THE BUCCAL NERVOUS SYSTEM OF *OCTOPUS*

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(*Received* 21 *July* 1964)

[Plates 8 to 11]

CONTENTS

The operations of killing and eating food by an octopus are under the control of a series of nervous centres. The poison centre lies most posteriorly and is probably activated first, since it lies close to endings of fibres from the arms. The fibres of the nerves to the posterior salivary gland run without synapse from the superior buccal lobe to the glands, passing first far forward and then back along the duct. There is thus no peripheral synapse on this path, perhaps because no continuing rhythmic operations are involved in the secretion, and no reflex guidance is needed.

The actual injection of the poison by the salivary papilla is controlled through the subradular ganglia. The cerebro-subradular connectives arise from the front of the superior buccal ganglia, near the entrance of the labial nerves, and run direct to the subradular ganglia, bypassing the inferior buccal ganglion.

The interbuccal connectives also arise from the front of the superior buccal lobe and run to the inferior buccal ganglion. The inferior buccal ganglion sends nerves to the muscles of the jaws and radula and to the anterior salivary glands, buccal palps and oesophagus. Through the sympathetic nerve it communicates with the gastric ganglion. The inferior buccal ganglion has a complicated internal structure. From its outer surface arise numerous strands of the juxta-ganglionic tissue, which end at the surfaces of the buccal sinus.

The proportion of large cells decreases in the sequence posterior buccal, superior buccal, inferior buccal, subradular and gastric ganglia.

1. Introduction

The structure and mode of action of the buccal mass of *Octopus* are not well known. Heinrich (1904) described many features of the musculature in various cephalopods. Bogoraze & Cazal (1944) have more recently dealt with some features of the innervation, but knowledge of the pathways involved in feeding remains incomplete. There are no good descriptions or figures of the remarkable salivary papilla by which poison is emitted, nor of the subradular ganglion that controls it. Fundamental facts about the pathways are unknown. Are there two synapses on the pathway from the brain, one in the inferior buccal and another in the subradular ganglion? The neural pathway for activation of the posterior salivary glands has often been stimulated to obtain saliva (see Ghiretti 1960) but there is no information as to where the cells of origin may be. There is need for information as to whether there are any afferent fibres in the sympathetic nerves, which might control hunger from the oesophagus or crop.

Knowledge of the nervous centres that are involved in feeding is essential for an understanding of the parts of the brain of an animal that constitute the memory. Learning often involves making a record of the cues provided by, say, vision or touch that are likely to lead to food. The afferent pathways of taste, as of pain, must therefore be known if we are to understand how the memory is correctly informed. Conversely, it is probable that the motor pathways by which food is either taken or rejected provided the original motor machinery that was controlled by the memory (Young 1963 *a*, 1965 *a*).

Evidence will be given on these and other questions in relation to *O. vulgaris* Lam. The condition of the feeding apparatus is obviously a fundamental feature of any animal and it is hoped therefore to deal with the problem later in various other octopods and in decapods. In the course of the present investigation much has been learned of the curious juxta-ganglionic tissue that was first described by Bogoraze & Cazal (1944). Further details of this tissue will be published later.

2. Methods

A main reason for the current ignorance about the buccal mass of cephalopods is no doubt that it is difficult to cut sections because of the chitinous beaks. However, it is possible to cut the muscles away from the beaks using a fine sharp scalpel, with little disturbance to other tissues. Series of sections in various planes have been prepared, mainly after staining with Cajal's method after formol fixation (Young 1939). Sections of embryos and young octopuses that had just relinquished their previous pelagic existence were also made. Young *O. briareus* Robson are especially useful since they have no pelagic phase and hatch in a much more advanced stage than *O. vulgaris* (Messenger 1963).

Something of the actions of the nerves was learned by dissection of the nerves of the buccal mass and stimulating them electrically. No attempt has been made to provide a full analysis of the actions of the muscles of the jaws and radula.

Degeneration methods were used where possible.

3. Plan of the feeding system

The stages involved in catching and eating by an octopus may be classified as (1) visual approach, (2) catching with the arms and drawing to the mouth, (3) poisoning, (4) holding with the beak, (5) rasping or raking with the radula, which perhaps also sucks, (6) movement, by muscular action, along the oesophagus to the crop, (7) digestion. The divisions are somewhat artificial and there is uncertainty about the sequence of (3) and (4). However, the stages are reasonably distinct and are mostly served by separate nerve centres, each with its own afferent and efferent pathways and in some cases its own memory store (figure 1).

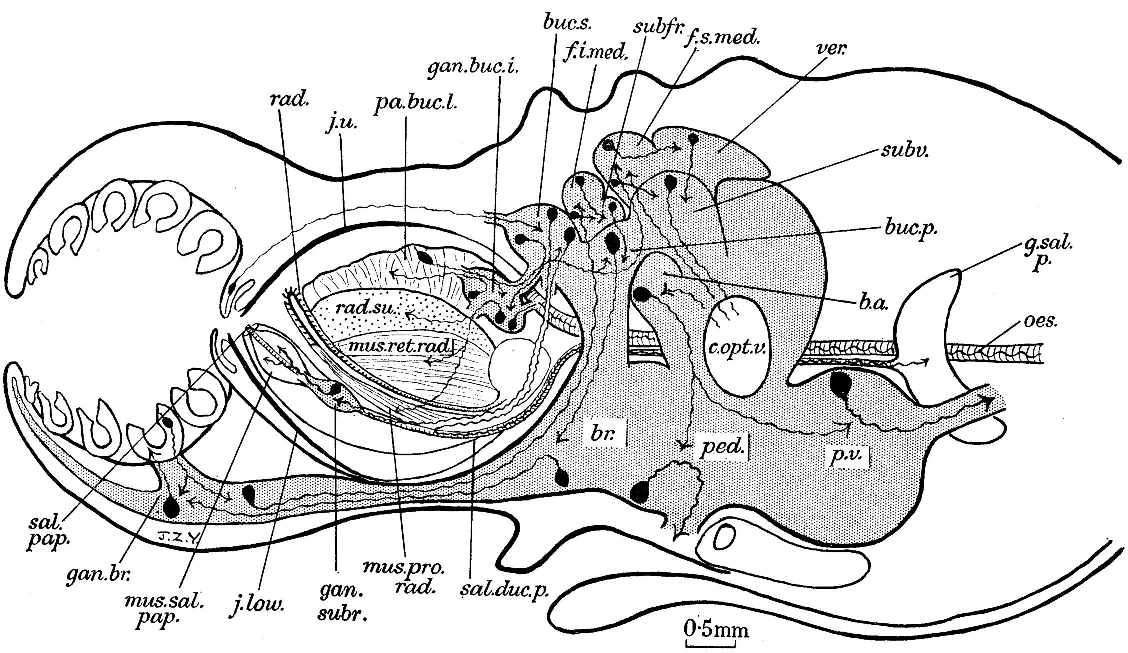


Figure 1. Diagram of the feeding system of an octopus. The main outlines have been drawn from a single sagittal section of a late embryo, but details of the nervous organization are included from various sources (abbreviations on p. 44).

The nervous centres producing these actions lie in serial order, with those responsible for the earlier actions (vision) more posteriorly, and the centres for controlling ingestion and digestion of food anteriorly (inferior buccal ganglion). The hindermost part of the supraoesophageal lobe is occupied by centres for the control of retreat and for other functions with which we are not here concerned. The centres for vision occupy the middle part of the brain and include the optic lobes, which are lateral extensions of the supra-oesophageal lobe. They are of course involved in eliciting actions of retreat, as well as producing the first of the above stages of feeding, namely approach to an object in the visual field. The octopus swims to the object and then catches it with the arms. The actions of the arms are largely directed by their intrinsic nervous system but the decision whether or not to seize the object touched depends upon the memory system of the inferior frontal and related lobes (Wells 1959, etc.; Young 1965*a*). These lie immediately in front of the visual centres, closely connected with them, and include, like the visual system, lower and upper pairs of centres. The lateral inferior frontal and posterior buccal lobes make the lower pair, the median inferior frontal and subfrontal lobes the upper pair.

The superior buccal lobe lies in front of the inferior frontal system. It contains the basic reflex centres for the stimulation of the posterior salivary glands, which it controls directly, and also for the ejection of saliva, controlled through the subradular ganglia, and for holding and breaking up the food, controlled through the inferior buccal ganglia. Ingestion and the actions of the anterior salivary glands, oesophagus and crop are also controlled through the inferior buccal ganglia. The later stages of digesting by the gizzard, caecum and hepatopancreas are controlled through the gastric ganglion, which has been little studied (see Alexandrowicz 1928).

If this analysis is correct, feeding involves the operation one after another of a series of centres of 'motor' type. These are, proceeding from behind forwards, the subvertical, posterior buccal, superior buccal, subradular, inferior buccal and then the gastric ganglion (lying of course more posteriorly). All of these contain some moderately large cells. The first two operate under the control of the elaborate receptor analysers and memory centres of the visual and tactile systems. These latter contain many small neurons, but the 'lower' centres of the series are composed mainly of motorneurons, presumably under more strictly reflex control. The function of the smaller cells that are also found in these lower centres is however one of the most interesting problems that they present.

The present paper is concerned with evidence about the structure and connexions of the superior buccal lobe and the inferior buccal and the subradular ganglia.

4. Parts of the buccal mass

There is some confusion in the terminology of the various lobes and glands in the mouth of cephalopods and their functions are uncertain. The term 'tongue' has been used for the structure that bears the radula by Griffin (1900) in *Nautilus* and Isgrove (1909) in *Eledone*. In *Sepia* Tompsett (1939) has described the structure through which the papilla of the posterior salivary duct emerges as the 'tongue'. This structure had been previously described as the subradular organ. It is surrounded by a sack of glandular tissue, which has been called the 'submandibular gland' (see Wülker 1910). In view of these ambiguities it has been decided to use the name 'salivary papilla' for the structure that carries the duct of the posterior salivary glands. The glandular tissue around it will be called the submandibular gland.

The naming of the organs above the radula, forming the floor of the buccal cavity, is even more difficult. Griffin (1900) described in *Nautilus* a central 'tongue' with two fleshy prelingual processes in front of it and a pair of 'salivary processes' at the sides, within which the salivary glands lie (there are no posterior salivary glands in *Nautilus*). This is approximately the condition in *Sepia*, where the paired lobes are conspicuous and contain the anterior salivary glands; Tompsett (1939) called them 'palatine lobes'. They are separated by a groove.

In *Octopus* there is a somewhat comparable pair of lobes but they do not contain the anterior salivary glands. These lie more posteriorly but their ducts pass through the pair of palps to open far forwards, near the teeth of the radula. In view of this it is advisable to call these lobes the lateral buccal palps. They form the floor of the mouth and are active organs, playing a large part in the ingestion of food.

5. The superior buccal lobe

5·1. *Position and cell composition*

This unpaired lobe stretches across the front of the supraoesophageal mass (figures 2 and 3, plate 8). It receives numerous labial nerves in front. From its antero-ventral end arise the interbuccal and bucco-subradular connectives and the salivary nerves. It receives the bucco-brachial connectives at its postero-lateral corners. Posteriorly it is broadly continuous with the posterior buccal lobes.

The cell layers of the superior buccal lobe resemble those of suboesophageal centres in containing large cells peripherally and some smaller ones near the neuropil (figure 4, plate 8). There are estimated to be 97000 cells with nuclei up to 5 μm in diameter, 78000 of 5 to 10 μm, and 26000 of 10 to 15 μm (table 1, Young 1965*a*). Some of these are final motorneurons whose axons run direct to the lips or posterior salivary glands. Others are interneurons, leading to the inferior buccal and subradular ganglia.

The neuropil has in the main the characteristics of a motor centre, namely a dense tangle, without obvious regularities, or complex interweaving bundles. There are however some regions of different composition at the back of the lobe (see below).

5·2. *Afferent fibres of the superior buccal lobe*

(1) *Labial nerves*

These form an arch of about twenty bundles as they enter the lobe (figure 3, plate 8). They run round the buccal mass to the lips. They are estimated to contain about 42000 fibres, mainly between 2 and 6 μm in diameter (Young 1965*b*). After severing them degeneration is seen in both stumps; they therefore include motor fibres to the lip muscles, as well as afferents, presumably taste fibres (figure 7, plate 8). The much-folded lip epithelium contains numerous receptor cells with large vacuoles, which are probably the taste receptors (Graziadei, personal communication).

(2) *Brachial to superior buccal tract*

The superior buccal to brachial connective arises as a complex set of bundles turning back and down to form part of the cerebro-brachial connective (figure 8, plate 8). After section at the level of the oesophagus many of its fibres degenerate above the lesion and these are presumably chemotactile and perhaps pain afferents. There are also some fibres that degenerate below the lesion (see below).

(3) *Subvertical to superior buccal tract*

The close connexion between the superior buccal lobe and the rest of the supraoesophageal mass is a characteristic feature of octopods. It allows the passage of afferents from the labial nerves and buccal mass directly to the learning centres. There is no evidence as to whether there are also fibres arising in the superior buccal lobe and running backwards. It will be assumed that they do not exist. There are certainly some fibres running in the reverse direction. Three days after removal of the supraoesophageal centres that lie behind the inferior frontal system degeneration granules are found in the superior buccal lobe. They probably originate in the subvertical lobe.

(4) *Inferior frontal to superior buccal tract*

The lateral inferior frontal and posterior buccal lobes send many fibres to the superior buccal lobe, which is filled with degeneration granules after a cut made immediately behind it.

(5) *Oesophageal to superior buccal tract*

After section of the sympathetic nerve trunks degenerating fibres have been seen in the interbuccal connectives (figure 9, plate 8). These are presumably afferent fibres from the oesophagus or crop, concerned with the regulation of digestion and perhaps with hunger. It is not known whether there are also fibres from within the buccal mass ascending to the superior buccal lobe. Fibres presumed to come from receptors are numerous in the lateral buccal palps (p. 37) and some of these may reach the superior buccal lobe.

(6) *Salivary to superior buccal tract*

Fibres that are probably afferent occur in the epithelium of the posterior salivary duct (p. 35). Presumably they reach the superior buccal lobe.

5·3. *Efferent fibres of the superior buccal lobes*

(1) *Labial nerve efferents*

Degeneration is seen in the peripheral stumps during the days after section of the labial nerves. These fibres presumably control the movements of the lip.

(2) *Superior buccal to brachial tract*

As described above there are descending fibres in the bucco-brachial connective. Their significance is not known.

There is no definite evidence of pathways arising in the superior buccal and ending in other centres within the brain and they are assumed not to exist.

(3) *Posterior salivary nerves*

The nerves for the posterior salivary glands arise from cells of the dorsal wall of the extreme hind end of the superior buccal lobe (figure 10, plate 9). The fibres of each nerve probably arise in part from both sides, since there are numerous crossing bundles of fine fibres in this region (figure 11, plate 9). However, after section of the nerve on one side, changes, believed to be retrograde degeneration, were seen mainly in cells of the same side (figures 17*a* and *b*, plate 9). The details of the changes cannot be decided from these Cajal preparations. The normal cells are filled with vague dark granules. Most of those on the operated side have a clear cytoplasm with a few very large granules, accompanied by smaller particles. The cell layers from which the nerves arise are very thick, with large cells (up to 30 μm diameter) at the outside and numerous smaller ones within (figure 4, plate 8).

The hinder region of the superior buccal lobe receives the brachio-buccal connective from below, whose ascending fibres presumably record the presence of a crab in the arms and thus initiate the process of poisoning it, by sending impulses down the posterior salivary nerves. The origin of the nerves also lies close behind the endings of the labial nerves, which may also play a part in initiating the flow of poison.

The fibres of the posterior salivary nerves are all small ($< 3\ \mu m$) (see Young 1965*b*). They pass through the superior buccal lobe as a conspicuous bundle on each side, staining only lightly with Cajal's stain (figures 10 and 11, plate 9). Each salivary nerve then leaves the superior buccal lobe at its antero-ventral edge. Here it lies at the centre of a complex bundle of nerve trunks (figure 12, plate 9). Lateral and dorsal to it lie labial nerve bundles. Ventro-medially is the cerebro-subradular connective, and medially the interbuccal connective. The nerve runs with the connectives round the back of the buccal mass to the side of the inferior buccal ganglion. For the greater part of this course it is accompanied by labial nerves lying laterally to it, but is not tightly bound to them, as it is to the two connectives. The salivary fibres are easily recognized in the early posterior part of their course as they are small and pale-staining, but become deeper staining more distally. As the bundles pass round the buccal mass the posterior salivary nerves lie most ventrally, the cerebro-subradular connectives above them and the interbuccal connective most dorsally (figure 13, plate 9).

At the sides of the inferior buccal ganglion the salivary nerves and cerebro-subradular connective leave the interbuccal connective, and continue ventrally (figure 14, plate 9) lateral to the strand of juxta-ganglionic tissue (figure 15, plate 9). Here the two bundles that have come from the central nervous system (on each side) are joined by the inferior mandibular nerve, arising from the inferior buccal ganglion (figure 16, plate 9).* The three trunks twist around each other as they pass ventrally. Where they finally enter the buccal mass, lateral to the posterior salivary duct, the three bundles are clearly distinct. The salivary nerve lies between the other two, with, at first, the inferior mandibular nerve medial and the cerebro-subradular connective lateral to it. The salivary nerve fibres at this level stain darkly with silver and the bundle appears black by contrast with the larger yellow or orange fibres of the other two bundles.

After running forward together for a short distance the bundles separate. The posterior salivary nerves and cerebro-subradular connectives turn medially and the inferior mandibular nerves laterally (figure 18, plate 9). However, two or more small bundles of larger fibres probably originating from the inferior buccal ganglion leave the inferior mandibular nerve to run with the salivary nerve for a while before ending in the muscles on either side of the duct.

The posterior salivary nerves continue forward and medially to the base of the salivary papilla. Here they turn sharply backwards and accompany the salivary duct along the whole of its course to the posterior salivary glands (figures 19, 21, plate 10). At the base of the papilla they are joined by at least two bundles of fine fibres arising from the subradular ganglion (figure 20). These smaller bundles will be called salivary duct nerves, on the assumption that they innervate the duct and that the posterior salivary nerves

* This has been called the inferior buccal nerve elsewhere (Young 1964*b*).

innervate the glands themselves. Both groups consist entirely of small fibres, none larger than 3 μm (Young 1965*b*).

The origin of the posterior salivary nerves here described differs from that given by Bogoraze & Cazal (1944). These authors say that the fibres of the nerve arise in the sub-radular ganglion, although their schematic figure IV A (p. 120) clearly shows the bundle turning back *behind the ganglion* to run with the duct.

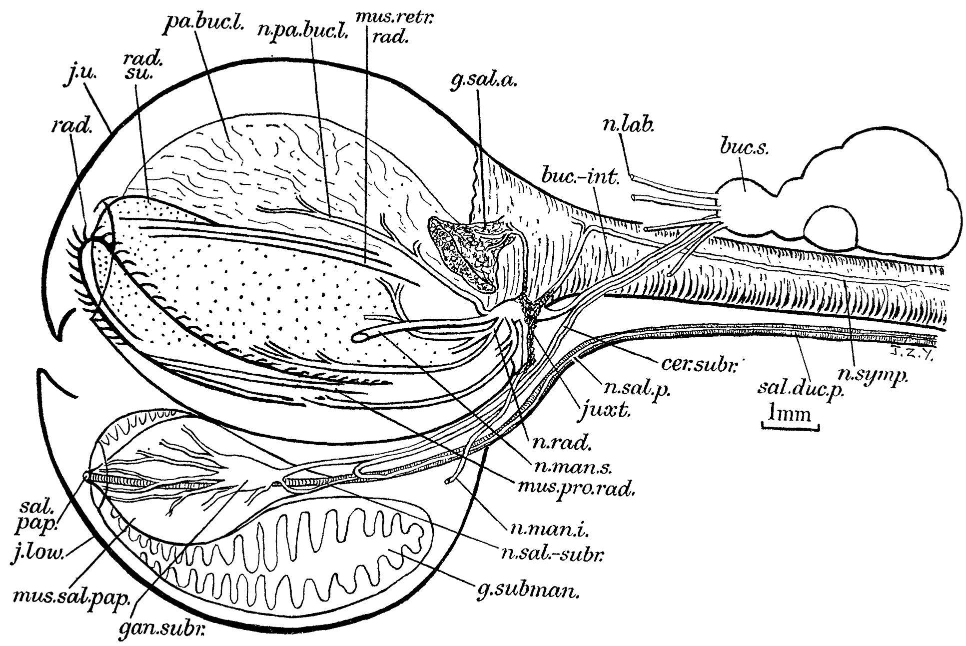


FIGURE 20. Diagram of the buccal mass and its nerves, reconstructed from serial sagittal sections.

