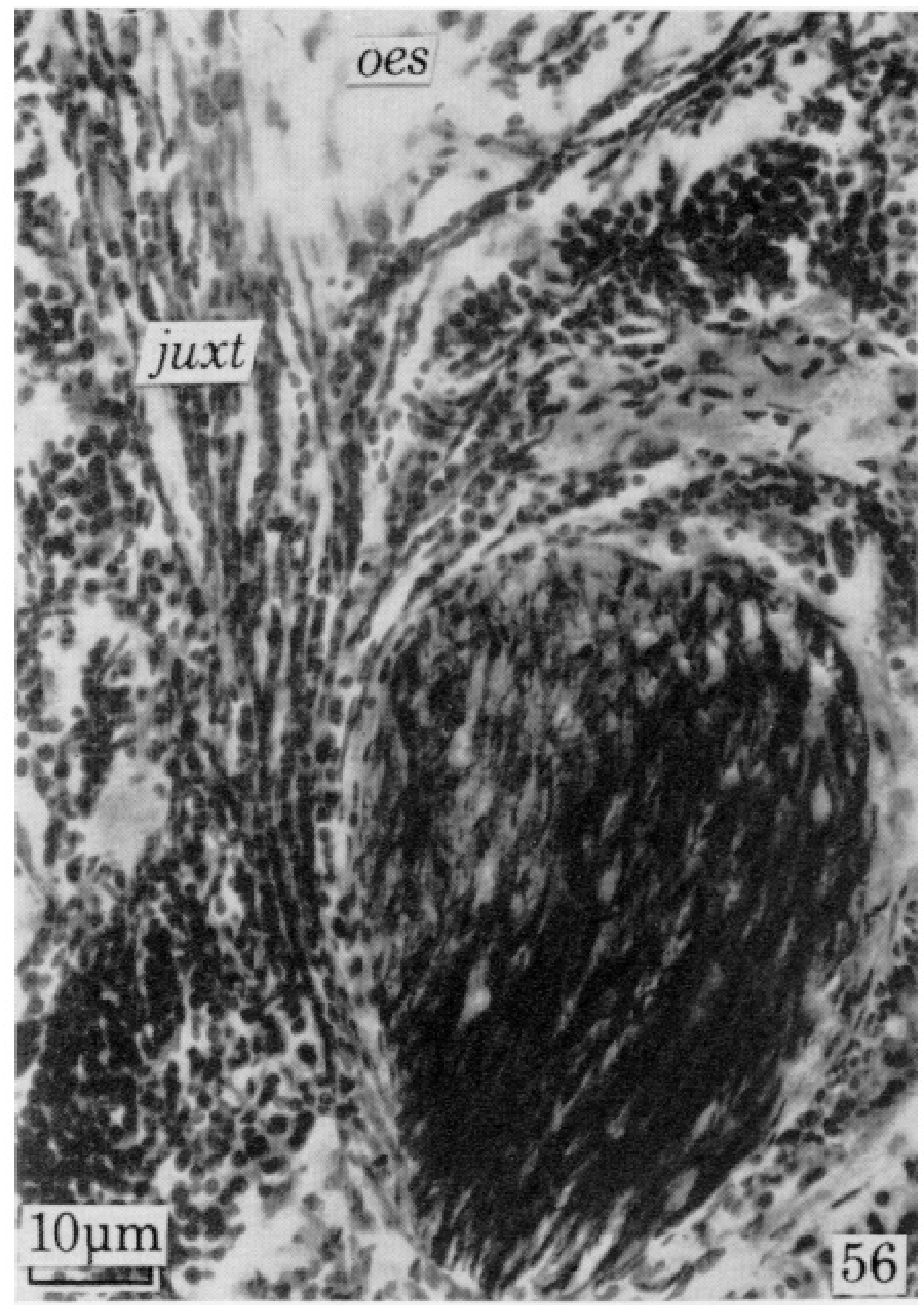
51

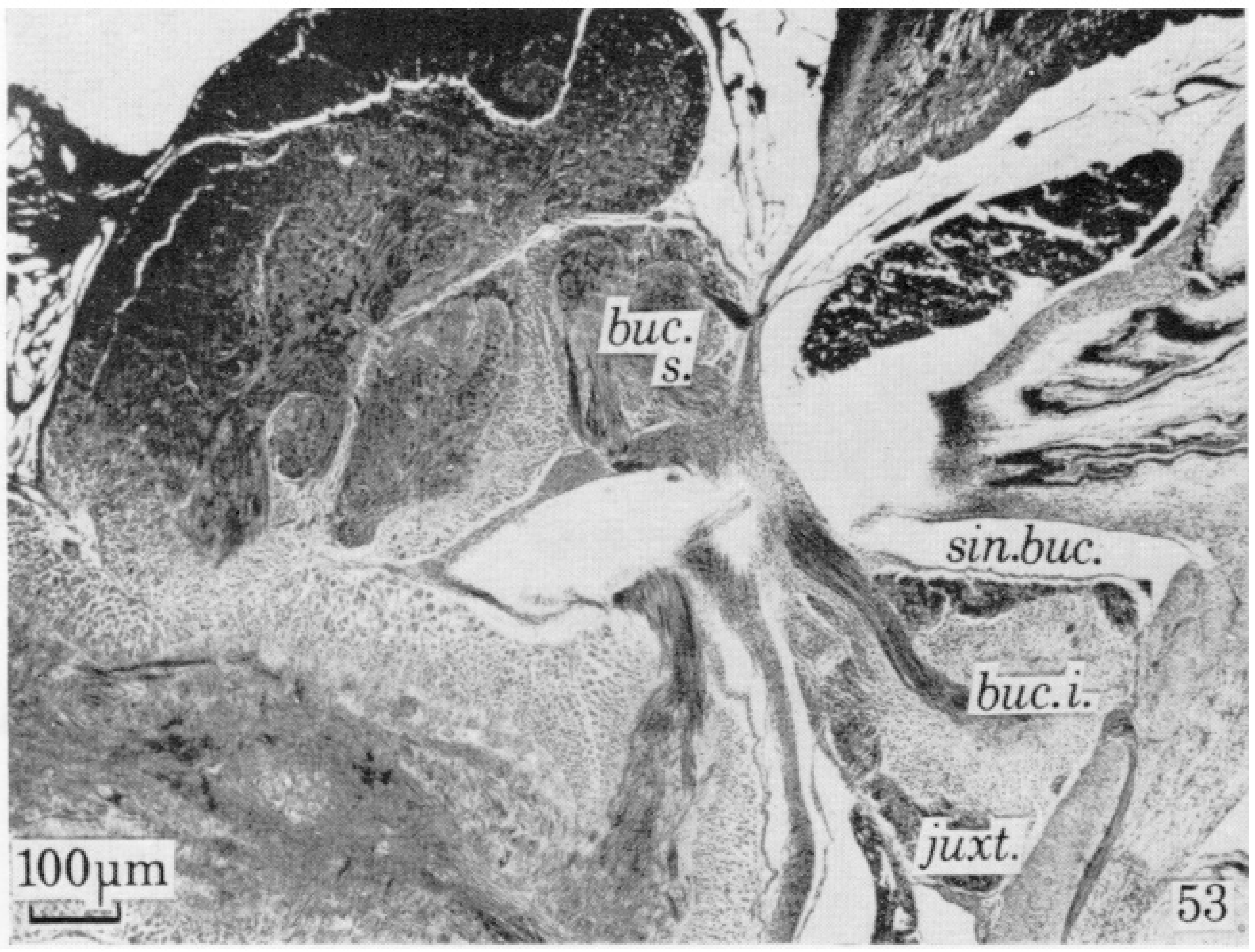


