THE VISCERAL NERVES OF *OCTOPUS*

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[Plates 1 to 8]

The gastric ganglion of cephalopods is connected with the central nervous system by three pathways: (1) the sympathetic nerves; (2) from the visceral nerves through the rectal and intestinal nerves; (3) from the visceral nerves through the abdominal (hepatic capsule) nerves. None of these are direct efferent pathways, but proceed through plexuses innervating the walls of the viscera along which they run.

The ink sac and duct are innervated by branches from both visceral nerves. The innervation of the hearts, renocoele, gonocoele and ctenidia are described. The oviducal gland (spermatheca) contains a very rich plexus of nerve fibres and cells, presumably regulating the rate of fertilization and laying of the eggs. The folded epithelium around the opening of the female duct is richly innervated. The male duct is innervated only along the ridge of the vas deferens; the spermatophores are therefore formed by ciliary action only partly under nervous control. The innervation of the penis is described; there is no special afferent plexus around the aperture.

The pericardial body is very richly innervated and may provide a system involved in regulation of circulation and/or excretion. The walls of the pericardial and genito-pericardial canals also contain many nerve fibres.

The nerve fibres of the branchiae not only innervate the muscles but also make an elaborate plexus beneath the epithelium (presumably afferent).

The nerves of the viscera of octopus thus resemble those of vertebrates in that: (*a*) they contain very numerous fibres, (*b*) these form plexuses, (*c*) there are many peripheral nerve cells. The peripheral centres such as the gastric ganglia and ganglia of the oviducal gland receive no direct through trunks from the central nervous system and it may be that they operate mainly as autonomous pacemakers or reflex centres.

Introduction

Although much information is available about the visceral nerves of invertebrates there is not yet sufficient understanding of them to allow comparison with the autonomic system of vertebrates. Design features that are characteristic of visceral nervous systems seem to be (1) the presence of plexiform arrangements of the peripheral nerves, (2) numerous and small nerve fibres, (3) nerve cells scattered in the plexuses, close to their end organs. These features are presumably related to the slow and relatively 'autonomous' actions of some of the viscera. It is less clear what may be the principles of the control of the viscera from the central nervous system. In cephalopods, for example, it is not known whether the 'visceral nerves' send any branches at all to the alimentary canal. The present investigation was undertaken to clarify this and other points of obscurity. Earlier works on the visceral nervous system are summarized by Bauer (1909), who also gave moderately complete drawings left by Jatta. In his classical work on the nervous system of octopods Pfefferkorn (1915) provides some descriptions of the two 'sympathetic' trunks, which leave the inferior buccal ganglia and run back along the oesophagus. He showed that they divide and anastomose, but he found difficulty in following them along the crop. In one example he was able to follow the right sympathetic all the way to the gastric ganglion (a connexion seen already by Chéron in 1866 in *Eledone* and indeed by van Beneden (1838) in *Argonauta*). Pfefferkorn (1915) gives a description of the gastric ganglion and its nerves but specifically states that 'Eine Commissur desselben (Ganglion) mit dem Visceralsystem konnte ich bei keiner Form entdecken' (p. 518).

Alexandrowicz (1928) provided an excellent account of the plexus in the wall of the oesophagus (of *Sepia*) and of the nerve cells that are found there. As he points out, the main trunks of the 'sympathetic nerves' are 'des voies principales d'un riche plexus' (p. 71). He prefers to call them stomatogastric connectives, but since only a part of each runs to the gastric ganglion this name also is not perfect and we shall keep to 'sympathetic'. He points out that the right is larger than the left. The two join shortly before running to the gastric ganglion. The ganglion and the nerves coming from it are fully described, but again there is no mention of any connexion with the visceral nerves.

A further description of the gastric ganglion was given by Bogoraze & Cazal (1944), who also make no mention of a connexion with the visceral nerves. In spite of these negative anatomical descriptions there is evidence that the visceral nerves can influence the alimentary canal. Falloise (1905) reported movements of the stomach and caecum following stimulation of either visceral nerve. These responses might have been mediated by connexions such as that described by Pfefferkorn leading from the left visceral nerve to the lower end of the rectum. The right visceral nerve in its further course lies close to the intestine but there have been no reports that it gives branches to the latter. A further possible pathway for a connexion with the gastric ganglion is through branches from each visceral nerve to the capsule around the liver. Carlson (1904) reports a direct connexion of the left visceral nerve with the gastric ganglion in *Ommastrephes*.

The remaining course of the visceral nerves to the heart, ctenidia, urinary and genital systems is also here described. Some aspects of this posterior part of the course of the visceral nerve have been recently described by Alexandrowicz in decapods and in *Octopus* (1960, 1964, 1965).

An account of the innervation of the ink sac has beeen given by Girod (1882). He includes no mention of the atrio-rectal nerves described here, but writes of 'filets vésiculaires' more posteriorly and 'nerfs de la glande' farther back still. The latter are almost certainly the abdominal nerves, which in the present investigation have been shown to innervate the hepatic capsule.

Methods

The greater part of the description is based upon analysis of serial sections stained with a modified Cajal method (Young 1939). Serial transverse sections were prepared through the whole body of small octopuses, about 50 to 100 g, fixed whole in formalin and then cut up. These allowed the visceral nerve and its branches to be followed. The detailed innervation of the various organs was then studied in pieces of each organ obtained from larger animals and sectioned and stained in the same way.

The main conclusions about distribution of the branches were obtained by dissection, sometimes assisted by methylene-blue staining. Treatment with alcohol (50%) assists dissection.

The plexuses in the oesophagus were followed in whole mounts after Cajal staining. The muscle layers can then be separated from the mucosa. Such preparations can also be made of the intestinal plexuses. The preparations are much improved by the method devised by Miss P. Stephens in which the viscera are tied at both ends and inflated by an injection of formalin (10% in sea water).

Results

Visceral nerve main trunk

The trunks of the visceral nerves pass through the muscular capsule that surrounds the liver, reaching positions above the funnel on either side of the vena cava (figure 1, and figure 2, plate 1). Each is accompanied by the trunk that Alexandrowicz (1964, 1965) has called 'medial NSV trunk' or 'nerve of the medial NSV trunk' (figure 2, plate 1 and figure 8). The nerves lie somewhat dorsal to the vein and are not very easy to expose at this level by dissection.

Each visceral nerve consists of about fourteen bundles, not well separated. All have approximately the same composition (figure 3, plate 1 and figure 4). A few of the fibres

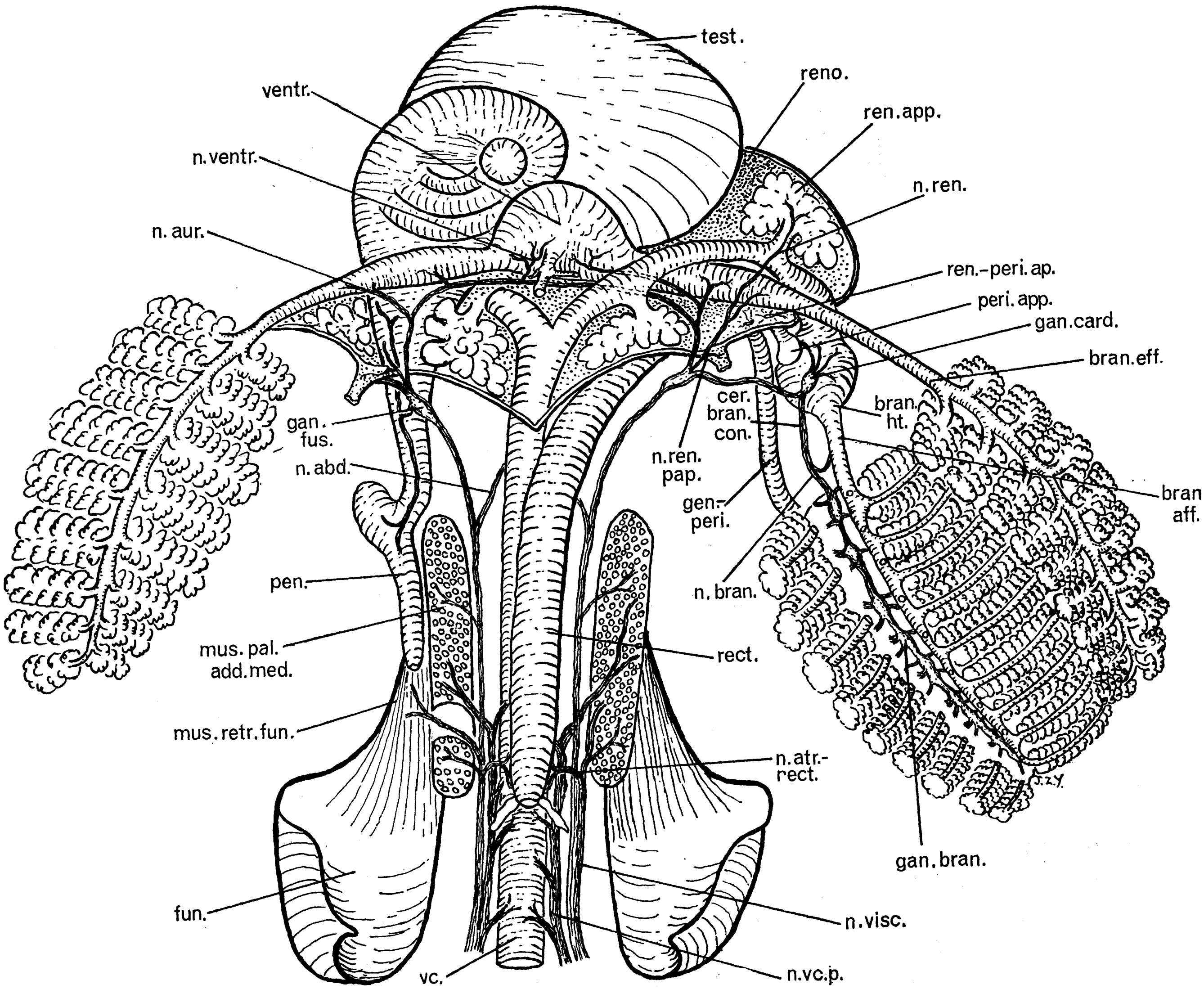

FIGURE 1. Drawing of the visceral nerves and their branches, seen from the ventral side.

reach 20 μm diameter and there are all gradations down to less than 1 μm. The region with fibres above 12 μm occupies the lateral part of the nerve and probably runs to the nerves of the depressor of the funnel and median pallial adductor. The remaining bundles of the visceral nerve contain fibres only up to 12 μm, but they have considerable numbers of

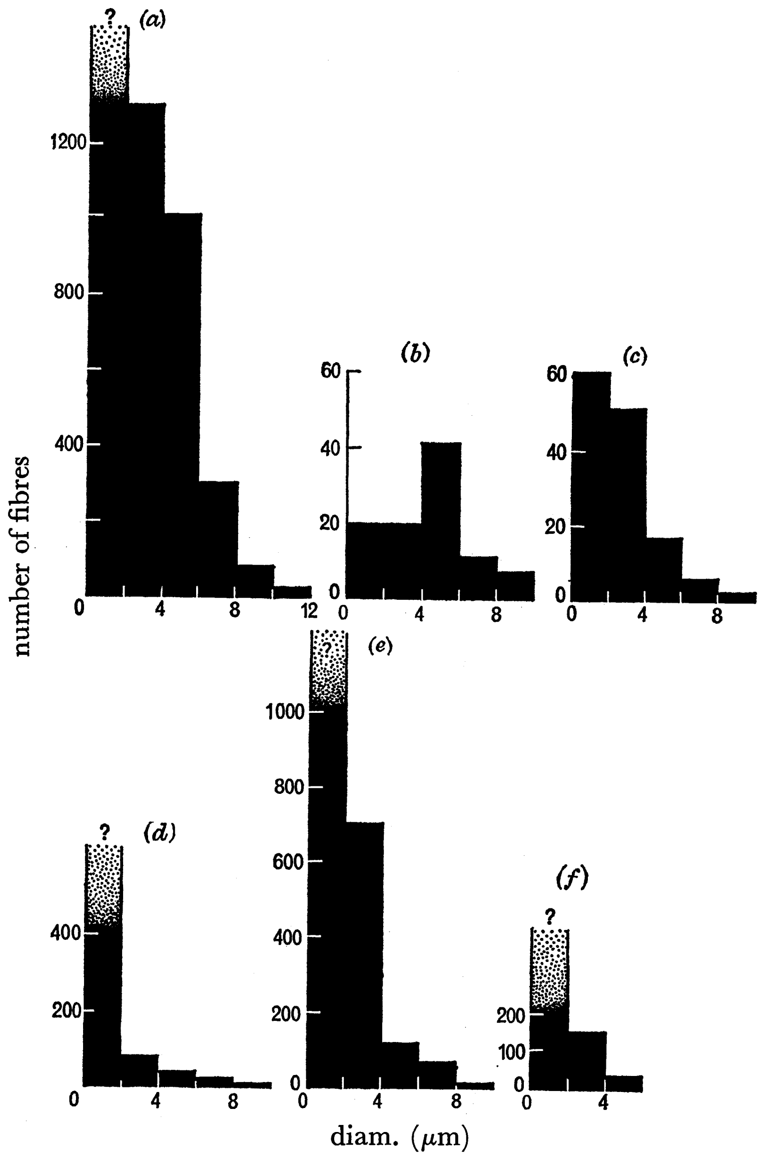

FIGURE 4. Histograms to show the composition of various branches of the visceral nerve, from a small octopus (38 g). (*a*) Left visceral nerve in front of anus. (*b*) Nerve of medial pallial adductor muscle. (*c*) Ink sac nerve. (*d*) Left abdominal nerve. (*e*) Left visceral nerve behind abdominal nerve. (*f*) Ventricular nerve.

fibres approaching this diameter. No single bundle differs outstandingly from the rest, or consists mainly of small fibres. The numbers of the smaller fibres cannot be determined from these preparations, but the nerves are not made up of large numbers of very small fibres as are the sympathetic trunks.

The first branches to come off from the visceral nerves run medially to the ink sac and rectum and laterally to the median pallial adductor muscle (figures 5, 6, plate 1; 8*a* and *b*).

In spite of their different courses the two branches arise together. Moreover, they have a somewhat similar fibre composition, including a considerable number of fibres up to 12 μm or more in diameter (figure 4 and figure 7, plate 1). It may well be that the muscles that these branches control act together in regulating the release of ink (and faeces?). The median pallial adductor muscle embraces the rectum and ink duct and part of the ink

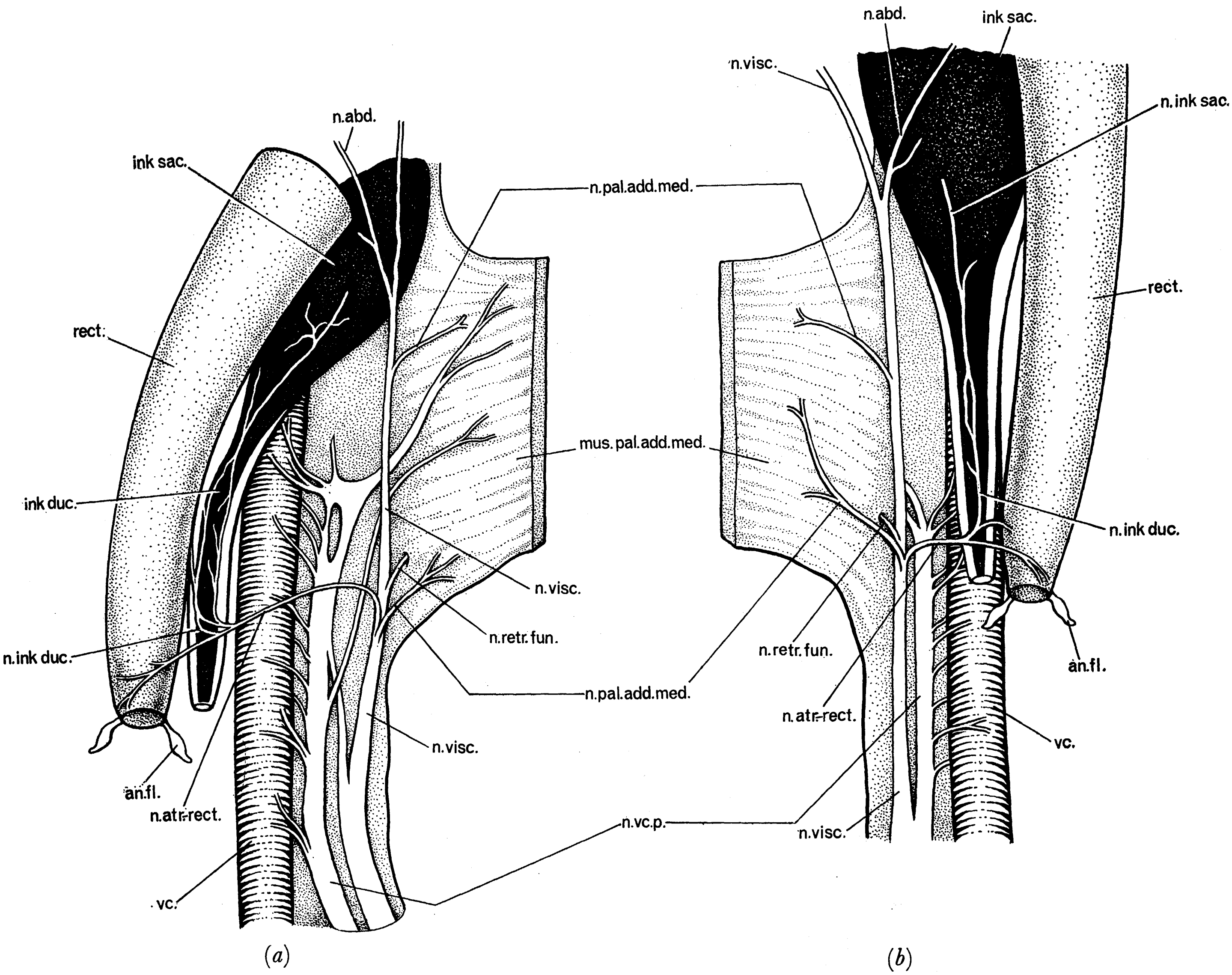

Figure 8. Drawing of the left (*a*) and right (*b*) atriorectal nerve.

sac and may be the agent that actively expels the ink. The median pallial adductor muscle receives one or more further branches from the visceral nerve more posteriorly. These also include mainly relatively large fibres ($\sim$10 μm) together with some smaller ones. The nerves to the depressor (retractor) muscles of the funnel leave the visceral nerves shortly behind those to the median pallial adductor. They run laterally dorsal to the adductor muscle (figure 1).

The nerves to the ink sac and rectum correspond to those called 'n. atramenti' by Hillig in *Sepia* (1912) but it is more appropriate to call them 'atrio-rectal'.

The atrio-rectal nerves run ventrally round the vena cava. Both the ink sac and the rectum receive fibres from the nerves of both sides. Each nerve divides into a complex system of small bundles in the tissue that lies between rectum and ink sac. Twigs run forwards to the terminal regions of both organs and branches turn back along them (figures 8*a* and *b*).

Ink sac nerves

The main trunks running back along the ink duct contain fibres up to 10 μm in diameter as well as smaller ones (figure 9, plate 1). The trunks divide several times and make a plexus along the duct. Branches have been followed back to the ink sac, but their terminal portions are hard to trace either by dissection or in sections because of the ink.

The duct has thick outer circular muscular coats and an inner longitudinal one (figure 11, plate 1). All are richly innervated, with fibres up to 8 μm, perhaps larger. The terminal portion is provided with a very thick circular sphincter muscle (figures 10 to 12, plates 1 and 2). At the tip the ink duct and anal canal are confluent and share a common circular muscle sphincter. The ink sac portion of the sphincter appears to be more richly innervated than the anal portion. Farther back the circular layer is divided, the outer dorsal layers forming an inverted 'sling' ending at the sides attached to outer longitudinal bundles (figure 13, plate 2).

Proceeding backwards the wall of the ink duct becomes thinner and gradually passes over into that of the sac, which thus has outer circular and inner oblique and longitudinal muscle layers composed of rather large muscle fibres (figure 14, plate 2). These muscles continue into the septae that divide up the cavity of the sac. They are richly innervated, presumably by fibres of the atrio-rectal nerves. However, the greater part of the musculature served by this nerve acts as a circular sphincter around the duct. Ejection is therefore presumably produced by the action of the muscles of the ink sac, hepatic capsule, median pallial adductor and of the mantle, with control of release by loosening of the sphincter.

Nerves of the intestine

There is no sharp change of structure between intestine, rectum and anal canal. Correspondingly there is no clear separation between the more anterior region, innervated by branches of the atrio-rectal nerves and the posterior region innervated by the intestinal nerves, which spring from the gastric ganglion.

At the lower end there is a thick outer coat of circular muscle and an inner layer of longitudinal muscles, the latter more prominent near the anus than further proximally. These muscles of the anal canal are all richly innervated by fibres of the atrio-rectal nerves, some up to 10 μm diameter, (figures 15 to 17, plate 2). The longitudinal muscle bundles are very marked ventrally, near the aperture.

The anal flaps contain some muscle, innervated by relatively large fibres ($\sim$5 μm). In addition, there is a loose plexus of fine single fibres. These collect into bundles near the surface, from which fibres run to the epidermis, presumably a receptor system (figure 18, plate 2).

The terminal portion of the intestine ('rectum') has simple villi, covered with a secretory epithelium. The muscles are mainly circular, with a few longitudinal ones internal to them

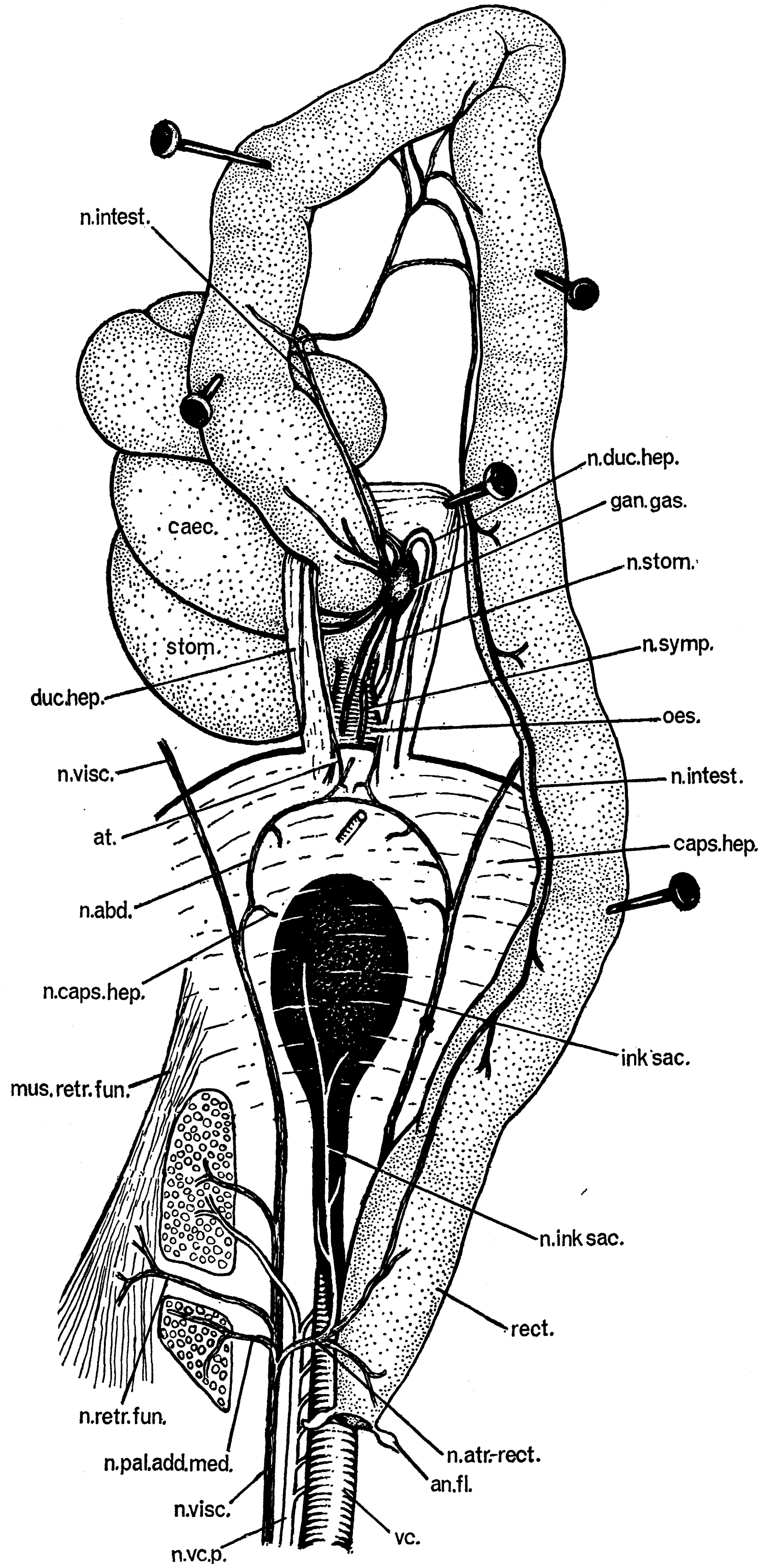

FIGURE 22. Drawing of the visceral nerves and gastric ganglion to show the connexions between them. The intestinal nerves are also shown, but the lower portion and connexion with the atrio-rectal nerve is diagrammatic. There are actually several trunks, not a single one as shown. They are very difficult to dissect.

and a few in the villi (figures 20, plate 3). Numerous small bundles of nerve fibres run back along its surface, forming an elaborate plexus. The intestinal plexuses differ from those of the oesophagus because of the presence of numerous conspicuous longitudinal bundles in the former. These lie superficially, accompanied by an elaborate network of vessels. They are connected with a fine plexus, including some nerve cells, lying more deeply among the muscles. This plexus was described by Alexandrowicz (1913, 1928). Altogether as many as eighteen of the smaller ventral bundles have been counted, distributed round the periphery. These are connected to the atrio-rectal nerves and also with the intestinal nerves of the gastric ganglion. In particular there are also two larger bundles dorsally, which join both systems (figure 22). These rectal nerves are more distinct than the smaller bundles and have their own sheaths (figure 21, plate 3). None of their fibres is above 5 μm, most of them are very small.

Fibres from the bundles around the rectum innervate the muscle layers and many penetrate the villi, but no complex submucous plexus has been seen. The fibres of these nerves are all small, but some reach 5 μm. It is not possible to make any accurate estimate of their numbers but there must be at least 500 in many of the bundles and therefore 10000 in all. The absence of larger fibres is especially conspicuous in contrast with the terminal (anterior) branches of the atrio-rectal nerves, which contain fibres up to 10 μm. Ganglion cells occur irregularly along these trunks (figure 21, plate 3).

More proximally the condition of the intestine is essentialy the same. The muscles and villi are less richly innervated. The longitudinal muscle layer is rather more prominent. The right visceral nerve runs close to the intestine for a long distance but no branches from it to the intestine have been reported by any author, other than the atrio-rectal nerves. None has been found in the present investigation, either by dissection or in sections. However it would be easy to miss them and although they have been carefully looked for, it is hard to be sure that none exists.

The main part of the intestine is innervated by the intestinal nerves, springing from the left-hand (posterior) end of the gastric ganglion (figure 22). Small branches run to the more proximal part and a large trunk accompanies the main loop of the intestine as it passes over to the right side. This nerve runs in its own sheath in the mesentery and is readily accessible for stimulation. Like all the nerves emerging from the gastric ganglion it contains

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Description of plate 1

All sections are stained by Young's (1939) modification of the formol-Cajal method.

Figure 2. T.S. Visceral nerves and nerves of the vena cava at a level in front of the anus.

Figure 3. Part of the visceral nerve at the level of figure 2.

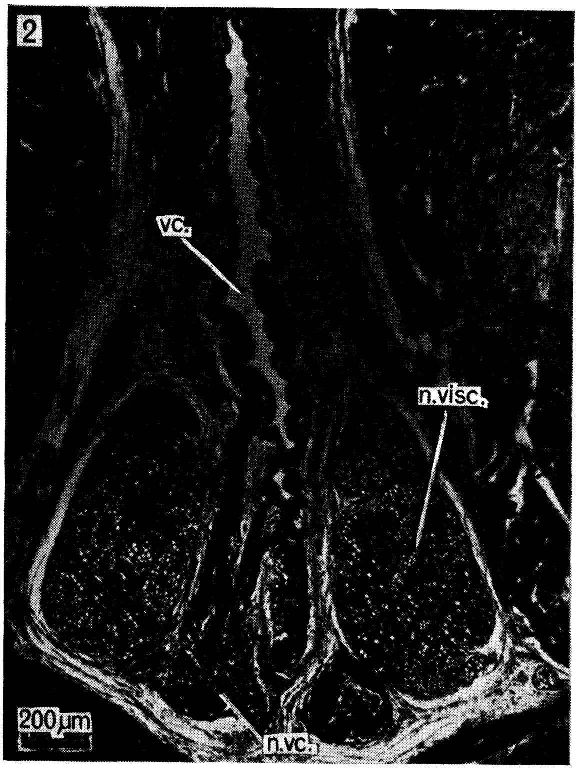
Figures 5, 6. T.S. to show the origins of the atrio-rectal nerves and nerve to the median pallial adductor muscle from the medial side of the visceral nerve.

Figure 7. T.S. Nerve to median pallial adductor muscle.

Figure 9. Ink duct nerve.

Figure 10. T.S. Terminal portion of ink duct and anal canal, showing their confluence.