(4) *The cerebro-subradular connective*

This connective leaves the superior buccal lobe medio-ventral to the salivary nerve and lateral to the interbuccal connective. The roots of the two connectives are very close together and their fibres probably intermingle. The cells of origin have not been traced in detail but are probably in the front part of the superior buccal lobe.

DESCRIPTION OF PLATE 8

FIGURE 2. Sagittal section of the brain of *Octopus* to show superior buccal lobe and origins of labial and posterior salivary nerves.

FIGURE 3. Horizontal section of superior and posterior buccal lobes, showing labial and posterior salivary nerves.

FIGURE 4. Transverse section of cell wall of superior buccal lobe.

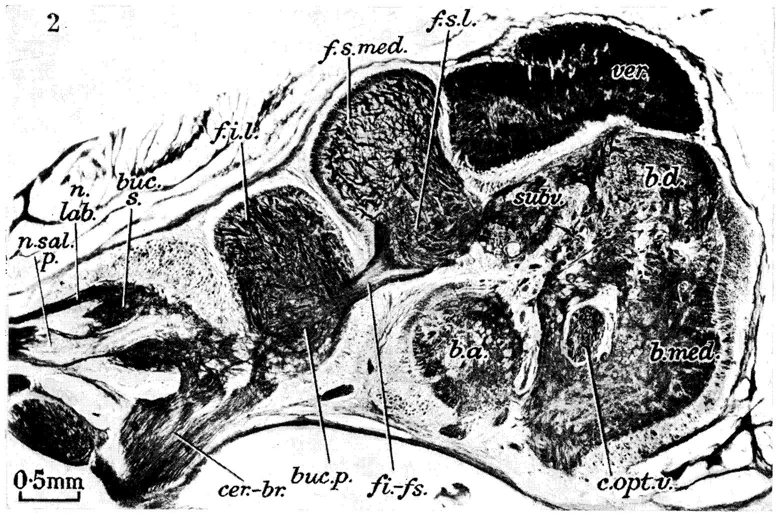
FIGURE 5. Transverse section of cell wall of inferior buccal ganglion.

FIGURE 6. Transverse section of cell wall of subradular ganglion.

FIGURE 7. Degenerating fibres in labial nerves 2 days after they had been severed peripherally.

FIGURE 8. Transverse section of superior buccal lobe to show compound origins of superior buccal to brachial tracts.

FIGURE 9. Sagittal section to show fine degenerating fibres in the interbuccal connective 2 days after severance of the sympathetic trunks.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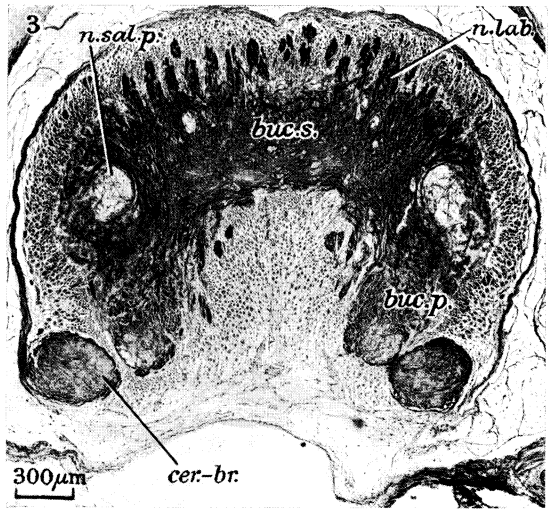
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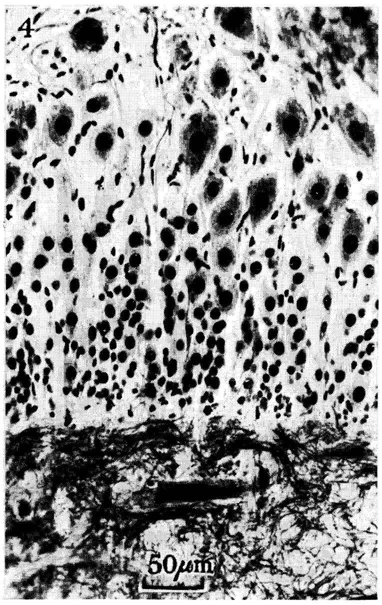
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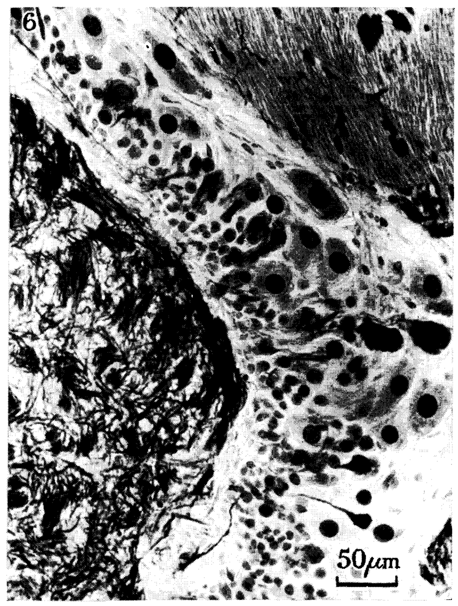
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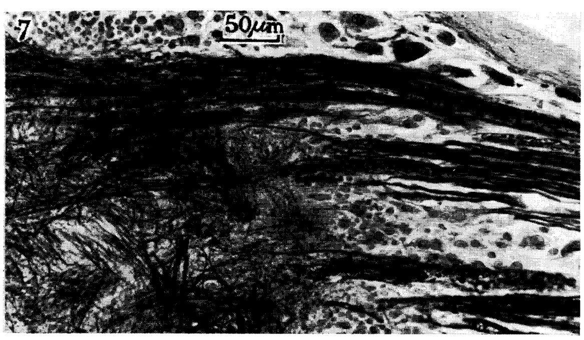
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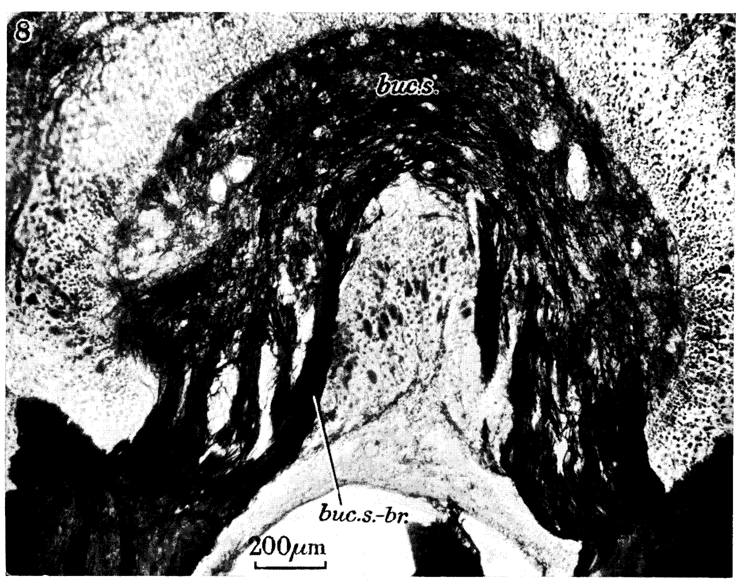
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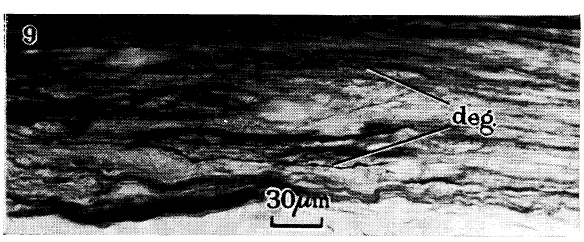
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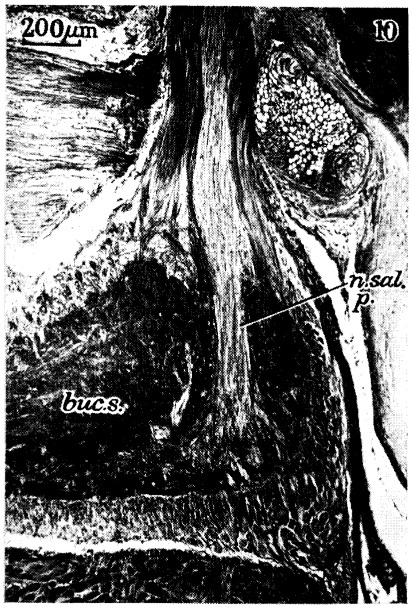
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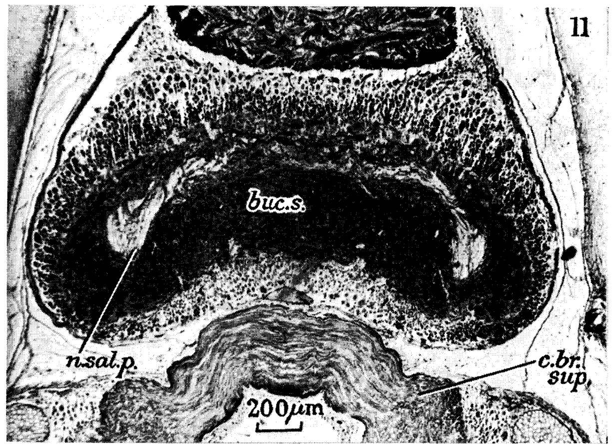
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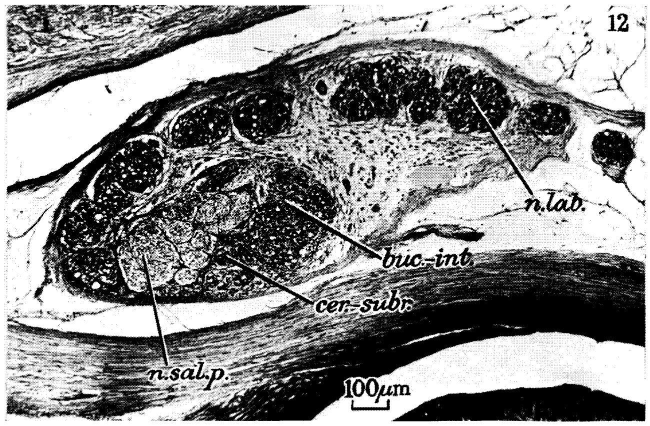
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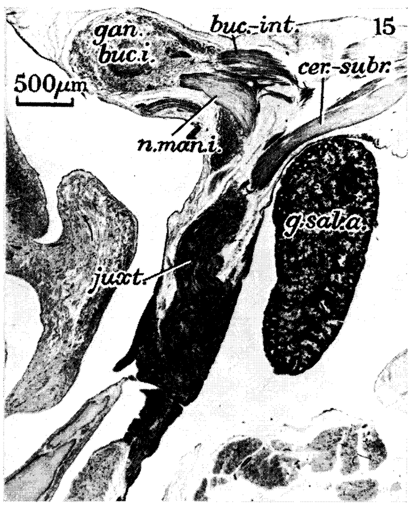
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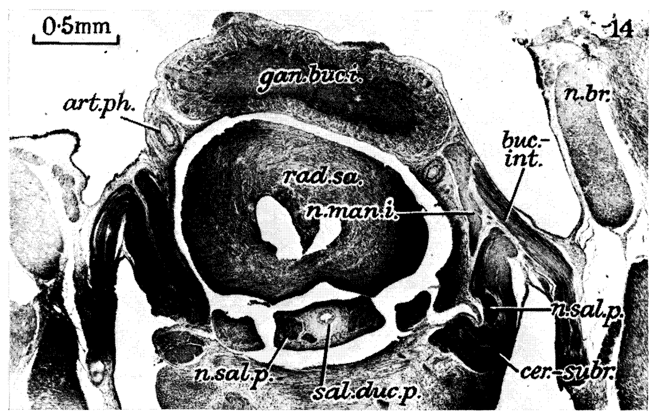
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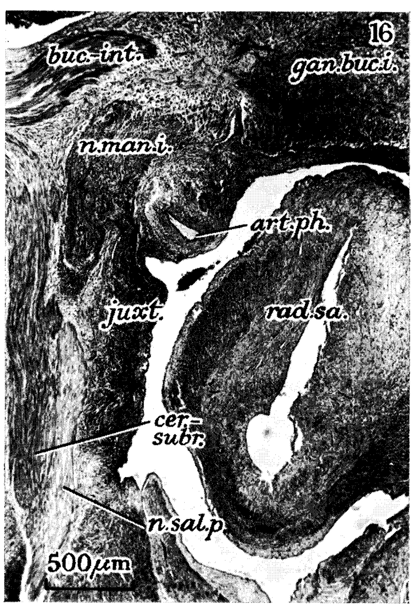
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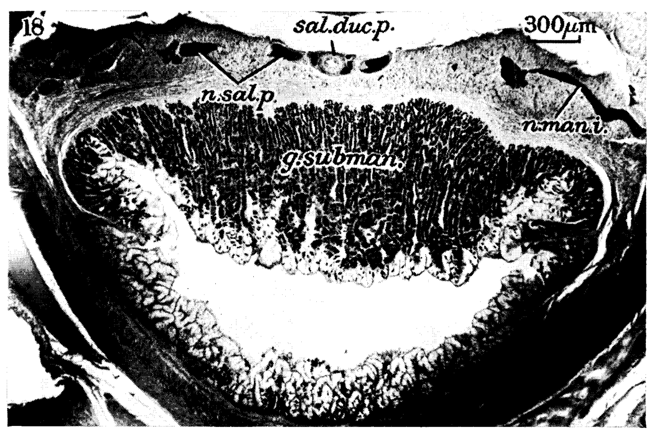
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g.subman.

Plate 9

Figure 10. Horizontal section of superior buccal lobe to show origin of posterior salivary nerve.

Figure 11. Transverse section of superior buccal lobe to show origin of the posterior salivary nerves apparently partly through commissures.

Figure 12. Transverse section in front of superior buccal lobe to show the labial nerves and origins of the interbuccal and cerebro-subradular connectives.

Figure 13. Section across the interbuccal and cerebro-subradular connectives and posterior salivary nerves.

Figure 14. Transverse section of inferior buccal ganglion, showing some of the nerve trunks that connect with it.

Figure 15. Sagittal section of inferior buccal ganglion showing the neighbouring nerve trunks and the juxta-ganglionic tissue.

Figure 16. Transverse section of the inferior buccal ganglion and neighbouring trunks.

Figure 17. Retrograde degeneration after severance of the posterior salivary nerve. (*a*) Normal cells from back of superior buccal lobe. (*b*) Cells from the opposite side of the same lobe, where the salivary nerve had been crushed close to the brain 9 days previously.

Figure 18. Transverse section of posterior salivary duct and subradular organ. The inferior mandibular nerve is shown leaving the other trunks laterally.

Plate 10

Figure 19. Horizontal section showing the posterior salivary nerve leaving the cerebro-subradular connective and turning back to join the posterior salivary duct.

Figure 21. Transverse section of posterior salivary duct and its nerves. The salivary nerve is accompanied by a bundle of extremely fine, lightly stained fibres. The salivary duct nerves probably all arise in the subradular ganglia.

Figure 22. Transverse section of buccal mass showing subradular ganglia, joined by a commissure. The jaws have been removed.

Figure 23. Sagittal section of subradular ganglion. The anterior end is to the left.

Figure 24. Transverse section of base of salivary papilla and subradular ganglion.

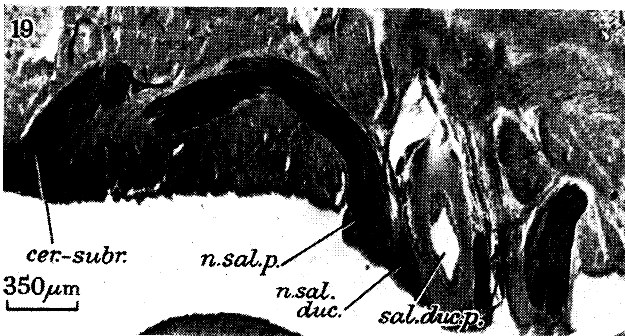
Figure 25. Transverse section of salivary papilla.

Figure 26. Transverse section of subradular ganglion, showing at bottom left the special region of neuropil where the small fibres of the salivary-subradular nerves end.

Figure 29. Oblique longitudinal section of duct of posterior salivary gland, showing beaded fibres running close to the lumen.

Figure 30. Sagittal section of tip of salivary papilla.

Figure 31. *a* and *b*. Transverse section of extreme hind end of radular sack showing plexus of fine nerve fibres.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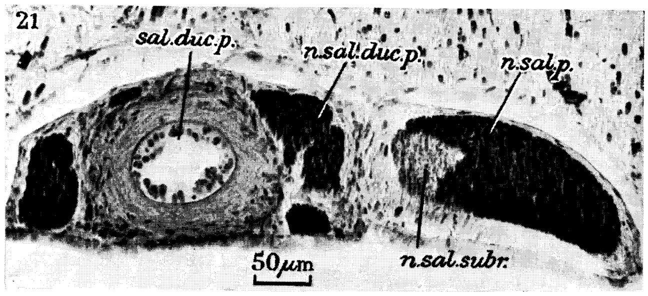
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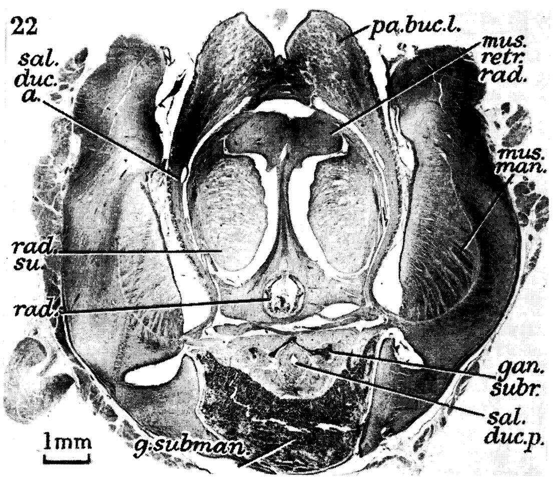
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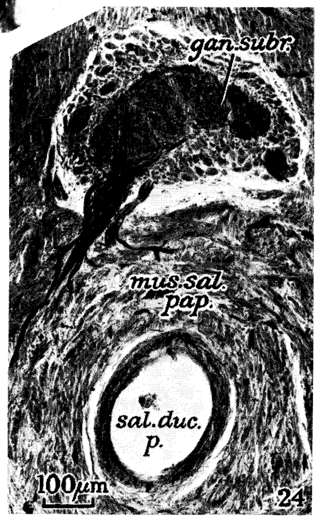
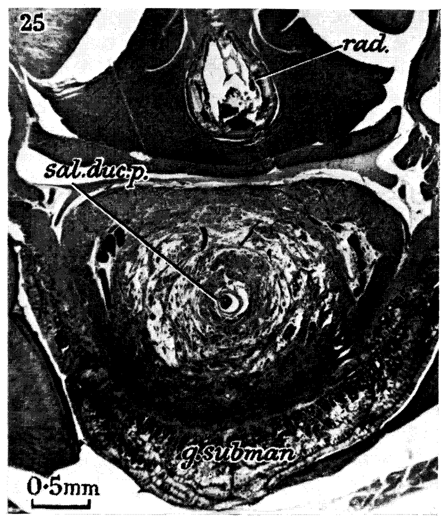
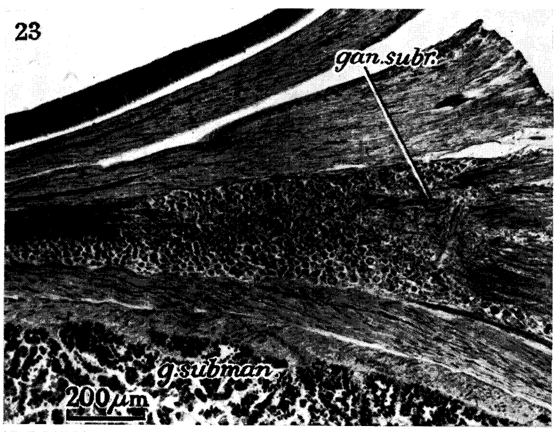
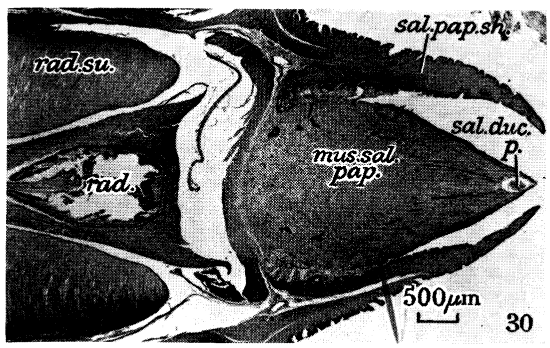
1mm
g.subman.