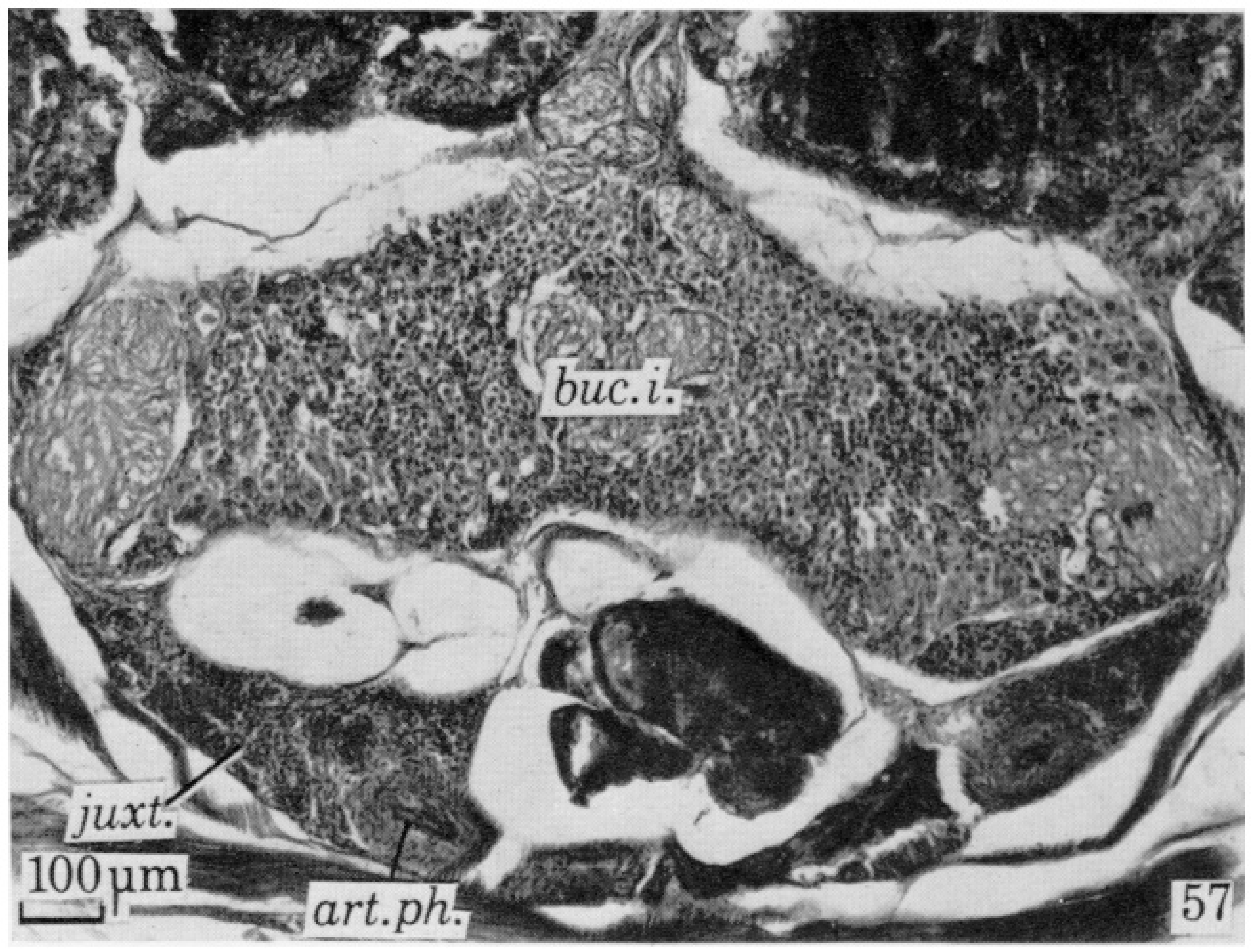
52

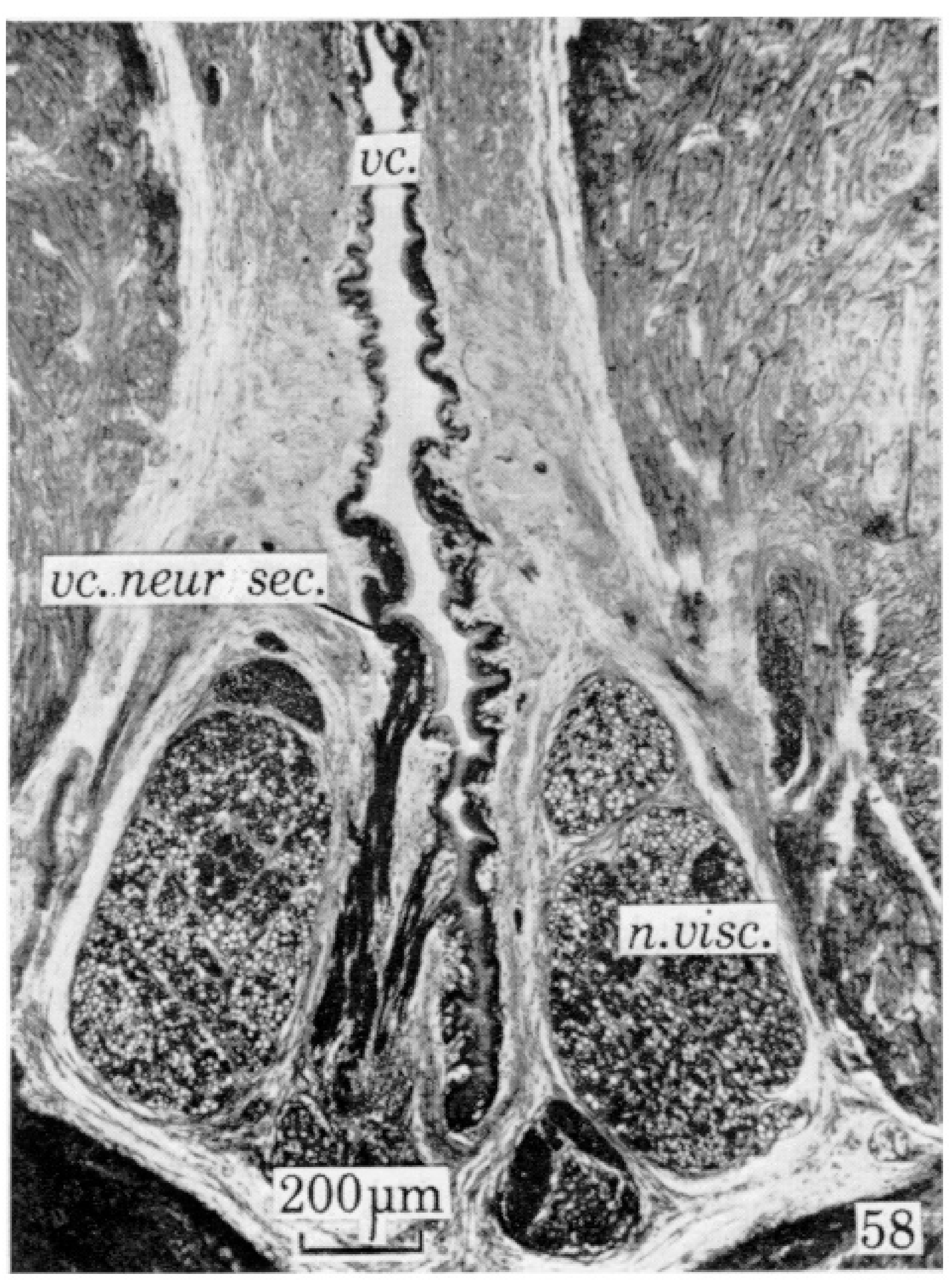