Figure 11. T.S. Ink duct more posteriorly. (See also figure 12, plate 2.)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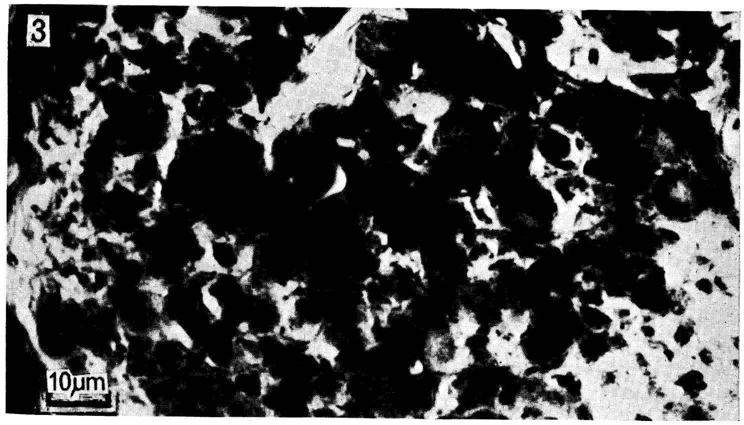
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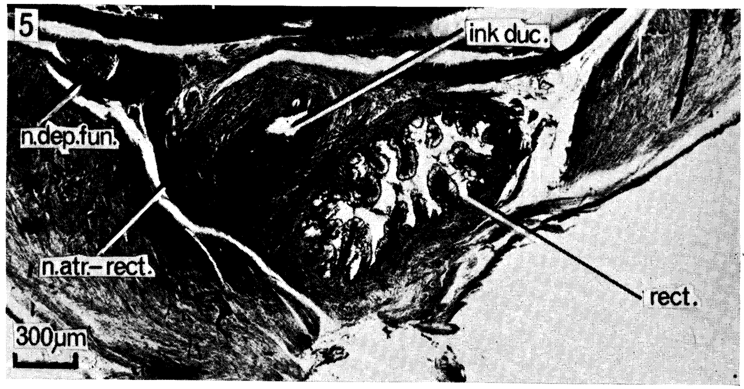
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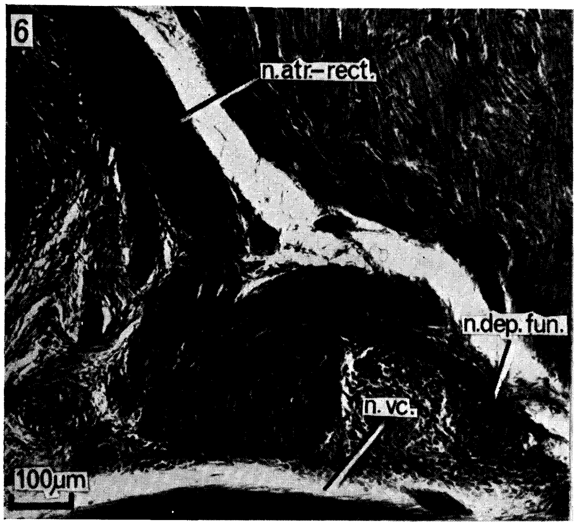
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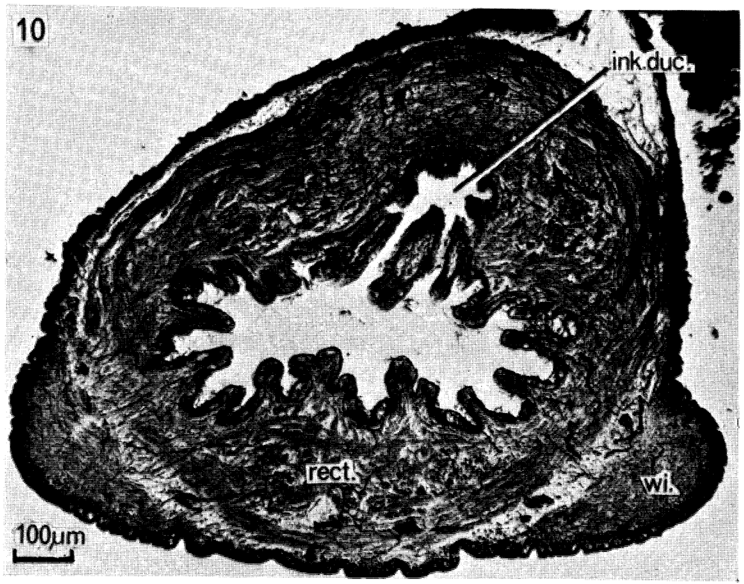
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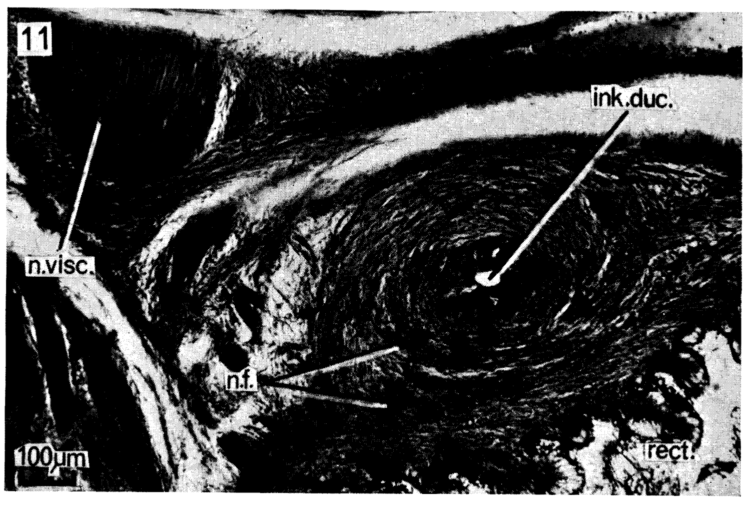
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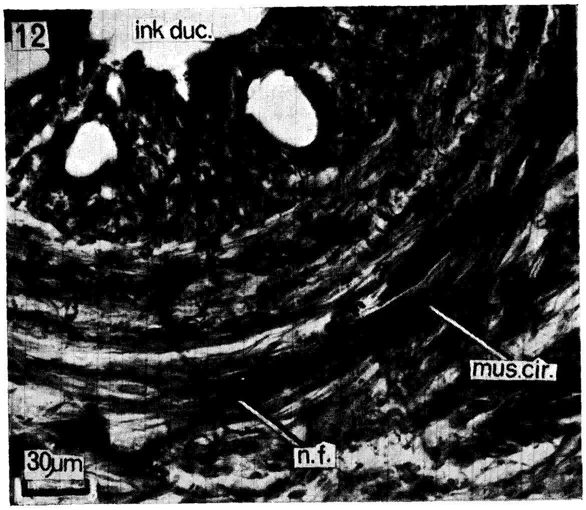
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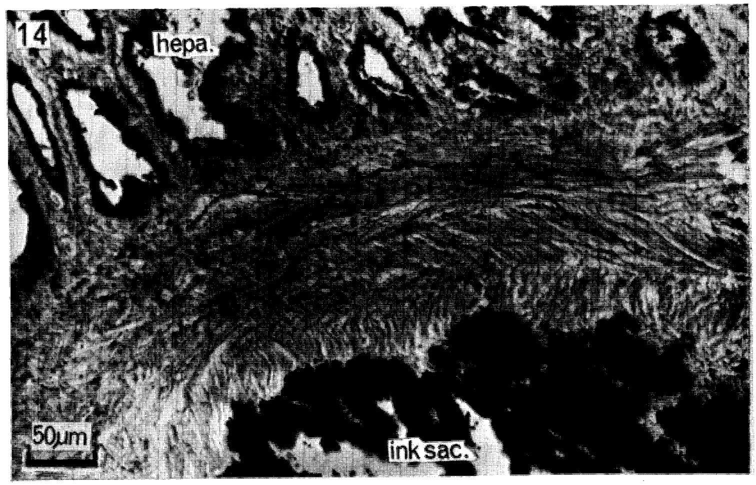
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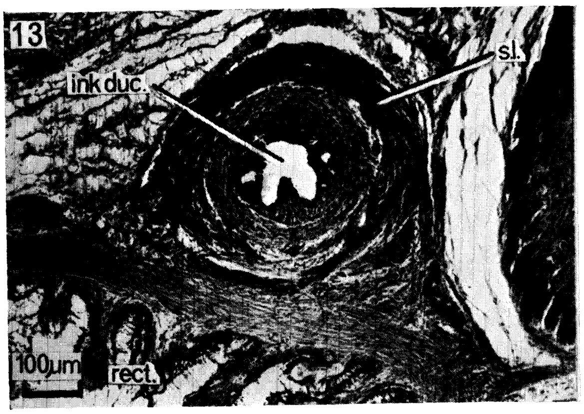
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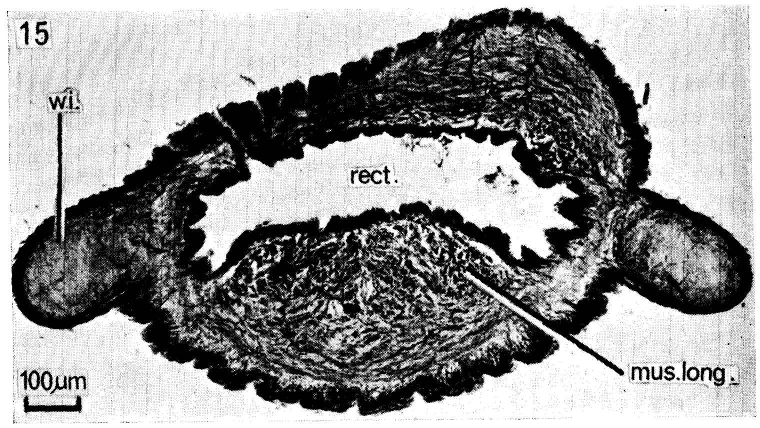
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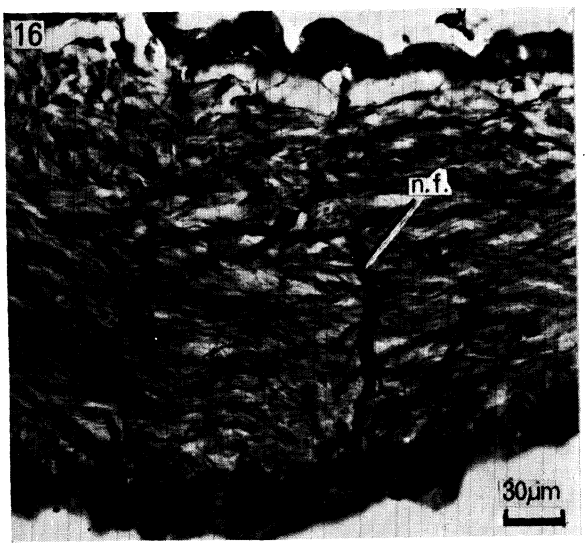
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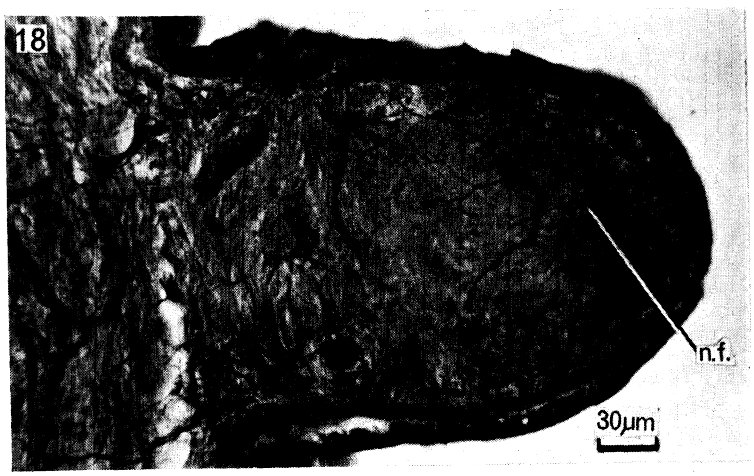
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17
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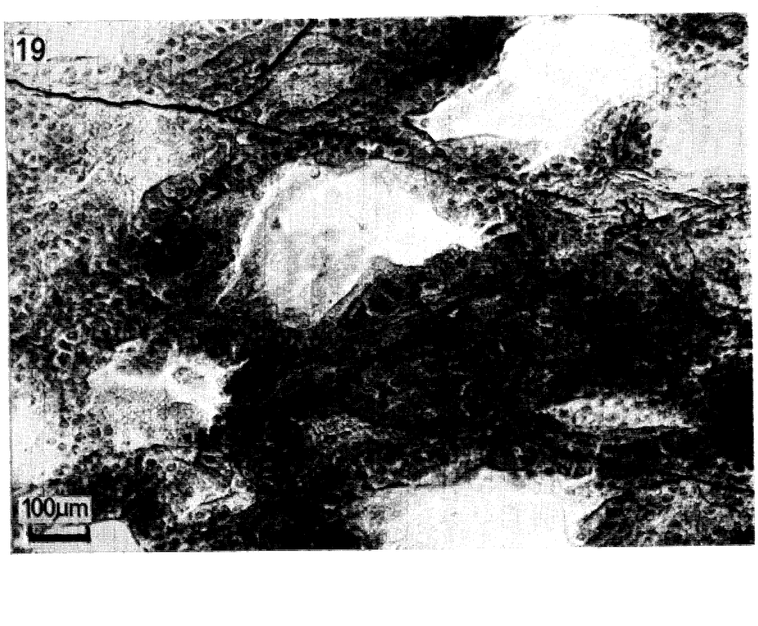
19
100μm

large numbers of small fibres, none above 3 μm (figures 23 and 24, plate 3). No estimate of the number has been made but it must exceed 10000.

The intestinal nerves, originating in the gastric ganglion, give rise to an elaborate plexus, with several large trunks and many small ones. Many of the large trunks run alongside the blood vessels, which form an elaborate network on the surface of the intestine. Within the intestinal wall the main trunks anastomose and divide repeatedly. No one of them runs directly through from the gastric ganglion to the anus, but there must be numerous possible through pathways. Afferent or efferent fibres could thus pass from the visceral nerve to the gastric ganglion or vice versa.

From the major trunks of the plexus smaller branches separate to run among the muscles. The finest trunks consist of a very few fibres, from which spring short terminating collaterals. These are similar to those found in the oesophageal plexus and may be close to the final termination.

Nerve cells occur either singly or as small ganglia in the intestinal plexus.

Nerves of the stomach

The thick wall of the stomach consists mainly of an outer layer of circular muscle, quite richly innervated (figure 25, plate 3). Within this is a smaller layer of irregularly longitudinal fibres, also with nerves. The high epithelium is very heavily cuticularized. A complex submucous plexus is evident in the Cajal preparations (figure 26, plate 3). Graziadei (1960) showed that this is present in *Sepia* and Botar (1961*a*, *b*) in *Octopus*. No nerve cells have been seen in the stomach wall.

Nerves of the caecum

The caecum receives large bundles of nerves from the gastric ganglion. They innervate its outer wall and run into the septa that divide its lumen. The outer wall has a rather thin layer of circular muscles. Longitudinal bundles run opposite each of the trabeculae, and muscle bundles also run up the latter.

Nerves of the hepatic ducts and liver

The hepatic ducts have thick outer coats of circular muscles, very richly innervated by fibres with markedly varicose endings (figures 27 and 28, plate 3). Deep to the circular

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Description of plate 2

FIGURE 12. T.S. Ink duct, more posteriorly. (See also figure 11, plate 1.)

FIGURE 13. T.S. Ink duct showing 'sling' of circular muscles dorsally.

FIGURE 14. T.S. Portion of wall of ink sac.

FIGURE 15. T.S. Terminal portion of anal canal.

FIGURE 16. Part of figure 15, to show large nerve fibres (up to 10 μm).

FIGURE 17. T.S. Small bundle of nerve fibres in the wall of the anal canal to show large fibres.

FIGURE 18. T.S. Anal flap showing plexus of fine fibres (perhaps afferent).

FIGURE 19. 'Pancreatic region' of the liver, showing nerve fibres.

coat are scattered longitudinal fibres, with few nerves. The low cuboidal epithelium is thrown into shallow folds. There are a few nerve fibres in these villi but no rich submucuous plexus and few fibres reaching to the epithelium.

The nerves accompany the branches of the ducts within the liver and fibres are distributed even among the finest alveoli (figure 19, plate 2). There is little muscle in this region and it seems probable that the gland cells are directly innervated, at least in the posterior (pancreatic) part of the liver. In the more anterior part the alveoli are surrounded by much argyrophil tissue and it has not been possible to decide whether they are innervated.

Post-rectal visceral nerves

Behind the branches to the ink sac and rectum the nerves run for a short distance near the mid-line and then begin to diverge: that on the right accompanies the intestine, that on the left the vena cava.

At this level the nerves contain fibres up to 10 μm diameter and down to < 1 μm. They do not consist of a mass of small fibres like the sympathetic trunks or intestinal nerves (figure 29, plate 3). There are about six major bundles in both right and left nerves (which are similar in size in a female). All the bundles have a similar make-up, with both large and small fibres. Bundles containing large fibres run to the hind part of the median pallial adductor.

As each nerve begins to pass laterally it gives off medially the branch that Pfefferkorn called the abdominal nerve. These nerves pierce the capsule surrounding the liver and send branches to it. The two nerves then approach each other in the mid-line and join the plexus of nerves accompanying the hepatic ducts from the gastric ganglion (figure 22 and figure 30, plate 4). Analysis of this region has proved especialy difficult because the nerve bundles run among the muscle bundles of the hepatic capsule. Many of the branches of the abdominal nerves run to the muscles, but in nearly all dissections that were made small bundles could be followed to the hepatic duct nerves (figure 30, plate 4). Occasionally dissection failed to reveal the connexion, raising the suspicion that all the branches run to the muscles. However, the continuity was traced also in some serial sections stained with Cajal's method, though this again was not easy. The connexion is certainly present, but is not large.

Each abdominal nerve has the typical composition of one of the bundles of the visceral nerve (figure 4, and figure 31, plate 4). It pierces the hepatic capsule, to which it then

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Description of plate 3

Figure 20. T.S. Rectum.

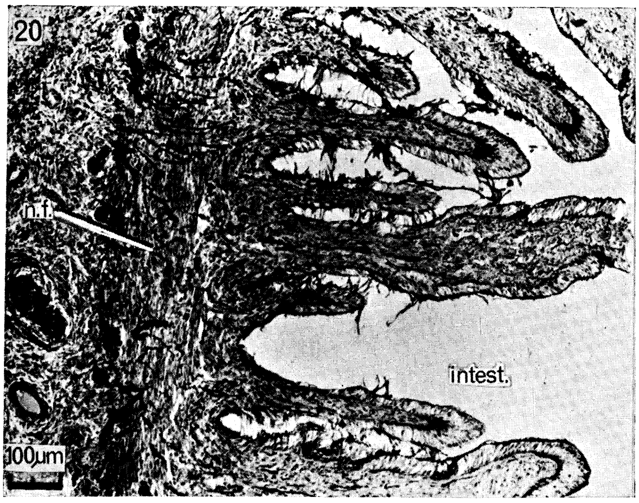
Figure 21. T.S. Rectal nerve.

Figures 23, 24. T.S. Intestinal nerve as it emerges from the gastric ganglion.

Figures 25, 26. T.S. Wall of stomach. In figure 26 the epithelial plexus is seen cut both radially and tangentially.

Figures 27, 28. T.S. Hepatic duct.

Figure 29. T.S. Visceral nerve behind level of anus.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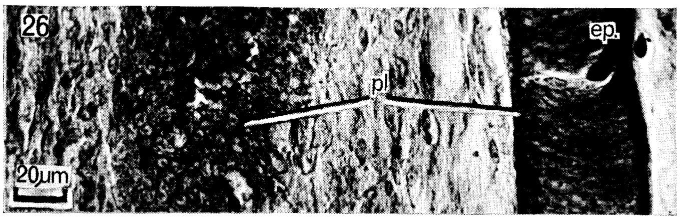
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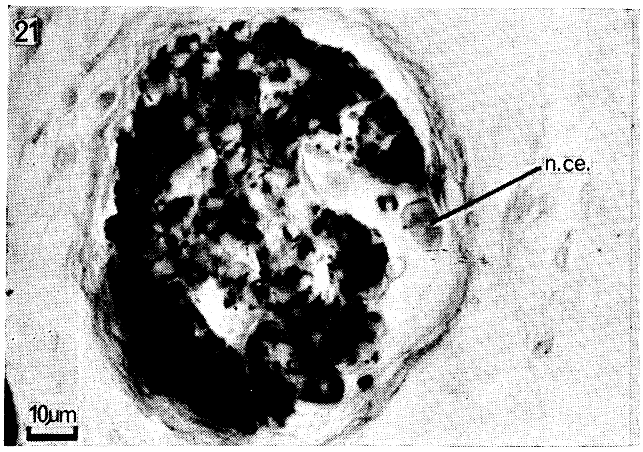
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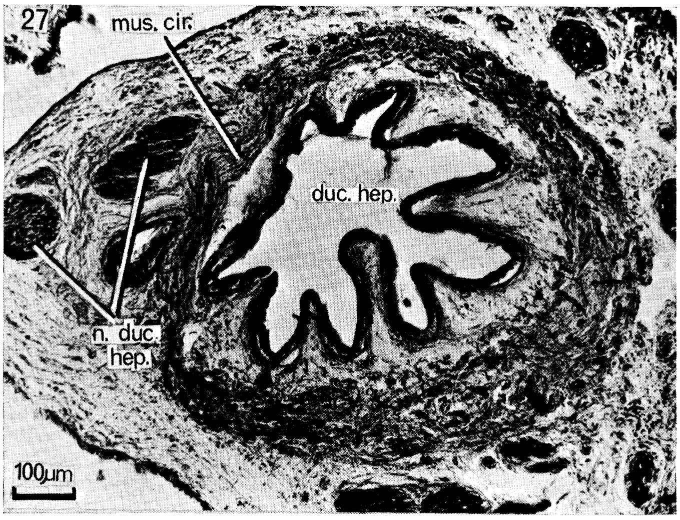
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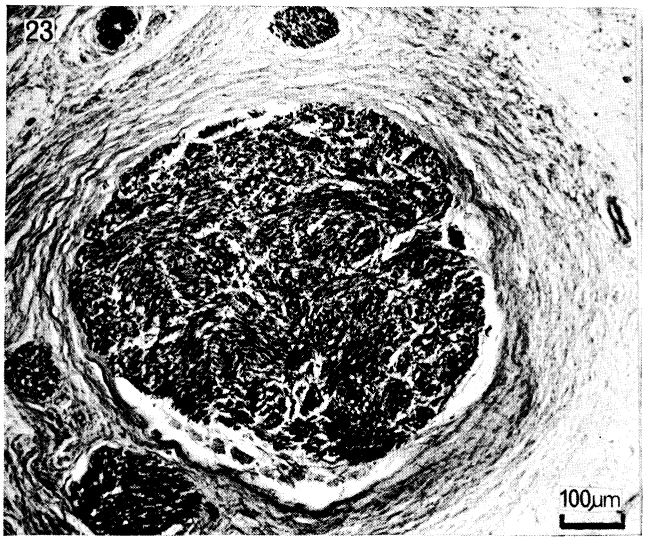
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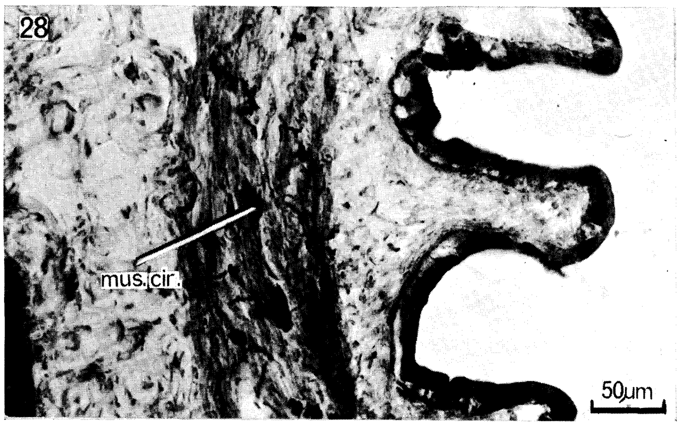
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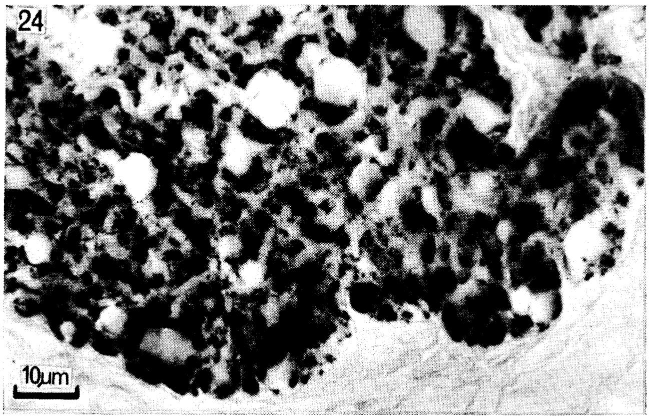
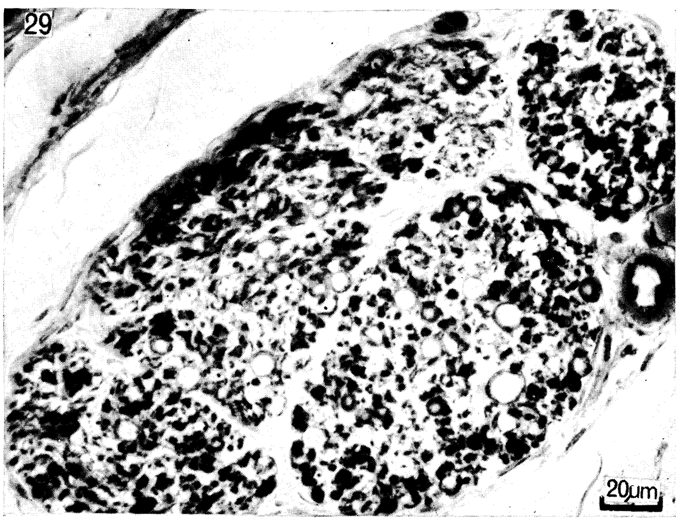
mus. cir.
50µm


24
10µm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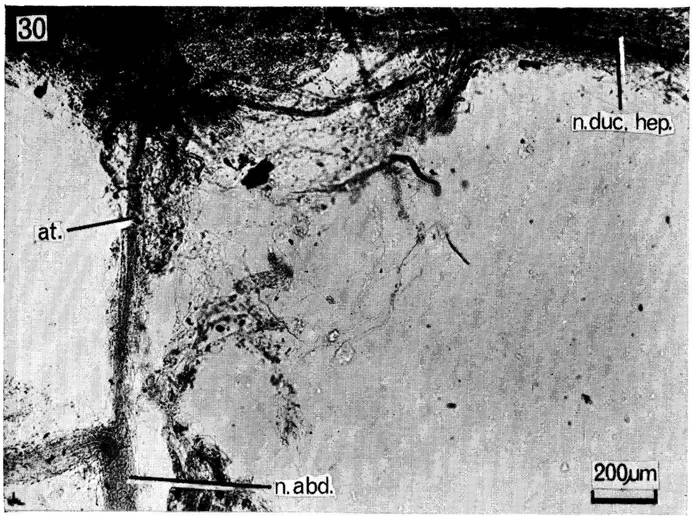
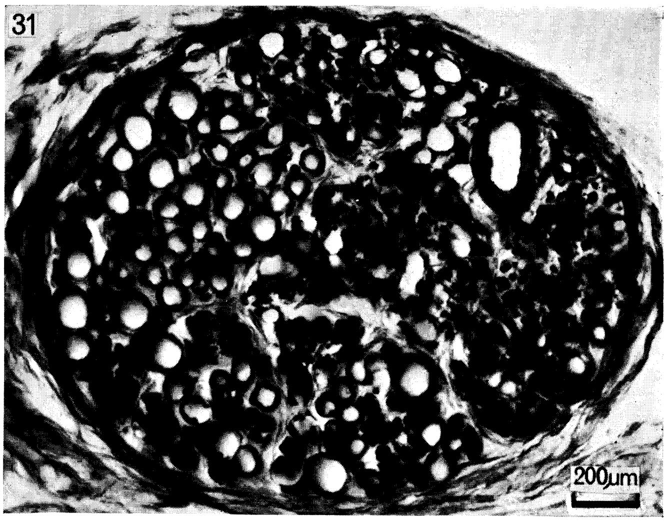
20µm


30
n.duc. hep.
at.
n. abd.
200µm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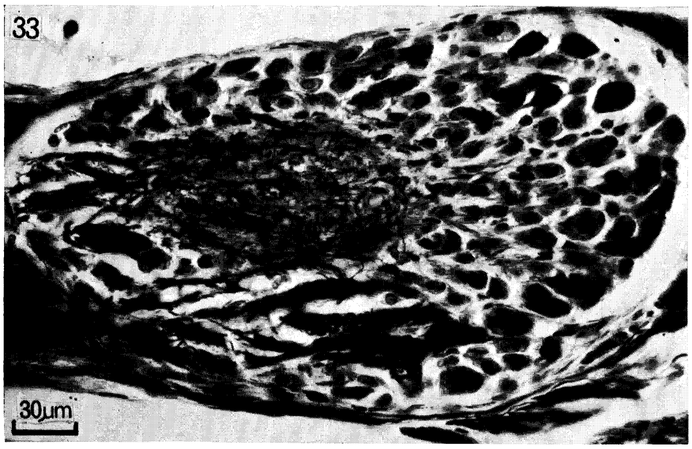
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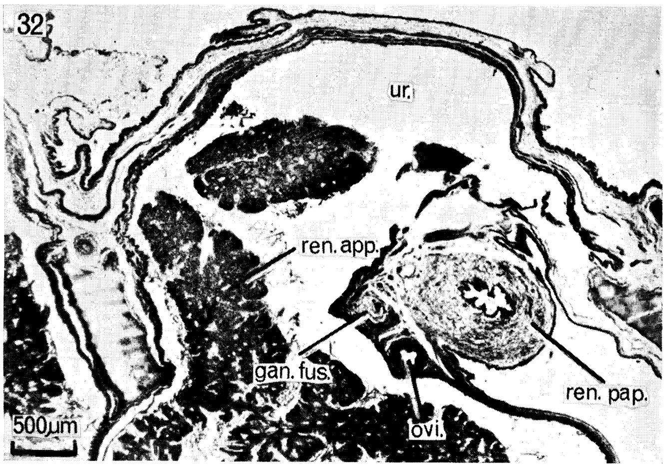
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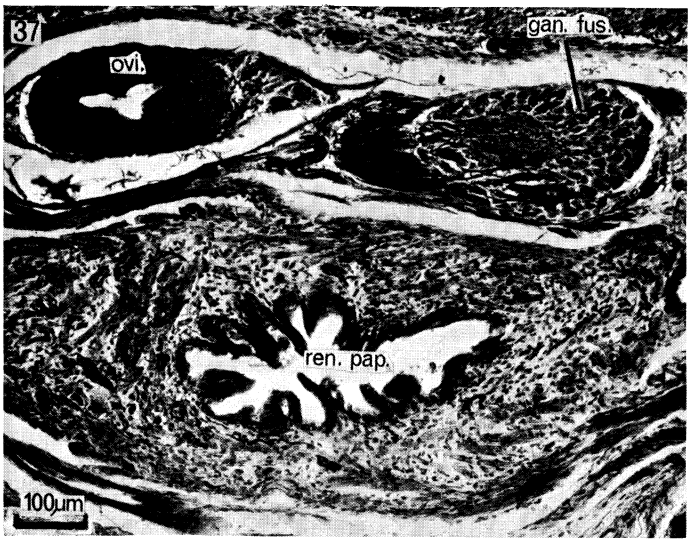
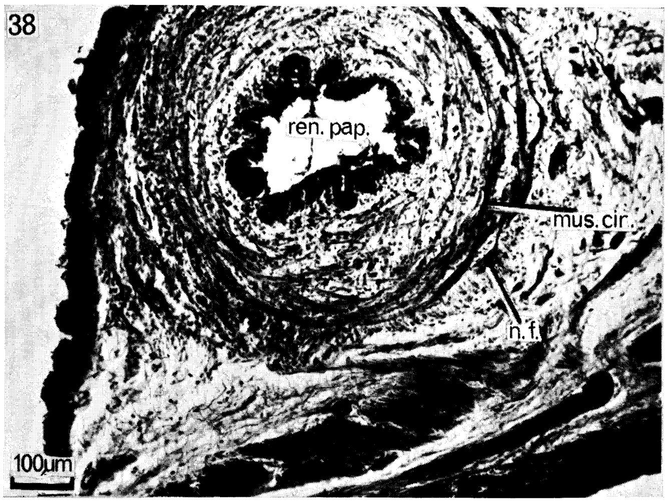
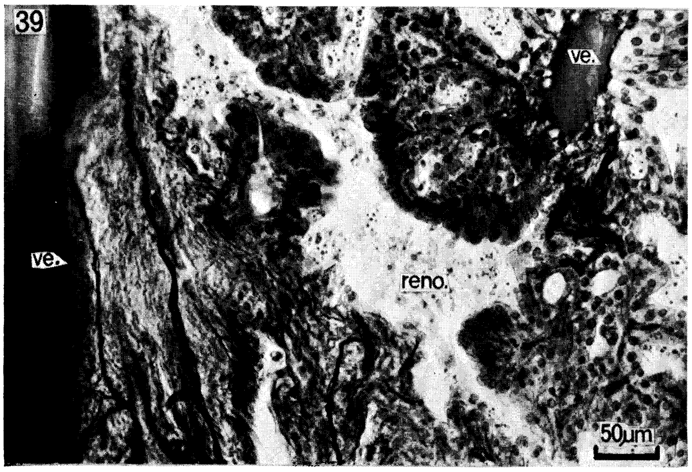
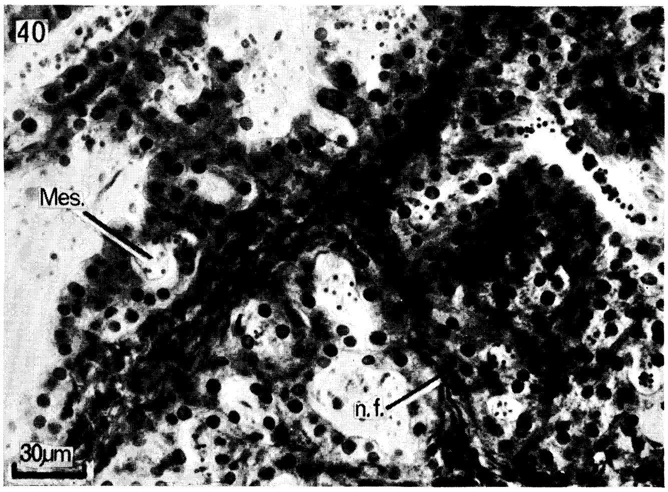
ur.
ren. app.
gan. fus.
ren. pap.
ovi.
500µm


37
ovi.
gan. fus.
ren. pap.
100µm


38
ren. pap.
mus. cir.
n. f.
100µm


39
ve.
ve.
reno.
50µm


40
Mes.
n. f.
30µm

gives branches. Each branch resembles the main nerve in composition. A group of small fibres is segregated in a separate part of the nerve, and may have a distinct destination. Perhaps it forms the branch that runs to the gastric ganglion and the larger fibres pass to the hepatic capsule. The liver capsule is composed of a main outer layer of circular muscle fibre and inner longitudinal ones, with a thin second coat of circular fibres at the inside.

Unfortunately the more posterior branches of the abdominal nerves cannot be followed to the hepatic ducts in the serial sections of whole juvenile animals, because of the effect of the liver and ink sac, making the stain very dark here.

Fusiform ganglion

At the base of the renal papillae the visceral nerves swell to form the small fusiform ganglia (figure 32, plate 4) and then turn sharply laterally and dorsally to continue to the cardiac ganglia. There has been some confusion in the naming of these ganglia, which is made difficult because of the difference between decapods and octopods (Alexandrowicz 1960, 1963). In *Sepia* there are commissures between the two visceral nerves at this level but no 'fusiform ganglion'. Since in *Octopus* the nerves of the auricle and ventricle arise from the fusiform ganglion it is tempting to call it the 'anterior cardiac ganglion'. However, other nerves also arise at this level and it is best to keep the name 'fusiform'. Several nerves arise near or from the fusiform ganglion, but it is not clear which of them contain fibres arising from its cells.

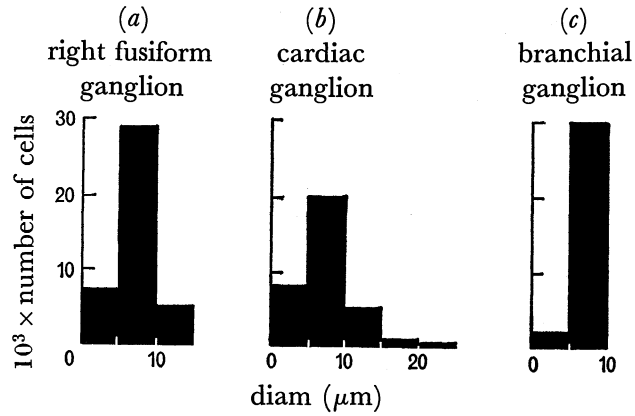


FIGURE 34. Sizes of nuclei of the cells of various ganglia.

DESCRIPTION OF PLATE 4

FIGURE 30. Preparation taken from the dissection drawn in figure 22 showing the fine anastomotic nerve.

FIGURE 31. T.S. Abdominal nerve.

FIGURE 32. T.S. Left fusiform ganglion, urocoele, urinary papilla and oviduct (immature).

FIGURE 33. T.S. Left fusiform ganglion.

FIGURE 37. T.S. Fusiform ganglion and proximal part of renal papilla.

FIGURE 38. T.S. Distal end of renal papilla.

FIGURE 39. T.S. Renal appendages.

FIGURE 40. T.S. Renal appendages, showing nerve fibres in the more peripheral regions.

The fusiform ganglion contains cells with nuclei up to about 15 μm in diameter at its outer edges (figure 33, plate 4). They become somewhat smaller towards the neuropil, but there are no very small ones. The majority of the 4000 cells of the ganglion have nuclei of 5 to 10 μm (figure 34). The neuropil is a loosely woven tangle. The main bundle of nerve fibres that proceeds to the cardiac ganglion certainly bypasses the fusiform ganglion. There are other fibres that run through, for example some of those to the ventricular nerve (but not all of them).

Nerves of the urocoele, renal papillae and renal appendages

Small nerves leave the proximal end of the fusiform ganglion for the renal papilla (figures 35, 36). The papilla has a folded lining and loose circular bundles of muscle fibres, which receive the nerves (figures 37, 38, plate 4).