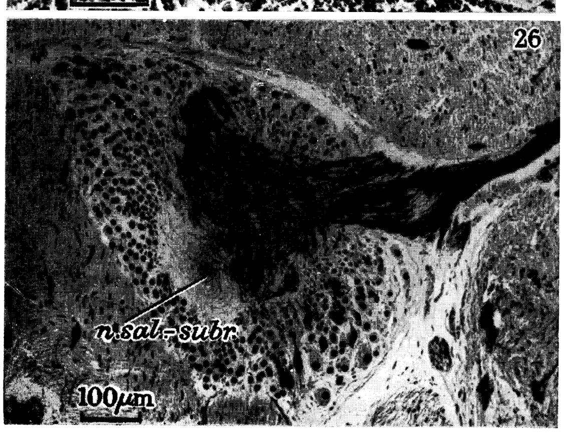

gan.subr.
mus.sal.
pap.
sal.duc.
p.
100μm
24

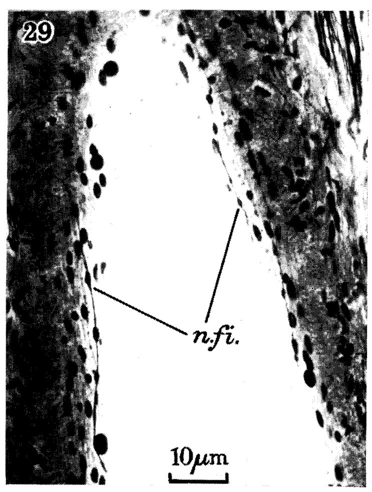

25
rad.
sal.duc.p.
g.subman.
0·5mm


23
gan.subr.
g.subman.
200μm

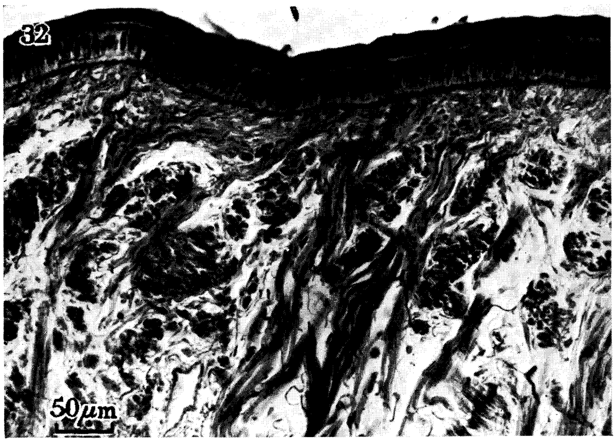

sal.pap.sh.
rad.su.
sal.duc.
p.
mus.sal.
pap.
rad.
500μm
30

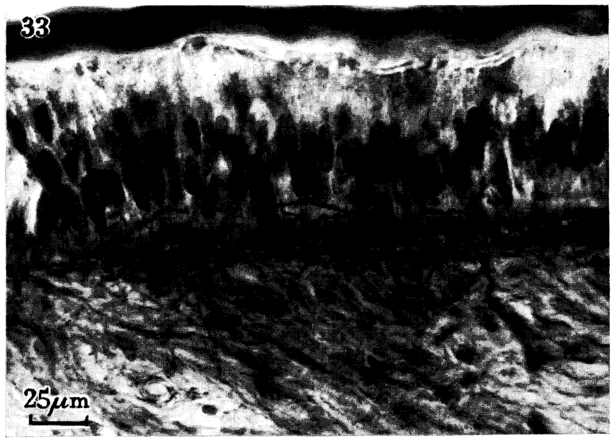

31b
10μm

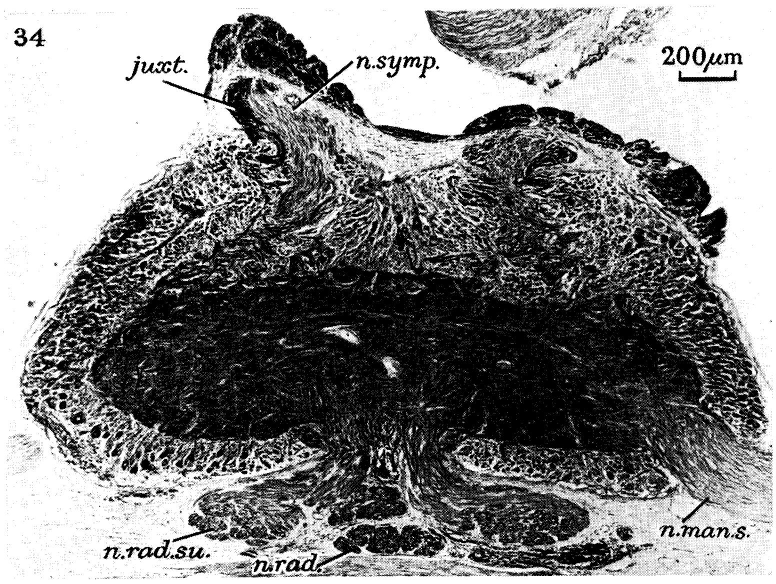

26
n.sal.-subr.
100μm


29
n.fi.
10μm


31a
10μm







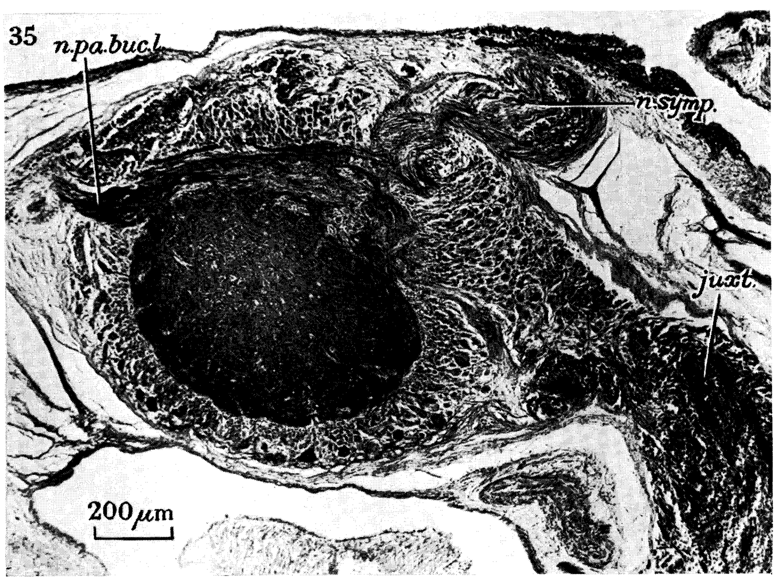


FIGURE 32. Transverse section of lateral buccal palp, showing loose web of muscle fibres and nerve trunks.

FIGURE 33. Transverse section of surface of lateral buccal palp, showing nerve fibres within the epithelium.

FIGURE 34. Transverse section of centre of inferior buccal ganglion.

FIGURE 35. Sagittal section of inferior buccal ganglion to show the part with small cells and the origin of the juxta-ganglionic tissue.

FIGURE 36. Transverse section of gastric ganglion.

FIGURE 37. Cells and neuropil of gastric ganglion.

The cerebro-subradular connective contains a few fibres up to 14 μm in diameter. There are some 50 fibres (on each side) greater than 10 μm, 250 of 6 to 10 μm, 1250 of 2 to 6 μm and over 3000 smaller than 2 μm (Young 1965*b*). The large fibres of this and the interbuccal connective spread out widely in the neuropil at the front of the superior buccal lobe, probably crossing to the opposite side. This branching suggests that some of them are afferent fibres.

The cerebro-subradular connective accompanies the salivary nerve almost to the subradular ganglion. The two can be readily distinguished by the larger fibres in the connective. It is less easy to distinguish between the connective and the inferior mandibular nerve, since both have large fibres. However, the nerve has few very small ones. The situation is complicated by the fact that branches of the inferior mandibular nerve run for some distance with the cerebro-subradular connective, as they do with the salivary nerve (see above).

Bogoraze & Cazal (1944) described the cerebro-subradular connective correctly and figure it bypassing the inferior buccal ganglion. They believed, however, that there was also a connective between the inferior buccal and subradular ganglia (their 'bucco-subradular connective'). There is indeed a nerve that starts on this course from the inferior buccal ganglion but it does not reach the subradular ganglion. It turns laterally as the nerve we have called the inferior mandibular nerve (see below).

6. The subradular ganglia

These lie on either side of the salivary duct, joined by commissures above it (figure 22, plate 10 and figure 22*a*). The ganglia have mainly large and medium-small cells (table 1, Young 1965*a*). In the two ganglia together there were 21000 cells less than 5 μm in nuclear diameter, 39000 of 5 to 10 μm and 5000 of more than 10 μm (figure 6, plate 8).

The nerves arising from the ganglia probably all run to the musculature of the salivary duct and especially to the salivary papilla (figures 24 and 25, plate 10; figure 22*a*). About ten trunks run forward on each side (figure 23, plate 10) and then branch profusely to innervate the thick muscle layers that surround the termination of the duct (figures 24 and 25, plate 10). The fibres of these nerves are medium-small, many less than 2 μm, none greater than 6 μm diameter. About five similar bundles turn back on each side and accompany the duct, probably all the way to the posterior salivary glands These salivary duct nerves are, of course, distinct from the posterior salivary nerves themselves, which arise from the superior buccal lobe (p. 32).

The nerve trunks that accompany the salivary duct consist therefore of medial bundles, the salivary duct nerves arising in the subradular ganglion and the more lateral bundles of the posterior salivary nerves (figure 21, plate 10) arising in the superior buccal lobe. In addition a bundle of very small fibres (all < 2 μm) runs with each posterior salivary nerve for most of its course (figure 21, plate 10) but where the nerve turns back the bundle continues forwards to the subradular ganglion. This bundle has been called the salivary-subradular nerve (figure 22*a*). It ends in a special part of the subradular ganglion, which is composed mainly of small cells (figure 26, plate 10). There is no evidence as to the nature of these fibres but they may be afferent. There are varicose fibres in the epithelium of the duct, lying very close to the lumen (figure 29, plate 10). The question of their nature raises many

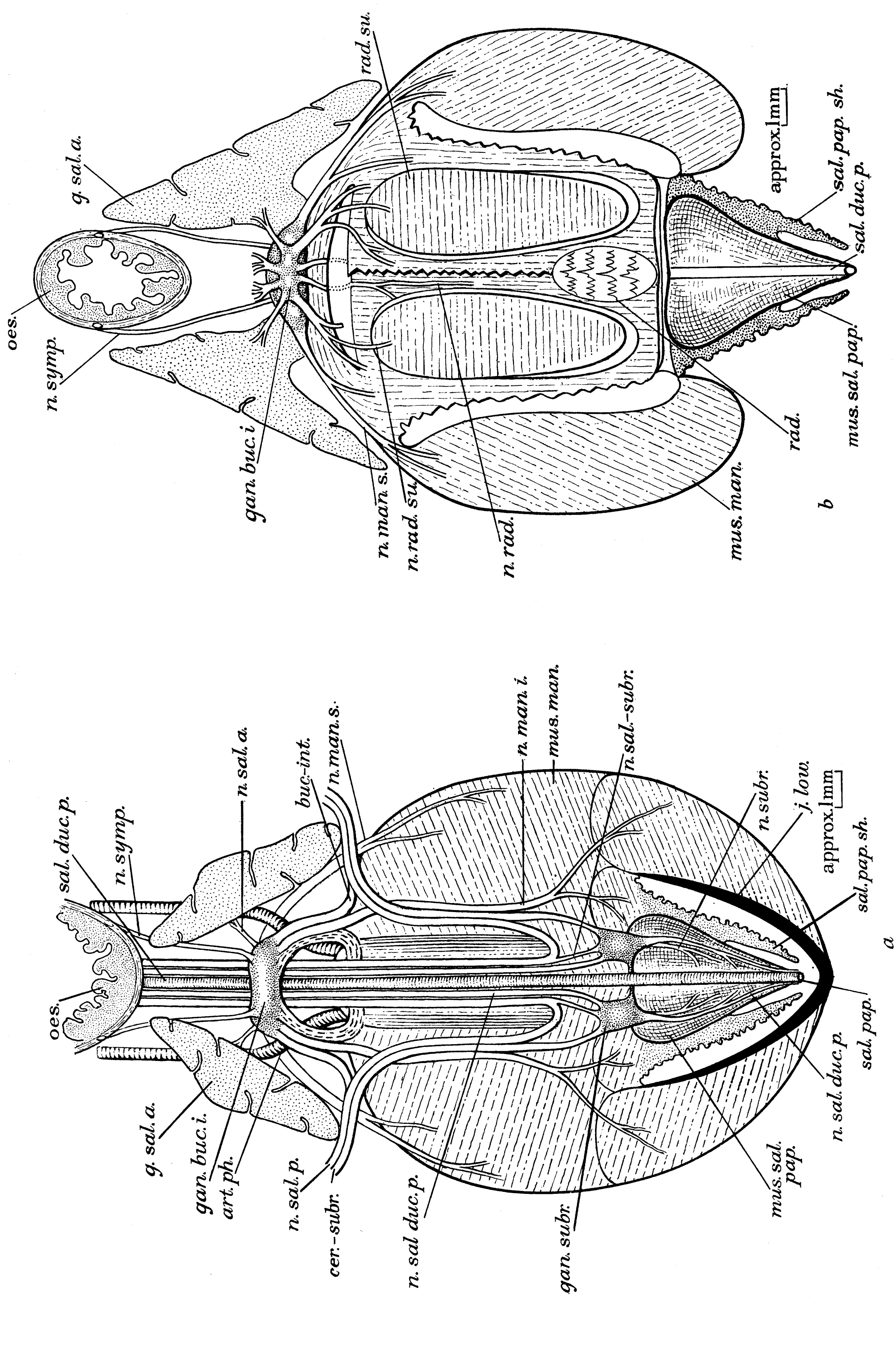


FIGURE 22. *a.* Schematic diagram of the buccal mass, seen from below, reconstructed from oblique horizontal sections.
b. Schematic diagram of the buccal mass seen from above, reconstructed from oblique horizontal sections.

difficulties. In this position they can hardly be efferent fibres. Yet if they are afferent, as they seem from their structure, where do their cell bodies lie? Near the tip of the salivary papilla there is a rich plexus of nerve fibres below the epidermis (figure 30, plate 10).

7. The interbuccal connectives and inferior buccal ganglia

The connectives arise from the superior buccal lobe with the cerebro-subradular connectives as already described. The two connectives have roughly the same fibre composition but the largest fibres in the interbuccal connective are smaller than those in the cerebro-subradular ($< 10\ \mu m$). Bogoraze & Cazal (1944) use the name cerebro-buccal connectives for the trunks that are here called interbuccal connectives. If the superior buccal lobe of *Octopus* is homologous with that of *Sepia* the term cerebro-buccal must be reserved for the trunk uniting that lobe with the brain.

The inferior buccal ganglia are a pair of lobes, united in the mid-line, lying below the oesophagus where it leaves the buccal mass (figure 14, plate 9; figure 22*a* and *b*). The cells and neuropil are partly similar to those of the superior buccal lobe, in that large and small cells are present and the neuropil is mostly of the irregular tangled type that is characteristic of motor centres. However, the ganglia have some very specialized and unusual regions (see below). The axons of their cells run to the muscles of the jaws, radula and lateral buccal palps, also to the anterior salivary glands and oesophagus. Some of them perhaps run to the gastric ganglion.

The interbuccal connectives enter the ganglia at the postero-lateral margins (figures 14 and 16, plate 9). Most of their fibres end in the ganglia but some afferents from the gut pass through the ganglia without synapse.

Seven pairs of nerves leave the ganglia (figures 20, 22*a*, *b*, 27 and 28).

The lateral buccal palp nerves arise from the dorsal surface of the ganglia near the mid-line. They run ventrally for a short distance as a single trunk and then turn dorsally into the lateral buccal palps. These palps are a pair of soft, mobile structures (figure 22, plate 10). The ducts of the anterior salivary glands enter the palps posteriorly and run through them near their medial borders, opening into the mouth by pores on the medial faces of the palps, near their anterior ends. The centre of each palp is occupied by a loose web of muscles and blood vessels (figure 32, plate 11). The muscles run in several directions and many strands pass dorso-ventrally and thus serve to depress the surface of the palp. Waves of depression have been seen to pass along the palps and probably serve to suck in the food and pass it backwards.

The nerves of the palps divide into several trunks running forward to supply the muscles and the epithelial surface of the tongue. Although this surface is cuticularized there are numerous fine fibres within the epithelium (figure 33, plate 11) probably including afferents. The buccal palp nerves have some medium-sized fibres but also numerous small ones, which are presumed to be the afferents. They thus differ markedly in composition from the nerves to the radula and jaw muscles, which have few small fibres and whose maximum fibre size is much greater. These nerves are probably those referred to by Bogoraze & Cazal (1944) as 'labial nerves'. However, no trunks run from the inferior buccal ganglia to the lips.

The radular nerves join the ganglia somewhat behind and below the buccal palp nerves. They pass downwards and divide into branches running backwards and forwards to enter the radula sack. The radula is operated by a complicated set of muscles whose anatomy and mode of functioning has not been elucidated (see Heinrich 1904; Tompsett

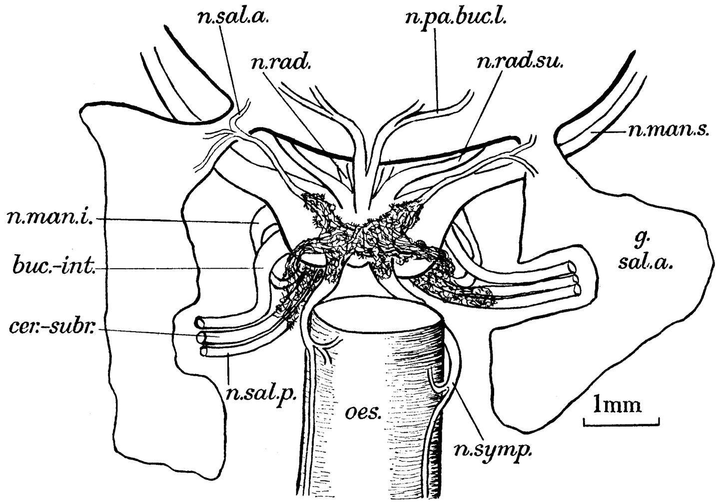


FIGURE 27. Inferior buccal ganglia seen from above, as reconstructed from horizontal sections.