buc.i.
pil.cort.e.
sin.buc.
500μm
54

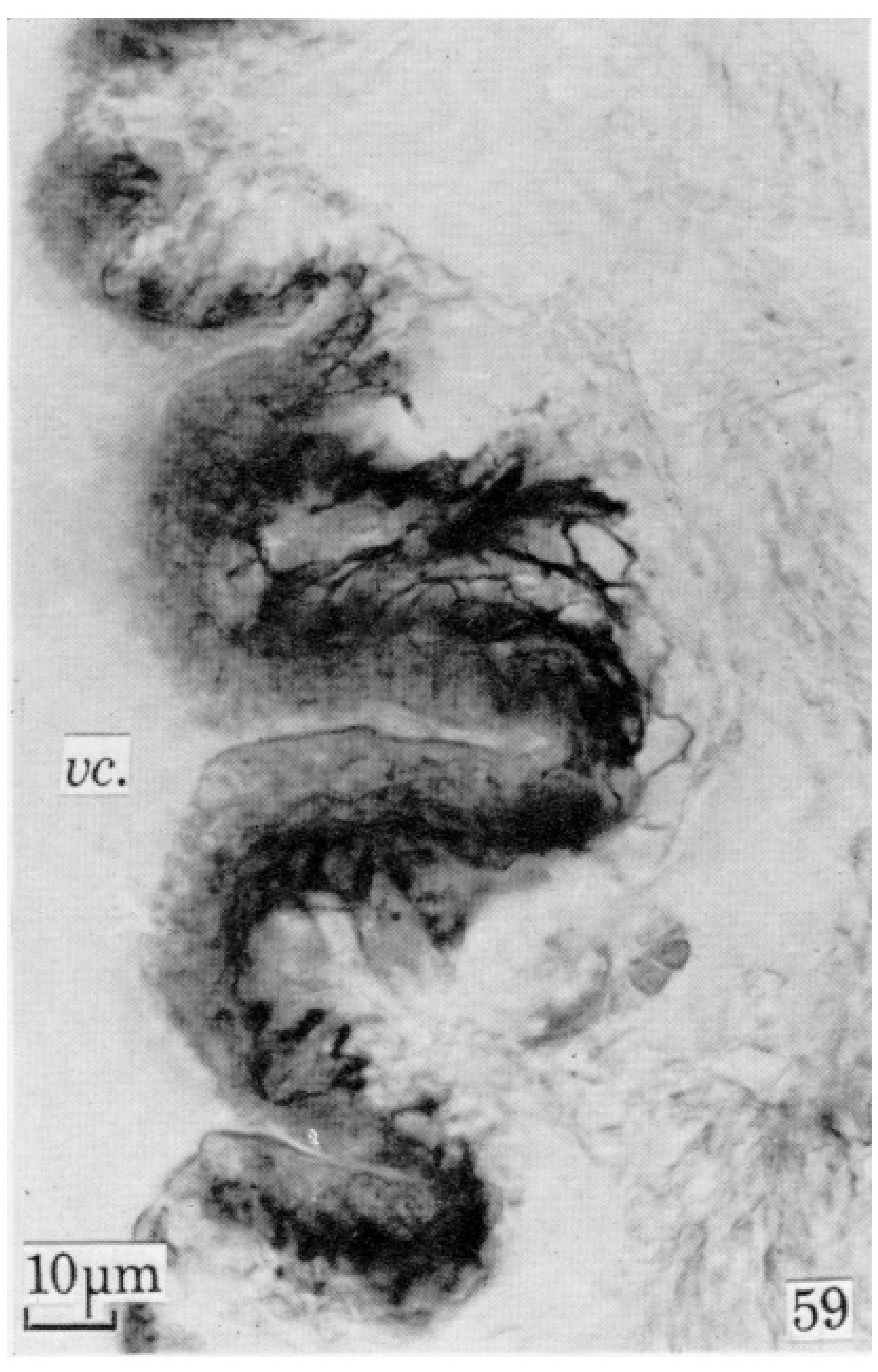

buc.i.