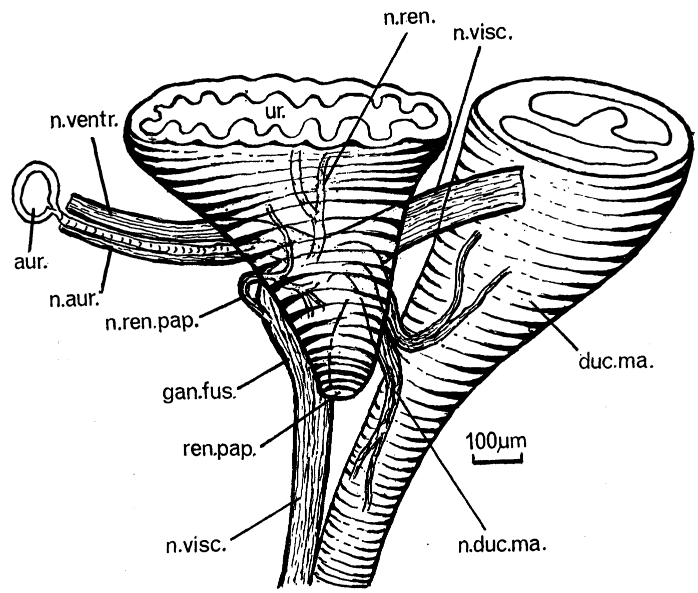


FIGURE 35. Drawing of the reconstruction of the left fusiform ganglion of a juvenile male, made from serial sections, seen from the lateral side. It shows the innervation of the urinary papilla and male ducts.

The nerves of the urocoele and renal appendages arise as several small trunks, difficult to follow by dissection or in sections. Some proceed ventrally from the proximal part of the ganglion, running in the ventral wall of the urocoele, others, more posteriorly, run medially with the veins. Both sets contain some of the large fibres of the main visceral nerve trunks, which have probably passed through the ganglion. It is not certain whether all the fibres pass through without synapse, but certainly a considerable bundle does so on the medial side of the ganglion, probably to the urocoele.

The fibres of the renal nerves accompany the veins, presumably ending on the muscles of their thick walls (figures 39 and 40, plate 4). The nerve fibres follow the major branches of the veins, but there are few or none in the more peripheral regions, where the walls of the veins are very thin.

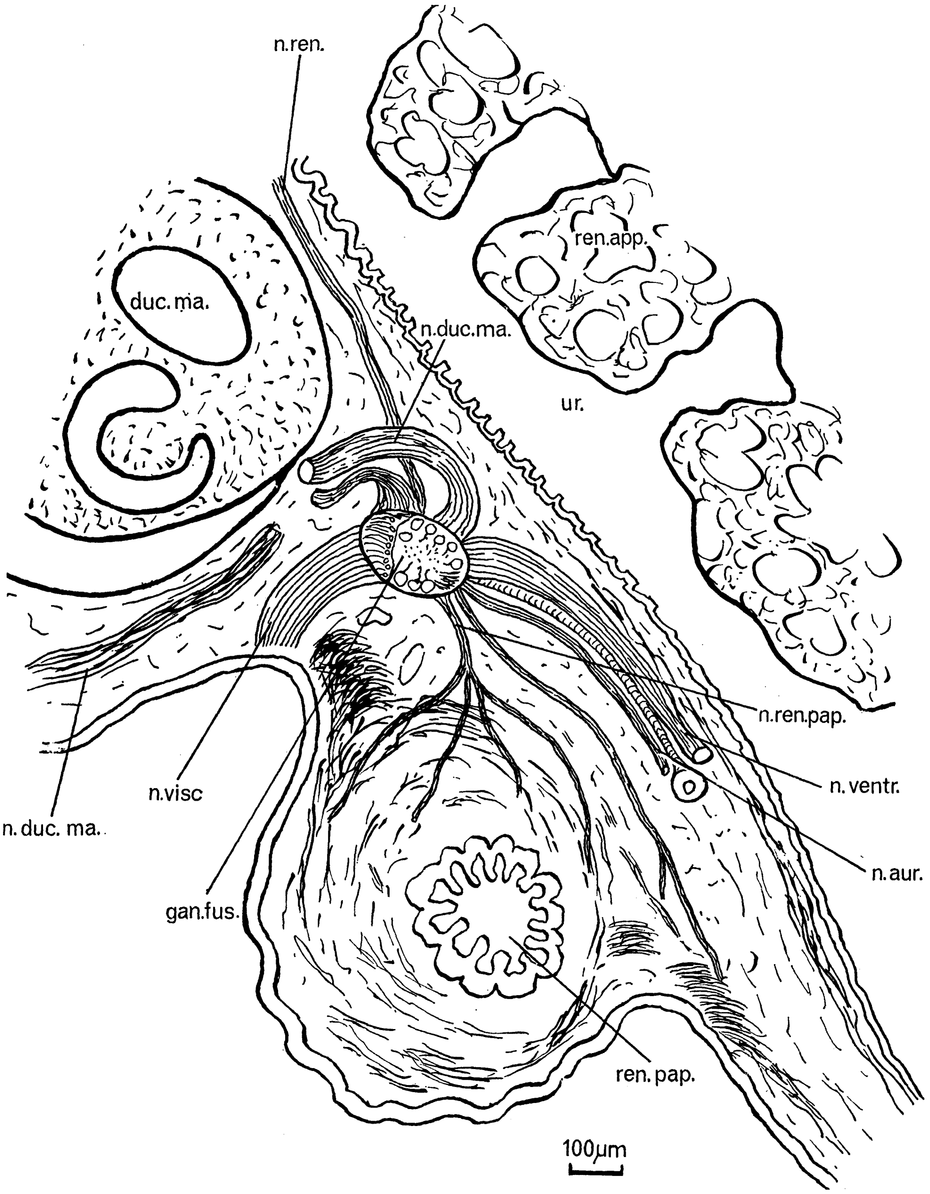


FIGURE 36. Composite transverse section through the region shown in figure 35, and figure 37, plate 4.

Nerves of the female reproductive tract

The nerves leave the fusiform ganglia, but it has not been determined whether their fibres arise from its cells. There are indications that some at least do not do so, but run straight through from the visceral nerves. The nerves divide and run upwards and downwards on the oviducts. Their finer details have been followed in series of sections through a juvenile and a mature female.

The gonocoele is supplied by nerves that form a plexus at its hilum, extending into the trabeculae that bear the ova (figure 41, plate 5). Some of these nerve fibres run in the arterial walls, but others ramify among muscle bundles at the centre of the trabeculae.

The outer wall of the gonocoele has a thin layer of muscle fibres, among which there are nerves. Near to the oviducal aperture the wall has a specialized and folded epithelial lining, below which is a rather extensive plexus of nerve fibres (figures 42 and 43, plate 5). Many of these are very fine and run singly. They may be afferents.

The upper portion of the oviduct has a folded epithelium and a rather thin wall, with a few layers of circular muscle fibres and a few nerve bundles (figure 44, plate 5). Many nerve fibres which may be afferents, enter the villi and form plexuses beneath the epidermis. The fibres were not seen penetrating among the epithelial cells. This whole system of nerves is little developed in the juvenile oviduct (figure 45, plate 5). The genito-pericardial canal ('water vascular canal'), which runs with the oviduct, is accompanied by several bundles of nerve fibres (figures 45 and 46, plate 5), arising from the region of the fusiform ganglion, but probably by passage direct from the visceral nerve. The canal has a few layers of circular muscles, but many of the nerve fibres terminate beneath the epithelium (figure 46). The tissue around the canal is richly vascular.

The oviducal gland probably has the two functions of storing sperms and secreting the egg cases (Wells 1960). However, according to Fort (1937) exploded spermatophores are found in the ovary (of *Eledone cirrhosa*) and presumably fertilization occurs there. The presence of spermatangia in the ovary was also reported for *E. moschata* by Orelli (1962). Peterson (1959) found spermatozoa in the oviducal 'gland' of *O. bimaculoides*, but believed that it was not also secretory. Wells had the advantage of using females stimulated by denervation of the optic gland and these showed definite signs of secretion. He described spermathecal chambers and two types of gland, the first probably producing the egg case and the second an aromatic reducing agent for tanning it. These two parts can be recognized in the preparations stained to show nerve fibres.

The gland is very richly innervated. The plexus of nerve fibres lying inside the circular muscle layer of the upper oviduct becomes greatly thickened during the course of the duct within the oviducal gland (figures 47 to 49, plate 5). It here consists of bundles of nerve fibres running around as well as along the length and interspersed with numerous nerve cells (figures 50 to 52, plate 6). This plexus or 'oviducal ganglion', lies between the central passage down which the eggs arrive from the ovary and the chambers that are believed to be spermathecal. These latter are blind diverticula, swollen at their ends, one arising at the base of each of the ducts that radiate from the central chamber (figure 49). They have a columnar ciliated epithelium, surrounded by a loose tissue containing blood vessels and a few isolated muscle fibres. Here there is a rich plexus of nerve fibres, reaching to the epithelium (figure 52). This plexus is an extension of that of the oviducal ganglion (figure 50): the whole system presumably ensures the proper timing of movement of the eggs and stored sperms.

The plexus also sends numerous bundles of nerve fibres along the ducts of the glands (figure 53, plate 6), accompanying them to their finest branches. The two parts of the gland seen by Wells can be distinguished, but their internal structure appears similar (in the immature female). The nerve fibres branch around the finest alveoli, whose cells they probably innervate directly.

The distal portion of the oviduct (anterior to the oviducal gland), has a similar wall to the proximal, with some nerve bundles innervating the circular muscles and some as a plexus beneath the epithelium (figures 54 and 55, plate 6). Many of the nerve fibres accompanying the duct, however, lie outside these layers. They accompany the duct to its extreme anterior end and there break up in a mass of vascular tissue around the lower end of the duct and female opening (figure 54, plate 6). These may be vascular efferents or afferent fibres. The epithelium of the lower end of the duct is folded into villi, at the core of each of which there is a plexus of nerve fibres (figure 55, plate 6). Around the tip of the duct the outer epithelium lining the mantle cavity is thrown into a number of folds (figure 56, plate 6). These contain some muscle and nerve fibres, the latter making a plexus beneath the skin, which may be afferent (figure 57, plate 6).

Nerves of the male reproductive system

Two branches leave from the middle of the length of the fusiform ganglion and run to the male duct (figure 35, p. 12). They contain some of the larger fibres of the visceral nerve, probably running directly from the nerve. It is not known whether other fibres arise in the ganglion. One nerve turns forwards and the other backwards.

The wall of the male gonocoele is thin and contains few nerve fibres. Nor have any been seen among the testicular tubules. The genito-pericardial canal, as in the female, is accompanied by several bundles of nerve fibres.

The wall of the proximal vas deferens (Peterson 1959) is thin and contains few muscle fibres and few nerve fibres. In the next region, the spermatophore-forming duct, however, there is a moderately rich plexus running along the axis of the rolled-in central portion (figure 58, plate 6). This plexus terminates as fine fibres immediately below the ciliated epithelium of this portion of the lining. The other portions of the wall have few or no nerve fibres.

The following region is more complex than described by Peterson. The 'accessory gland', joining the lower end of the 'proximal vas deferens' is a blind sac with thick glandular walls (figure 59, plate 7). Its lumen contains balls of sperms, and these are apparently transferred to a duct running along its side. This is continuous with the 'distal vas deferens' or Needham's duct, itself a structure with complex walls, which opens into Needham's sac (the spermatophore storage sac).

The accessory gland has a thin capsule, containing a few nerve fibres but few or none occur among the glandular tubules. The complex set of ducts constituting the distal vas deferens are heavily ciliated. In some parts the walls are folded into pockets with loops of nerve fibres around the neck of each pocket (figure 60, plate 7). The tubes contain bundles of sperms, whose appearance shows that they were fixed while rotating. Presumably the spermatophores are formed here, apparently with some neural direction.

Needham's sac has an outer fibrous coat and within this a muscular layer, fairly richly innervated (figure 61, plate 7). A few of the muscles and nerves enter the transverse partitions, which divide the sac into compartments, each carrying one spermatophore (figure 62, plate 7).

The process of manufacture of the spermatophores thus proceeds by ciliary action upon the balls of sperms and secreted material as they pass through the complex system of tubes. These tubes have some nerve fibres along the axis of the ridge of the proximal vas deferens and in the distal vas deferens.

The upper part of the penis has a thick muscular coat, composed mainly of circular fibres, but with bundles of longitudinal fibres central to these, and a few oblique ones (figure 63, plate 7). These muscles are all innervated. There are a few nerve fibres beneath the epithelium lining the duct. At the lower end of the duct the muscle bundles run more irregularly in various directions. The skin of the mantle here shows a folded surface epithelium, with a highly vascularized corium (figure 64, plate 7), as around the female duct, p. 15. There are numerous nerve fibres in this region, but they do not make any special plexuses or endings in relation to the epidermis. They appear mostly to run to the muscle fibres.

There are no specialized structures around the aperture of the penis (figure 65, plate 7). There are bundles of nerve fibres lying rather deeply in this region and probably running to the muscles. There is no especially developed innervation of the skin.

Auricular and ventricular nerves

These nerves come from the fusiform ganglion as separate trunks, more or less closely bound together in different specimens (figure 1 and figure 66, plate 7). They are accompanied by a small artery, running to the fusiform ganglion and neighbouring regions (figures 35 and 36, pp. 12 and 13). The auricular and ventricular nerves probably both contain fibres coming from cells of the fusiform ganglion. They probably also contain fibres that come from (or run to) the cardiac ganglion. The rhythm depends on continuity of the ganglia (Ransom 1884).

The auricular nerves include several bundles running to the efferent branchial vessel and to the auricle proper (figures 1, 35 and 36). They are similar in composition to the ventricular nerve (see later), but with the larger fibres not reaching 5 μm. The wall of the auricle contains muscle fibres (and nerve fibres) running through it radially, as well as around (figure 66, plate 7). This suggests that it may exert negative pressure on the ctenidia, as well as pumping blood into the ventricle.

The ventricular nerve contains medium-sized fibres, up to 6 μm diameter, as well as many smaller ones (figure 67, plate 8). The nerves of the two sides are united by several smaller commissural strands at the base of the ventricle. There is thus quite an elaborate plexus at this level (figure 1, p. 3). From this plexus bundles run to the wall of the ventricle, which is very thick and has four layers of circular muscle, alternating with three that contain mainly longitudinal fibres and some radial ones (figure 68, plate 8). All are

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DESCRIPTION OF PLATE 5

FIGURE 41. T.S. Ovary.

FIGURE 42. T.S. Opening of oviduct from ovary.

FIGURE 43. Higher power view of the inset area in figure 42.

FIGURE 44. Wall of upper portion of oviduct.

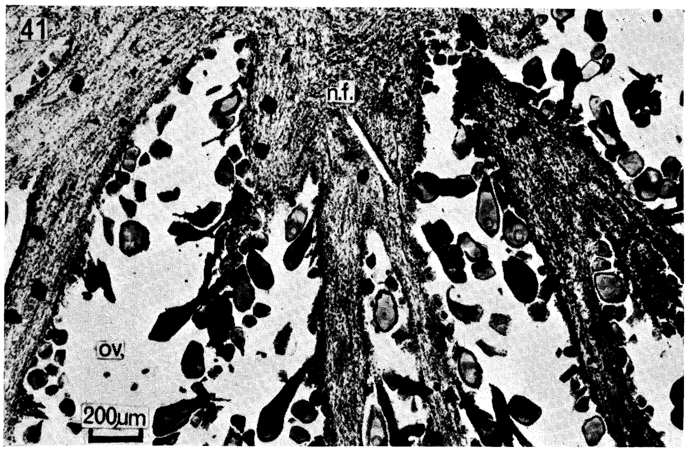
FIGURE 45. T.S. Oviduct and genito-pericardial canal of a juvenile.

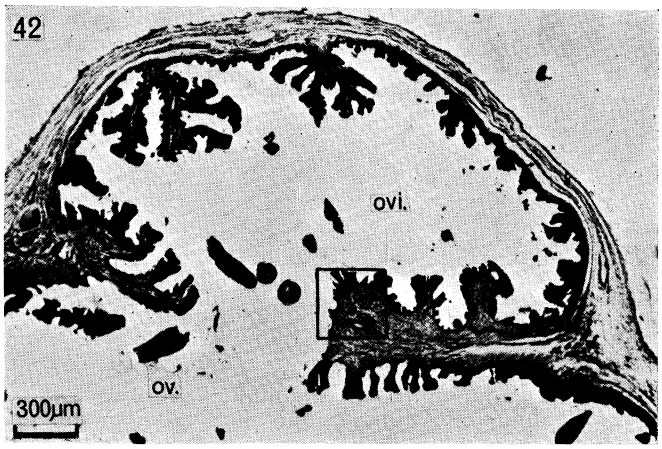
FIGURE 46. Villus of the genito-pericardial canal showing nerve fibre at the centre.

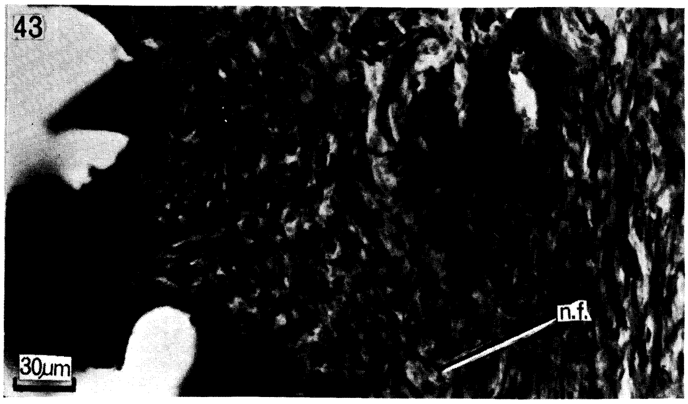
FIGURE 47. T.S. Oviducal gland.

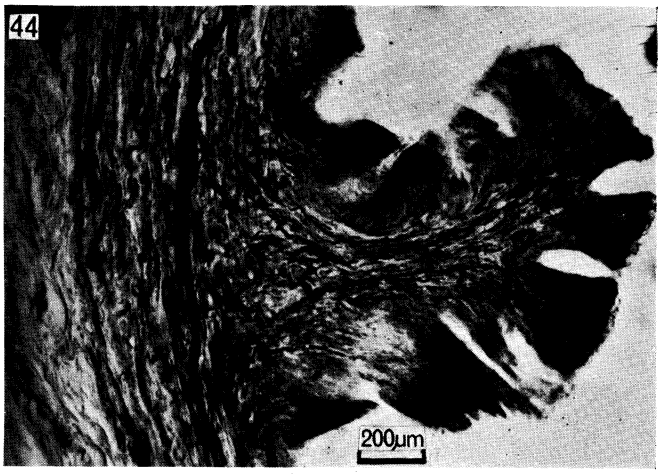
FIGURE 48. Longitudinal section through the centre of the oviducal gland, showing the two glands and the spermathecae.

FIGURE 49. Longitudinal section away from the centre of the oviducal gland, showing the nerve plexus.


41
n.f.
ov.
200µm


42
ovi.
ov.
300µm


43
n.f.
30µm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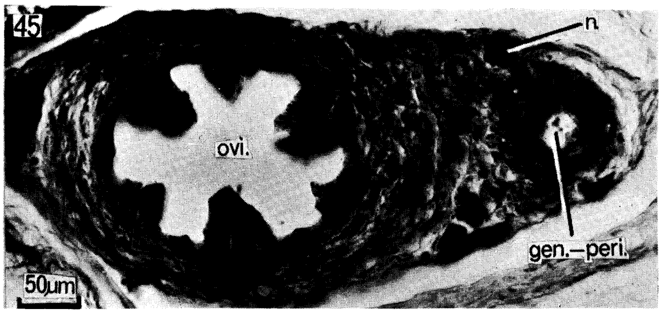
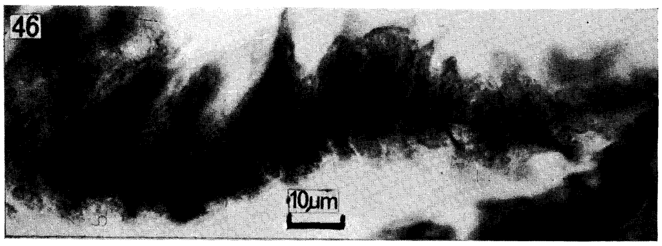
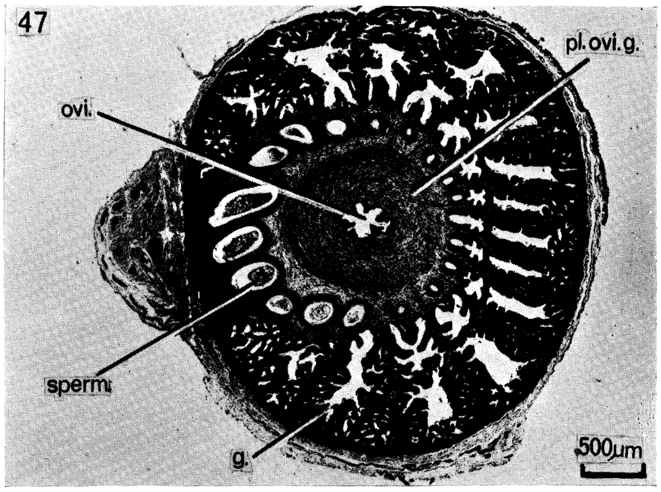
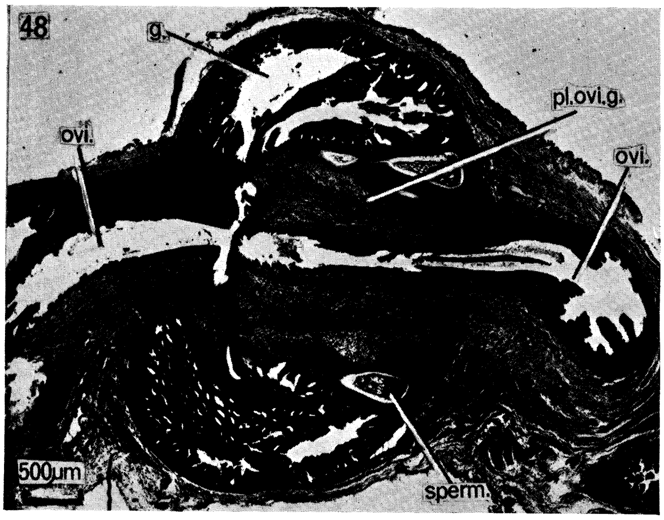
200µm


45
n
ovi.
gen.–peri.
50µm


46
10µm


47
pl. ovi. g.
ovi.
sperm.
g.
500µm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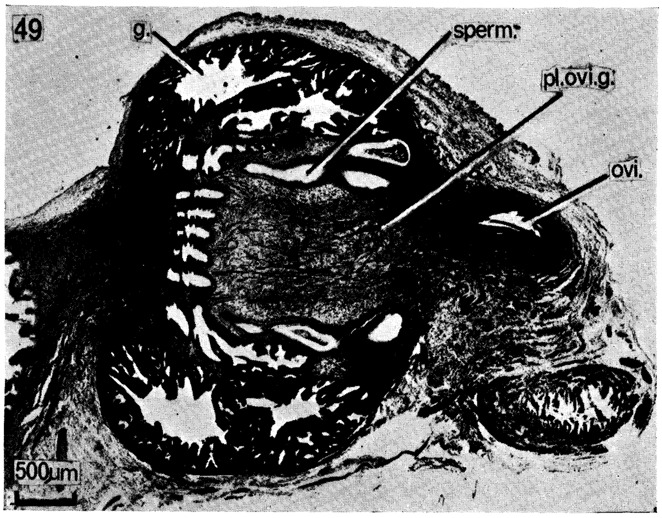
g.
pl. ovi. g.
ovi.
ovi.
500µm
sperm.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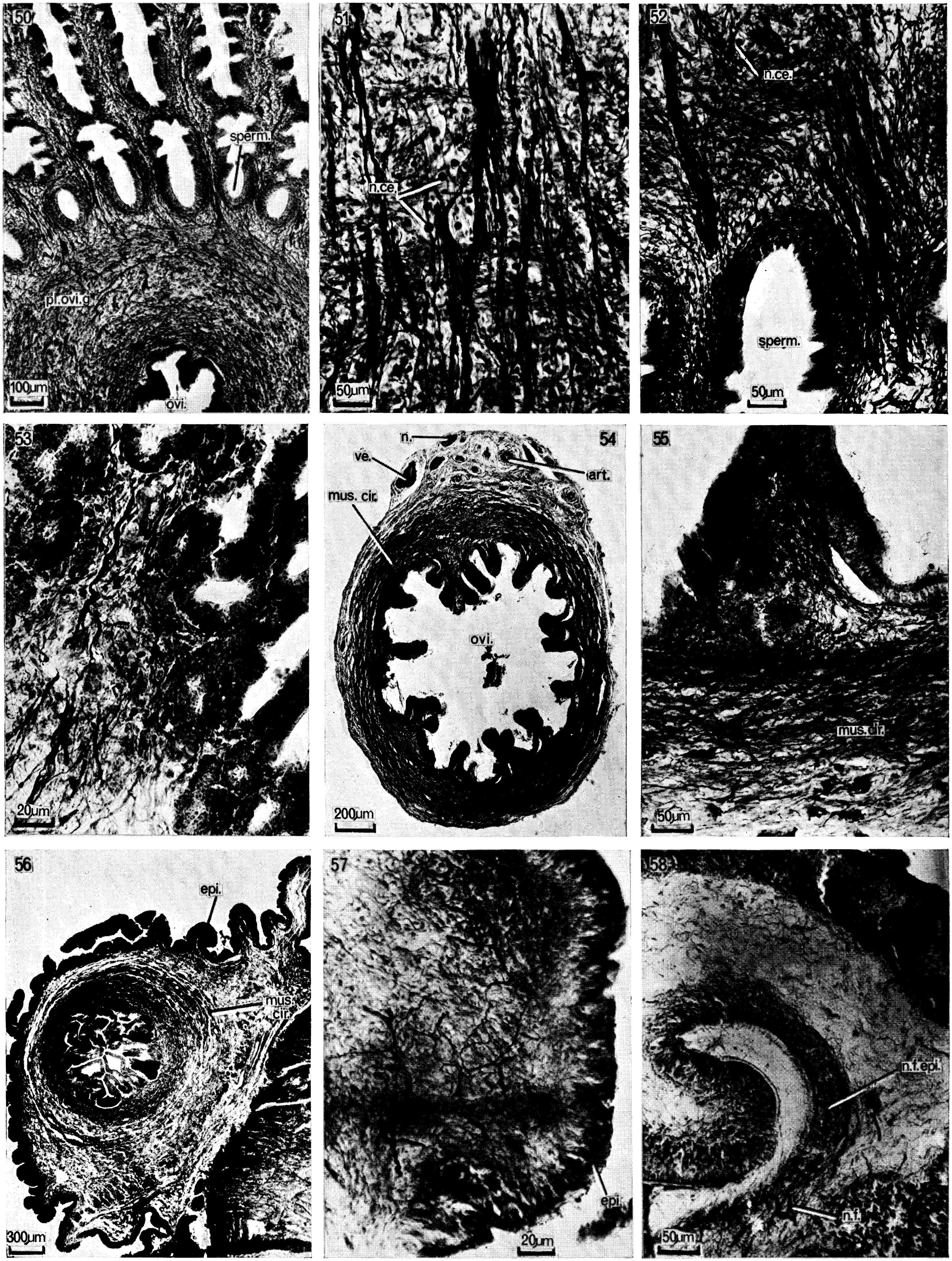
sperm.
pl. ovi. g.
ovi.
500µm


50
sperm.
pl.ovi.g.
100µm
ovi.
51
n.ce.
50µm
52
n.ce.
sperm.
50µm
53
20µm
n.
54
ve.
art.
mus. cir.
ovi.
200µm
55
mus. cir.
50µm
56
epi.
mus. cir.
300µm
57
epi.
20µm
58
n.f.epi.
n.f.
50µm

moderately richly innervated. Besides the fibres among the muscles, some reach close to the lumen and may be receptors. The folds that divide the ventricle longitudinally are richly innervated.

There are considerable differences between the innervation of the heart in decapods and octopods (see Alexandrowicz 1960, 1965). In both, the ventricle is innervated separately but in decapods the auricle is innervated from the cardiac ganglion (or its neighbourhood) rather than from the region of the fusiform ganglion. It may be that neither the ventricular nor auricular nerve fibres come from these ganglia but direct from the central nervous system. This is almost certainly true of the ventricular nerve of *Sepia* (Alexandrowicz 1960). Ganglion cells have been reported from the ventricle in *Octopus*, but are probably not numerous (Alexandrowicz 1913).

The cardiac ganglion

Distal to the fusiform ganglion the trunk of the visceral nerve turns sharply laterally and dorsally. It continues with approximately the same composition of large ($\sim 10\ \mu m$) and small fibres. Shortly before reaching the branchial heart it divides into two sets of bundles. Only one of these (containing three bundles) continues to the cardiac ganglion. The other is the cerebro-branchial connective (figure 1). The fibre contents of the divisions differ. Unfortunately no transverse sections good enough for complete enumeration have been made. The largest fibres occur in the branchial connective ($\sim 10\ \mu m$). The cerebro-cardiac connective contains fibres up to 5 μm.

The cardiac ganglion is a complex structure, including not only nerve cells and neuropil of the usual type, but also the pulsating 'intra-ganglionar body' described by Alexandrowicz (1963). The strictly ganglionic part at the more anterior region has a rather simple cell layer of large cells, with a few smaller ones and a loosely woven neuropil (figure 69, plate 8). This region includes only about 300 cells. However, the intra-ganglionar body itself contains numerous nerve cells, mainly small, whose trunks end in tufts in the neuropil, as described by Alexandrowicz. The body also has a complex arrangement of muscle fibres, connective tissues and blood vessels, whose plan is not clear. As Alexandrowicz has suggested, the organ may well have secretory as well as contractile functions. The total number

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Description of plate 6

Figure 50. T.S. Oviducal gland, showing the central canal, nerve plexus and bundles of nerve fibres between the ducts of the spermathecae.

Figure 51. Nerve plexus of the oviducal gland in longitudinal section.

Figure 52. Detail of the plexus and its relation to the ducts.

Figure 53. Secretary portion of oviducal gland, showing nerve fibres around the acini.

Figure 54. Distal (lower) portion of the oviduct and accompanying blood vessels and bundles of nerve fibres.

Figure 55. Distal portion of the oviduct with nerve fibres in the muscles and villi.

Figure 56. Terminal portion of the oviduct, surrounded by folded skin.

Figure 57. Plexus of nerve fibres beneath the epidermis of the terminal portion of the oviduct.

Figure 58. T.S. Upper portion of the spermatophore-forming duct. Nerve fibres are present at the base of the infolded portion, where some of them are very close to the epidermis. There are few or none elsewhere in the duct.

of neurons in the whole complex (of one side) was estimated at 3500, mainly medium small cells of the intra-ganglionar body (figure 34, p. 11). However, it is not easy to decide which of the cells of this body are neurons and the figure may be too high.

Numerous fine nerve trunks spring from the cardiac ganglion, though it is not known whether they are wholly derived from the ganglionic part or have afferent or efferent connexions to the intra-ganglionar body. Most of the nerves run to the branchial heart. This has a thin coat of circular muscle fibres, among which the nerve fibres branch (figure 72, plate 8). The fibres are mostly small (up to 3 μm). Around the distal end of the branchial heart, where it opens into the afferent branchial vein, there is a particularly rich plexus of nerve fibres (figure 73, plate 8).

The pericardial body ('gland') is a hollow but thick-walled appendage to the branchial heart (figures 70 and 71, plate 8). The cavity opens into the pericardium, which is a small diverticulum of the renocoele. The pericardial body contains some muscle and spongy tissue, richly supplied with branching nerve fibres. The cavity and haemopoietic tissue of the branchial heart penetrates its base (figure 71). The only previous mention of nerves to the 'pericardial gland' is that of Alexandrowicz (1960) in *Sepia*. He considered that the fibres run to smooth muscles.

The nerve fibres form webs and endings close beneath the pericardial surface. They run the short distance to the entrance of the pallial vein to the branchial heart and thence to the cardiac ganglion. There are also nerve fibres in the pericardial wall itself. These sets of nerve fibres may include many receptors, especially around the large vascular spaces (figure 72, plate 8). The contrast in this figure between the nerves in the walls of these spaces in the appendage and in the branchial heart itself is very marked, especially the rich terminal plexus of nerve fibres around the vessels of the appendage. This whole system perhaps includes receptors. It may be relevant that the genito-pericardial canal is also richly innervated. Elaborate receptor and motor systems may be necessary to regulate the pressures in the complex network of cavities, including the coelomic spaces, venous sinuses and afferent branchial arterial vessels serving excretion as well as respiration (Potts 1967).

Branchial ganglia

Beyond the branchial heart the remaining trunk of the visceral nerve turns forward and laterally along the base of the ctenidium (figure 1, p. 3). It may here be called the branchial

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DESCRIPTION OF PLATE 7

FIGURE 59. Section of the accessory gland, showing ball of spermatozoa at the centre.

FIGURE 60. Portion of the accessory gland showing a few isolated fibres, perhaps nervous, among the acini.

FIGURE 61. Transverse section across lower portion of the spermatophore-forming duct and Needham's sac.

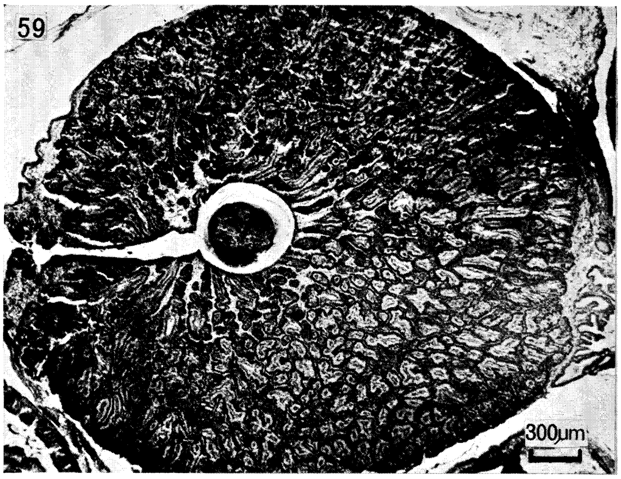
FIGURE 62. Detail of the wall of Needham's sac, with spermatophores forming on the right.