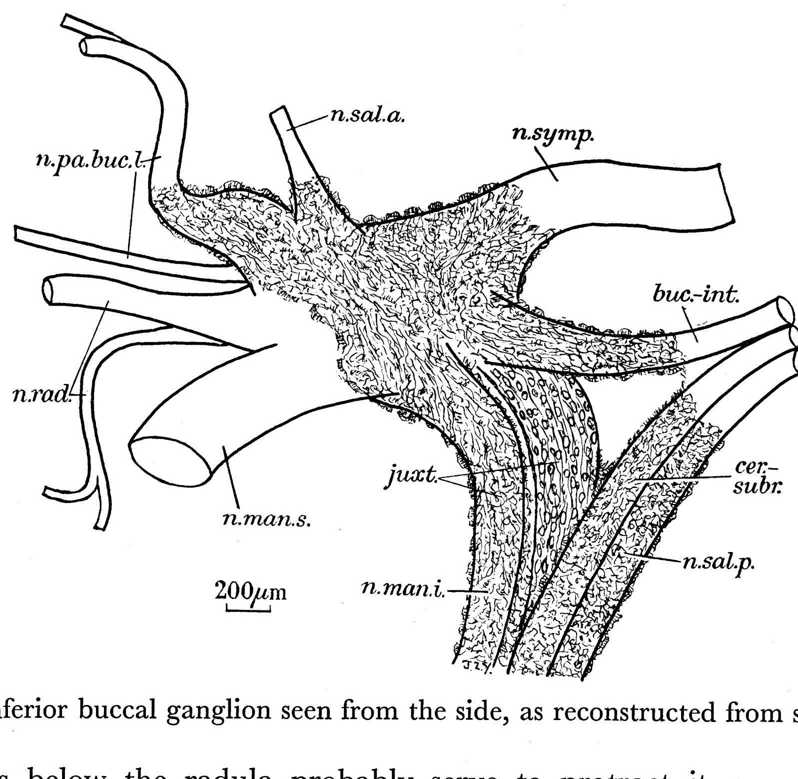


FIGURE 28. Inferior buccal ganglion seen from the side, as reconstructed from sagittal sections.

1939). Muscles below the radula probably serve to protract it, spreading the teeth laterally. A separate branch of the radular nerve reaches these muscles from behind and may be called the inferior radular nerve. Longitudinal muscles above the radula probably draw it and the whole front of the buccal mass backwards between the lateral buccal palps. This is the active action during which the lateral radular teeth fold inwards, raking material towards the mid-line, whose tooth then carries it backwards (see Fretter & Graham 1962 for the condition in gastropods).

Although there are longitudinal 'retractor' muscles that perform this action, the most conspicuous muscles of the radula are the so-called radula support muscles. These are barrel-shaped masses of tissue on either side of the radula. In many cephalopods they are mainly cartilaginous, but in *Octopus* they consist of transverse muscle fibres (figure 20, and figure 22, plate 10). These are attached laterally at the hind end but for much of their length they have *no attachment at either end.* Their action is therefore presumably to produce suction in the closed cavity within which they lie. Although the details are not clear, it is likely that this action would indeed serve to retract the radula and to pull its teeth inwards.

In accordance with this function the radular support muscles are innervated by large branches of the superior division of the radular nerve. Another branch of the same division innervates the longitudinal radular retractor muscles. The radular nerves also supply a rich plexus of branching fibres, in the wall of the posterior part of the radula sack (figure 31*a* and *b*, plate 10). This plexus contains many terminal rings and bulbs, which have all the appearance of afferents, though the position of their cells is not clear. The plexus originates from rather large fibres.

The radular nerves, like the mandibular, consist mainly of medium-sized fibres. No special component of small fibres similar to that of the lateral buccal palp nerves has been found (Young 1965*b*).

The muscles of the jaws are operated by two pairs of nerves (figures 20, 27 and 28). Close behind the radular nerves arise pairs of nerves that turn somewhat laterally and innervate the muscles that unite the upper and lower jaws and hence may be called superior and inferior mandibular nerves.* They consist mainly of fibres of medium diameter (Young 1965*b*).

The mandibular and radular nerves are essentially as described by Bogoraze & Cazal (1944). The radular nerves perhaps correspond to the 'nervi pharyngei' of Pfefferkorn (1915). The 'mandibular nerve' of the latter (in *Eledone*) is however probably the combined trunk of the posterior salivary nerve, cerebro-subradular connective and the nerve here called the inferior mandibular nerve. The last-named nerve leaves the ganglion at its extreme ventro-lateral edge and accompanies the posterior salivary nerve and cerebro-subradular connective around the sides of the back of the buccal mass. The three trunks enter the muscles together but the inferior mandibular nerves turn laterally. They innervate the muscles of the ventral part of the buccal mass (figure 22*a*). The inferior mandibular nerves have a composition similar to that of the radular nerves (Young 1965*b*). The main trunks of the juxta-ganglionic tissue accompany the inferior mandibular nerves (see below).

Besides these nerves that supply the muscles of the buccal mass the inferior buccal ganglia also give rise to nerves to the anterior salivary glands and the 'sympathetic' nerves to the gut. The larger fibres in both of these nerves are only 3 μm in diameter, while both contain smaller ones.

* The superior mandibular nerves have also been described as the lateral mandibular nerves (Young 1965*b*). The 'medial mandibular nerves' of that paper are those that innervate the radular support muscles.

The anterior salivary nerves leave the upper posterior part of the inferior buccal ganglia, near to the mid-line. They run dorsally, laterally and forwards, to the region where the anterior salivary glands are attached to the lateral buccal lobes, through which their ducts pass. The nerves join the ducts of the glands and then divide into several branches. Some of these run to the musculature of the wall of the oesophagus nearby, but the majority ramify throughout the glands. Fine nerve fibres are seen between the secretory acini and they probably innervate these.

The sympathetic nerves arise from the posterior faces of the ganglia and run straight up to the oesophagus. They run back within the wall of the oesophagus and are therefore not easy to dissect free. Their fibres innervate the muscles of the oesophagus and crop, through a plexus in which methylene blue preparations have shown the presence of nerve cells (Alexandrowicz 1928). These cells have not been seen in the silver preparations in the present investigations. Some of the fibres of the sympathetic nerves are also presumably pre-synaptic to the gastric ganglion, but the details of this relationship are quite obscure.

The sympathetic nerves contain afferent as well as efferent fibres. Three days after they had been sectioned degeneration is seen in the inferior buccal ganglia and interbuccal connective (Beverley & Young 1965). Methylene blue shows the presence of numerous receptor cells in the walls of the oesophagus and stomach (Alexandrowicz 1928).

The inferior buccal ganglia do not form a simple unit. The cell walls and neuropil include three separate and distinctly recognizable types of organization. The main ventral and anterior part of the ganglia consists of cell walls composed of large cells externally and smaller ones within (figure 5, plate 8; figure 34, plate 11). The neuropil of this part is of the usual 'reflex' type, a dense tangle, with no apparent order. From this neuropil arise the nerves that run to the muscles of the jaws and radula.

The postero-dorsal part of the ganglia consists of much more irregular cell walls, interspersed with promontories of neuropil proceeding from the main central mass. The cell walls of this part include a few large cells and more numerous small ones than in the remainder of the ganglion (figure 35, plate 11). The neuropil is also quite different, including a few thick fibres staining black with Cajal's method, also some thinner ones, and conspicuous areas staining light yellow and probably composed of very fine fibres. These areas recall the small-fibre areas of the subfrontal and vertical lobes; like them they appear to be developments of the outer region of the neuropil. These parts of the ganglia give rise to the sympathetic nerves and perhaps to those for the lateral buccal palps and anterior salivary glands. Many of the afferent fibres of the sympathetic nerves end in this part of the ganglia, which become filled with granules after these nerves have been cut (Beverley & Young 1965). These fibres presumably signal something about the amount or nature of food in the gut and may serve for regulation of the amount of food consumed ('hunger'). It is probable that this region constitutes some sort of pacemaker for part or even the whole digestive apparatus.

The third portion of the inferior buccal ganglia gives rise to the juxta-ganglionic tissue. It consists of ill-defined lobules of minute cells and neuropil, lying *outside* the main cell layer of the ganglia (figure 35, plate 11). These cells occupy an irregular area mainly above and at the sides of the ganglia, interweaving to some extent with the neuropil of the sympathetic part of the ganglion.

The juxta-ganglionic tissue consists of cords of cells, interspersed with nerve fibres and running alongside some of the nerve trunks, especially those of the inferior mandibular, sympathetic and anterior salivary nerves. More peripherally, and especially ventrally, these cords spread out into irregular plexuses of nerve fibres, which apparently come into close relationship with the buccal sinus. Some parts of this tissue contain rows of cells, lying in tubes, and resembling those of the subpeduncular tissue (Thore 1936; Boycott & Young 1956). In other places there are irregular lumps of neuronal material.

This is clearly the juxta-ganglionic tissue described by Bogoraze & Cazal (1944). Essentially similar tissue has been described by Alexandrowicz (1964) arising from the 'extracortical neuropil' at the back of the palliovisceral lobe and ending in the wall of the anterior vena cava. Alexandrowicz considers this to be 'neurosecretory' tissue. Not the least curious of its features is that it arises from small cells lying at the *outside* of the ganglia (figure 35, plate 11). This is the characteristic origin in regions as far apart as the palliovisceral and inferior buccal ganglia. The subpeduncular tissue may be related to control of pressures within the orbit and eyes (Boycott & Young 1956). It may be that all of these tissues are concerned with the regulation of the composition of fluids, perhaps in relation to flotation (Young 1965*c*).

8. Gastric ganglion

This lies at the point where the crop joins the stomach, and the caecum, 'liver' and intestine are all close together. It receives the lower ends of the two sympathetic trunks and sends nerves to the neighbouring organs. It is an oval body, measuring $1{\cdot}6 \times 2{\cdot}0 \times 1{\cdot}4$ mm in an octopus of 300 g body weight. It lies partly buried in the wall of the lower end of the crop and is therefore not easy to find.

The ganglion has a characteristic appearance in section, different from that of either of the buccal or subradular ganglia (figures 36 and 37, plate 11). The cell layers are thick, with larger cells at the outside and smaller ones within, but with less marked size differences than in other ganglia. There are no very large or very small cells. The neuropil contains a rather loose tangle of fibres, with many irregular bundles. There is no special region of small cells or neuropil of fine fibres, such as that lying at the origin of the sympathetic nerves in the inferior buccal ganglia. Neither is there any outer layer of small cells or juxta-ganglionic tissue.

9. Discussion

Analysis of the connexions of the various ganglia thus shows the outline of the plan of the mechanism for the control of feeding. The fibres that innervate the posterior salivary glands arise independently and behind the rest, and run, without synapse, from the superior buccal lobe to their destination. This is all the more remarkable since the nerves run forward almost to the front end of the salivary duct before turning back towards the glands. This course and the position of the papilla, far forward, suggest that perhaps the 'posterior' salivary glands lie, morphologically, in front of the glands that are now the more anterior. Presumably the poison glands have moved back as they have increased in size and became too large to be accommodated within the buccal mass.

The origins of the posterior salivary nerves lie close to the entry of fibres from the arms to the back of the superior buccal lobe. The secretion of poison may be begun as soon as the prey is touched, indeed perhaps even when it is seen. No peripheral synapse is involved along this pathway, possibly because no continuing rhythmic operations are involved, or because no local reflex guidance is needed, once the 'command' to secrete has been given.

The cerebro-subradular connectives, controlling the actual ejection of the poison through the papilla, arise from the front of the superior buccal ganglion. The process of emission is perhaps under the influence of afferent fibres from the lips, which enter here. However octopuses from which the lips have been removed can still poison crabs (Young 1965*d*). Presumably directing the salivary papilla is an important part of the process and this may be accomplished by reflexes through the subradular ganglia.

The operations of the other parts of the buccal mass are also probably initiated from the front of the superior buccal ganglion, through the interbuccal connectives. The inferior buccal ganglia have a complicated structure since they have to bring into action, in proper sequence, the jaws, radula, lateral buccal palps, anterior salivary glands and oesophagus and to co-ordinate all of these with the actions of the rest of the gut, controlled through the gastric ganglion. The inferior buccal ganglia cannot properly conduct these operations when isolated from the central nervous system (Young 1965*d*), but they certainly receive afferent fibres from the gut and some of their actions are of reflex character.

The activities of the gastric ganglion are even more obscure. It receives fibres from the sympathetic and perhaps also from the visceral nerves though there is no direct evidence of this. After severing the sympathetic nerves the octopuses are able to eat well, and they apparently digest food (Beverley & Young 1965). Severance of the visceral nerves has always killed the animal, apparently through damage to the veins.

The posterior buccal, superior buccal, inferior buccal, subradular and gastric ganglia all have characteristic microscopic appearances and distribution of nerve cell sizes. The proportion of large cells decreases in this sequence. In octopuses, as in vertebrates, it seems that large cells and axons are found only in the motor parts of the nervous system that come into relation directly with the outside world. Small cells are found in the motor centres for the control of the viscera. The large numbers of cells in the inferior buccal and gastric ganglia again emphasize the peculiarity that the number of final motorneurons is much greater in these visceral pathways than in the somatic motor systems, although presumably the actions of the latter systems in relation to the outside world are the more precise.

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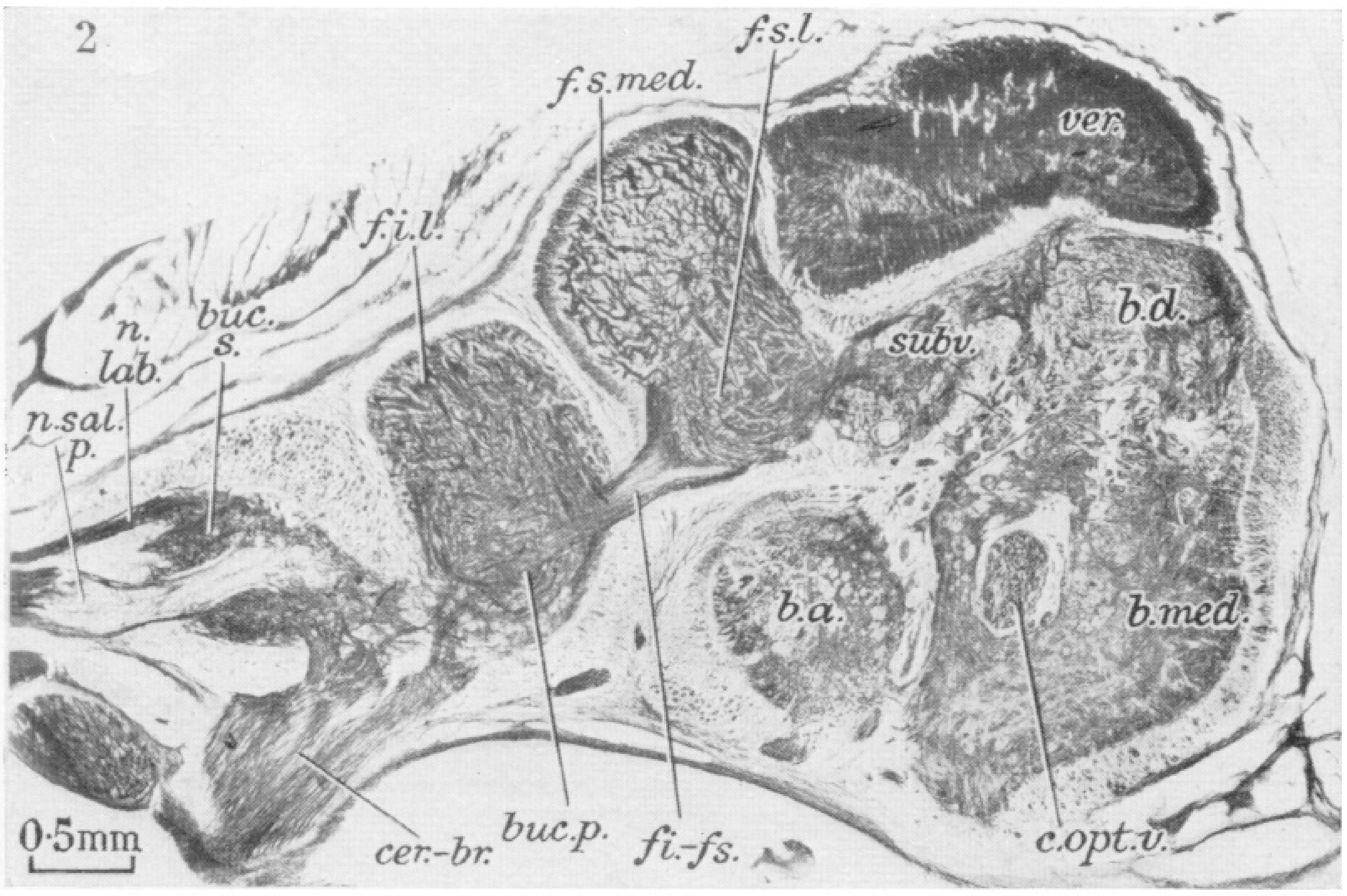
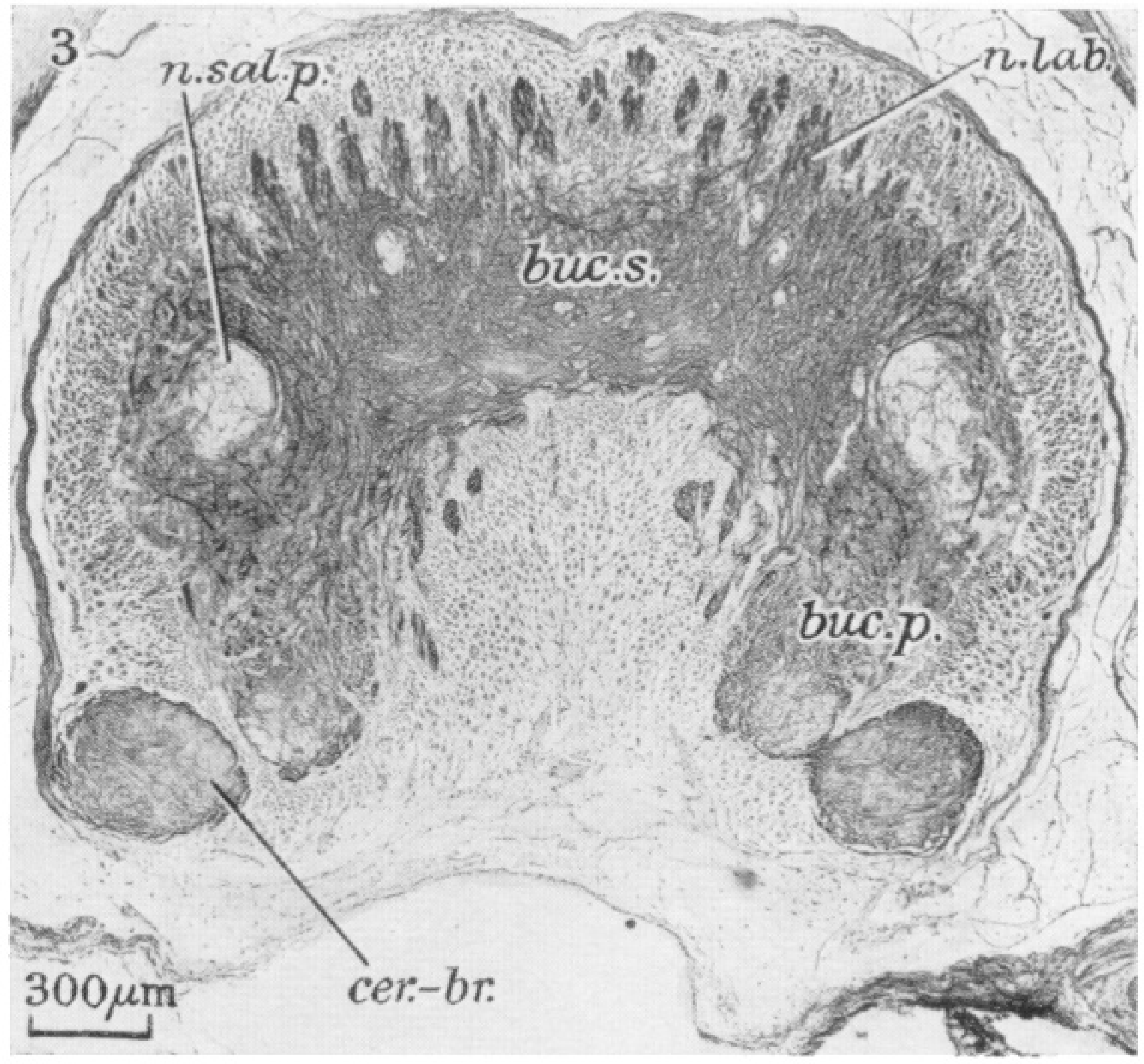
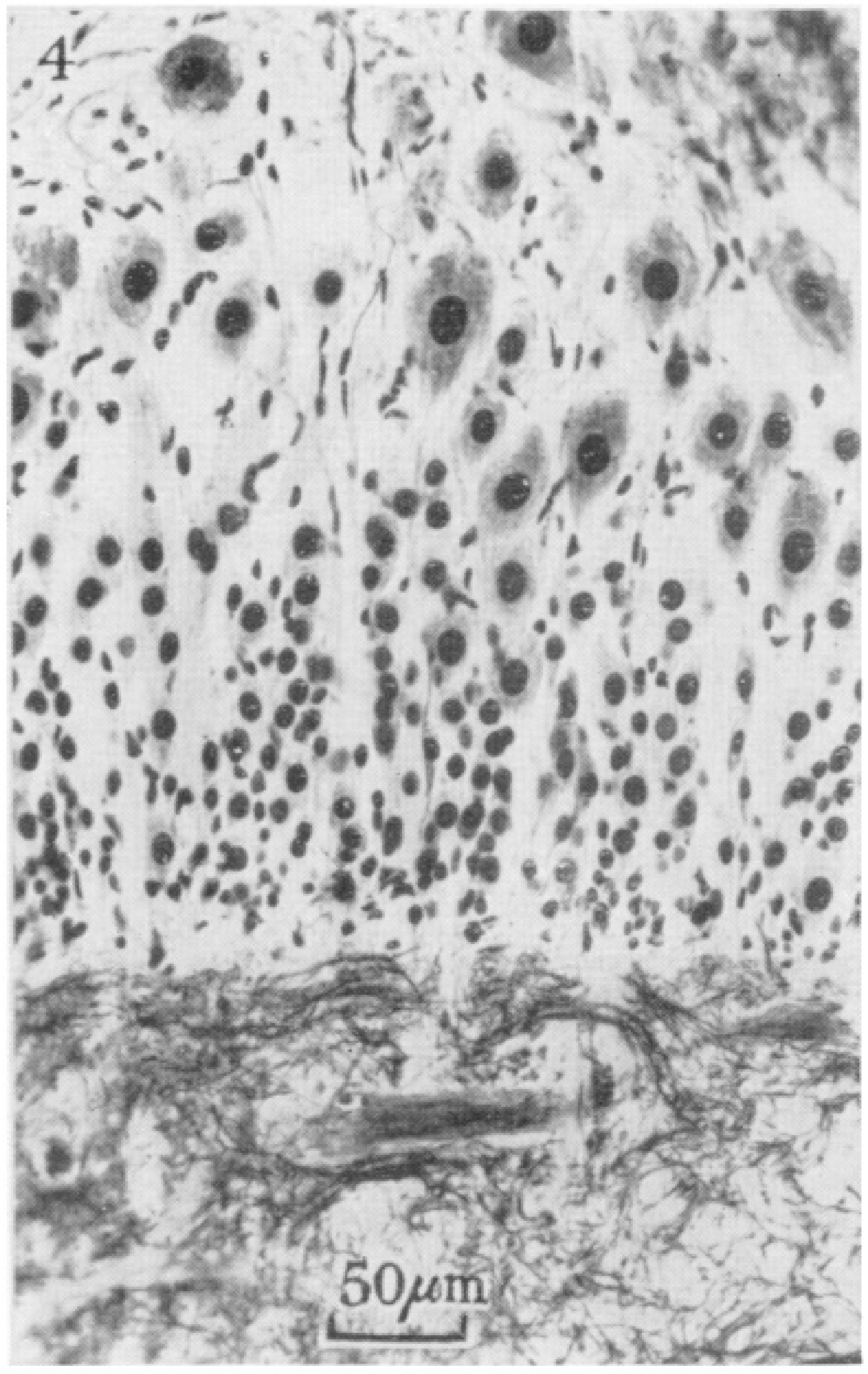
Abbreviations used on figures and plates