pil.cort.e.
100μm
sin.buc.
55

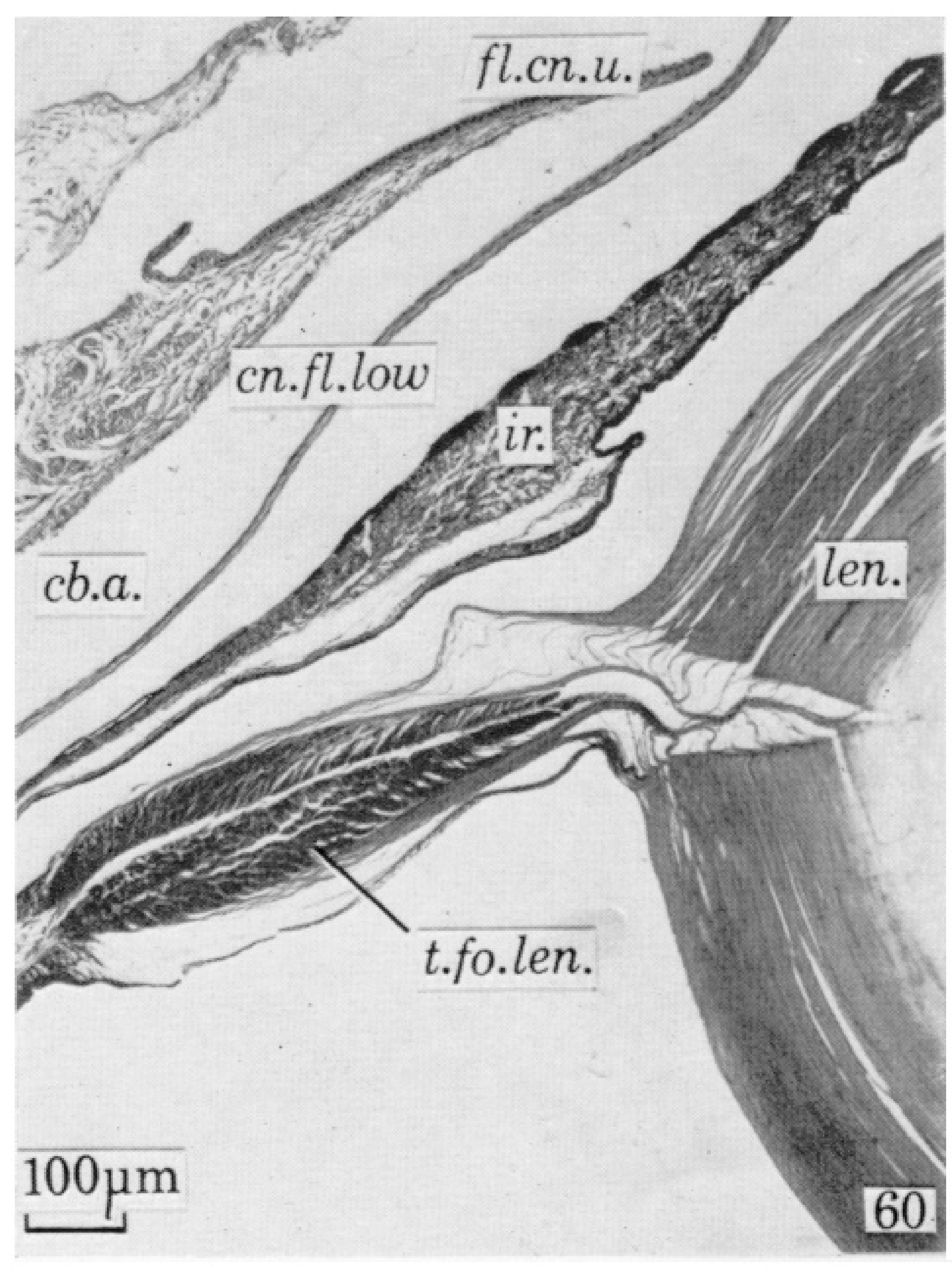

oes
juxt
10μm
56


buc.
s.
sin.buc.
buc.i.
juxt.
100μm
53


buc.i.
juxt.
100μm
art.ph.
57


vc.
vc.neur sec.
n.visc.
200μm
58


vc.
10μm
59


fl.cn.u.
cn.fl.low
ir.
cb.a.
len.
t.fo.len.
100μm
60