FIGURE 63. T. S. Penis.

FIGURE 64. T.S. Lower end of penis showing folds of thickened skin.

FIGURE 65. L.S. Tip of penis, with remains of a spermatophore.

FIGURE 66. T.S. Auricle, showing auricular and ventricular nerves.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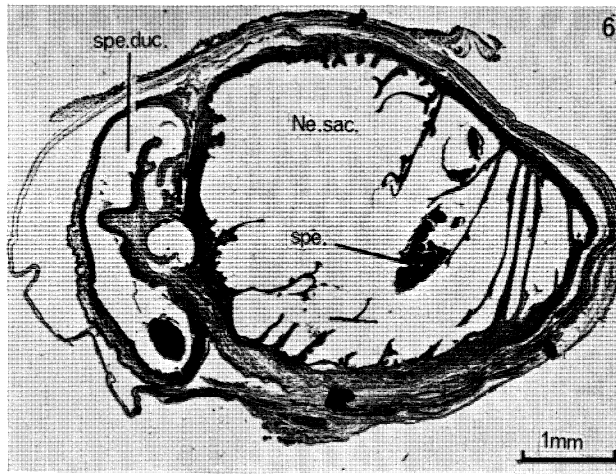
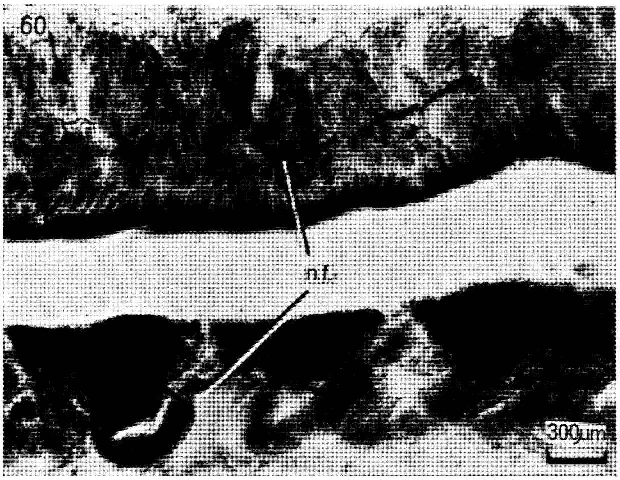
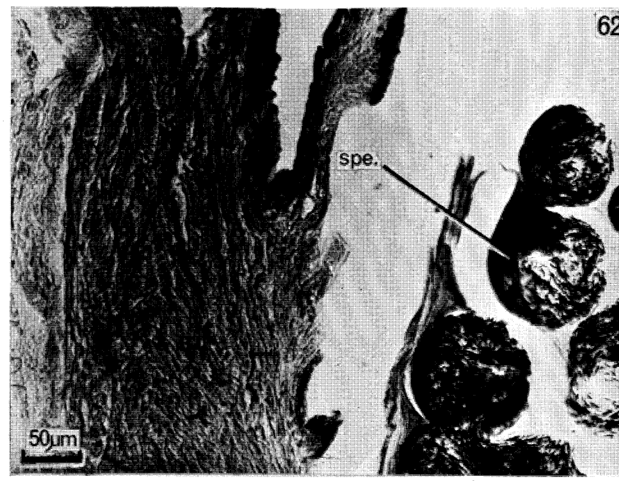
300µm


61
spe.duc.
Ne.sac.
spe.
1mm


60
n.f.
300µm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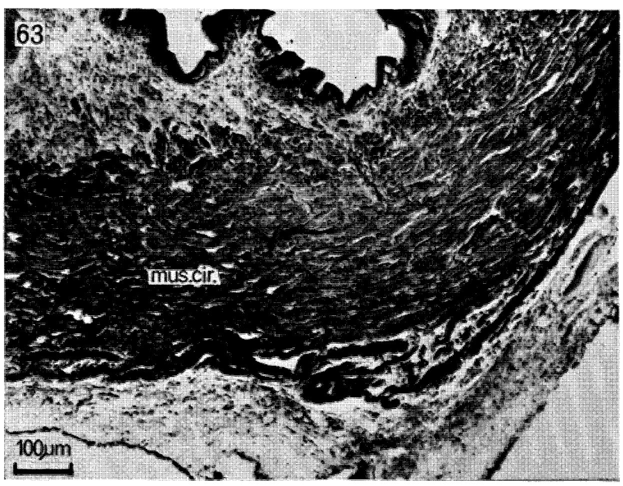
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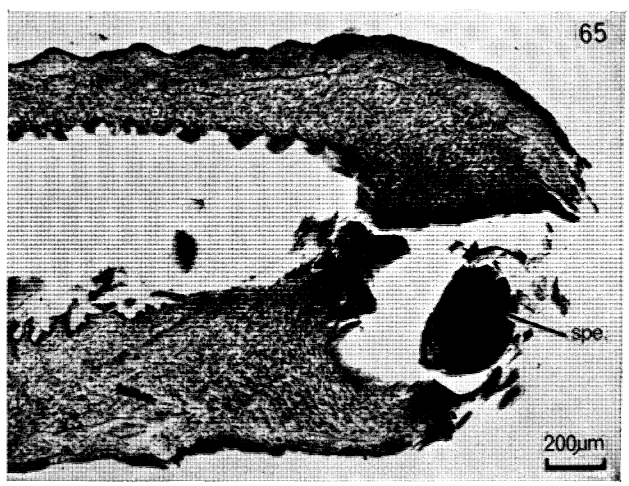
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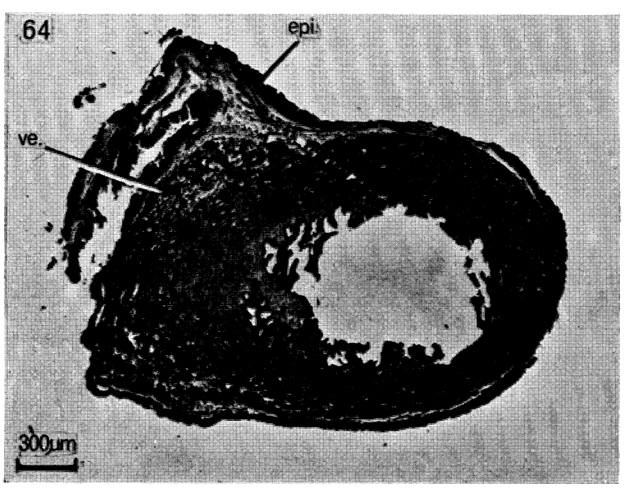
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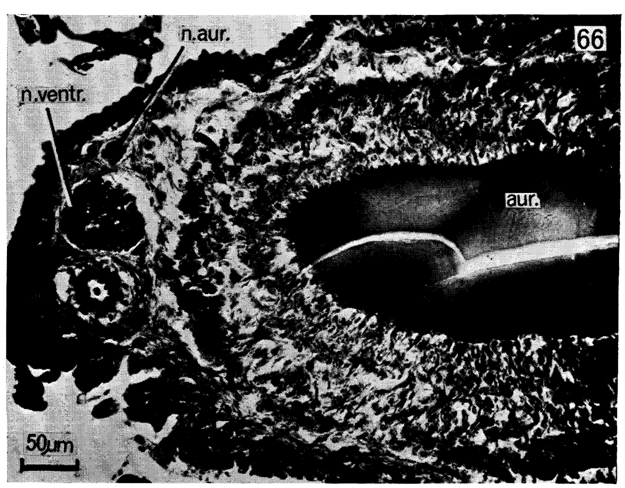
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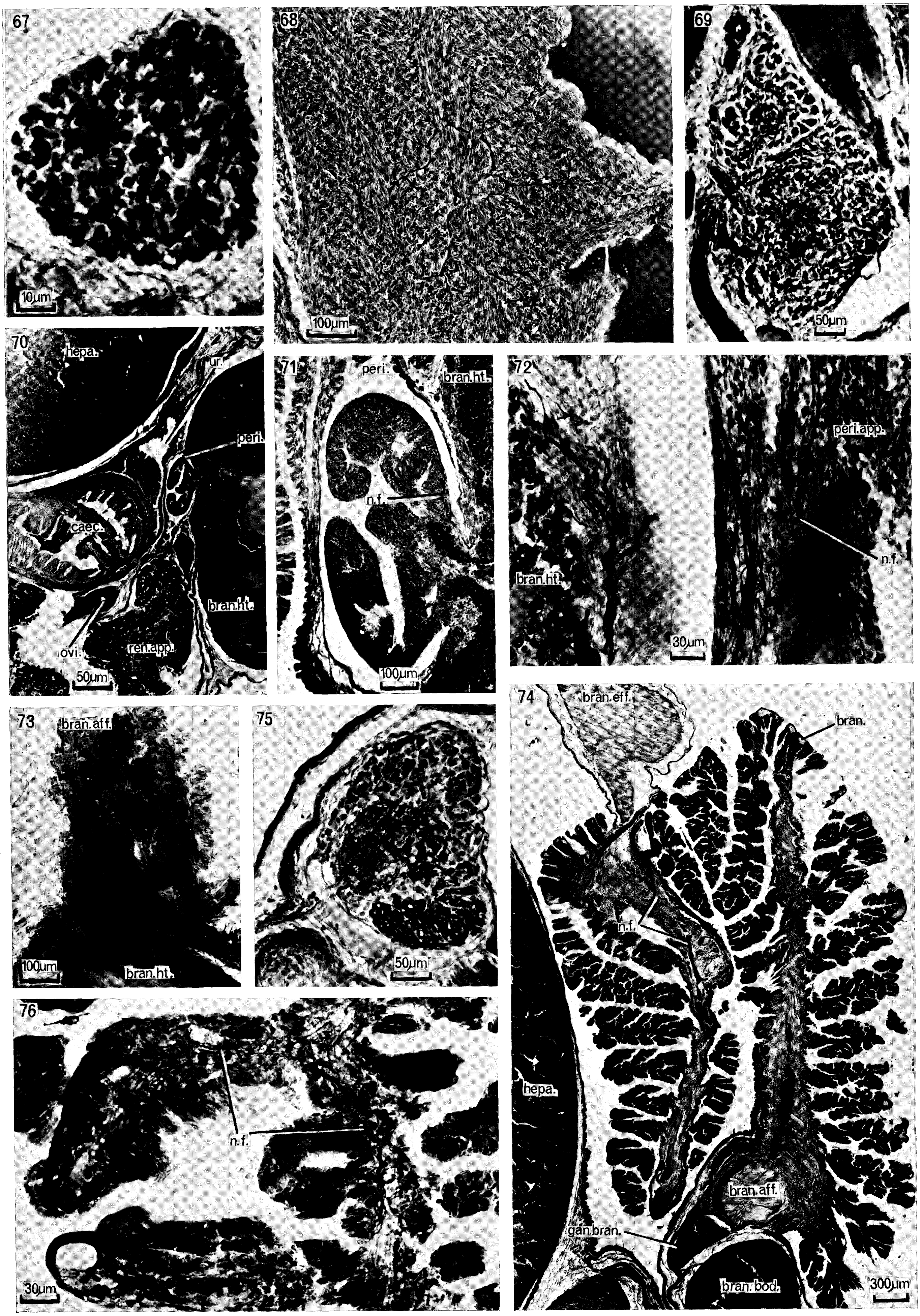
n.aur.
n.ventr.
aur.
50µm

(*Facing p.* 18)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hepa.
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50µm
71
peri.
bran.ht.
n.f.
100µm
72
peri.app.
n.f.
bran.ht.
30µm
73
bran.aff.
100µm
bran.ht.
75
50µm
74
bran.eff.
bran.
n.f.
hepa.
bran.aff.
gan.bran.
bran.bod.
300µm
76
n.f.
30µm

nerve, although more strictly it is a cerebro-branchial connective (or cerebro-ctenidial connective). The trunk at this level contains the usual mixture of small and medium fibres (up to 10 μm) but no count has been made.

The chain of branchial ganglia ('branchial ganglionic trunk' of Alexandrowicz 1960) runs along the dorso-medial side of the afferent branchial vessel, medial to the branchial appendage (figure 74, plate 8). The main bundle of fibres runs through the whole chain on the lateral side of the ganglia. Some medium fibres continue throughout (5 μm), perhaps running to the main retractor muscles (Alexandrowicz 1960). Cells are present along the whole trunk, but more nearly surround the cord where the ctenidial lamellae join the axis. This gives the effect of a series of ganglia.

The cells are only slightly larger at the periphery than next to the neuropil (figure 75, plate 8). Almost all fall within the range with nuclear diameter 5 to 10 μm, very few either larger or smaller (figure 34, p. 11). There are estimated to be 30000 cells in the whole chain (on each side).

Four branches are given off from the chain to each pair of lamellae. (The medial and lateral lamellae are arranged in pairs but are not exactly opposite to each other.) Branches of the nerves run along the lateral and medial sides of the vessel of each lamella (figure 74). They innervate the muscles at the core of the lamella and also run up into the branches (figure 76, plate 8). Some fibres reach to the finest extremities of the sub-branches of the lamellae and there is an elaborate plexus beneath the epithelium. There may well be receptors in this system. Alexandrowicz (1960) reports receptors in the branchiae of *Sepia*. Fibres continue to the tip of the lamella, where the efferent branchial vessel leaves (figure 74). Here they presumably meet the fibres from the fusiform ganglion and auricular nerves.

The branchial appendage (also called branchial body or gland) is a large mass of tissue lying along the base of the gill (Taki 1964). It consists of a thin capsule surrounding a mass of polygonal cells, thought to be secretory. As shown by Taki, nerve fibres proceed from the branchial ganglia to the capsule of the appendage, but do not penetrate among its cells.

Description of plate 8

Figure 67. T.S. Ventricular nerve.

Figure 68. T.S. Wall of ventricle, showing layers of muscle fibre running in various directions, also the base of one of the septae that divide the cavity.

Figure 69. Cardiac ganglion.

Figure 70. T.S. Branchial heart, pericardial appendage and related regions.

Figure 71. T.S. Pericardial appendage showing haemopoietic tissue extending from the branchial heart and communication with the pericardium.

Figure 72. Detail of wall of branchial heart and tissue of the pericardial appendage, with very rich innervation of the veins.

Figure 73. Plexus of nerve fibres at the opening of the branchial heart to the afferent branchial vein.

Figure 74. Transverse section of a pair of ctenidial lamellae to show afferent and efferent vessels, branchial ganglion, nerves and branchial appendage.

Figure 75. T.S. Branchial ganglion.

Figure 76. Detail of finest branches of ctenidium, showing nerve fibres close to the epithelium.

Discussion

Features commonly found in the innervation of visceral organs are: (1) plexiform arrangements with peripheral neurons, and (2) numerous small fibres. Plexuses including nerve cells are very marked in the oesophagus and intestine of *Octopus* but no nerve cells have been seen in the stomach, and few in the ventricle (see Alexandrowicz 1913, 1928, 1960; Graziadei 1960). There is an elaborate plexus with cells in the oviducal gland, but neurons have not been found elsewhere in the genital system. Of course, as Alexandrowicz emphasizes, evidence of the absence of cells is suspect, but less so when they can be found elsewhere in the preparations. From such differences it should be possible to discover whether the plexuses with cells serve to mediate some special reflex or rhythmic behaviour. In the plexuses of the intestine of arthropods there seem to be fewer cells than in molluscs (see Alexandrowicz 1928).

The number of nerve fibres in the viscera is even greater in *Octopus* than in *Sepia*, where it surprised Alexandrowicz (1960). He speaks of this profligacy as if it were in some way 'uneconomical', for example in contrast to Crustacea. It is more likely that in cephalopods, as in vertebrates, there is some positive advantage in the control of the viscera by numerous small fibres rather than fewer large ones. In the octopus none of the nerve fibres for the viscera is larger than 5 μm (the larger fibres of the 'visceral' nerve run to the median pallial adductor and depressor of the funnel). There are differences of diameter however even within the nerves running to visceral organs. Commonly there are a few rather larger fibres (up to 5 μm) accompanied by very numerous smaller ones. It may be that the larger fibres innervate particular muscle systems (for instance the longitudinal retractor muscles of the branchiae). Graziadei (1960) has shown that in some muscles of the stomach of *Sepia* each larger nerve fibre is accompanied by smaller ones to its termination.

The general plan of innervation of the gut is remarkably similar not only among molluscs, but also in arthropods (though they have fewer cells) and vertebrates (see Ábráham (1940) for gastropods; Alexandrowicz (1909) and Orlov (1929) for Crustacea). In addition to plexuses there are usually peripheral ganglia, receiving nerves from the central nervous system. A remarkable feature that has emerged from the present study is that there are three connexions of the gastric ganglion with the central nervous system. Yet none of them is by a direct nerve, all are through plexiform arrangements of (1) the oesophagus and crop, (2) the intestine and (3) the hepatic ducts. There may be through fibres in these plexuses, but the arrangement suggests that the gastric ganglion functions largely independently, or in some special reflex relationship to actions controlled by the plexuses of the crop and intestine. The connexions with the central nervous system may serve largely to convey afferents. In some preliminary experiments in which the sympathetic nerve trunks were severed, degeneration was seen centrally but not peripherally (even after as long as 14 days). Afferent impulses from the gut may well be needed to regulate the mechanisms of hunger, motivation and learning, while the actions of the alimentary canal itself proceed autonomously.

Unfortunately very little is known of the receptors of the gut or genital tracts, nor of their reflex pathways. It is hoped that the present data may provide a basis for their investigation.

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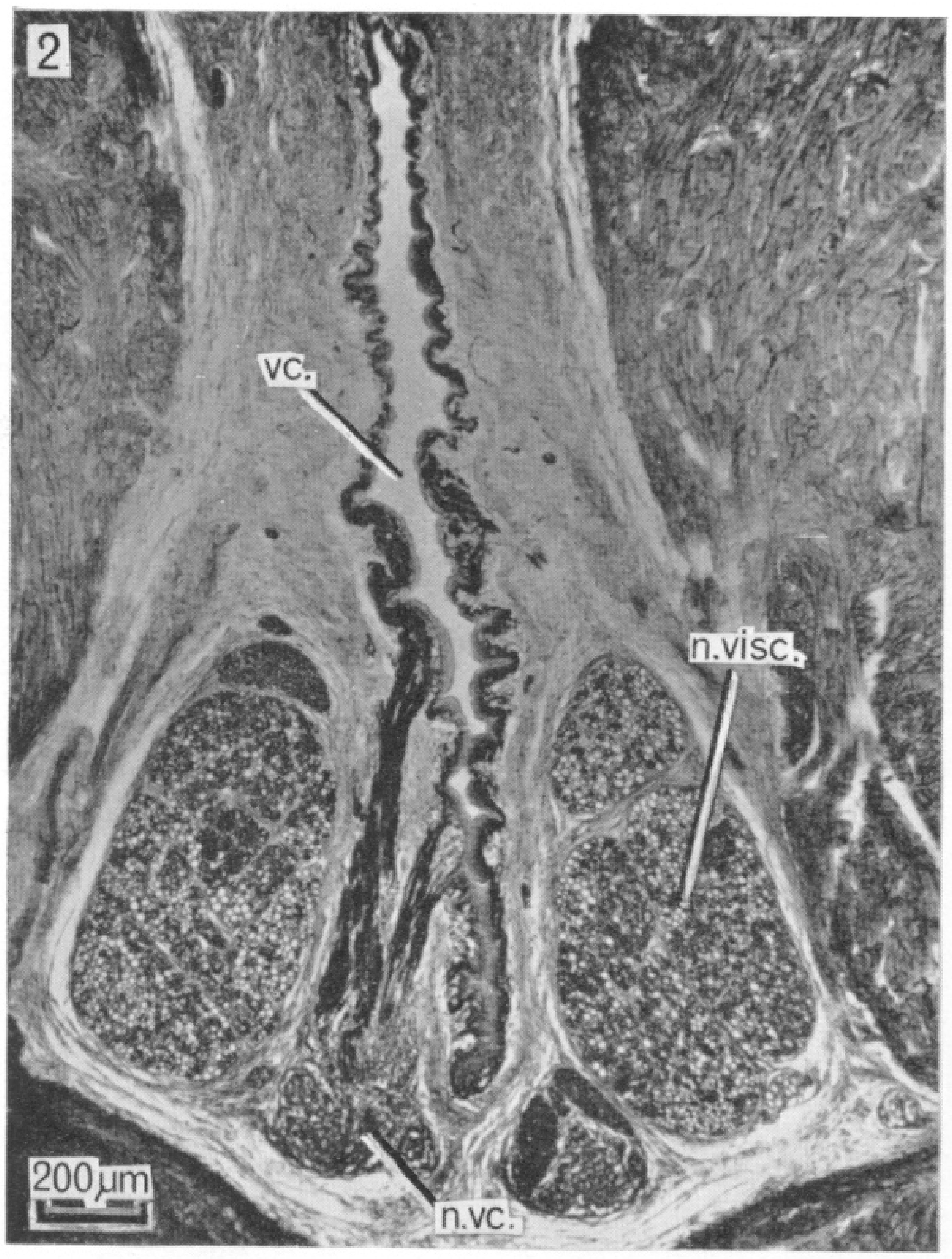
Abbreviations used on figures