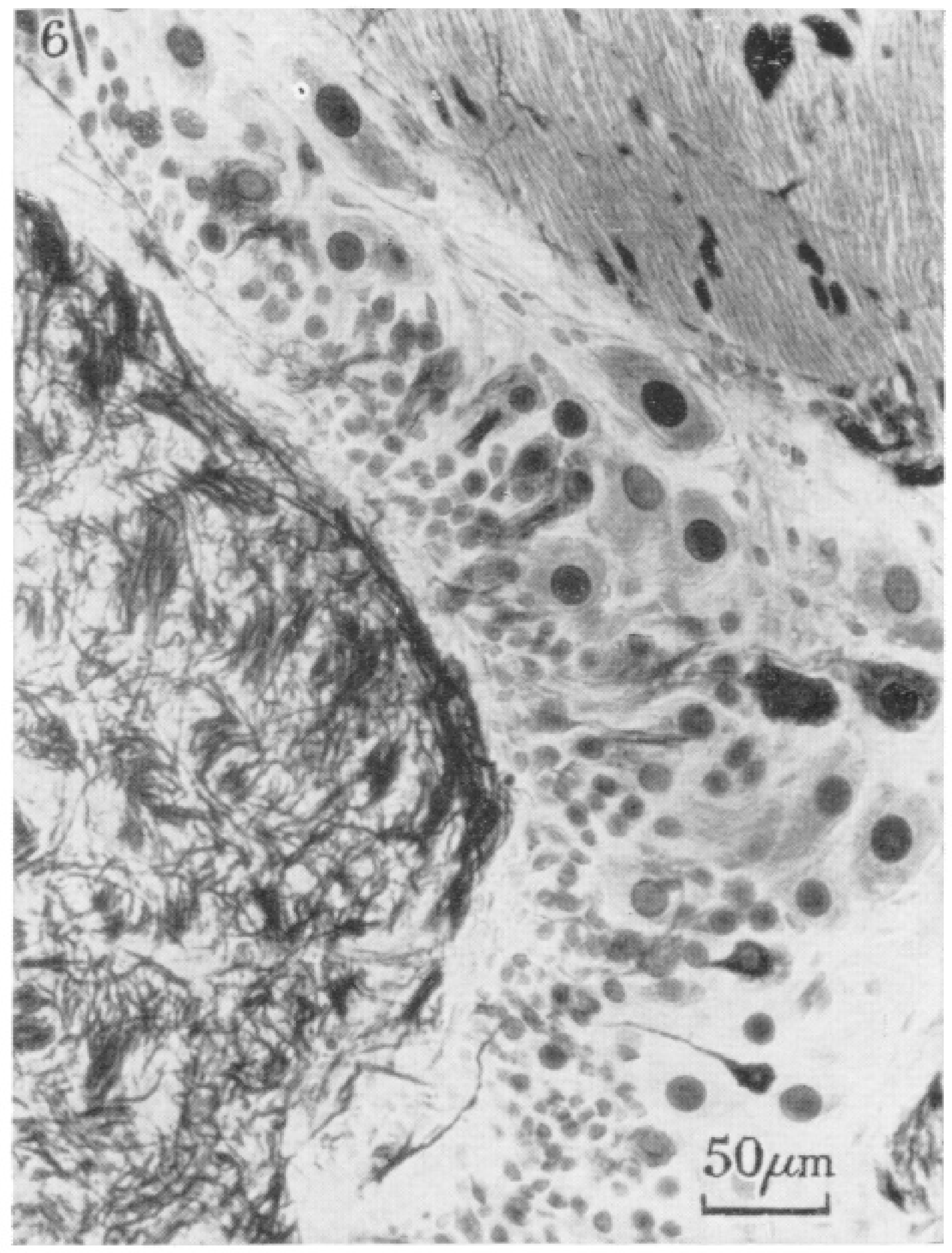
art.	arteriole
art.ph.	pharyngeal arteries
b.a.	anterior basal lobe
b.d.	dorsal basal lobe
b.med.	median basal lobe
br.	brachial lobe
br.pr.	prebrachial lobe
buc.-int.	interbuccal connective
buc.p.	posterior buccal lobe
buc.s.	superior buccal lobe
buc.s.-br.	superior buccal-brachial connective
buc.s.-buc.p.	superior buccal to posterior buccal tract
buc.-subv.	buccal to subvertical tract
c.br.sup.	suprabrachial commissure
c.buc.p.	commissure between posterior buccal lobes
c.opt.v.	ventral optic commissure
ce.lar.	large cell of posterior buccal (or subfrontal) lobe
cer.-br.	cerebro-brachial connective
cer.-br.l.	lateral cerebro-brachial connective
cer.-br.med.	medial cerebro-brachial connective
cer.-p.v.	cerebro-pallioviseral connective
cer.-subr.	cerebro-subradular connective
deg.	degenerating fibres
f.i.-br.	brachial to inferior frontal tract
f.i.-f.s.	median inferior frontal to median superior frontal connective
f.i.l.	lateral inferior frontal lobe
f.i.l.-buc.p.	lateral inferior frontal to posterior buccal tract
f.i.med.	median inferior frontal lobe
f.i.med.-subfr.	median inferior frontal to subfrontal tract
f.i.-opt.	inferior frontal (and posterior buccal) to optic tract
f.i.rud.	rudiment of inferior frontal system not yet differentiated into lobes
f.s.l.	lateral superior frontal lobe
f.s.med.	median superior frontal lobe
g.sal.a.	anterior salivary gland
g.sal.p.	posterior salivary gland
g.subman.	submandibular gland
gan.br.	brachial ganglion
gan.buc.i.	inferior buccal ganglion
gan.subr.	subradular ganglion
j.low.	lower jaw
j.u.	upper jaw
juxt.	juxta-ganglionic tissue
les.	position of lesion
mus.man.	mandibular muscle
mus.pro.rad.	radular protractor muscle
mus.retr.rad.	radular retractor muscle
mus.sal.pap.	muscle of the posterior salivary duct papilla.
n.br.	brachial nerve
n.fi.	nerve fibre
n.lab.	labial nerve
n.man.i.	inferior mandibular nerve
n.man.s.	superior mandibular nerve
n.pa.buc.l.	lateral buccal palp nerve
n.rad.	radular nerve
n.rad.su.	nerve to the radula support
n.sal.a.	anterior salivary gland nerve
n.sal.duc.p.	nerve of the duct from the posterior salivary glands
n.sal.p.	posterior salivary gland nerve
n.sal.-subr.	salivary to subradular nerve
n.subped.	subpedunculate nerve
n.subr.	subradular nerve
n.symp.	sympathetic nerve
oes.	oesophagus
opt.	optic lobe
pa.buc.l.	lateral buccal palp
p.v.	palliovisceral lobe
p.v.-buc.p.	palliovisceral to posterior buccal tract
ped.	pedal lobe
pil.cen.	central neuropil of subfrontal lobe
pil.out.	outer neuropil of subfrontal lobe
prec.	precommissural lobe
rad.	radula
rad.sa.	radula sac
rad.su.	radula support
sal.duc.a.	duct to the anterior salivary gland
sal.duc.p.	duct of the posterior salivary glands
sal.pap.	posterior salivary duct papilla
sal.pap.sh.	sheath of the posterior salivary duct papilla
subfr.	subfrontal lobe
subfr.-buc.p.	subfrontal to posterior buccal tract
suboes.m.a.	anterior suboesophageal mass
subv.	subvertical lobe
subv.a.	anterior subvertical lobe
subv.-buc.p.	subvertical to posterior buccal tract
subv.p.	posterior subvertical lobe
tr.buc.	buccal tract
tr.cer.	cerebral tract
tr.opt.	optic tract
ver.	vertical lobe
ver.-buc.p.	vertical to posterior buccal tract

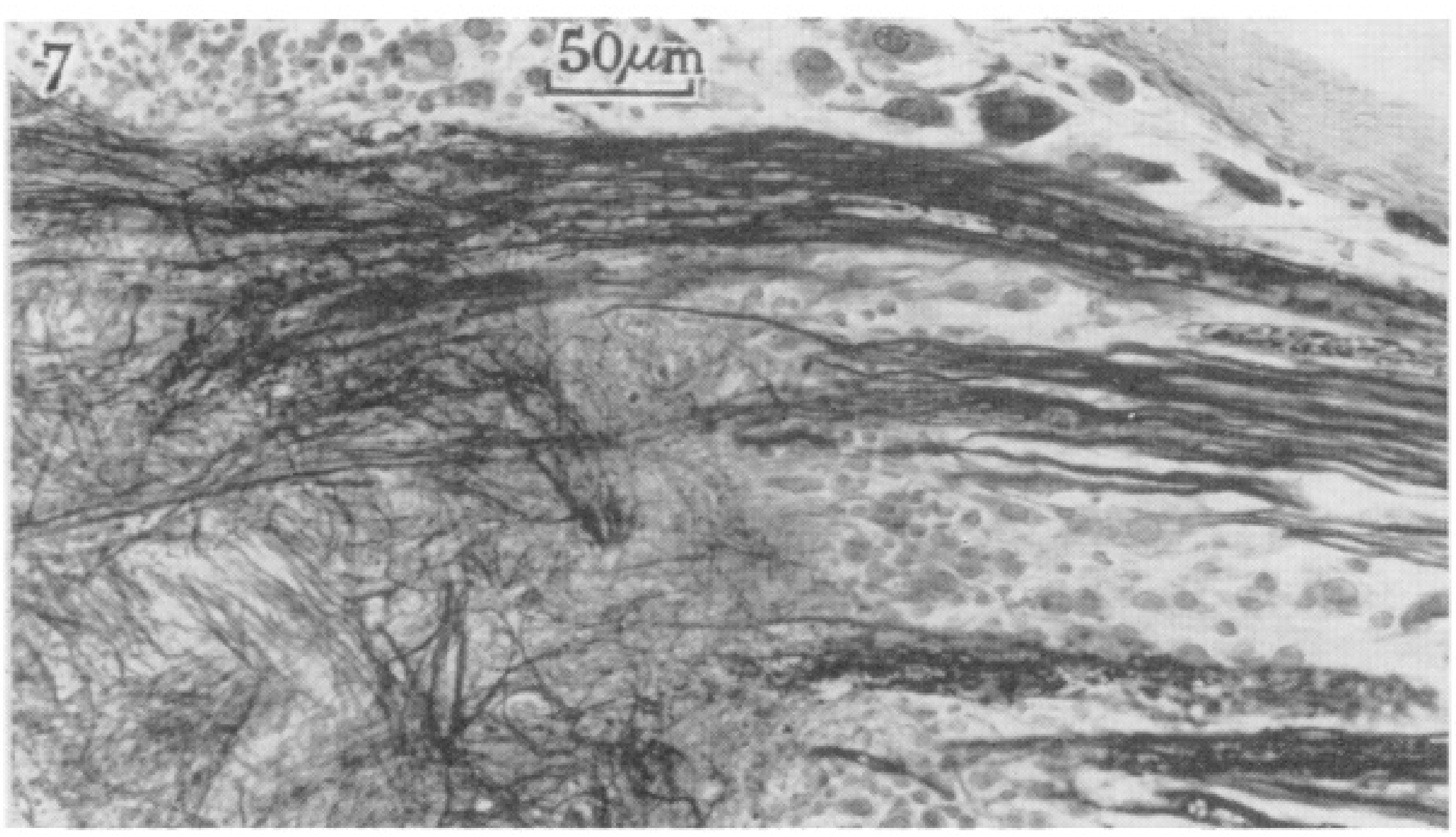

2
f.s.med.
f.s.l.
ver.
f.i.l.
b.d.
subv.
n.
lab.
buc.
s.
n.sal.
p.
b.a.
b.med.
0·5mm
cer.-br.
buc.p.
fi.-fs.
c.opt.v.

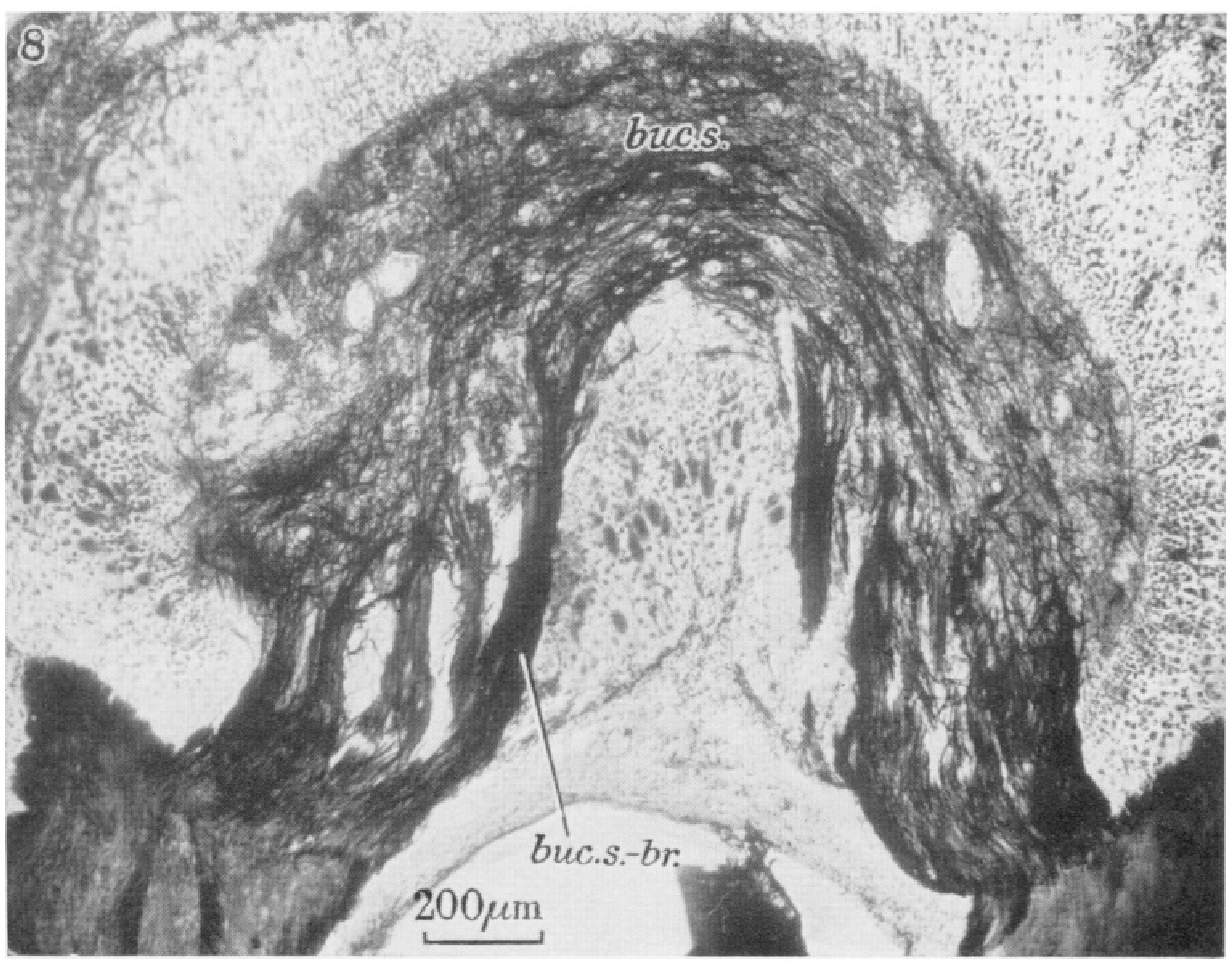

3
n.sal.p.
n.lab.
buc.s.
buc.p.
300μm
cer.-br.