an.fl.	anal flap
art.	artery
at.	anastomosis between abdominal and hepatic duct nerves
aur.	auricle
bran.	gill (ctenidium)
bran.aff.	afferent branchial vessel
bran.bod.	branchial body
bran.eff.	efferent branchial vessel
bran.ht.	branchial heart
caec.	caecum
caps.hep.	hepatic capsule
cer.-bran.con.	cerebro-branchial connective
duc.hep.	hepatic duct
duc.ma.	male duct
ep.	epithelium
epi.	epidermis
fun.	funnel
g.	gland
gan.bran.	branchial ganglion
gan.card.	cardiac ganglion
gan.fus.	fusiform ganglion
gan.gas.	gastric ganglion
gen.-peri.	genito-pericardial canal
hepa.	hepatopancreas
ink duc.	ink duct
ink sac	ink sac
intest.	intestine
mant.cav.	mantle cavity
Mes.	Mesozoan parasite
mus.cir.	circular muscle
mus.long.	longitudinal muscles
mus.pal.add.med.	median pallial adductor muscle
mus.retr.fun.	retractor muscle of funnel (=depressor)
n.	nerve
n.abd.	abdominal nerve
n.atr.-rect.	atrio-rectal nerve
n.aur.	auricular nerve
n.bran.	branchial nerve
n.caps.hep.	nerves to hepatic capsule
n.ce.	nerve cell
n.dep.fun.	nerve of the depressor muscle of the funnel
n.duc.hep.	nerves of hepatic ducts
n.duc.ma.	nerve of male duct
n.f.	nerve fibres
n.f.epi.	epidermal nerve fibres
n.ink duc.	nerve of ink duct
n.ink sac	nerve of ink sac
n.intest.	intestinal nerves
n.pal.add.med.	nerve to medial pallial adductor muscle
n.ren.	nerve of renal appendages
n.ren.pap.	nerve of urinary papilla
n.retr.fun.	nerve of funnel retractor
n.stom.	nerves of stomach
n.symp.	sympathetic nerve
n.vc.	nerve of vena cava
n.vc.p.	posterior vena caval nerve
n.ventr.	nerve of ventricle
n.visc.	visceral nerve
Ne.sac.	Needham's sac
oes.	oesophagus
ov.	ovary
ovi.	oviduct
pen.	penis
peri.	pericardium
peri.app.	pericardial appendage
pl.	plexus
pl.ovi.g.	plexus in oviducal gland
rect.	rectum
ren.app.	renal appendages
ren.pap.	renal papilla
ren.-peri.ap.	reno-pericardial aperture
reno.	renocoele
sl.	muscular 'sling'
spe.	spermatophore
spe.duc.	spermatophore forming duct
sperm.	spermatheca
stom.	stomach
test.	testis
ur.	urocoele
vc.	vena cava
ve.	vein
ventr.	ventricle
wi.	wings of anus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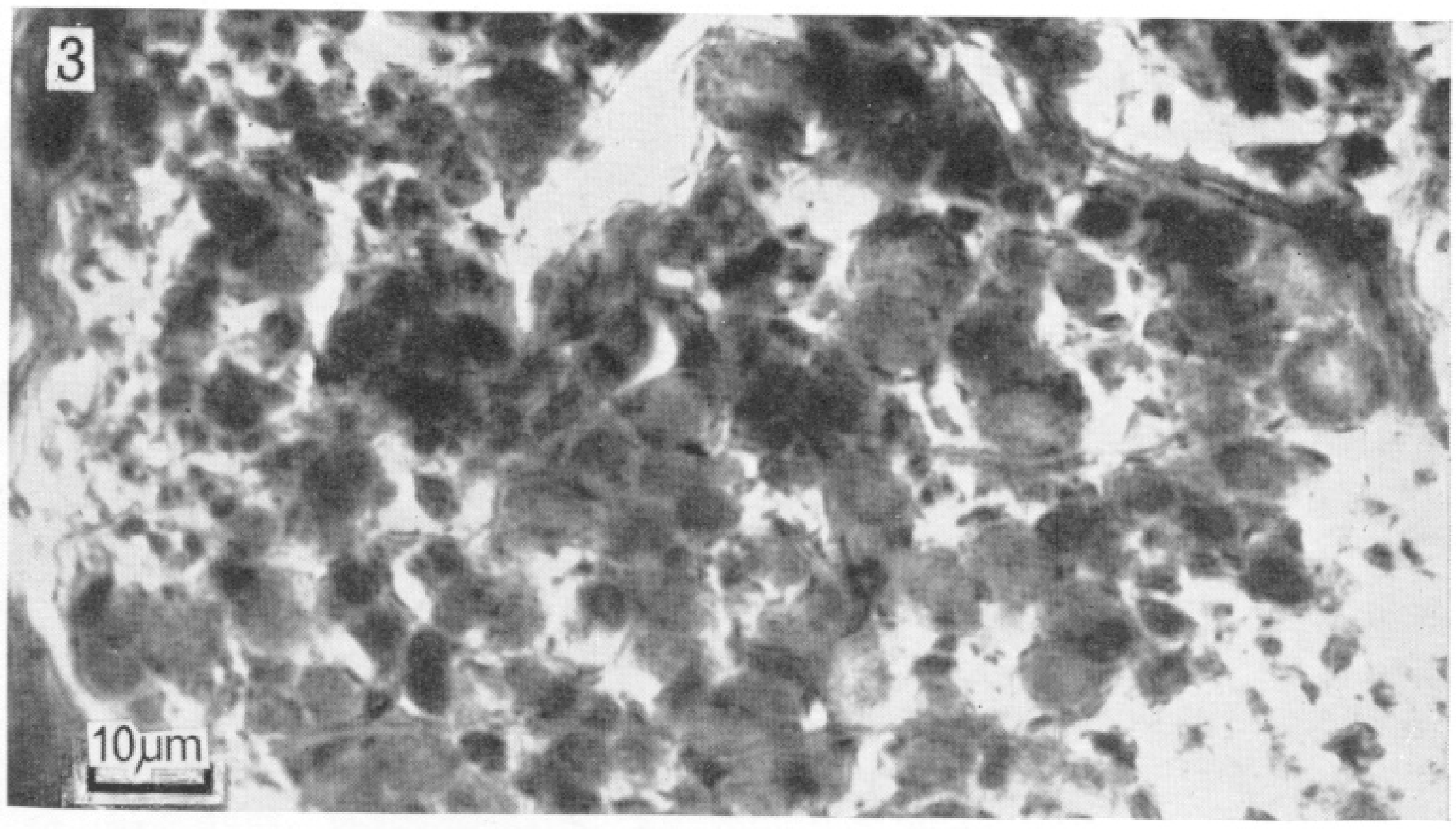
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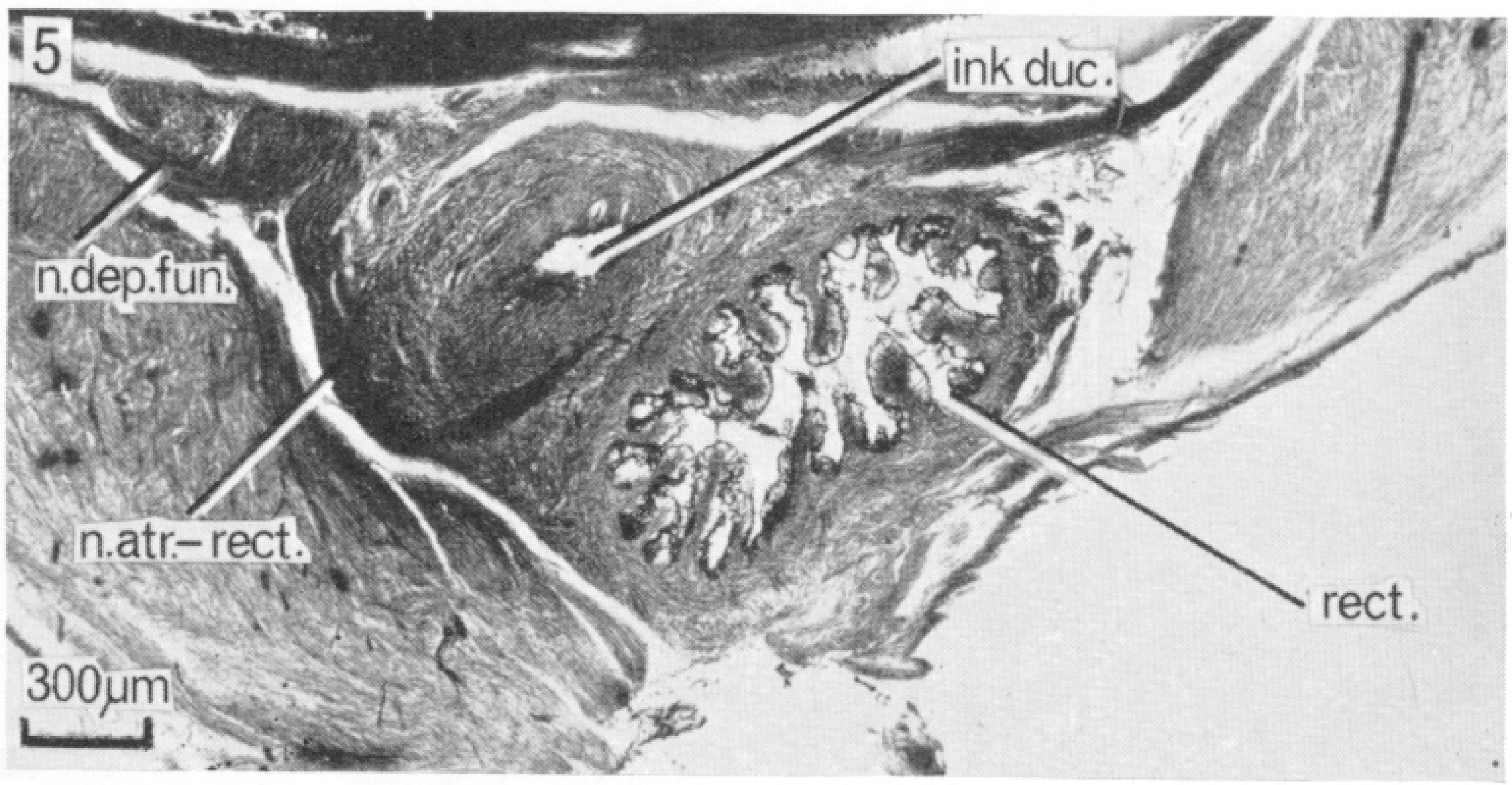
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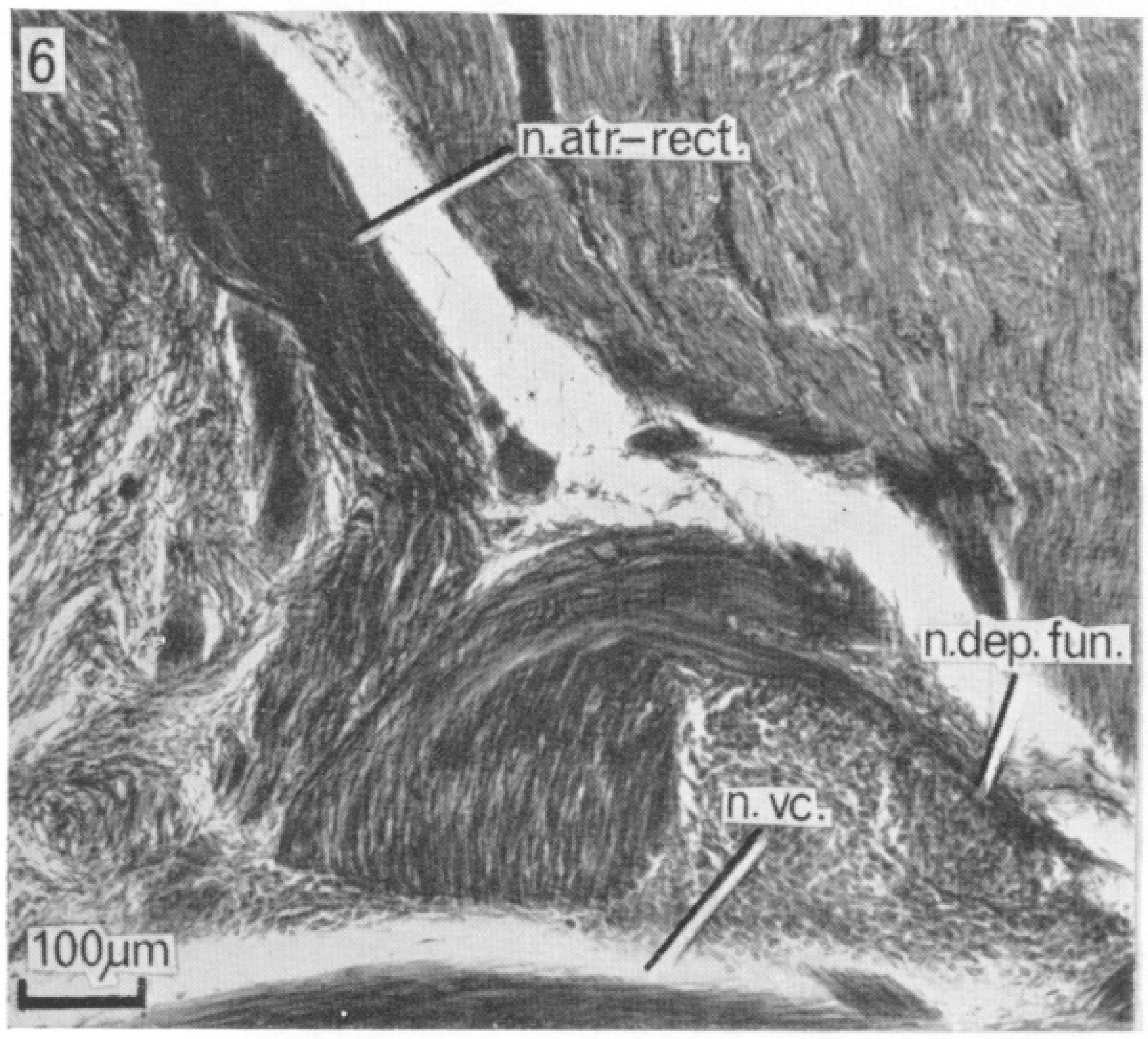
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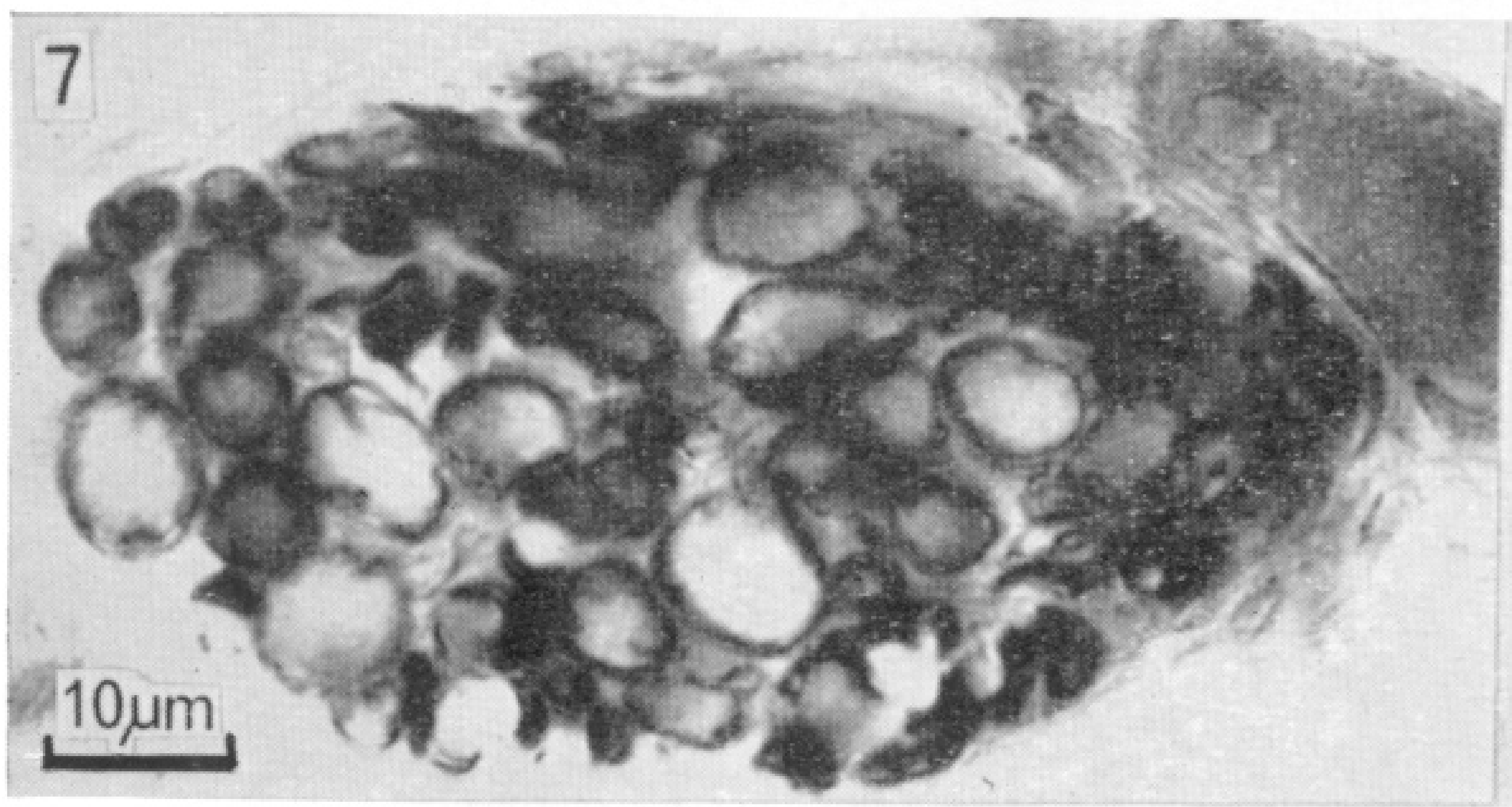
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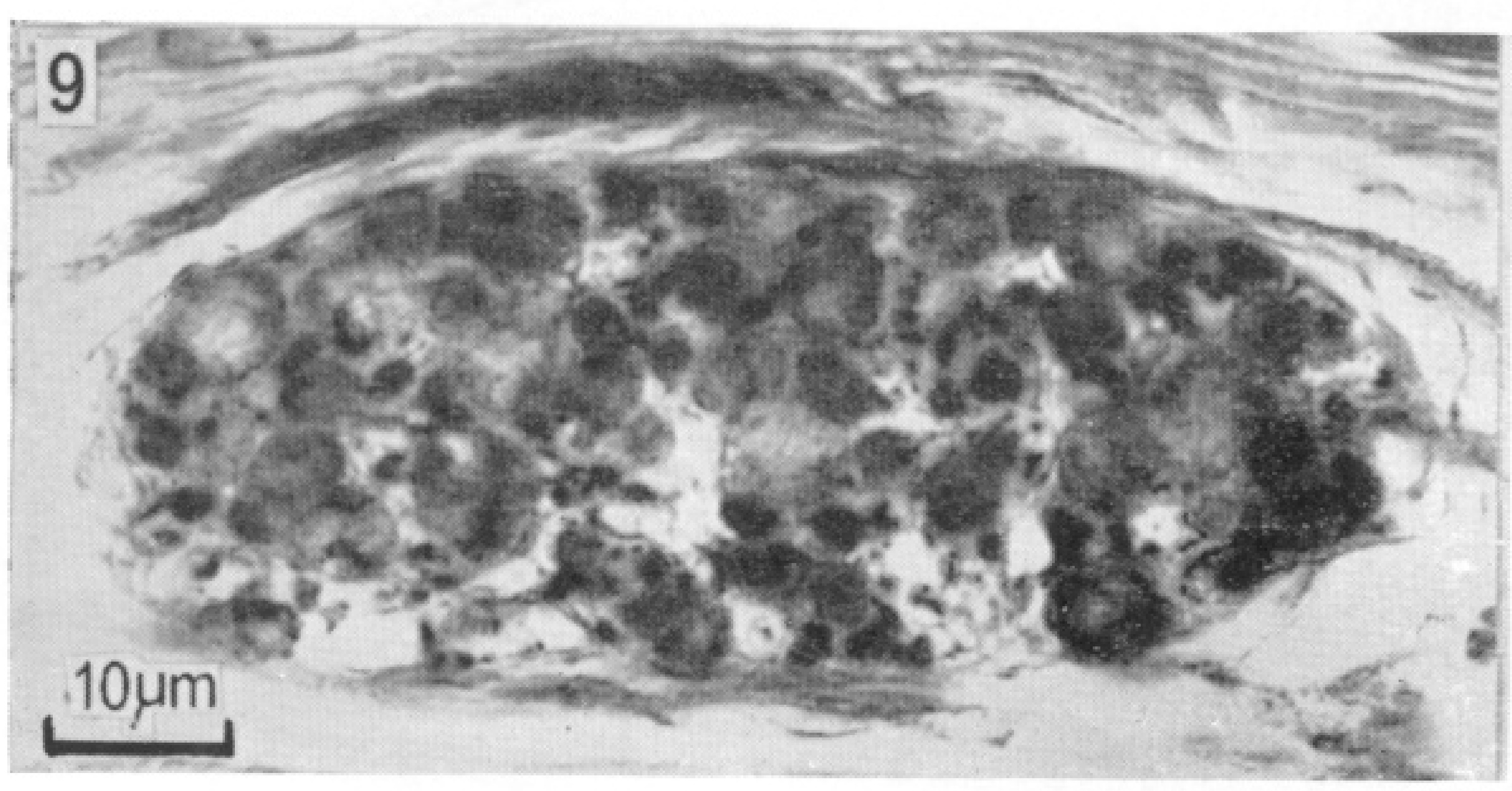
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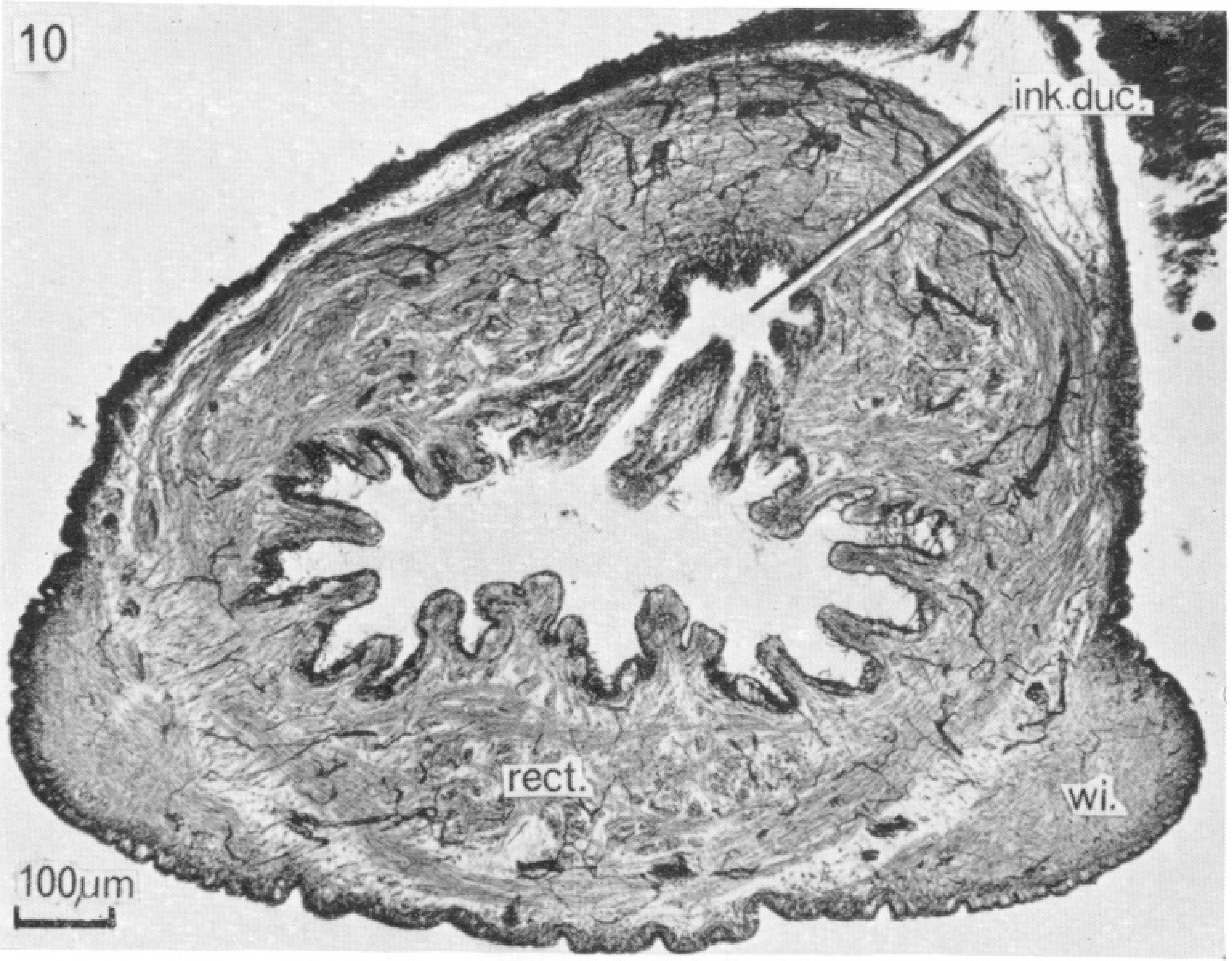
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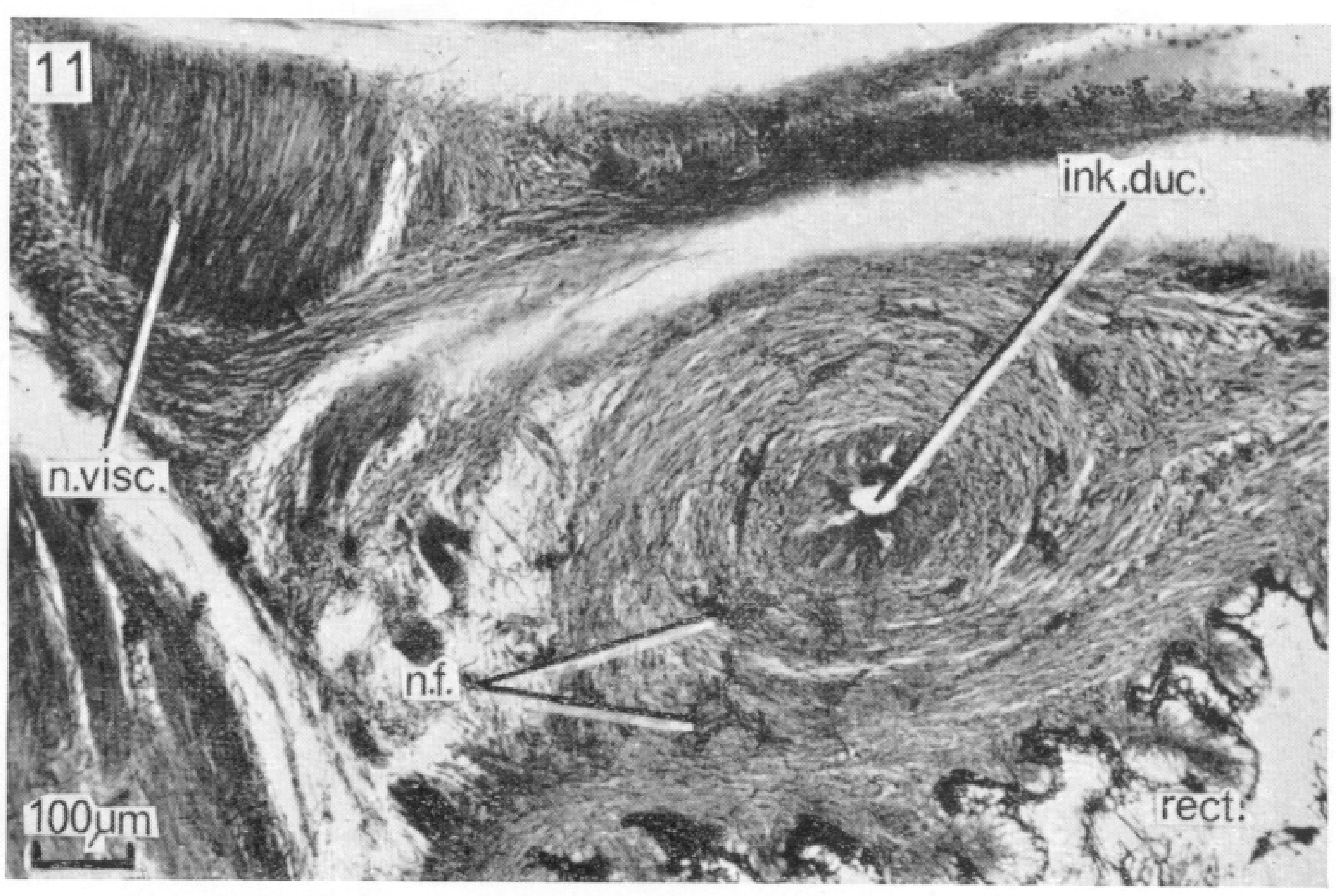
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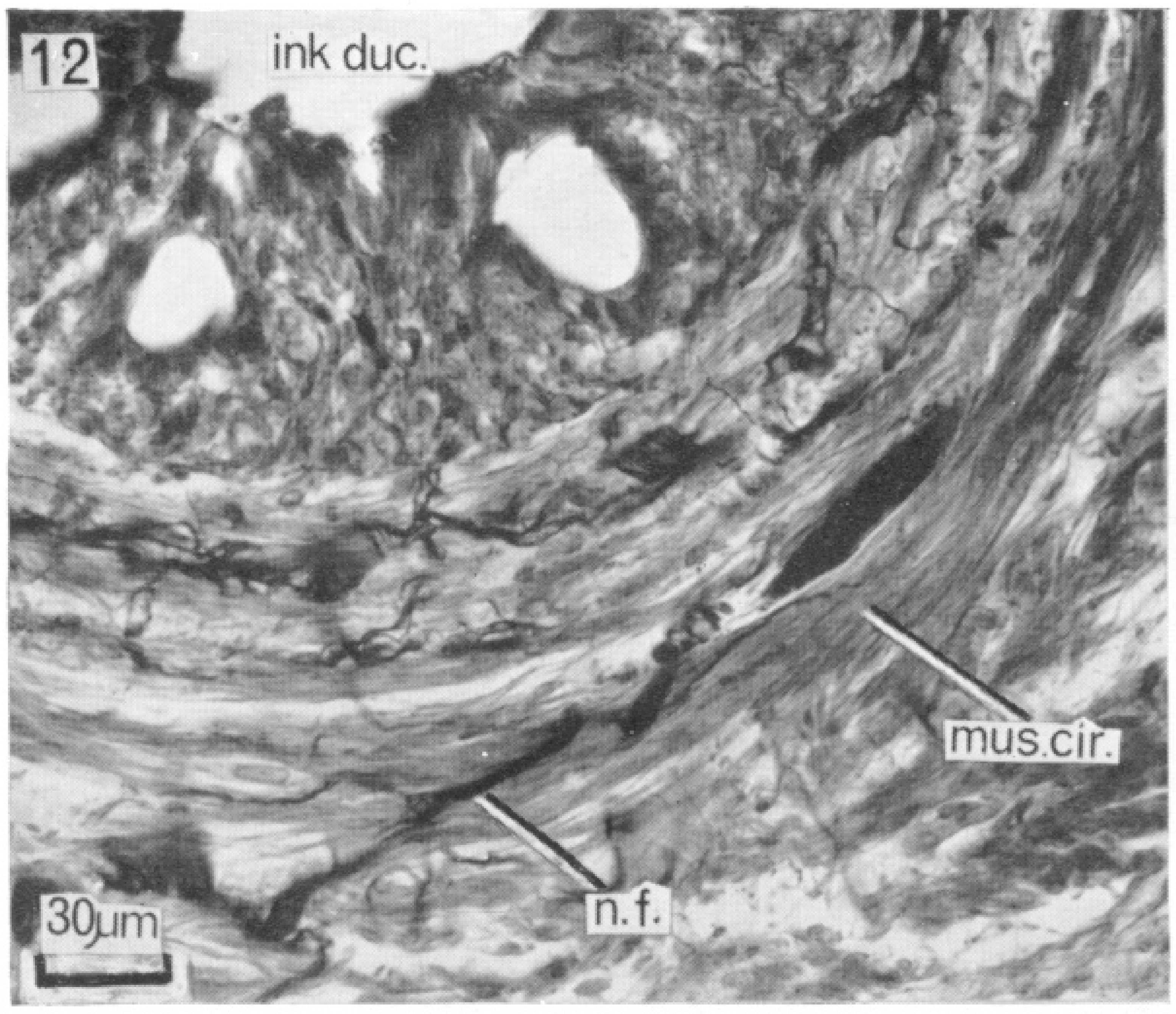
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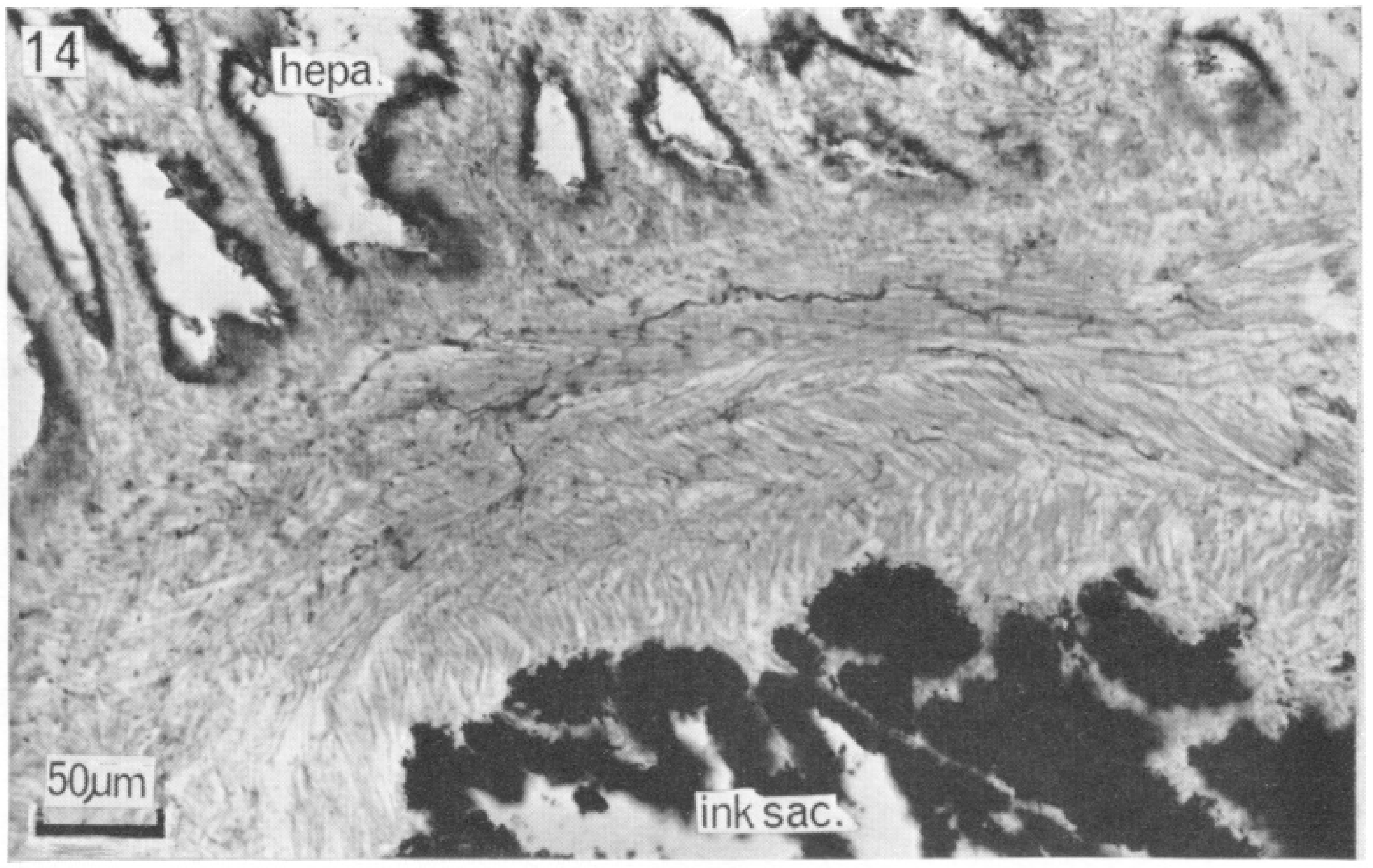
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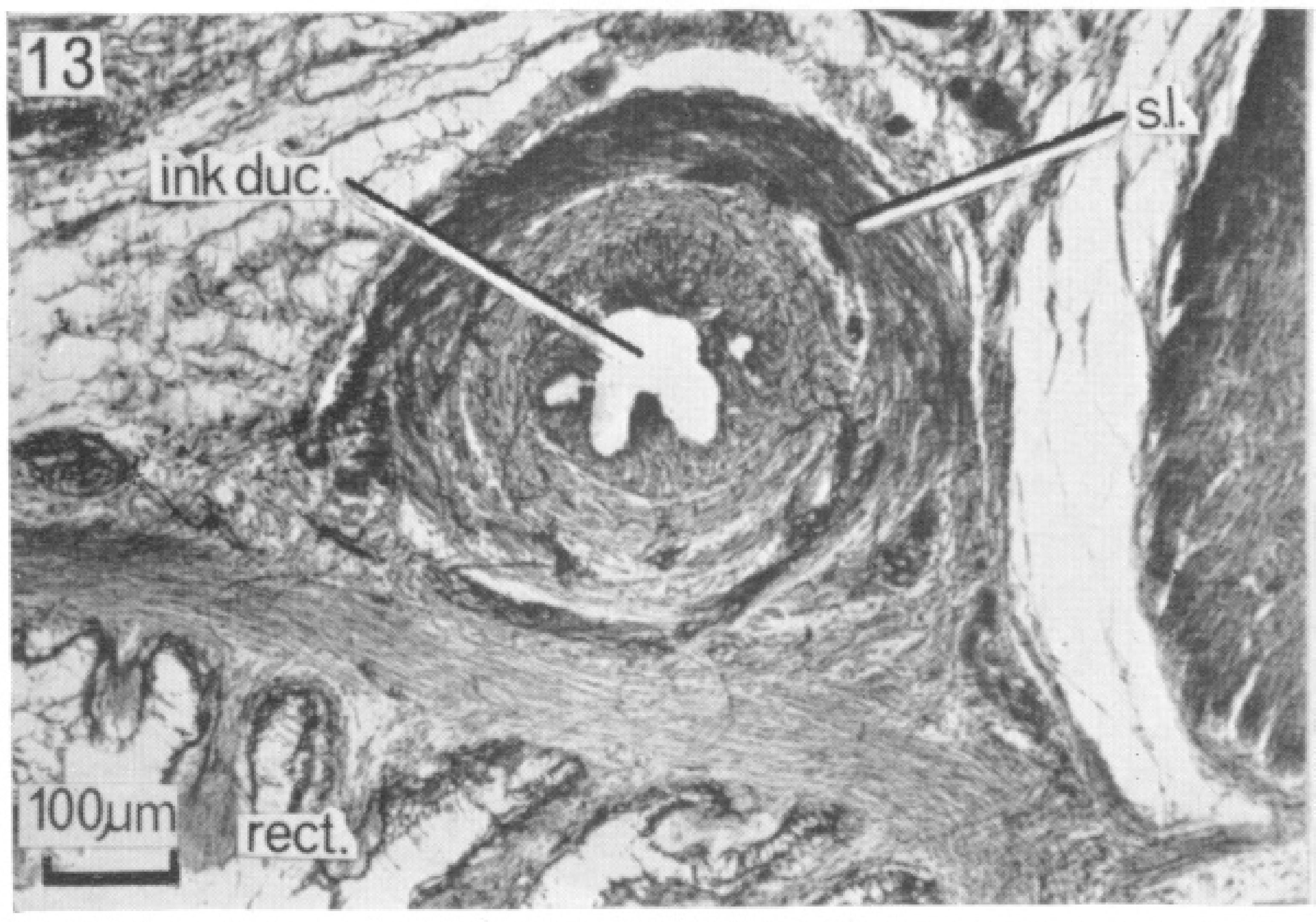
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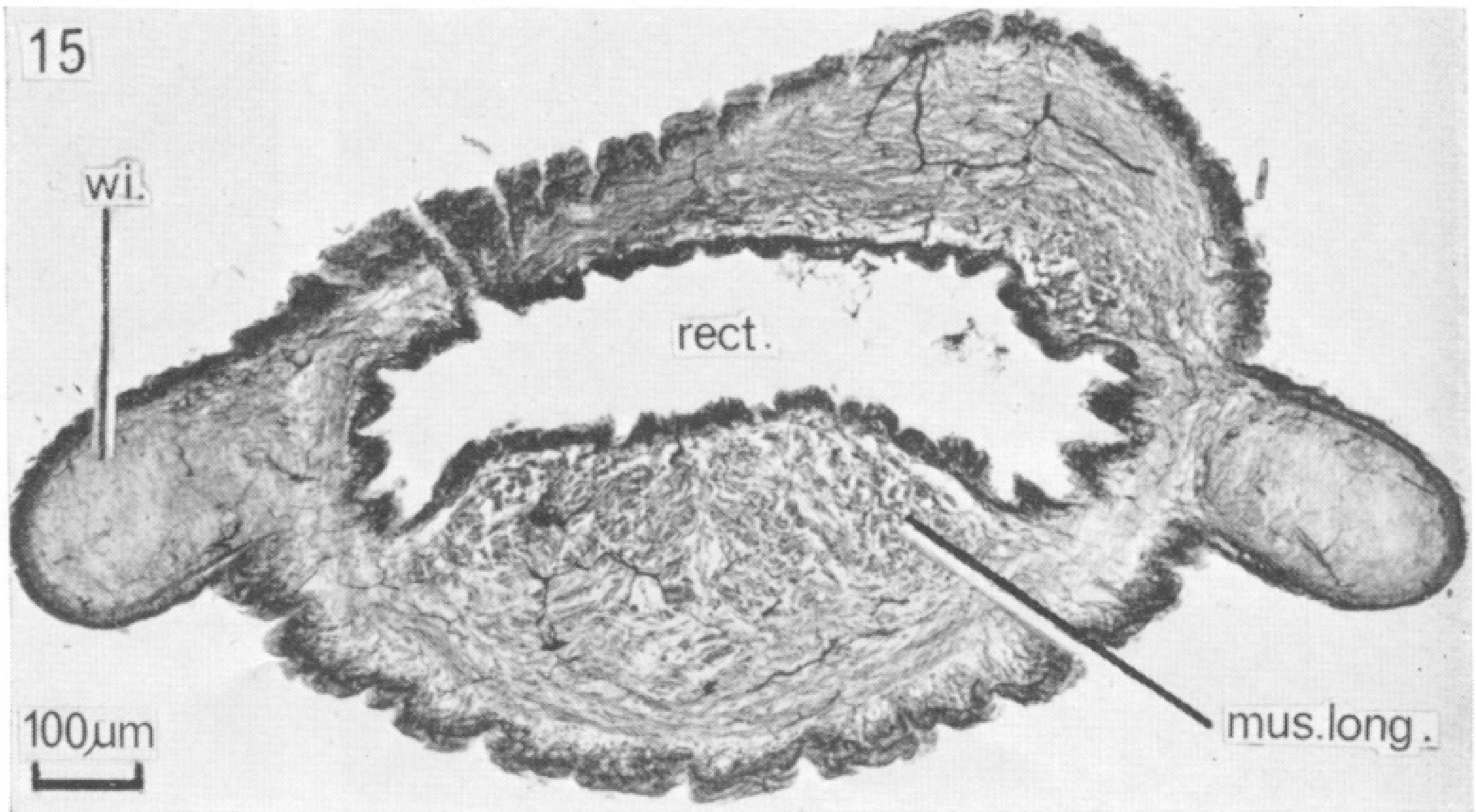