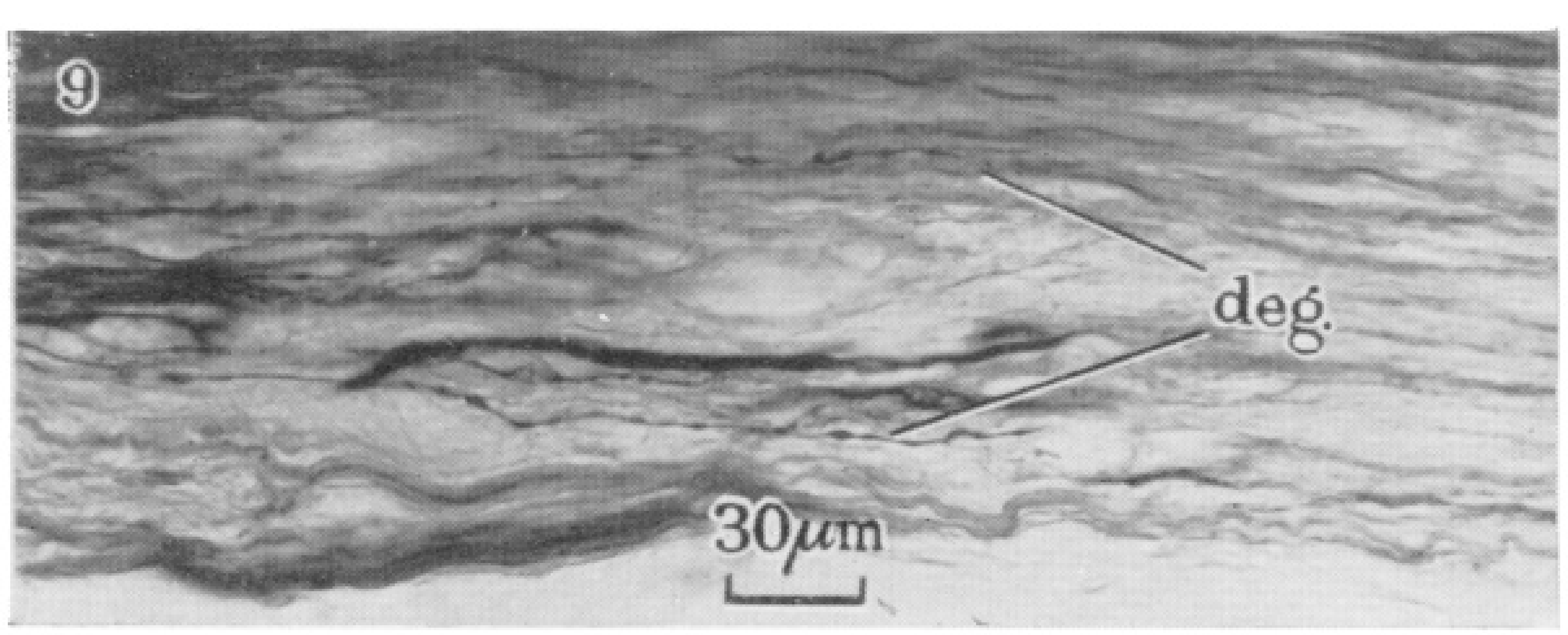

4
50μm

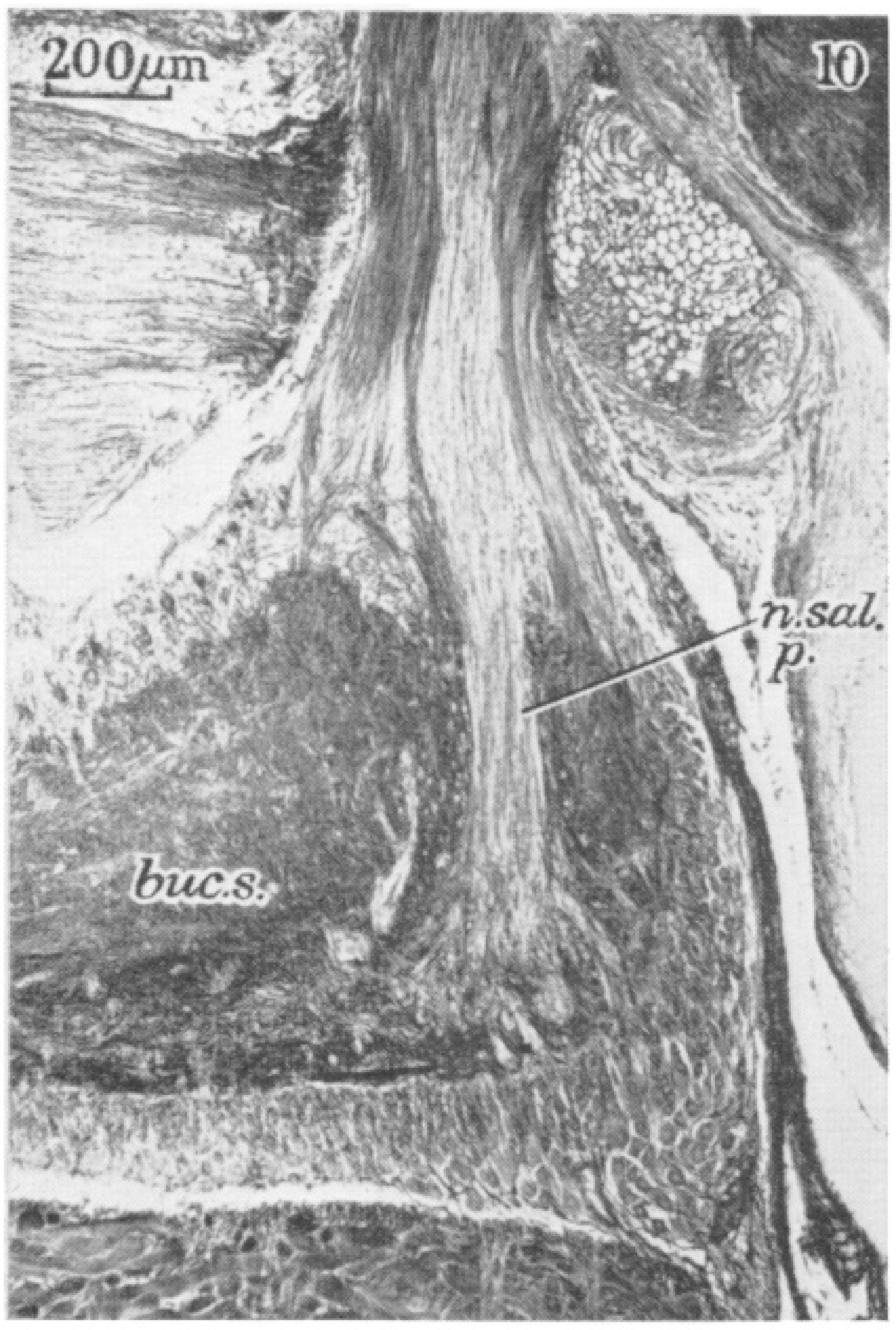

5
50μm

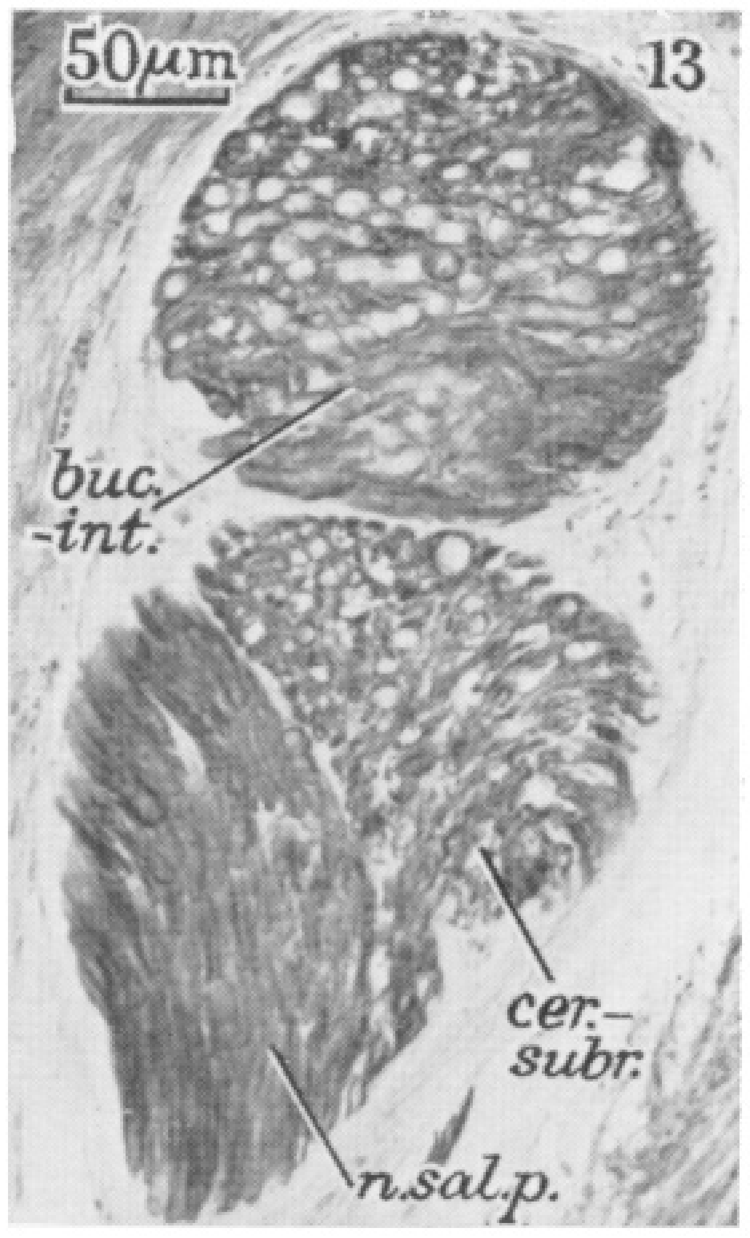

6
50μm

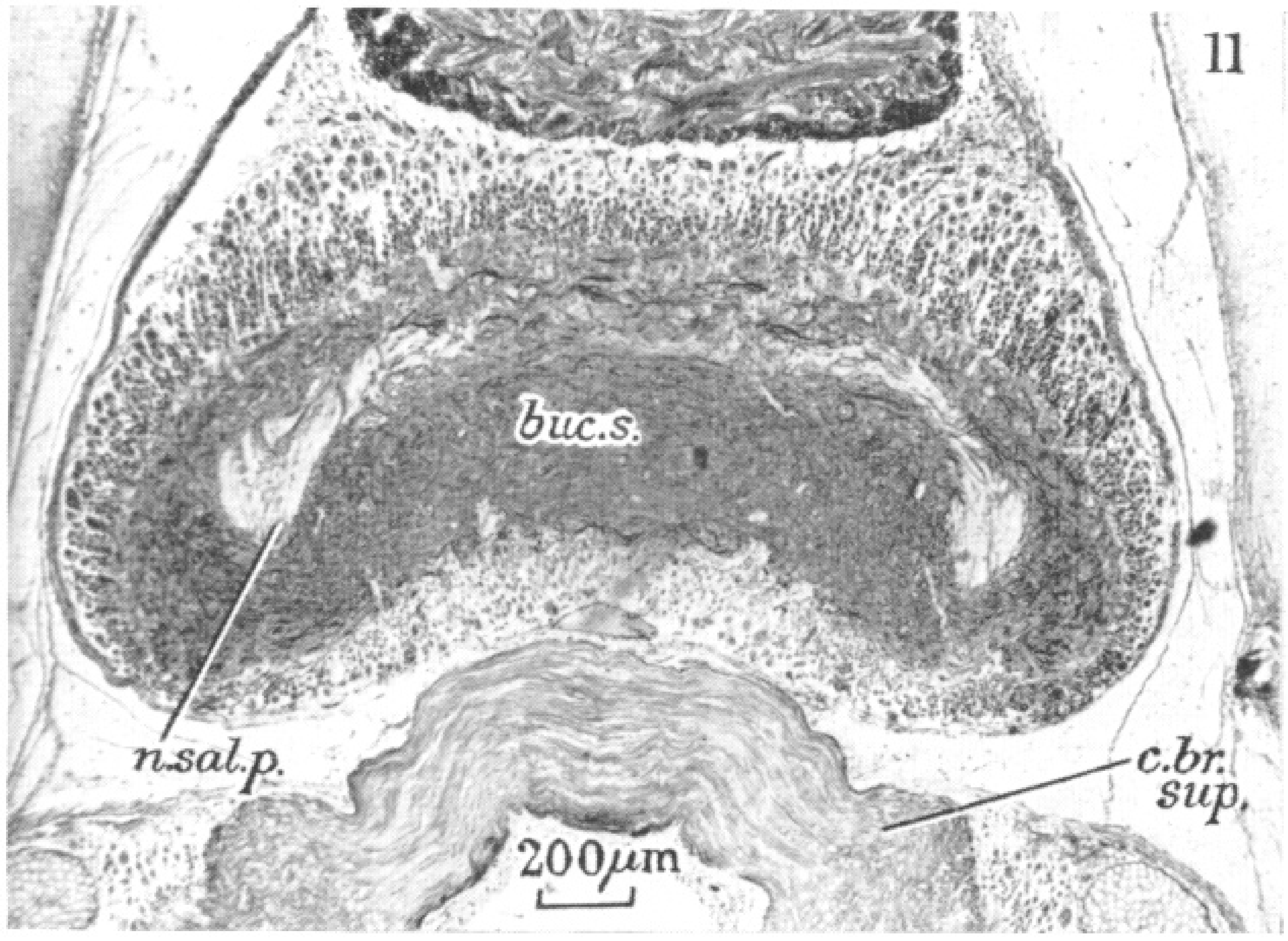

7
50μm

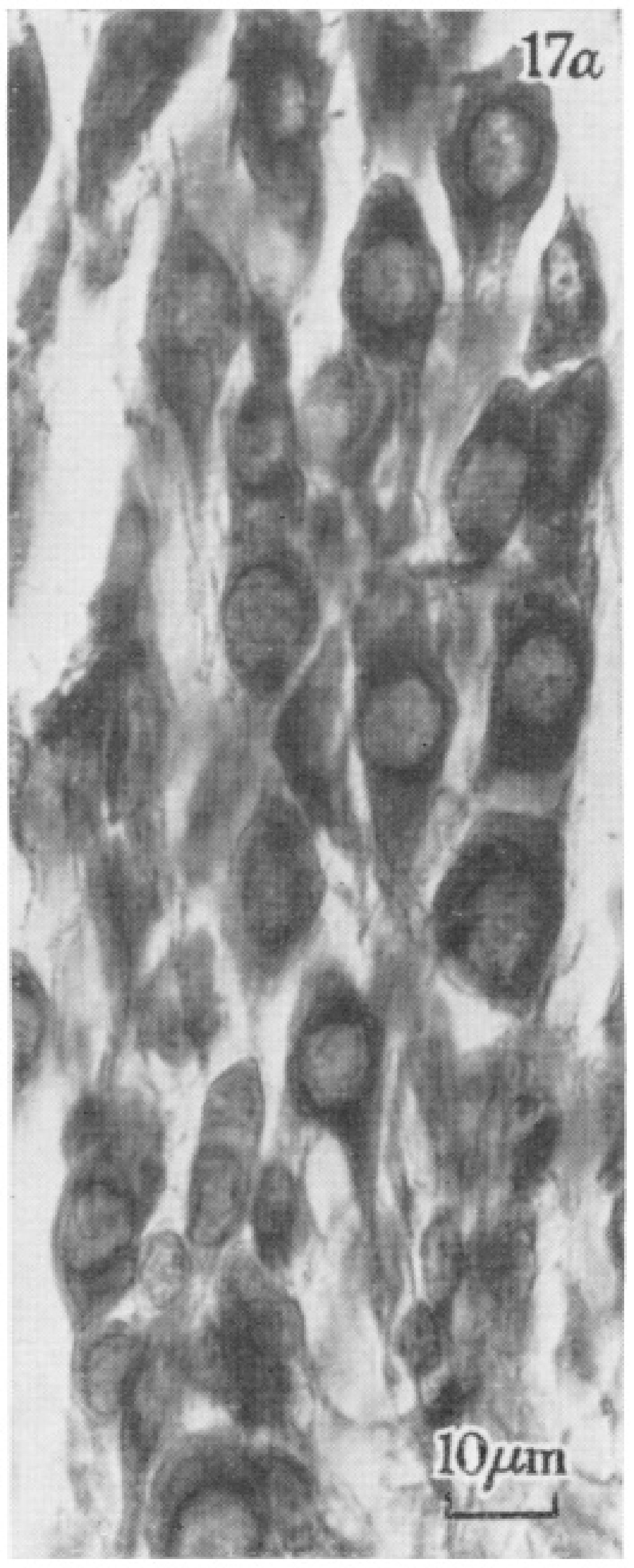

8
buc.s.
buc.s.-br.
200μm

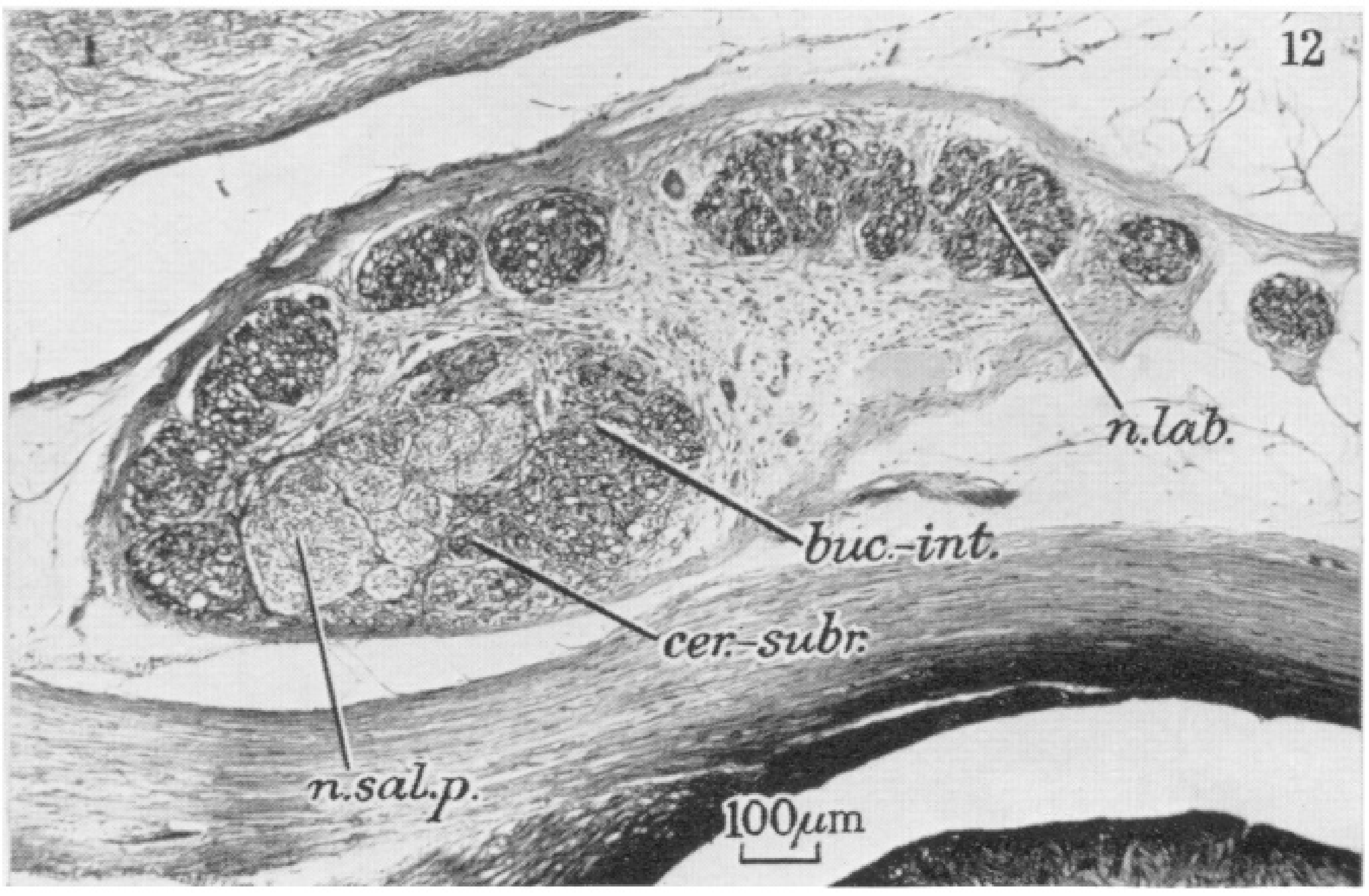

9
deg.
30μm

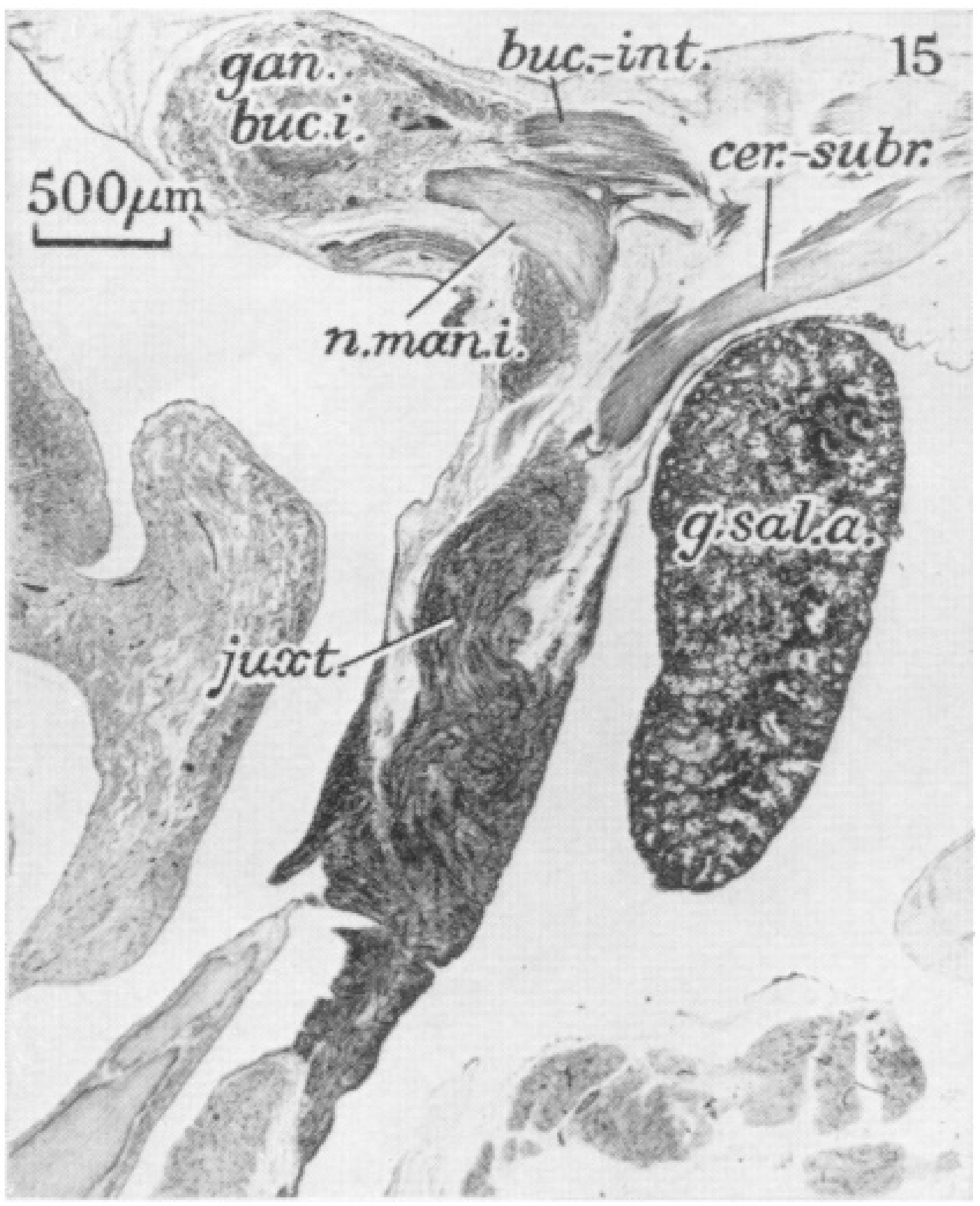

200μm
10
n.sal.
p.
buc.s.

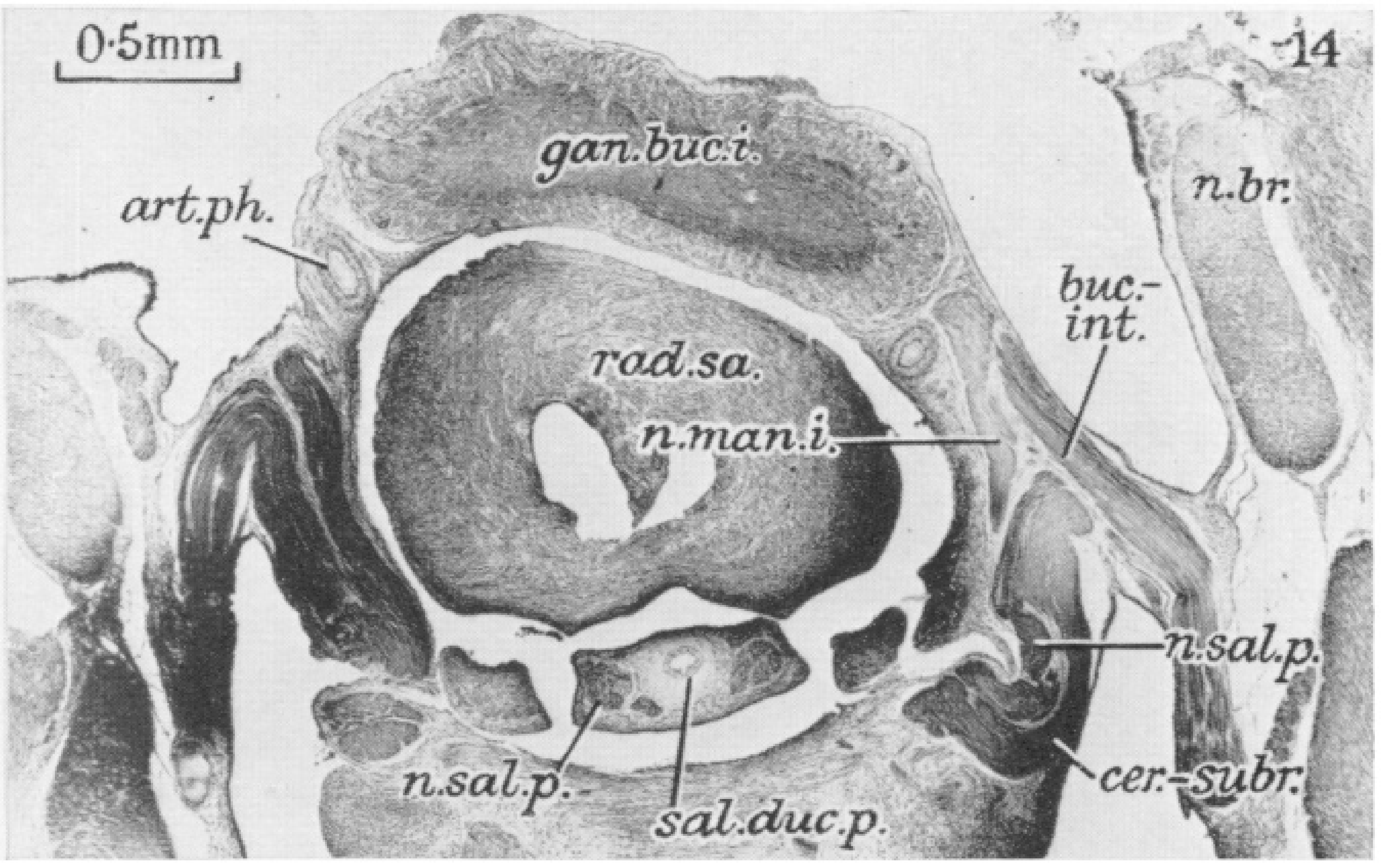