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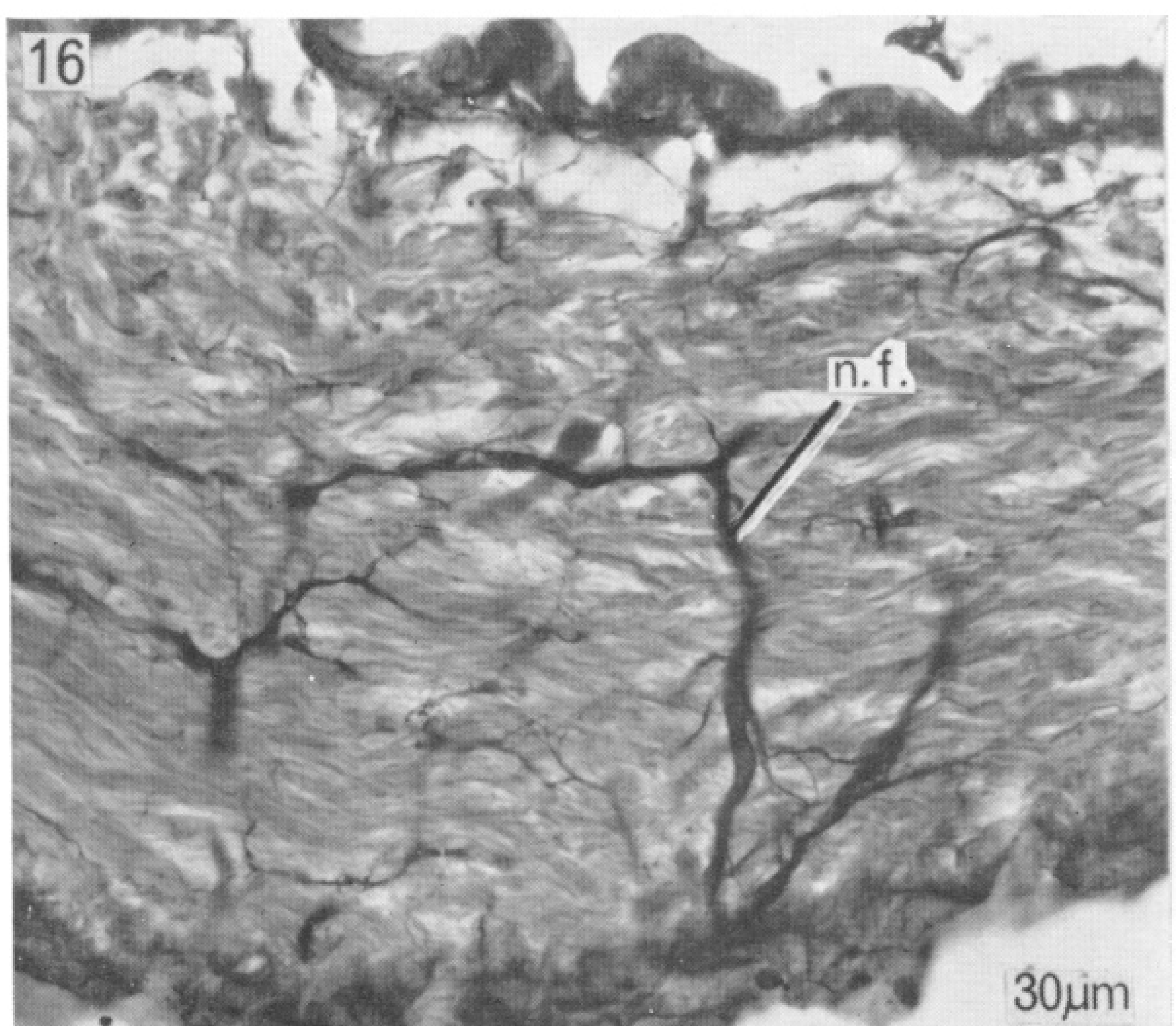
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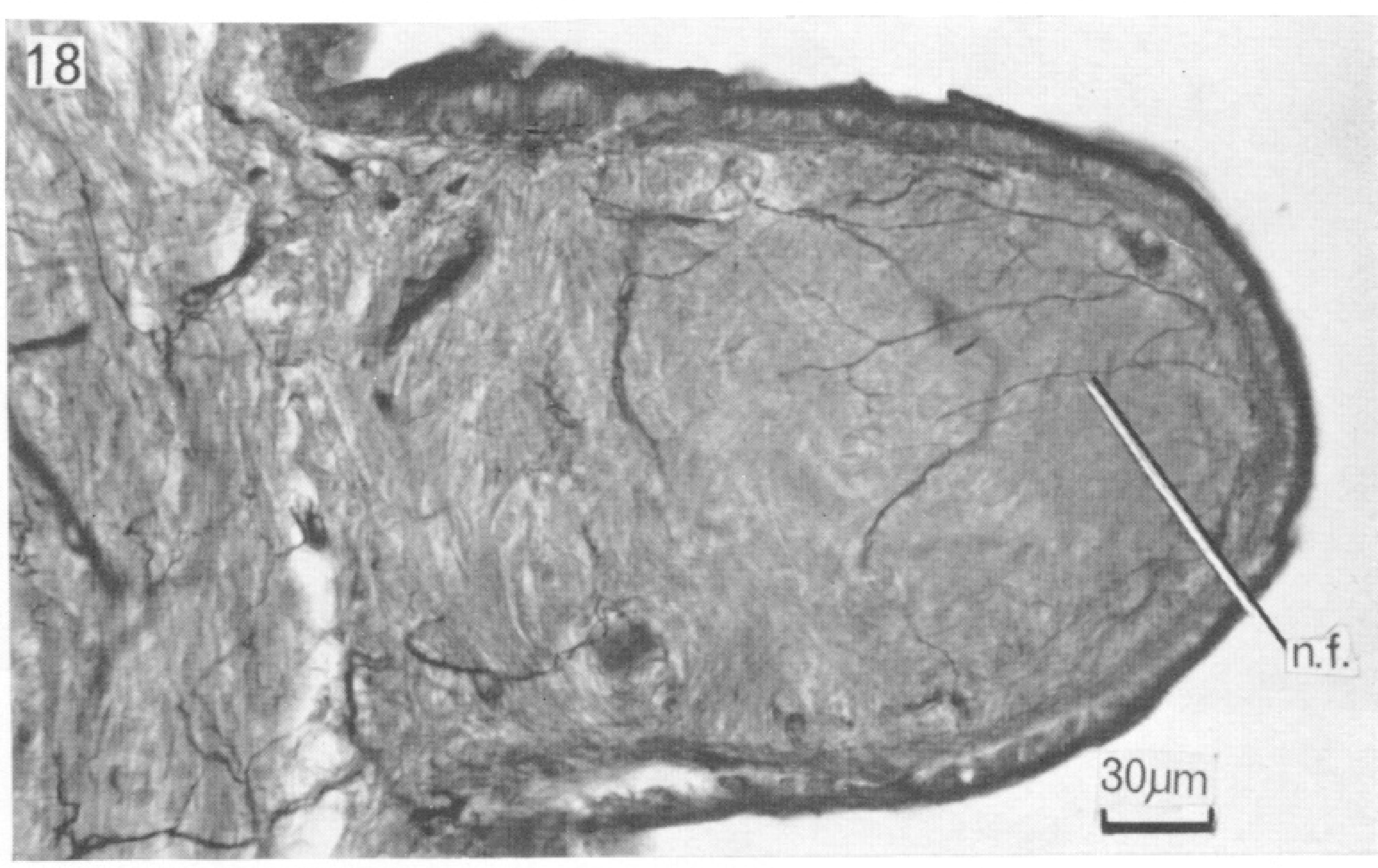
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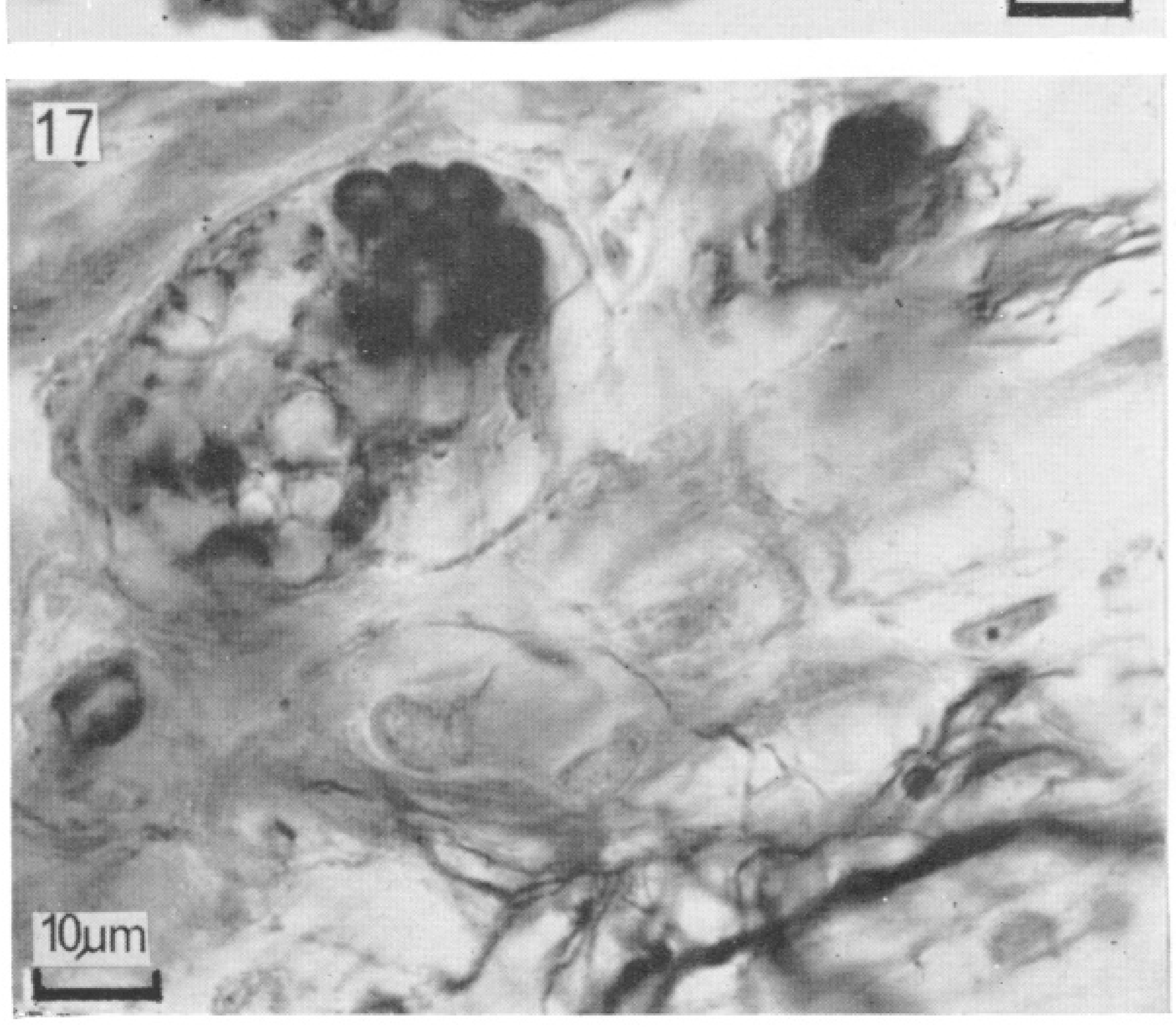
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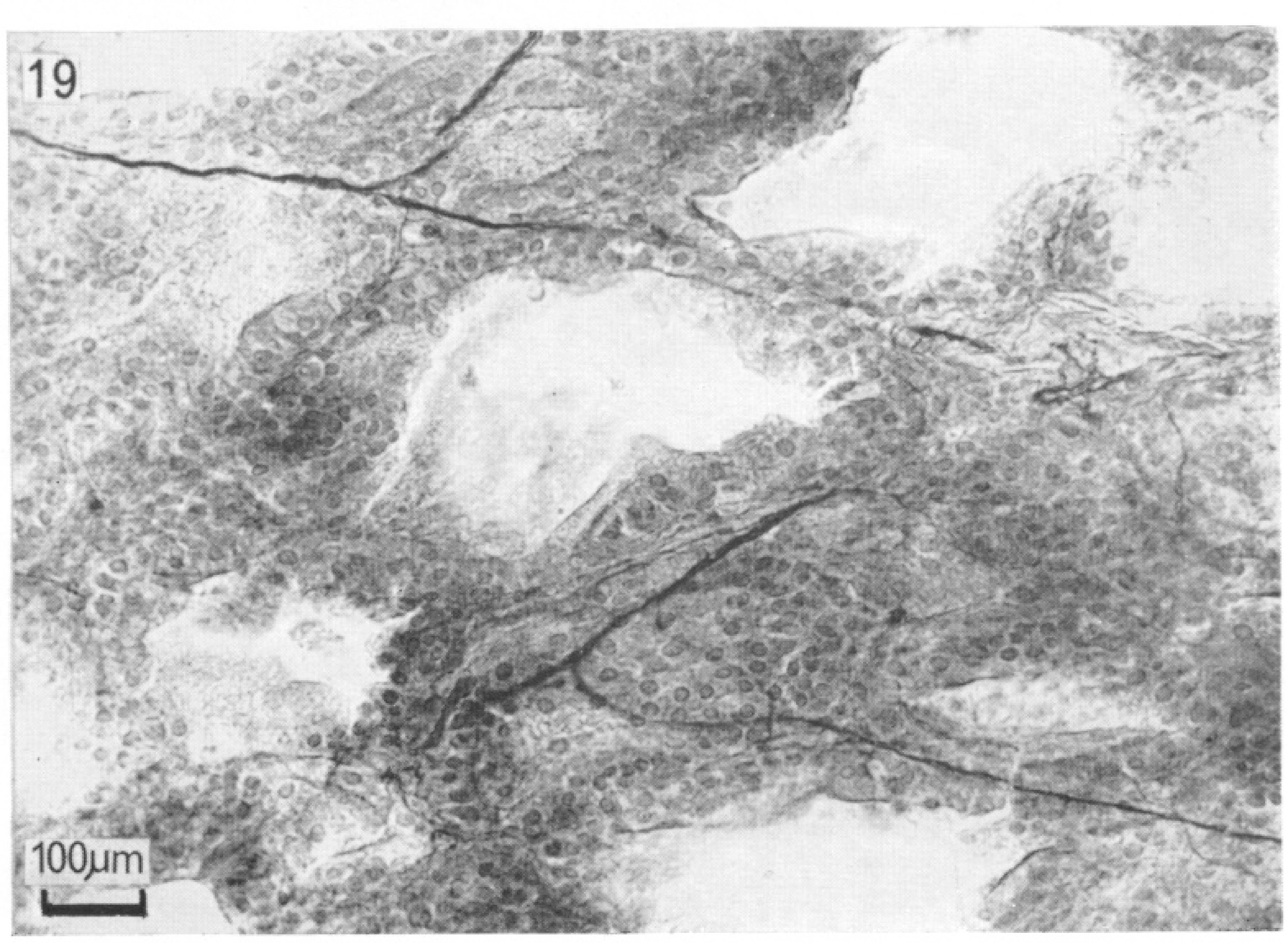
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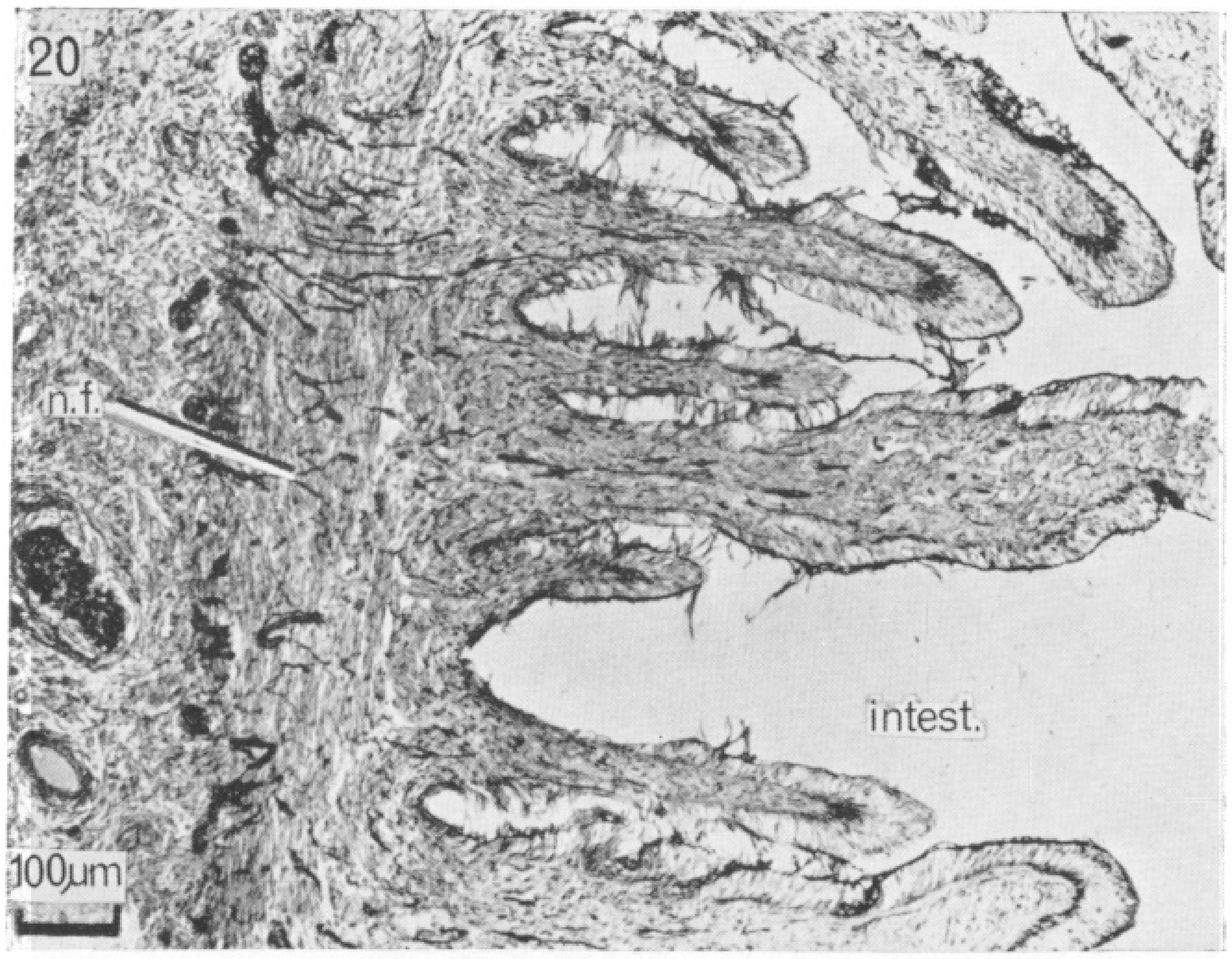
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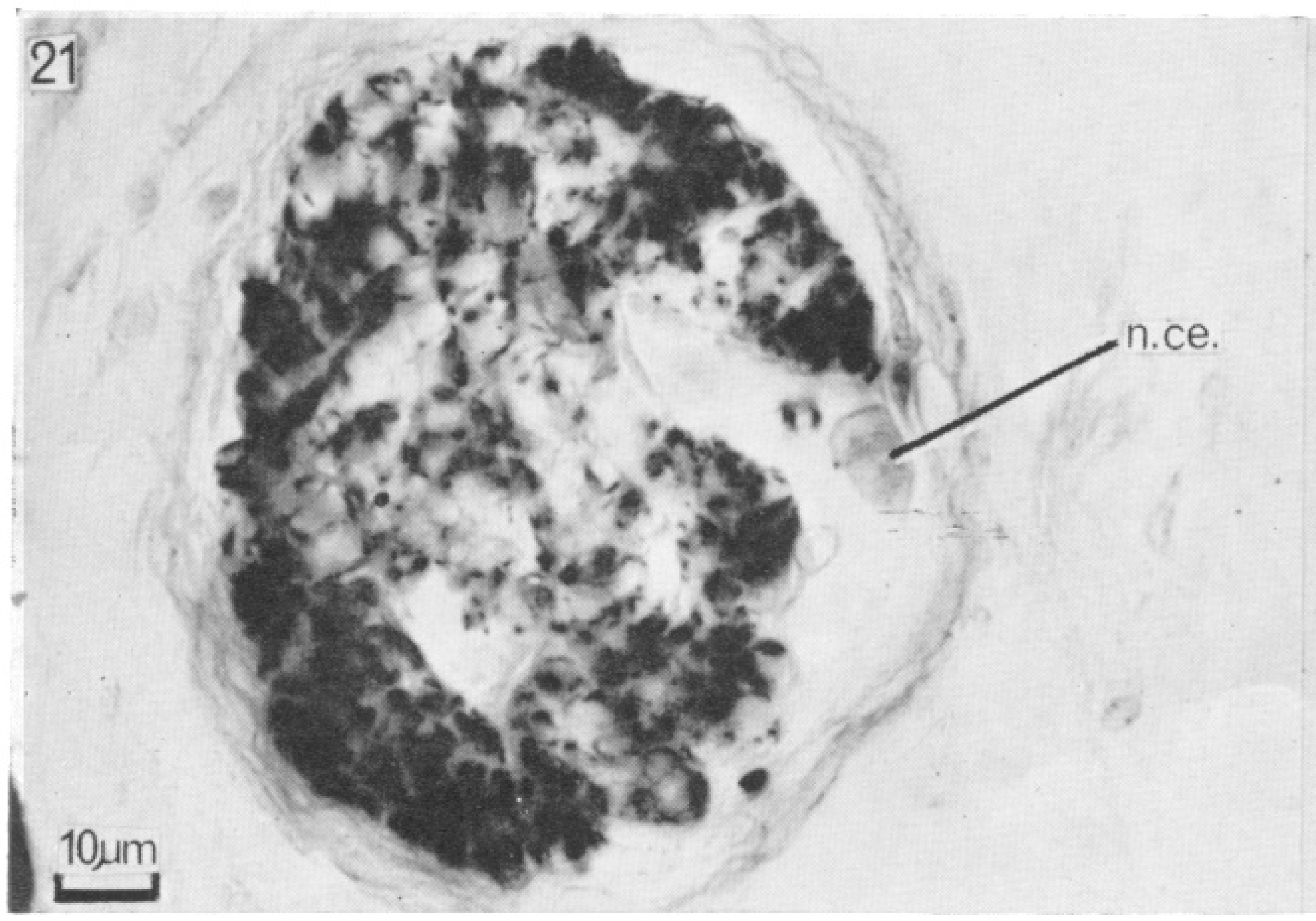
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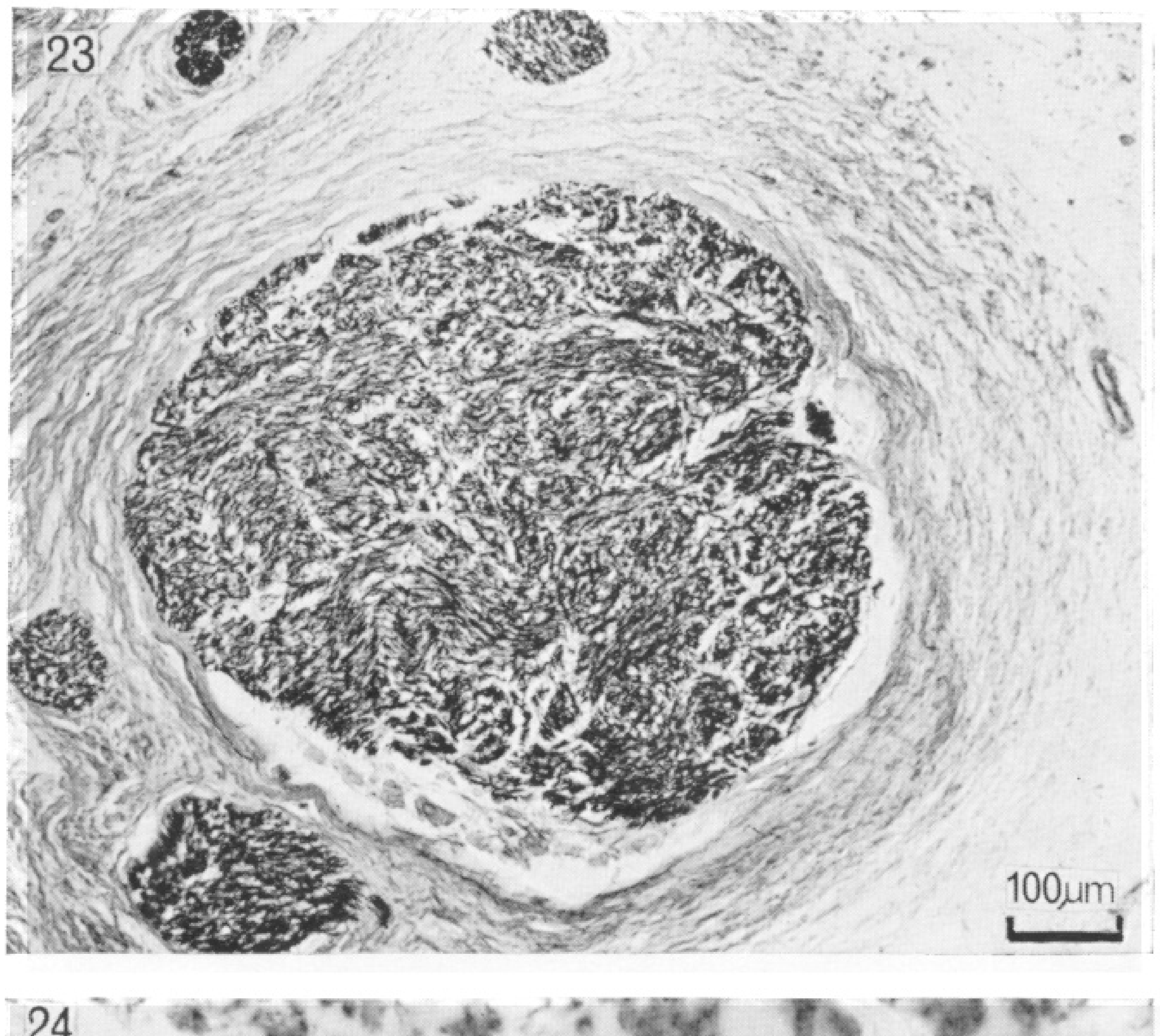
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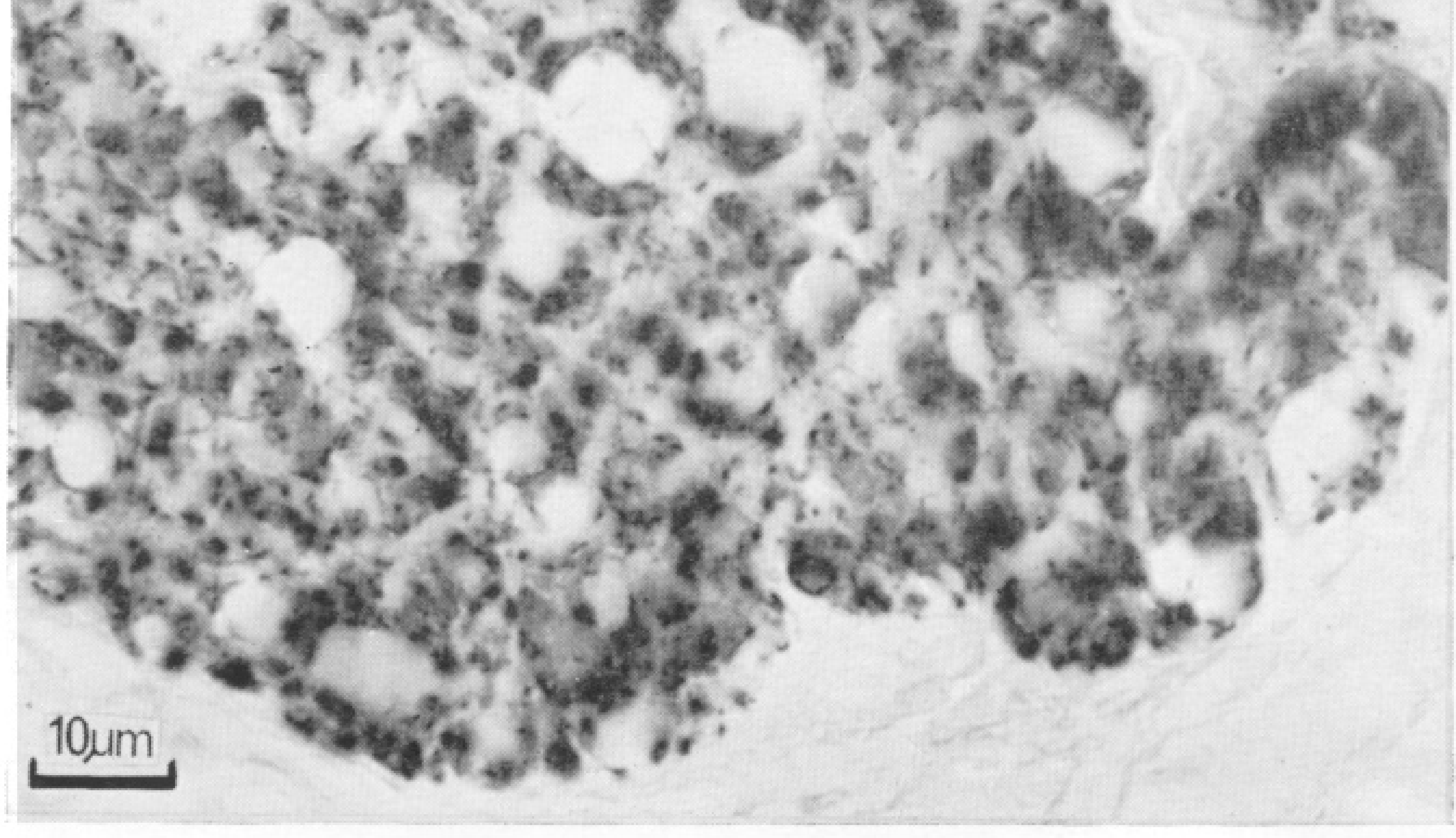
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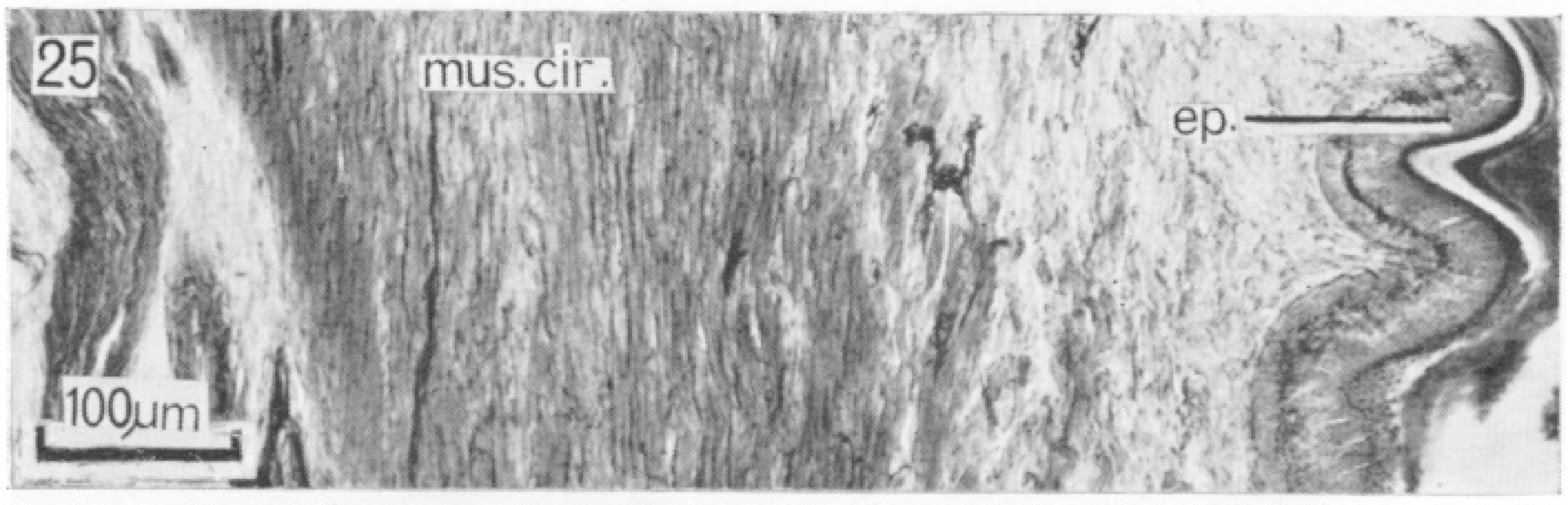
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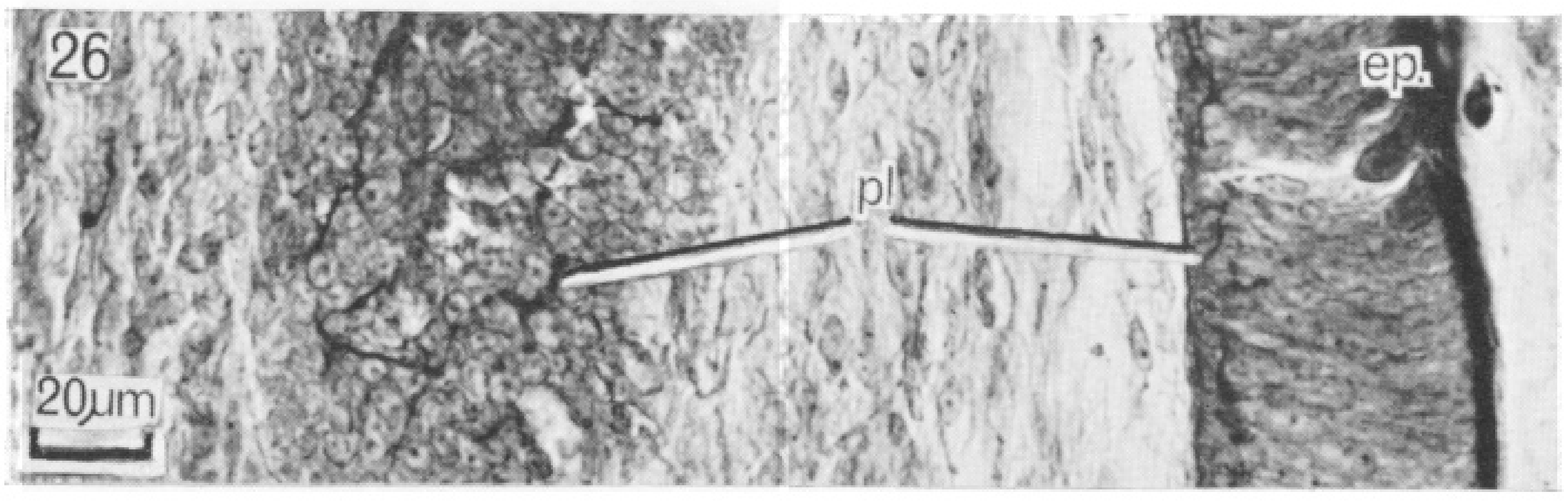
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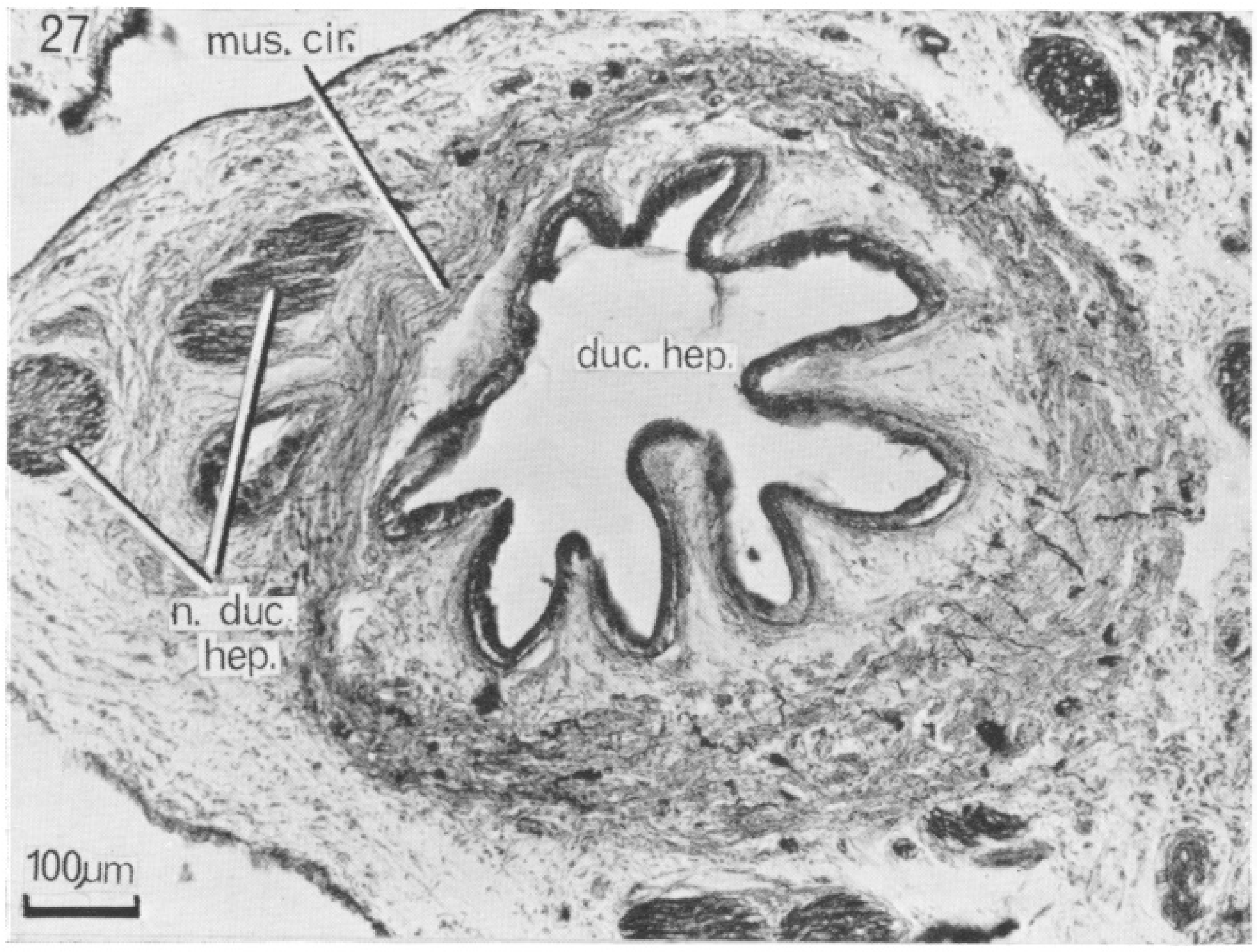
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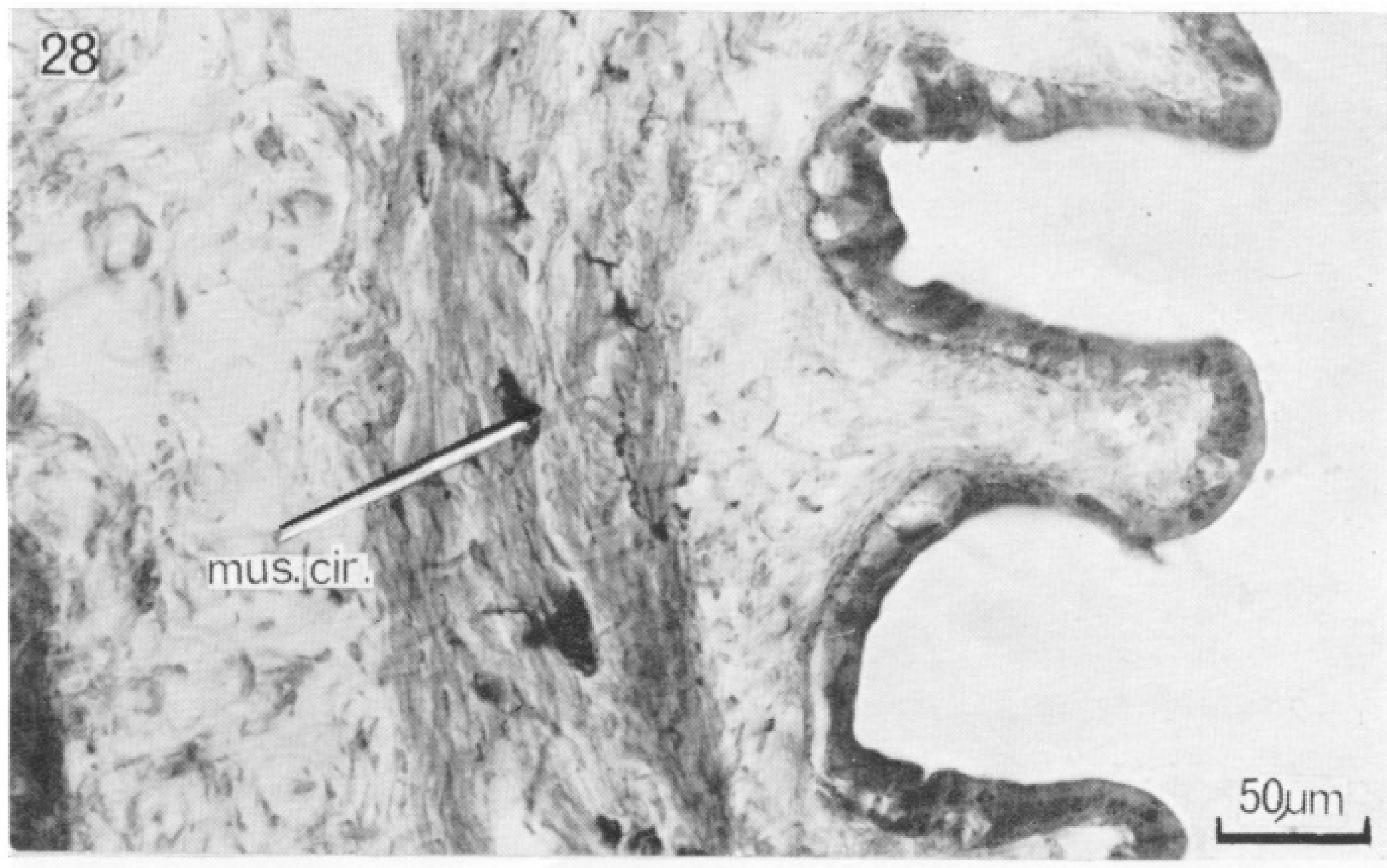
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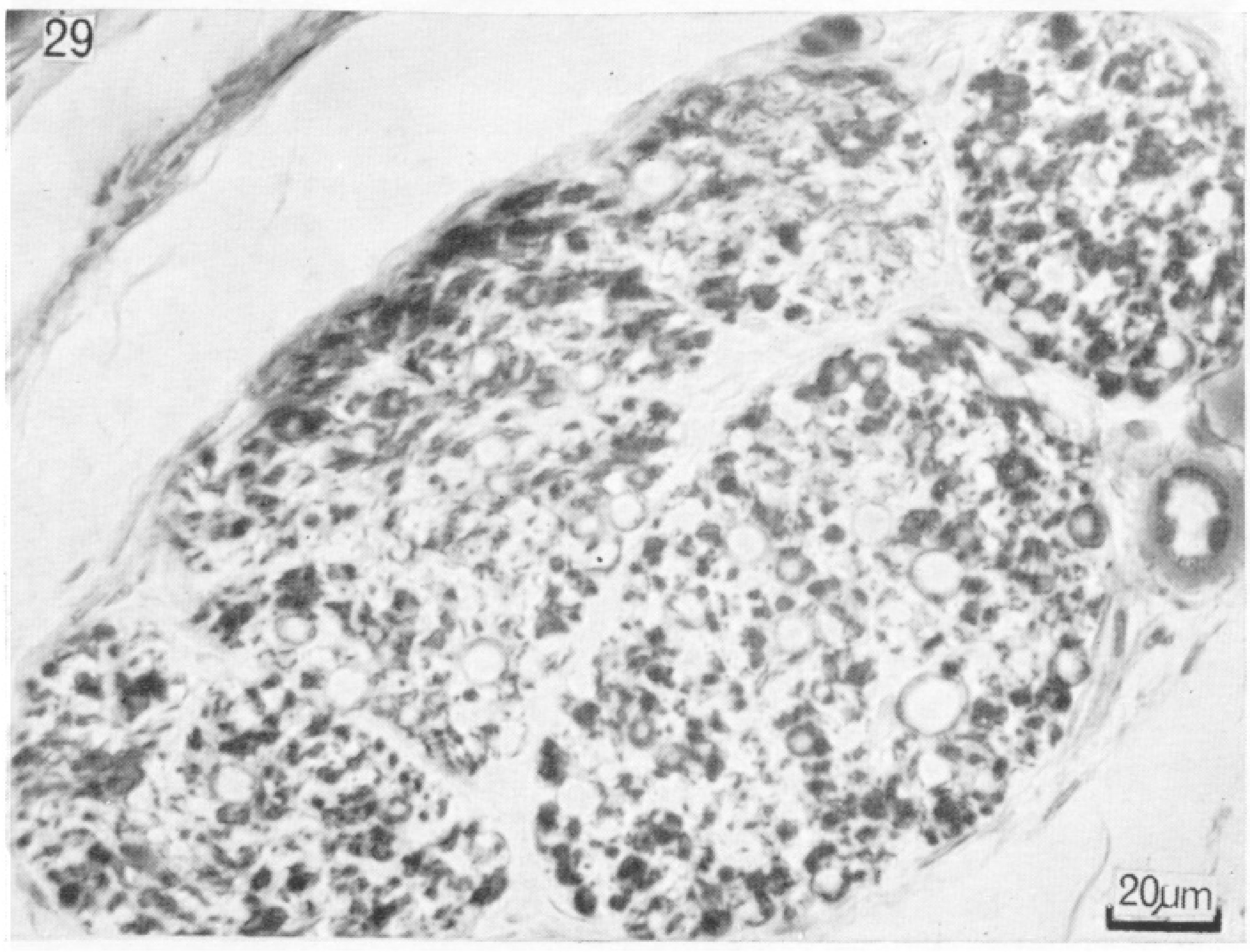
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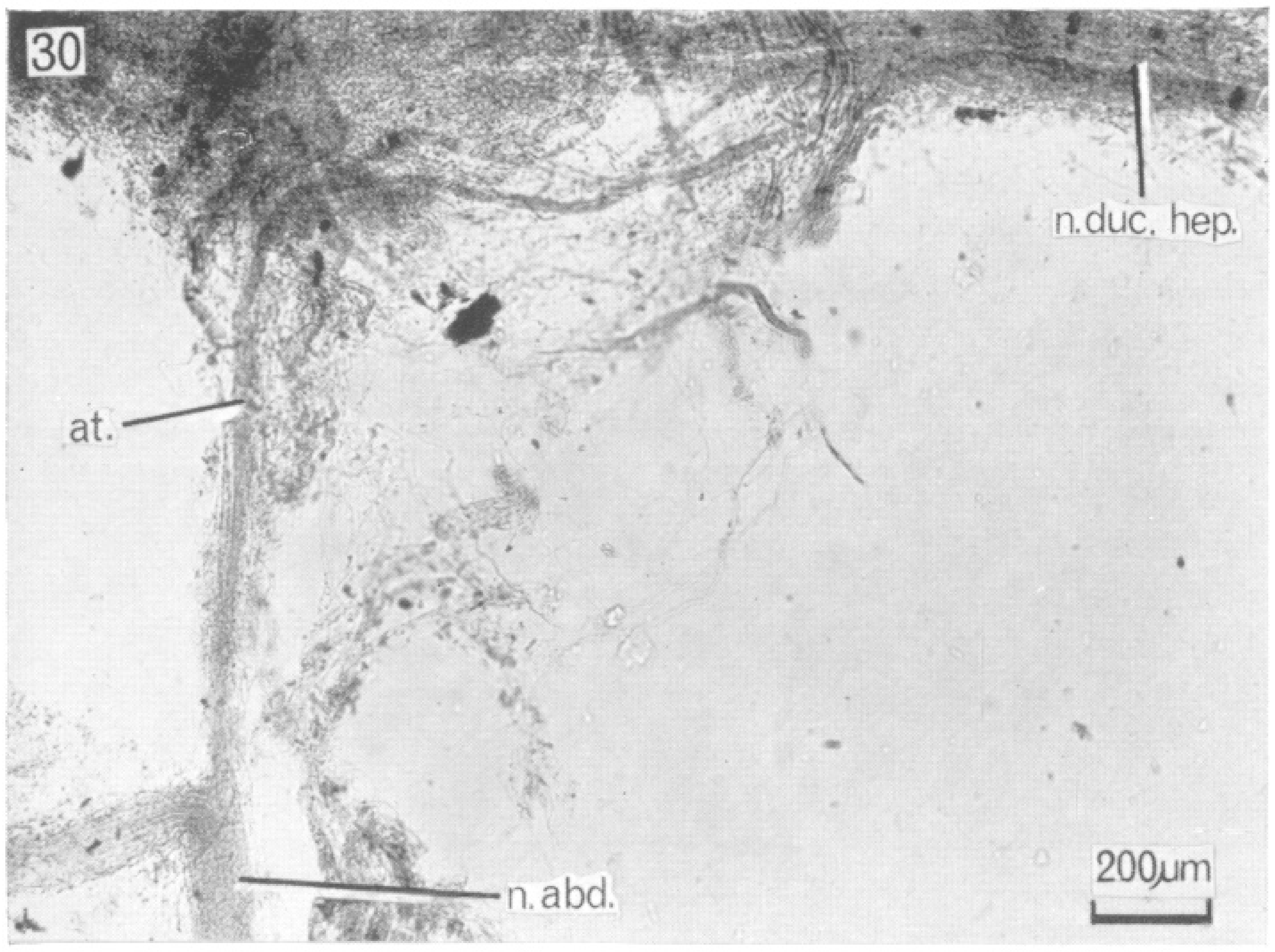
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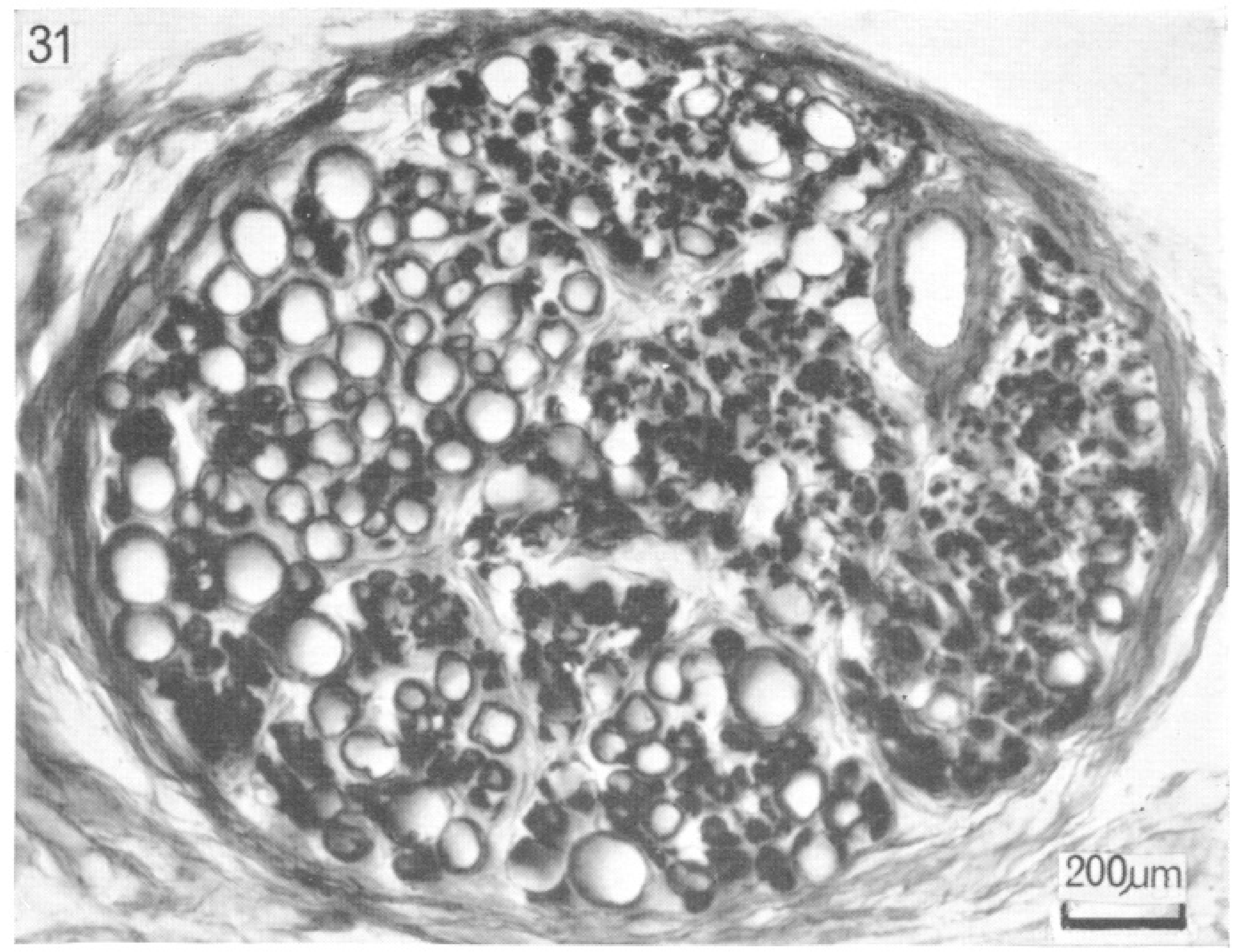
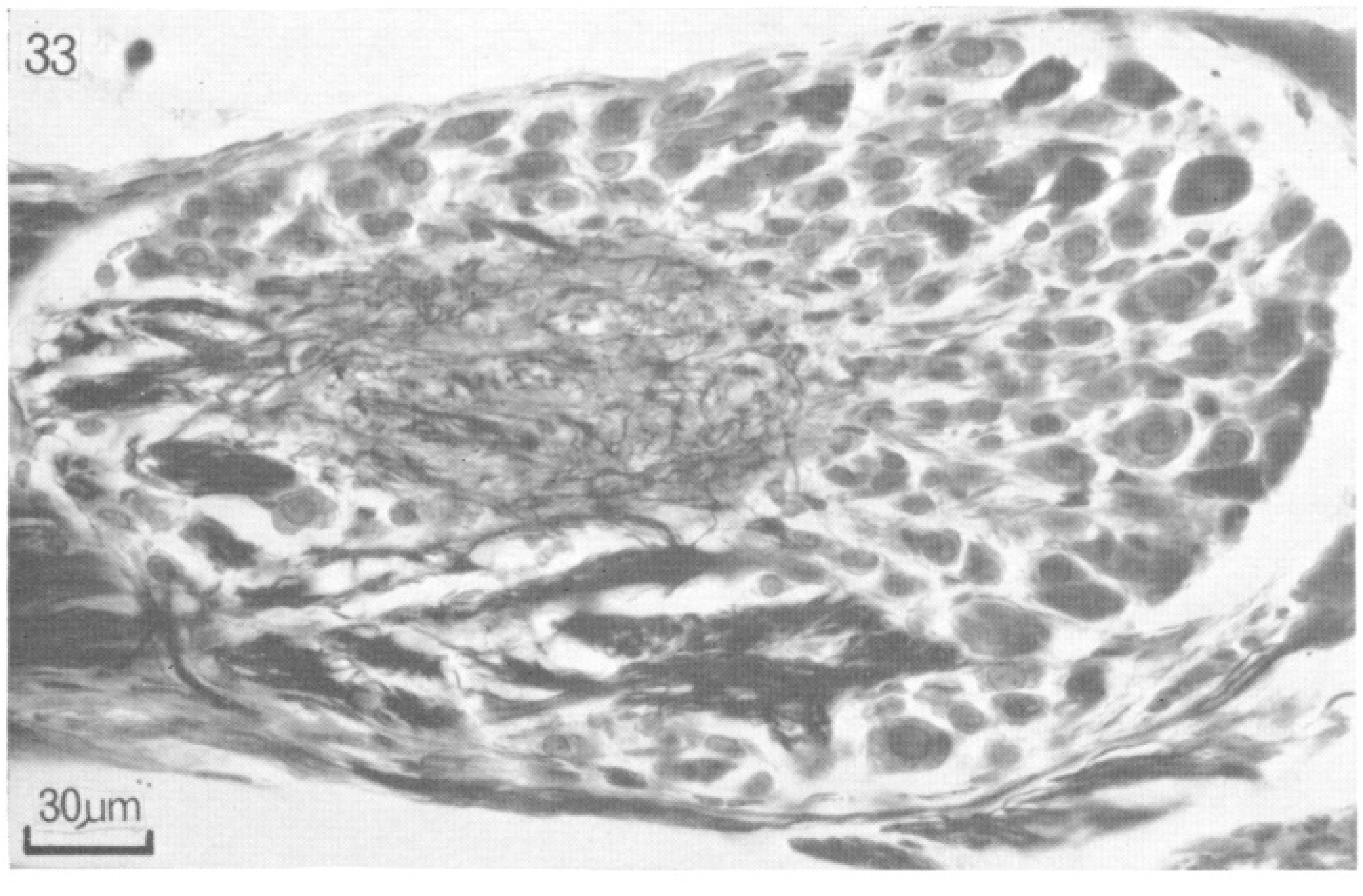
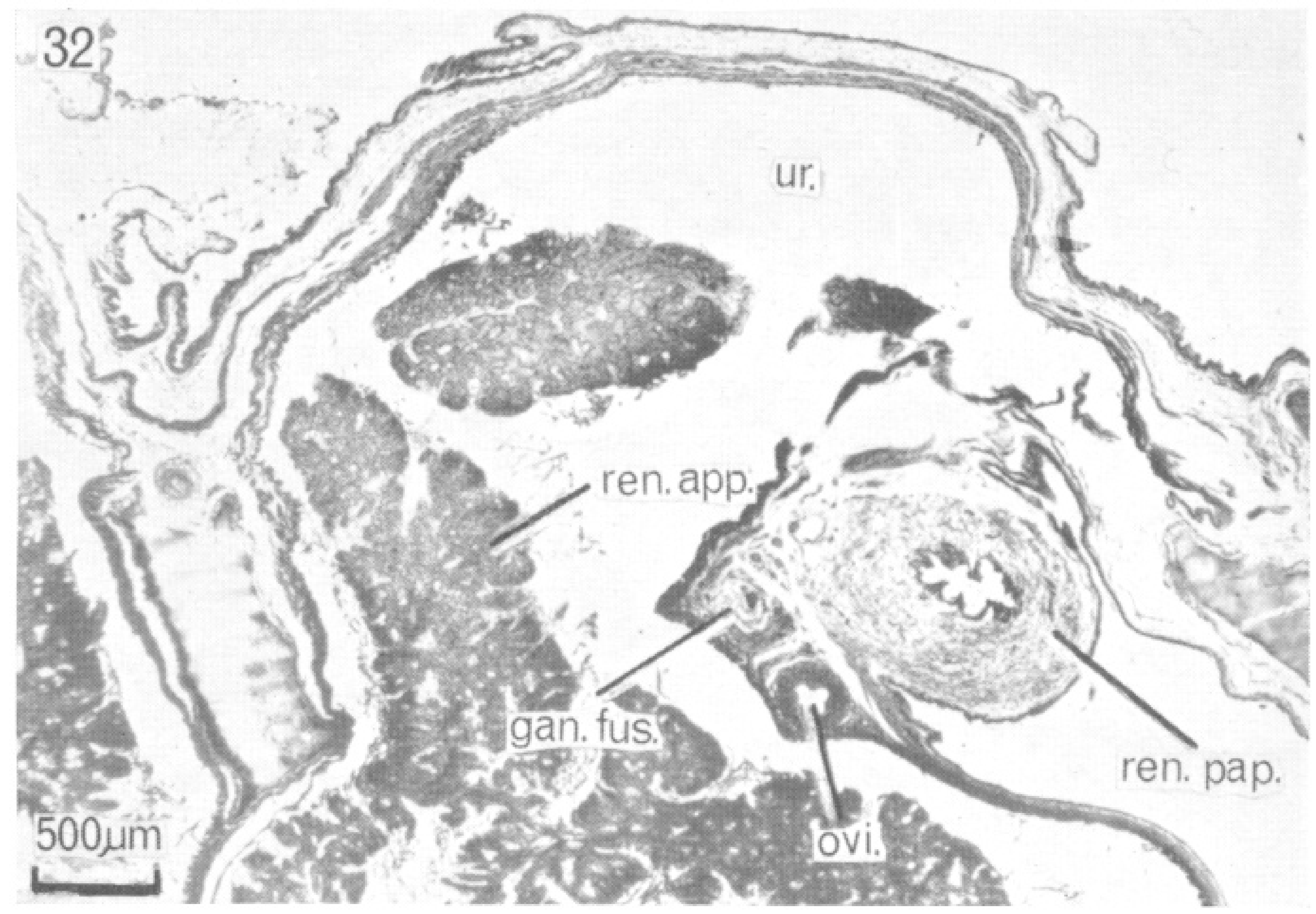
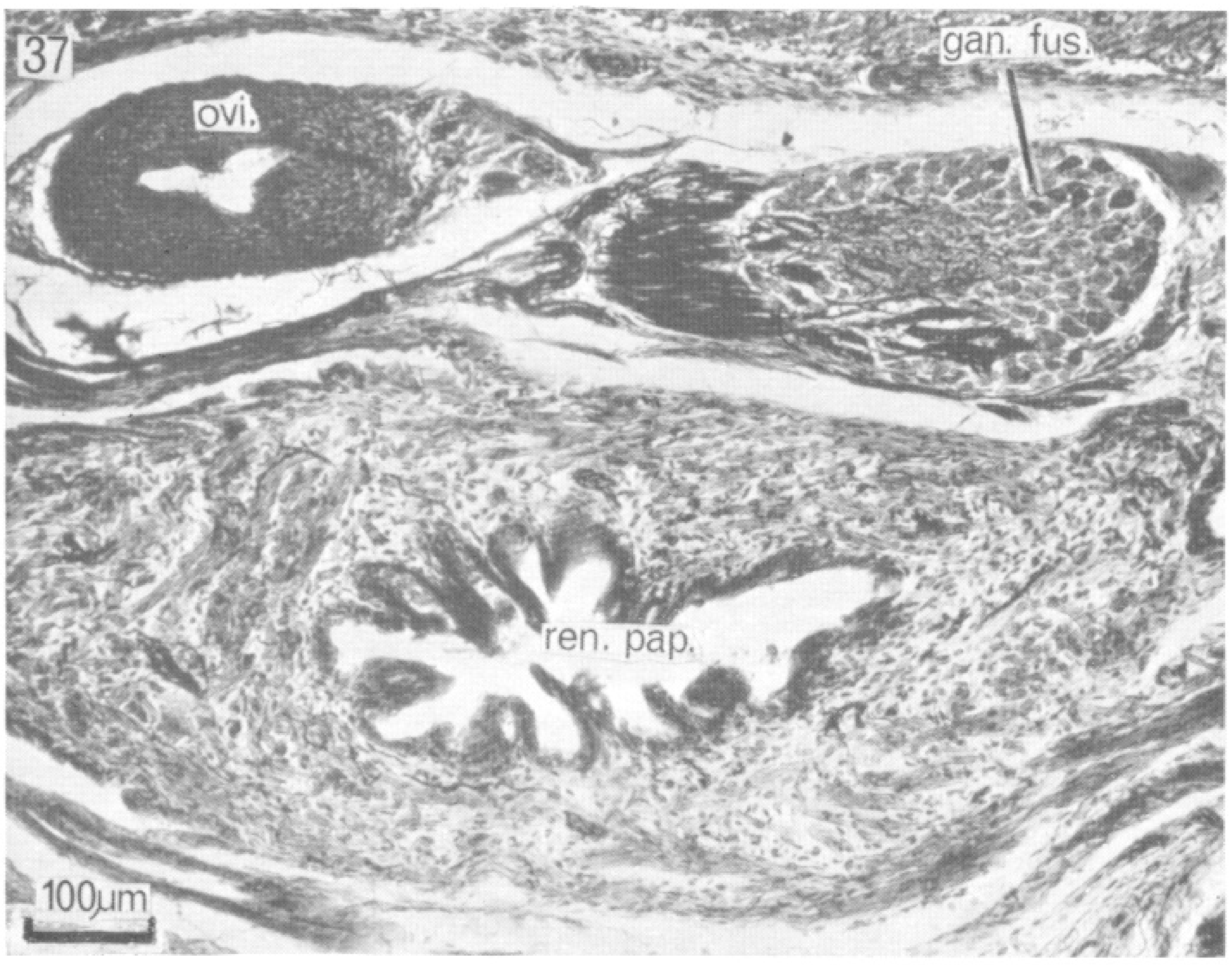
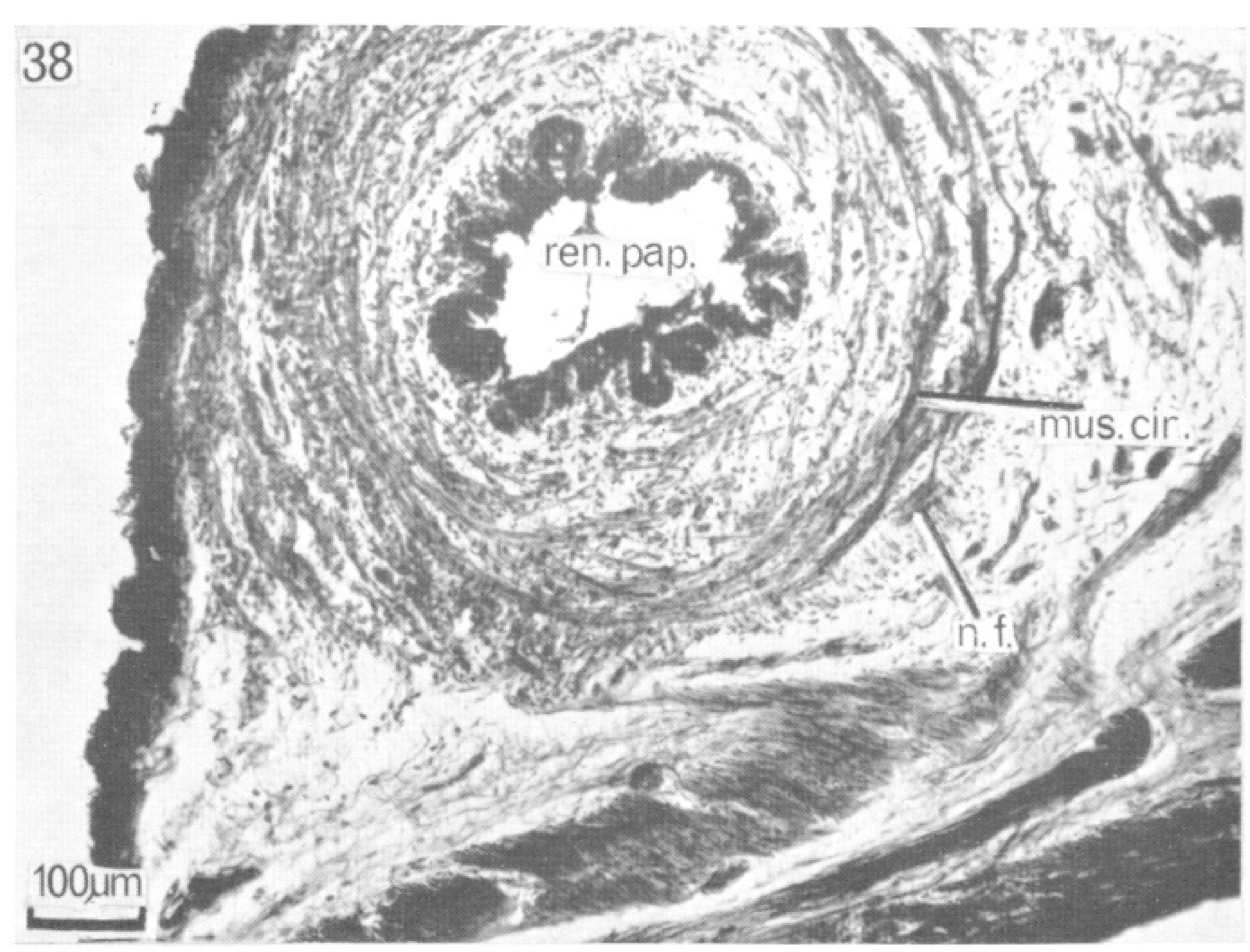
n. abd.
200µm