50μm
13
buc.
-int.
cer.-
subr.
n.sal.p.

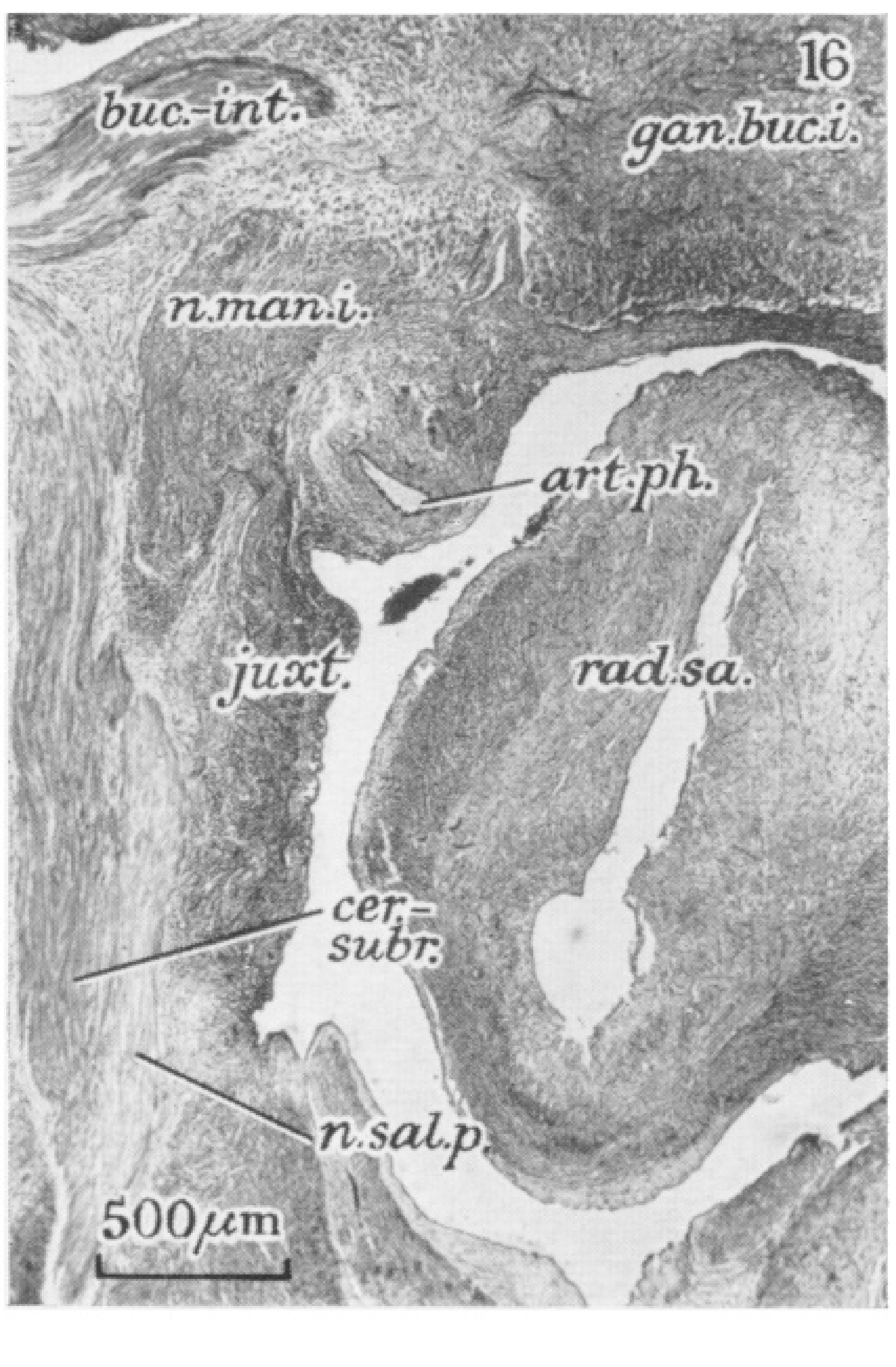

11
buc.s.
n.sal.p.
c.br.
sup.
200μm


17a
10μm

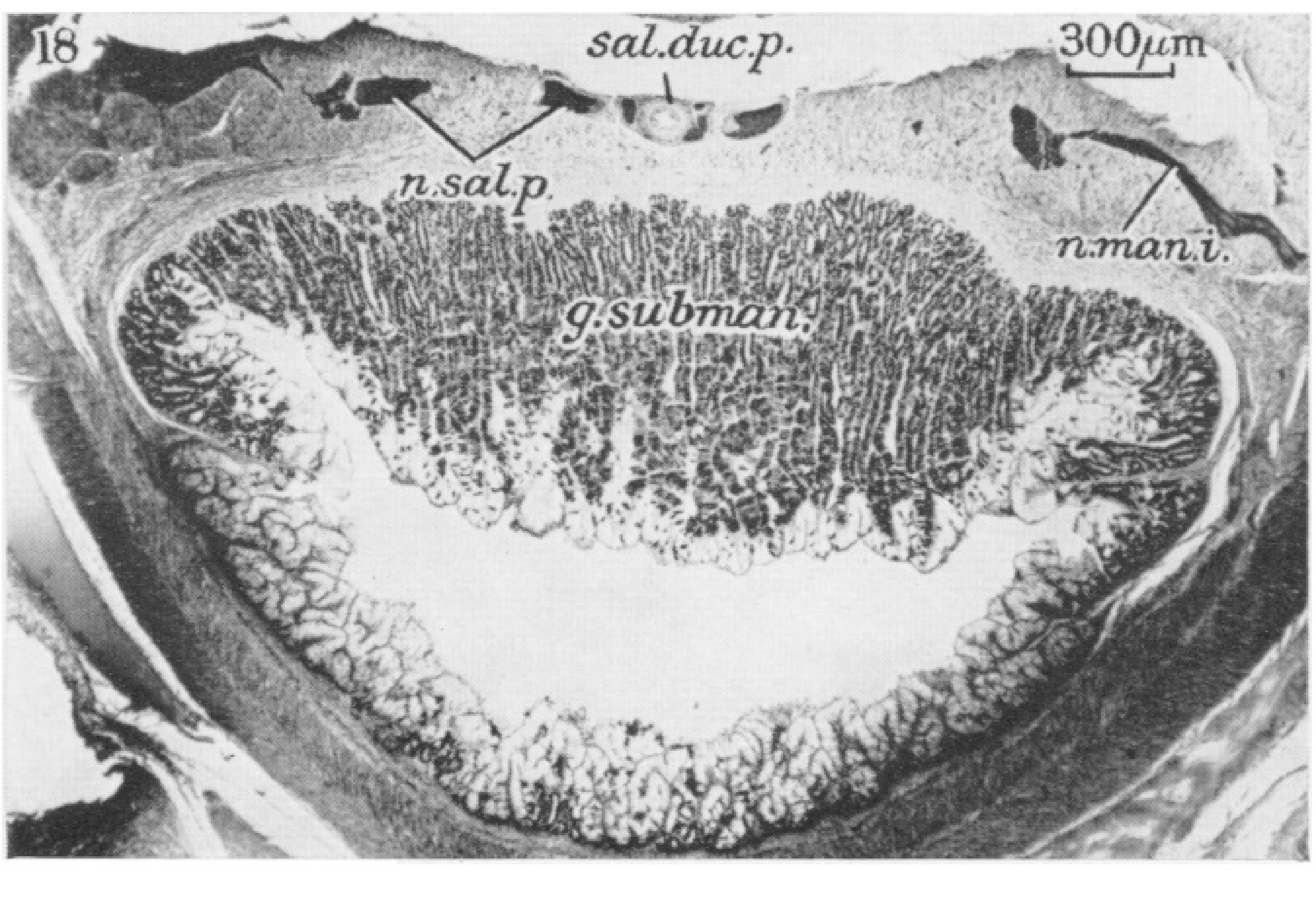

12
n.lab.
buc.-int.
cer.-subr.
n.sal.p.
100μm

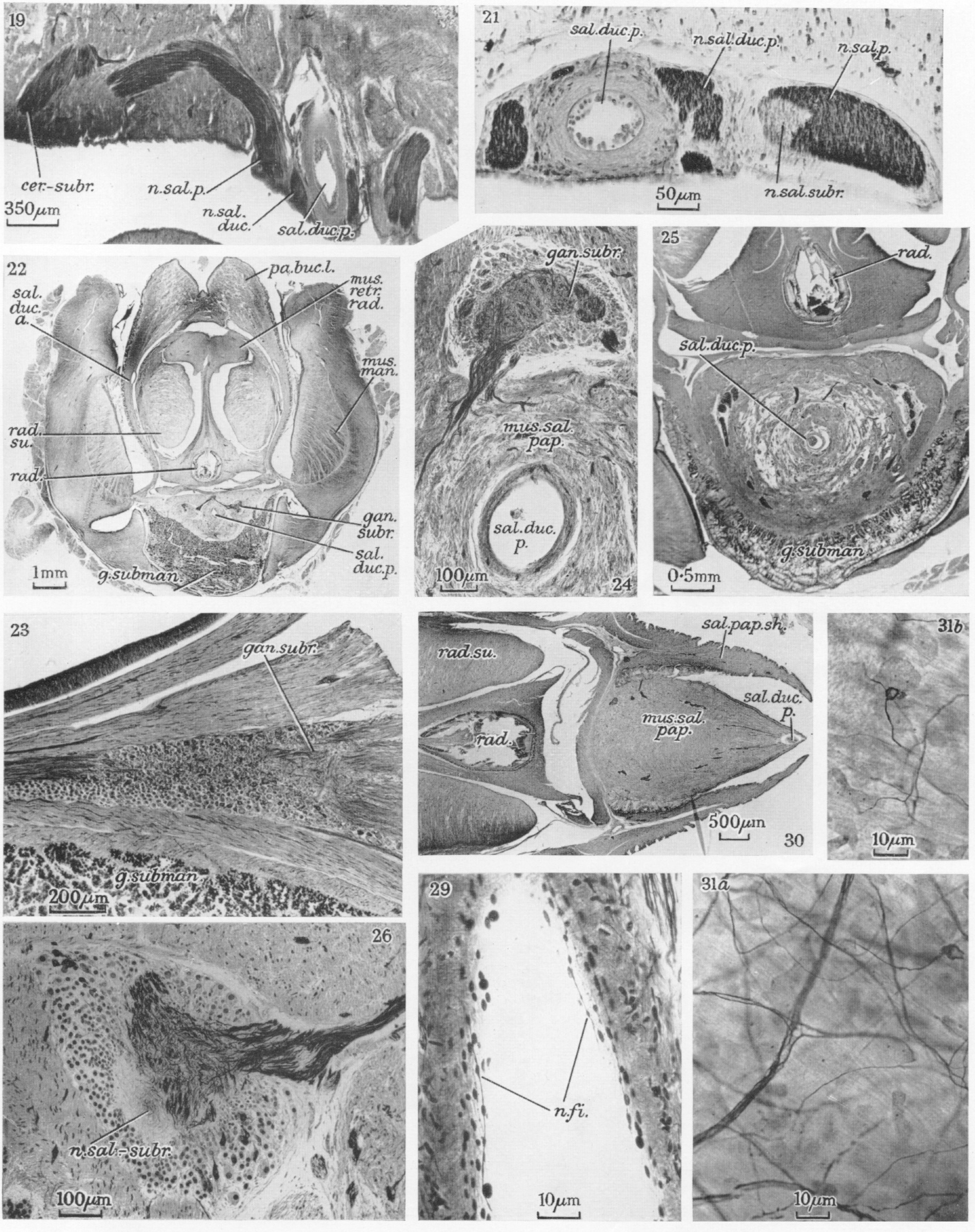

gan.
buc.i.
buc.-int.
15
500μm
cer.-subr.
n.man.i.
g.sal.a.
juxt.


0·5mm
14
gan.buc.i.
n.br.
art.ph.
buc.-
int.
rad.sa.
n.man.i.
n.sal.p.
n.sal.p.
sal.duc.p.
cer.-subr.

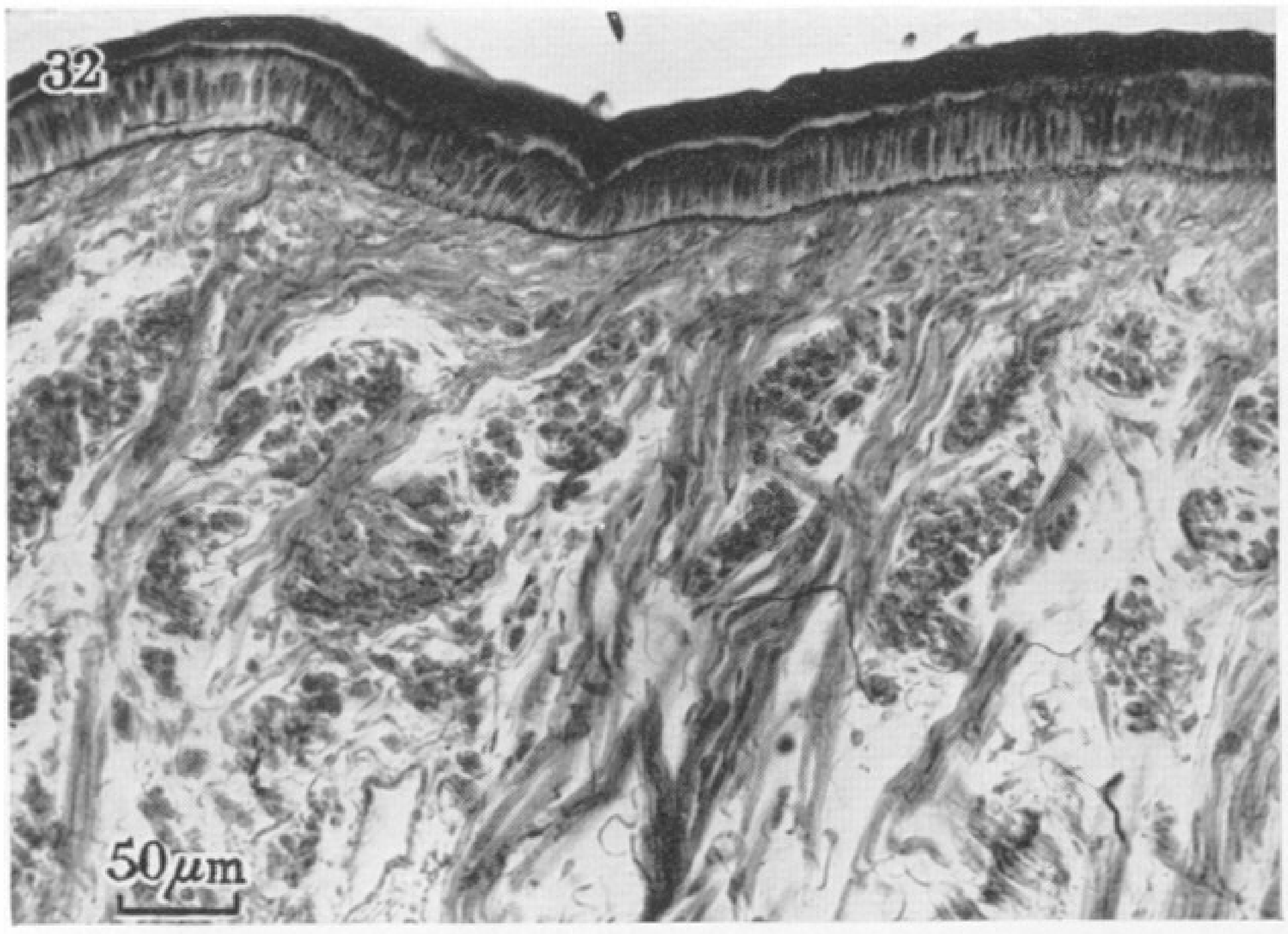

16
buc.-int.
gan.buc.i.
n.man.i.
art.ph.
juxt.
rad.sa.
cer.-
subr.
n.sal.p.
500μm

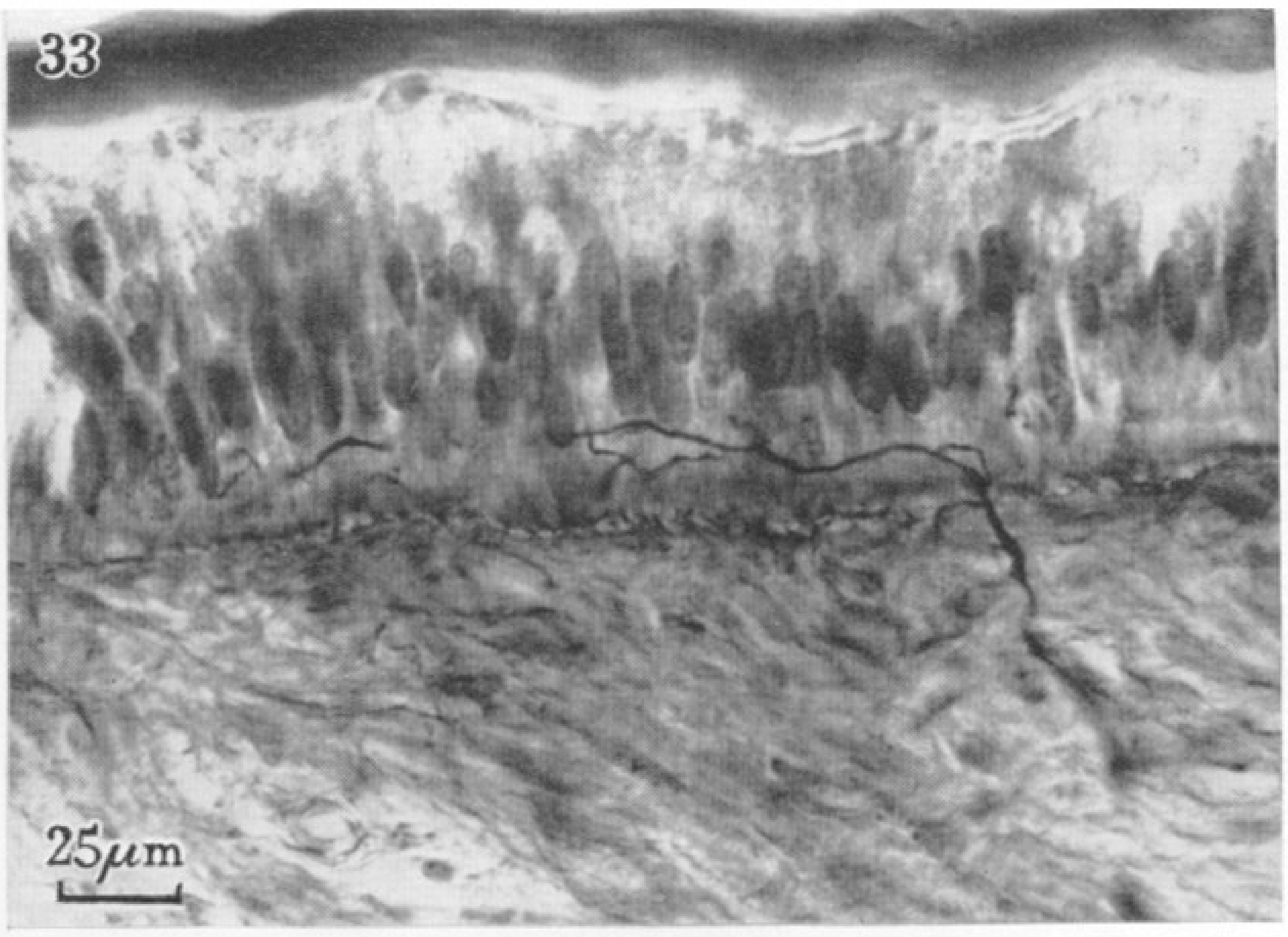

17b
10μm

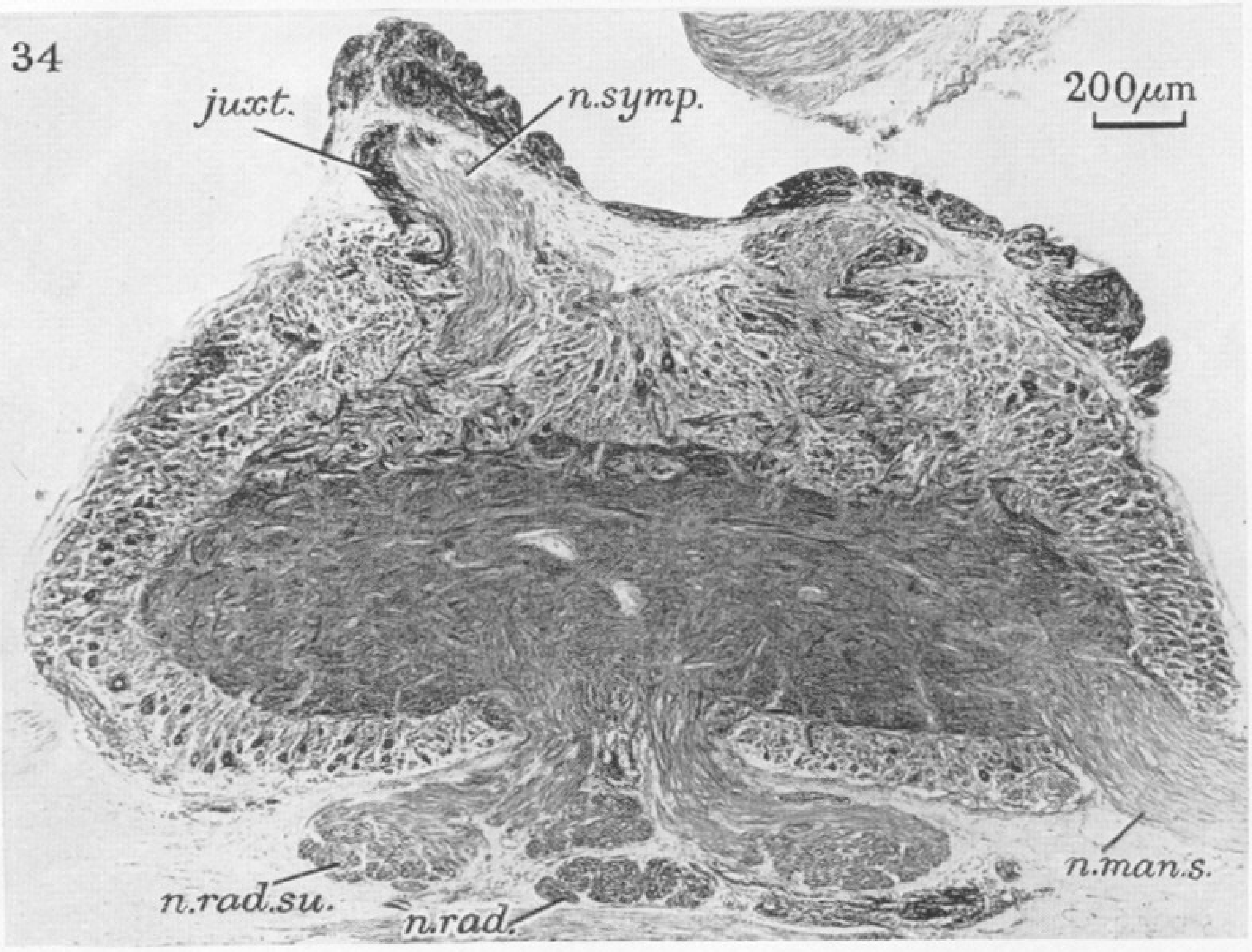

18
sal.duc.p.
300μm
n.sal.p.
n.man.i.
g.subman.

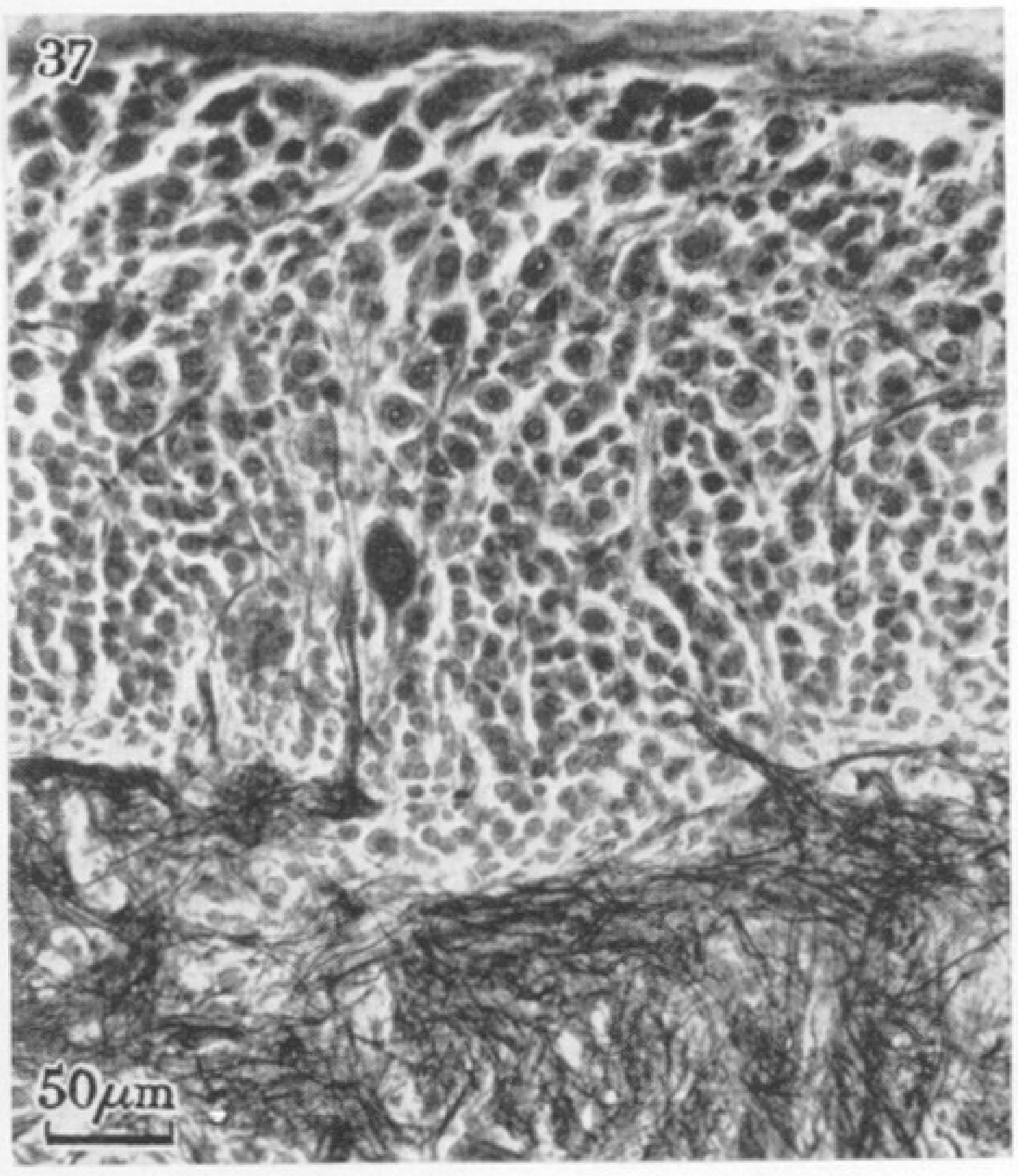


19
cer.-subr.
n.sal.p.
n.sal. duc.
sal.duc.p.
350μm
21
sal.duc.p.
n.sal.duc.p.
n.sal.p.
n.sal.subr.
50μm
22
pa.buc.l.
mus. retr. rad.
sal. duc. a.
mus. man.
rad. su.
rad.
gan. subr.
sal. duc.p.
g.subman.
1mm
gan.subr.
mus.sal. pap.
sal.duc. p.
100μm
24
25
rad.
sal.duc.p.
g.subman.
0·5mm
23
gan.subr.
g.subman.
200μm
sal.pap.sh.
rad.su.
sal.duc. p.
mus.sal. pap.
rad.
500μm
30
31b
10μm
26
n.sal.-subr.
100μm
29
n.fi.
10μm
31a
10μm









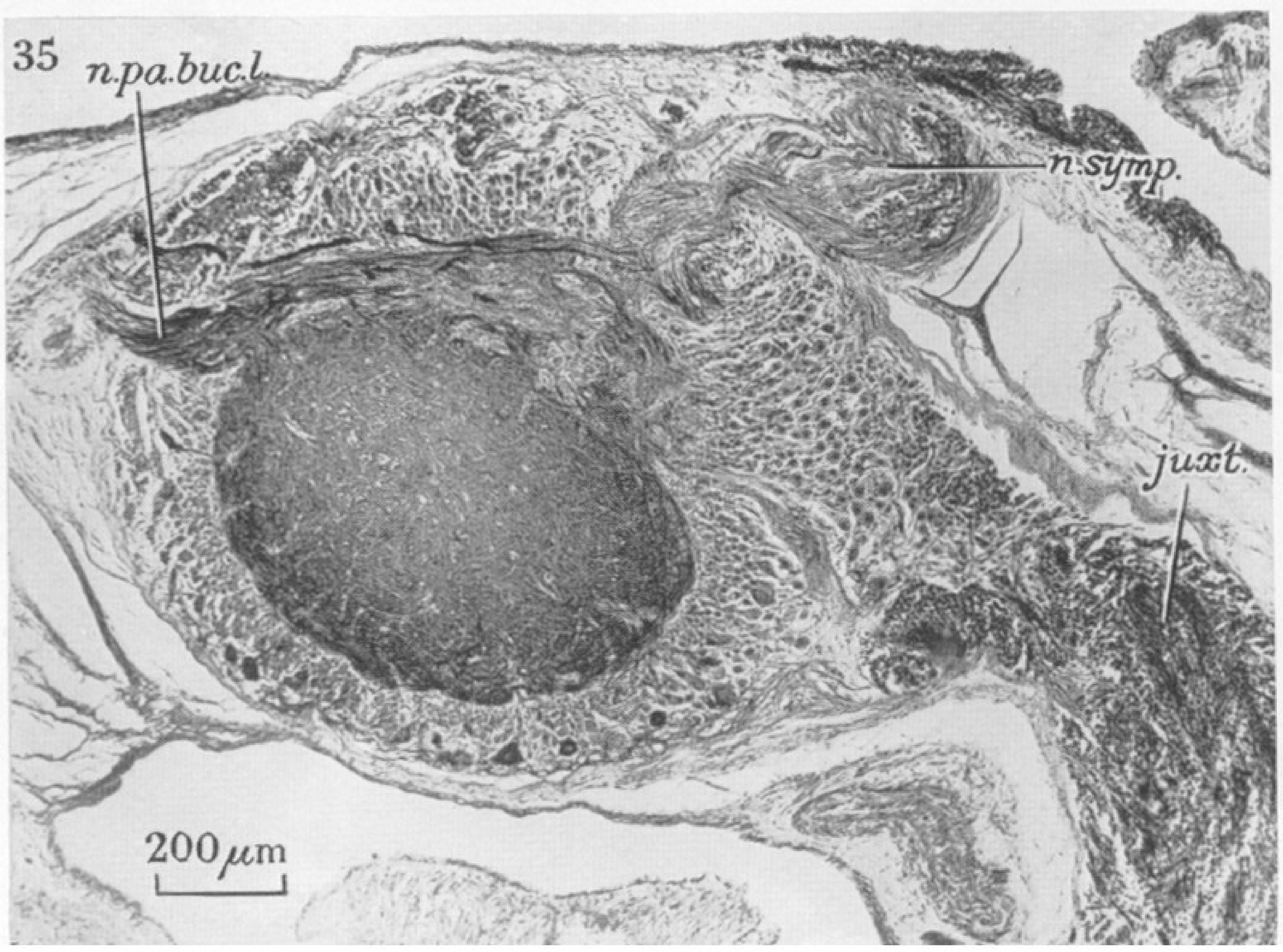


FIGURE 32. Transverse section of lateral buccal palp, showing loose web of muscle fibres and nerve trunks.

FIGURE 33. Transverse section of surface of lateral buccal palp, showing nerve fibres within the epithelium.

FIGURE 34. Transverse section of centre of inferior buccal ganglion.

FIGURE 35. Sagittal section of inferior buccal ganglion to show the part with small cells and the origin of the juxta-ganglionic tissue.

FIGURE 36. Transverse section of gastric ganglion.

FIGURE 37. Cells and neuropil of gastric ganglion.