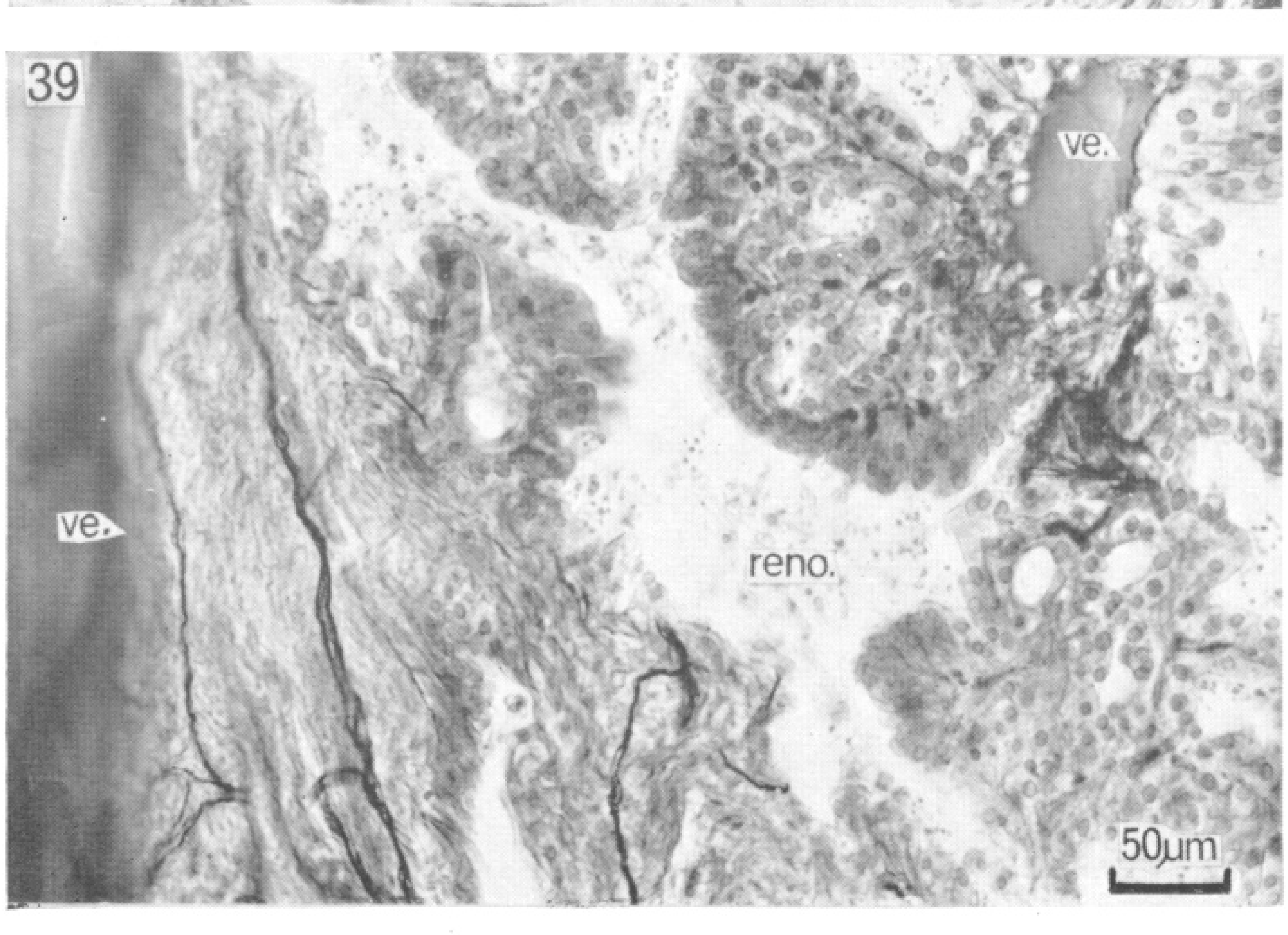

31
200µm

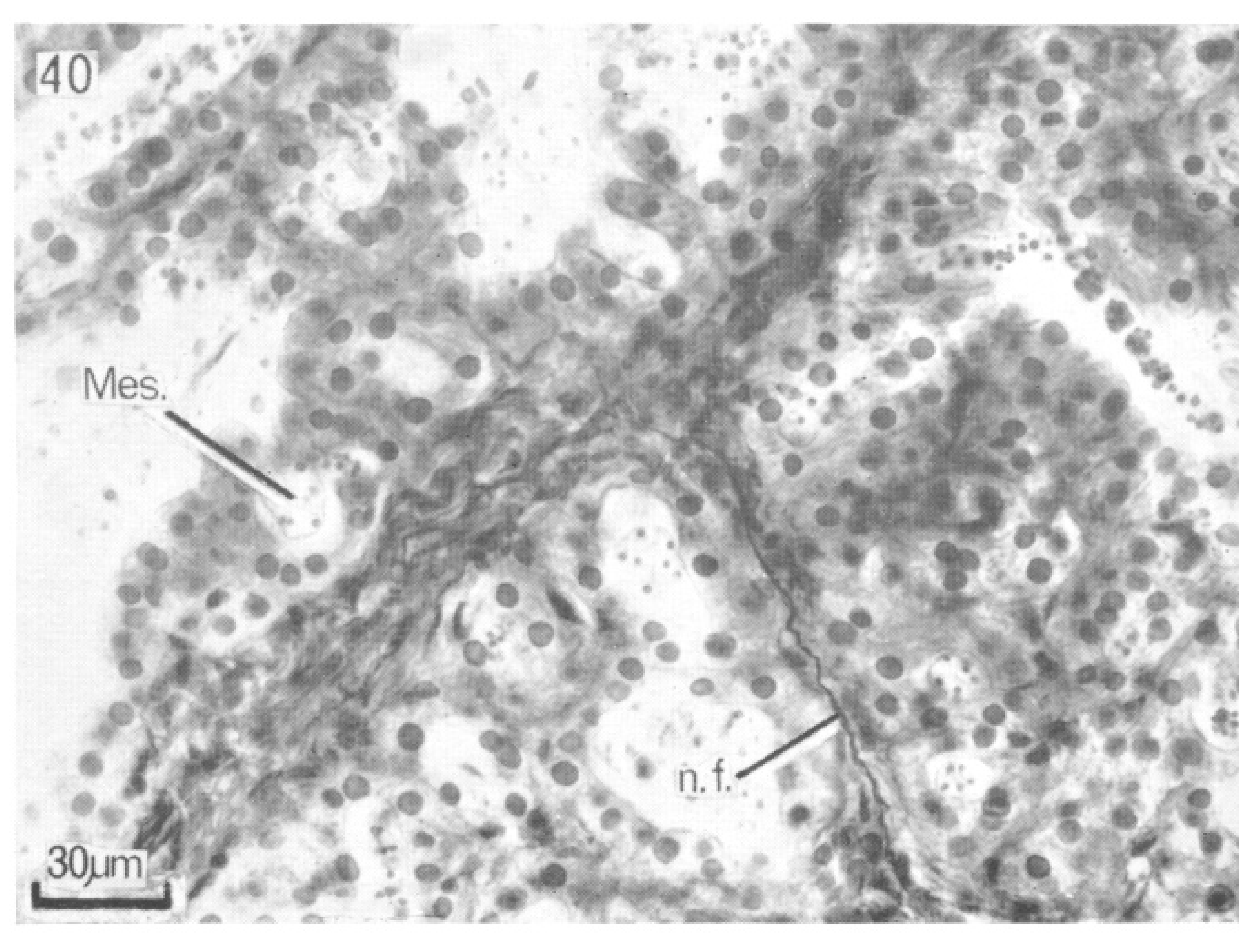

33
30µm

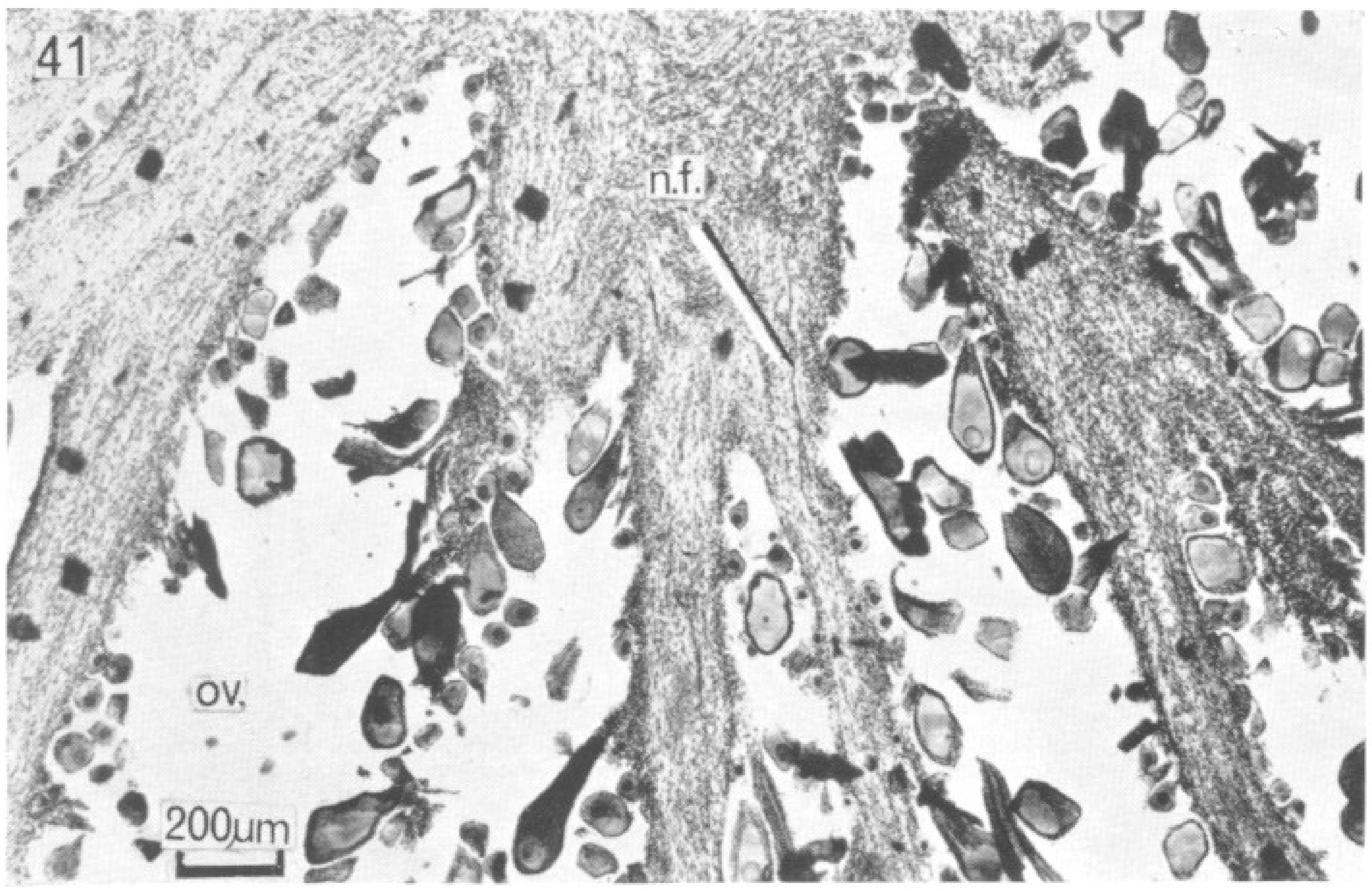

32
ur.
ren. app.
gan. fus.
ren. pap.
ovi.
500µm

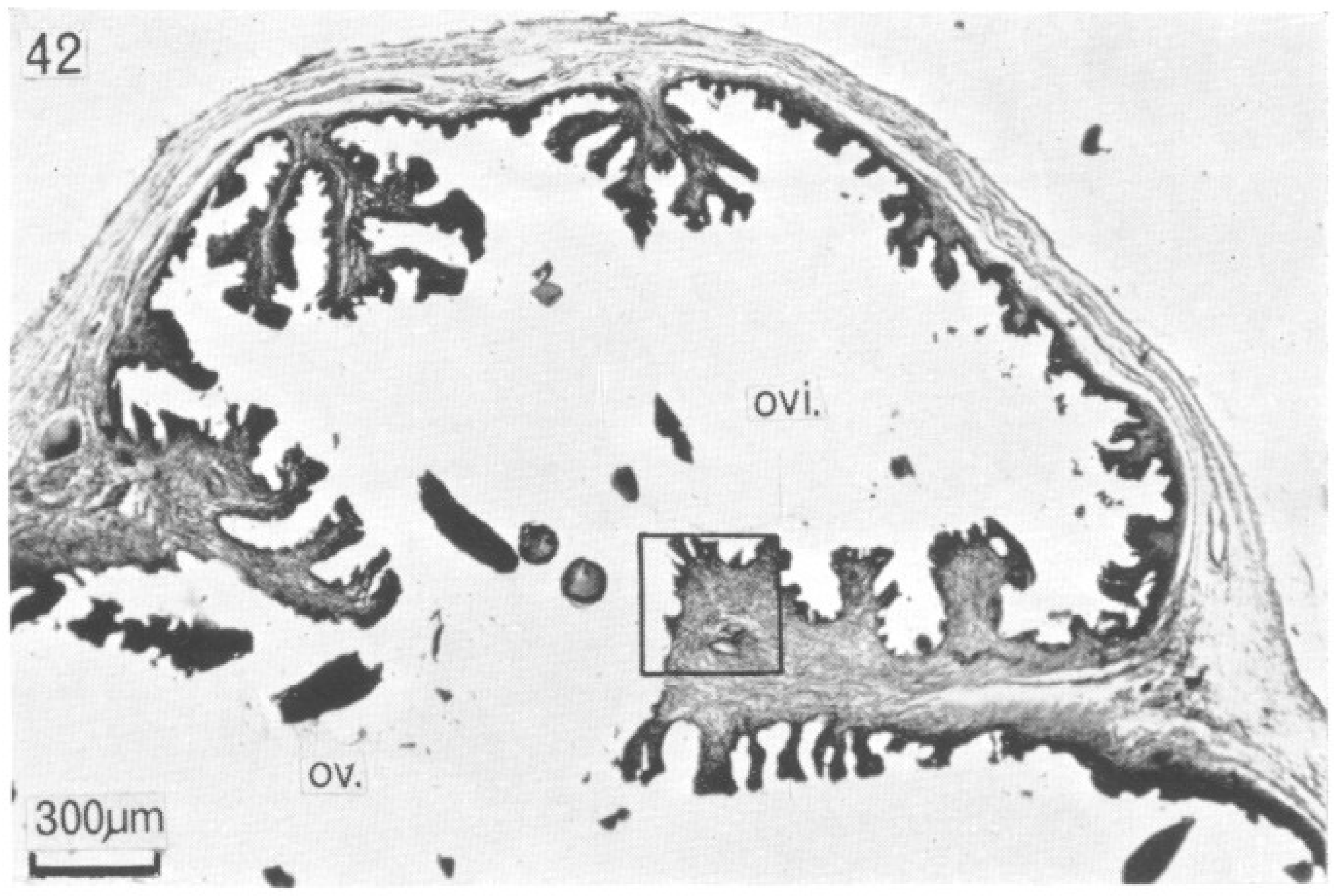

37
ovi.
gan. fus.
ren. pap.
100µm

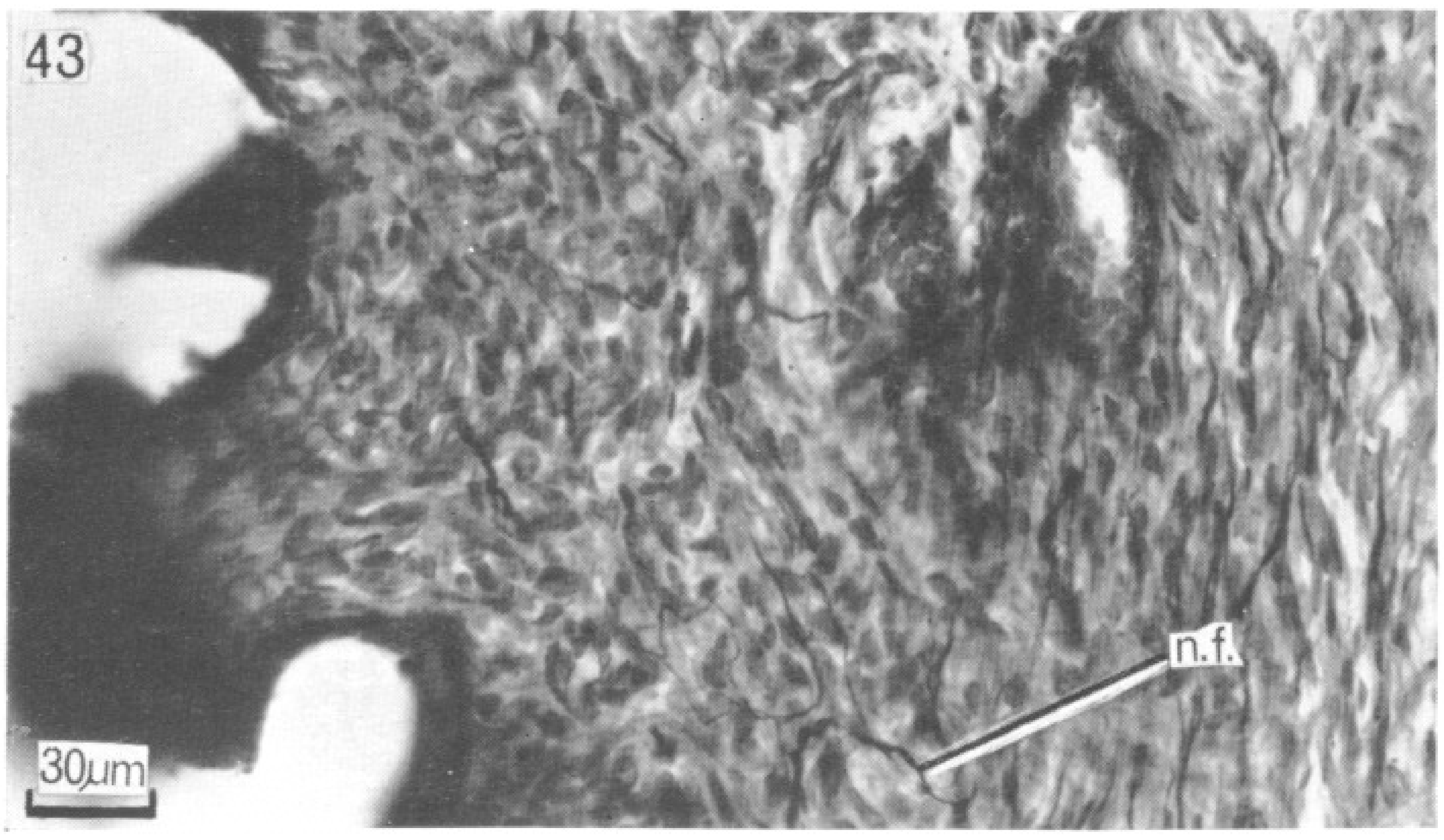

38
ren. pap.
mus. cir.
n. f.
100µm

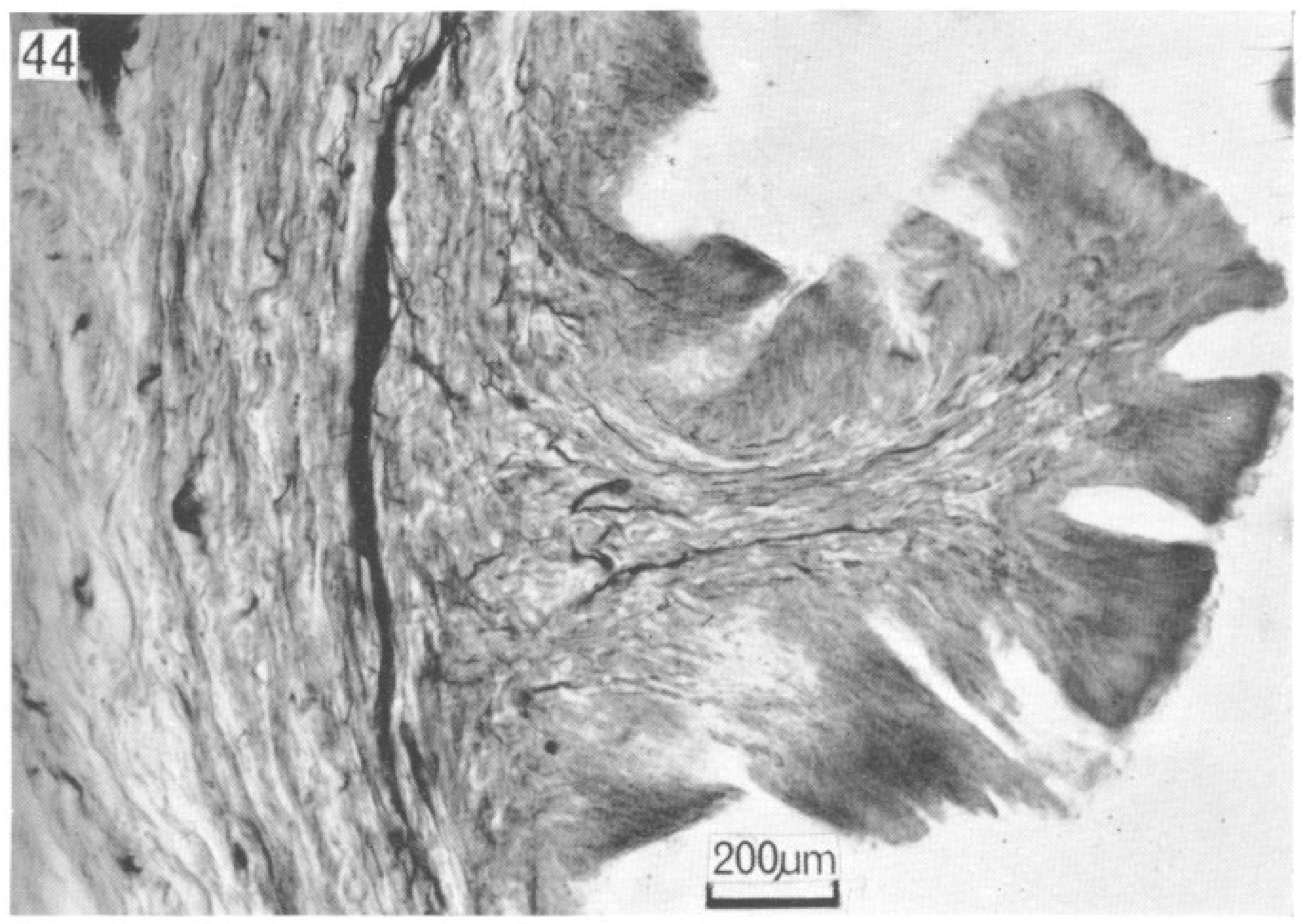

39
ve.
ve.
reno.
50µm

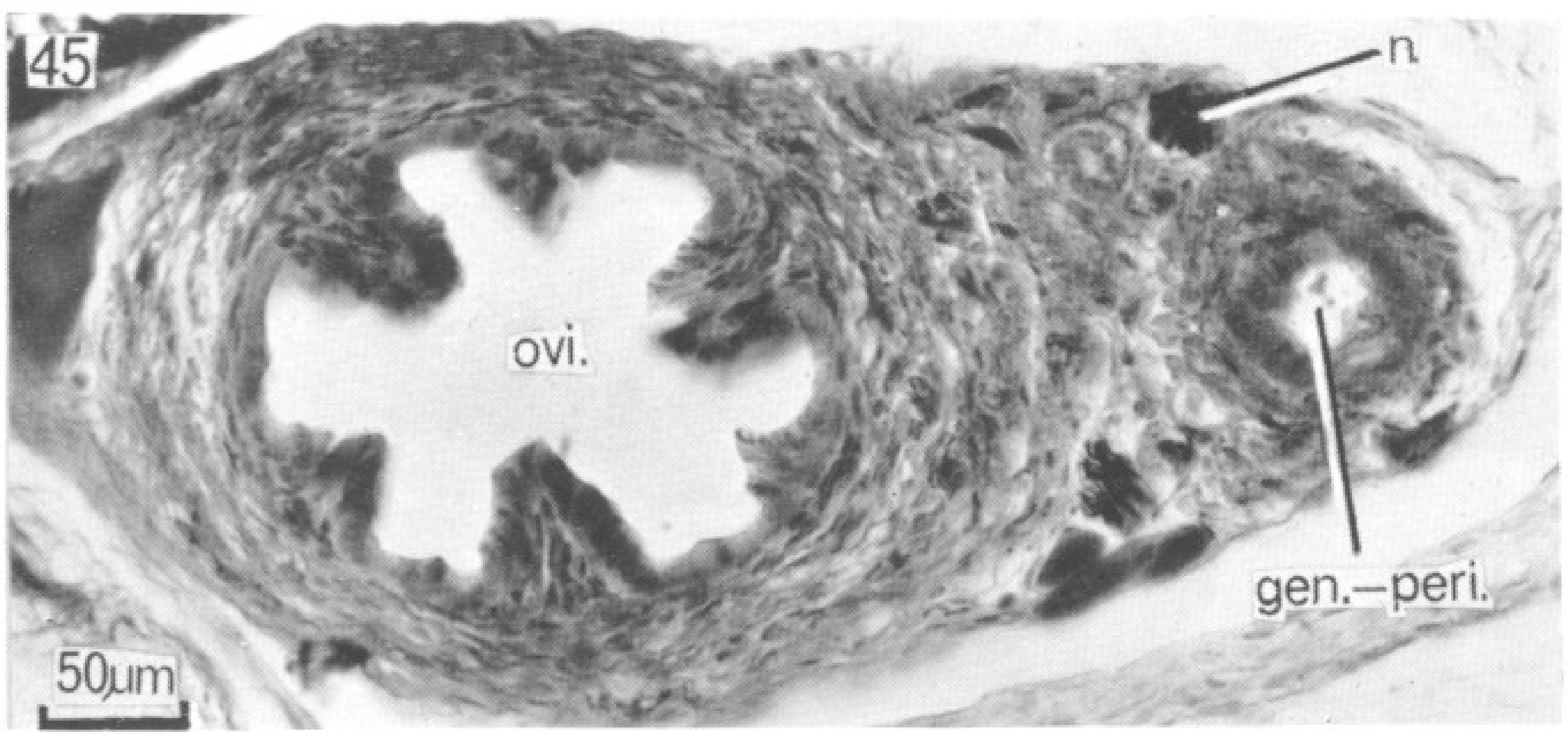

40
Mes.
n. f.
30µm

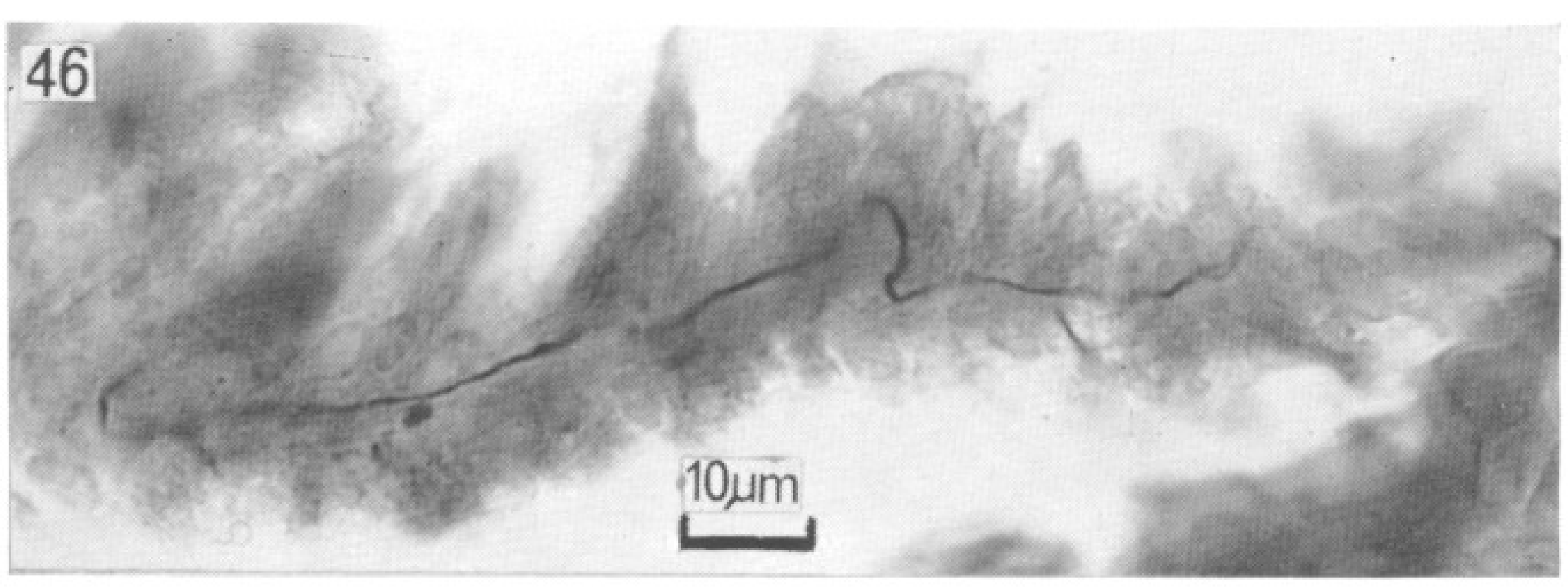

41
n.f.
ov.
200μm

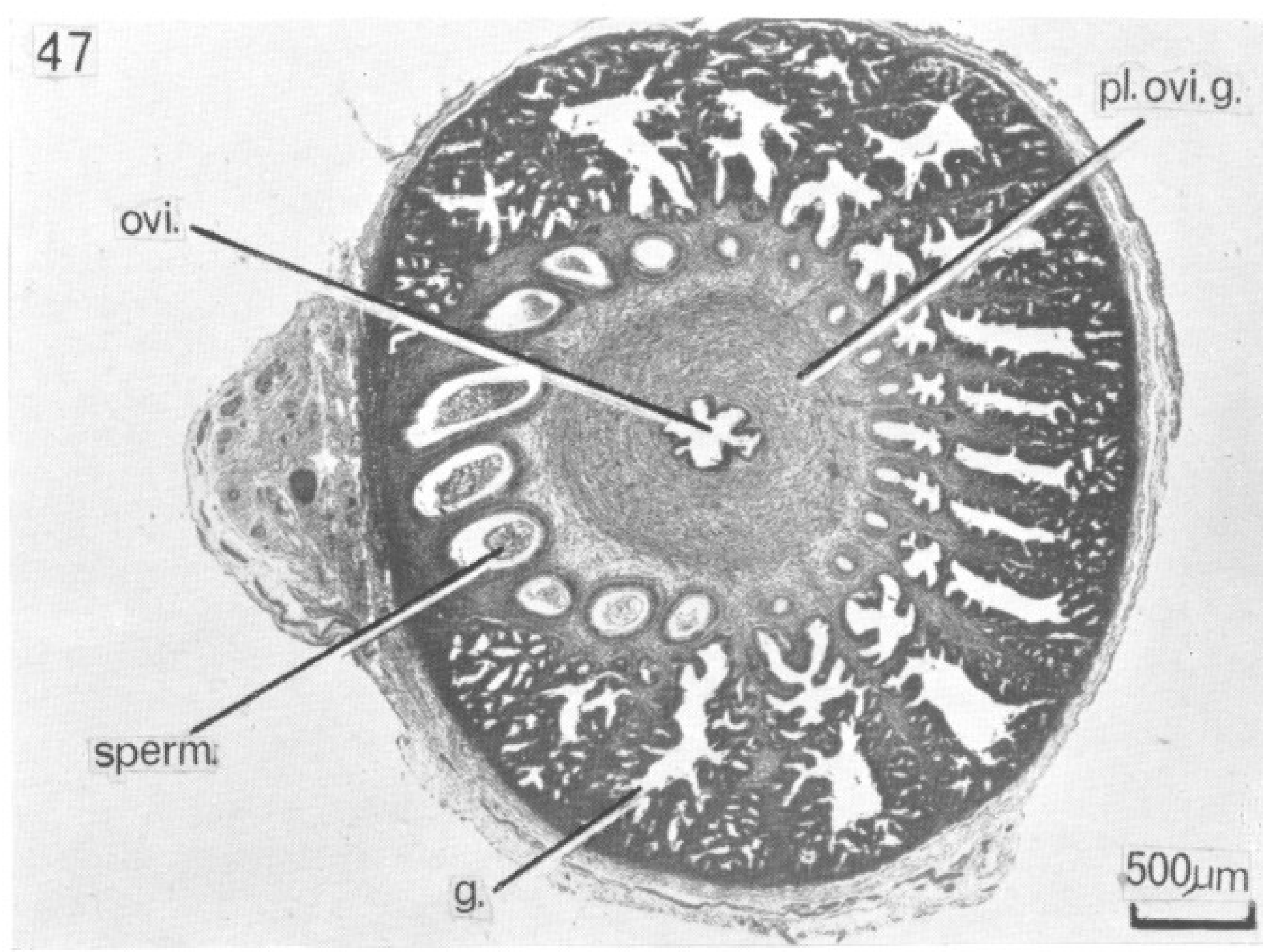

42
ovi.
ov.
300μm

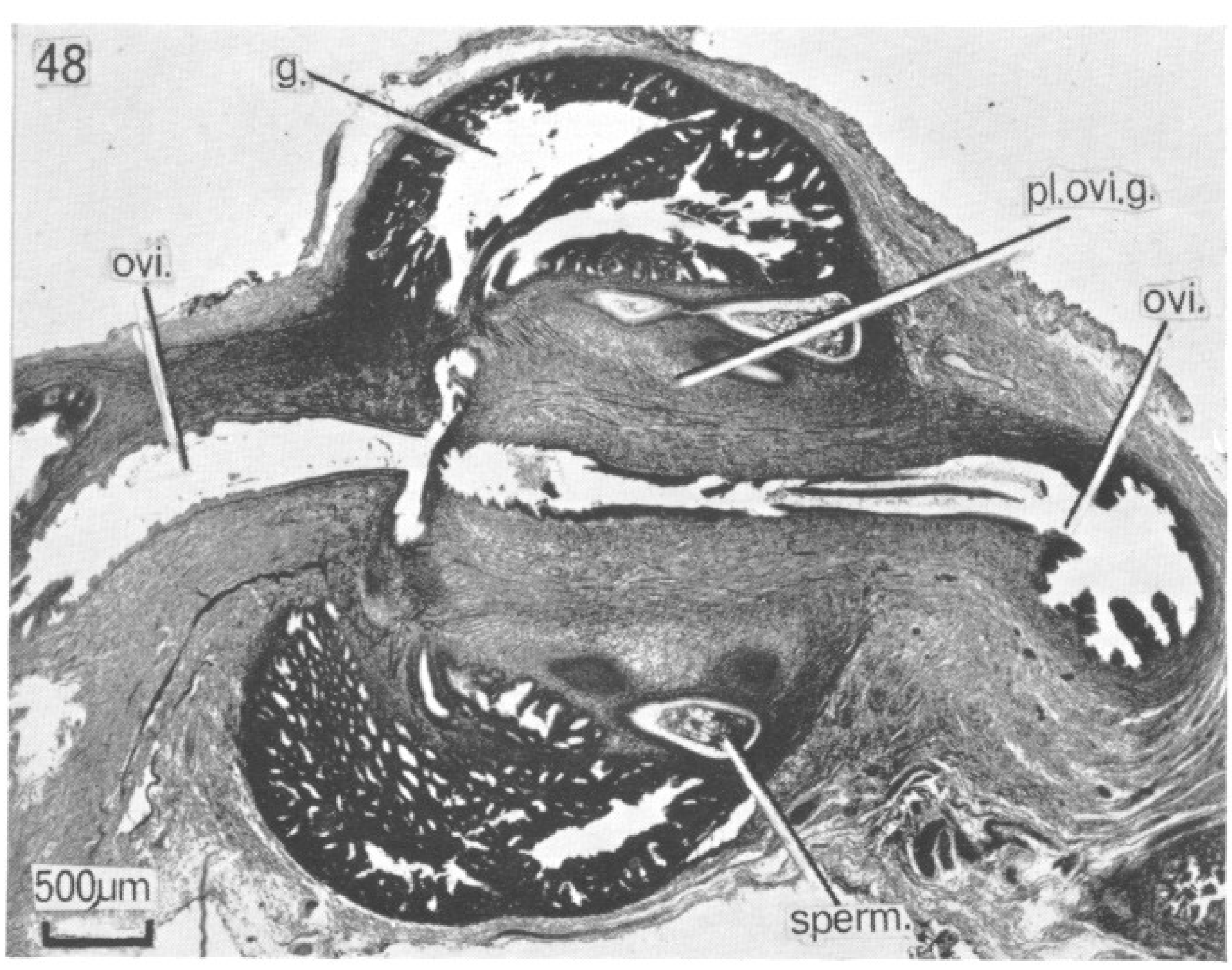

43
n.f.
30μm

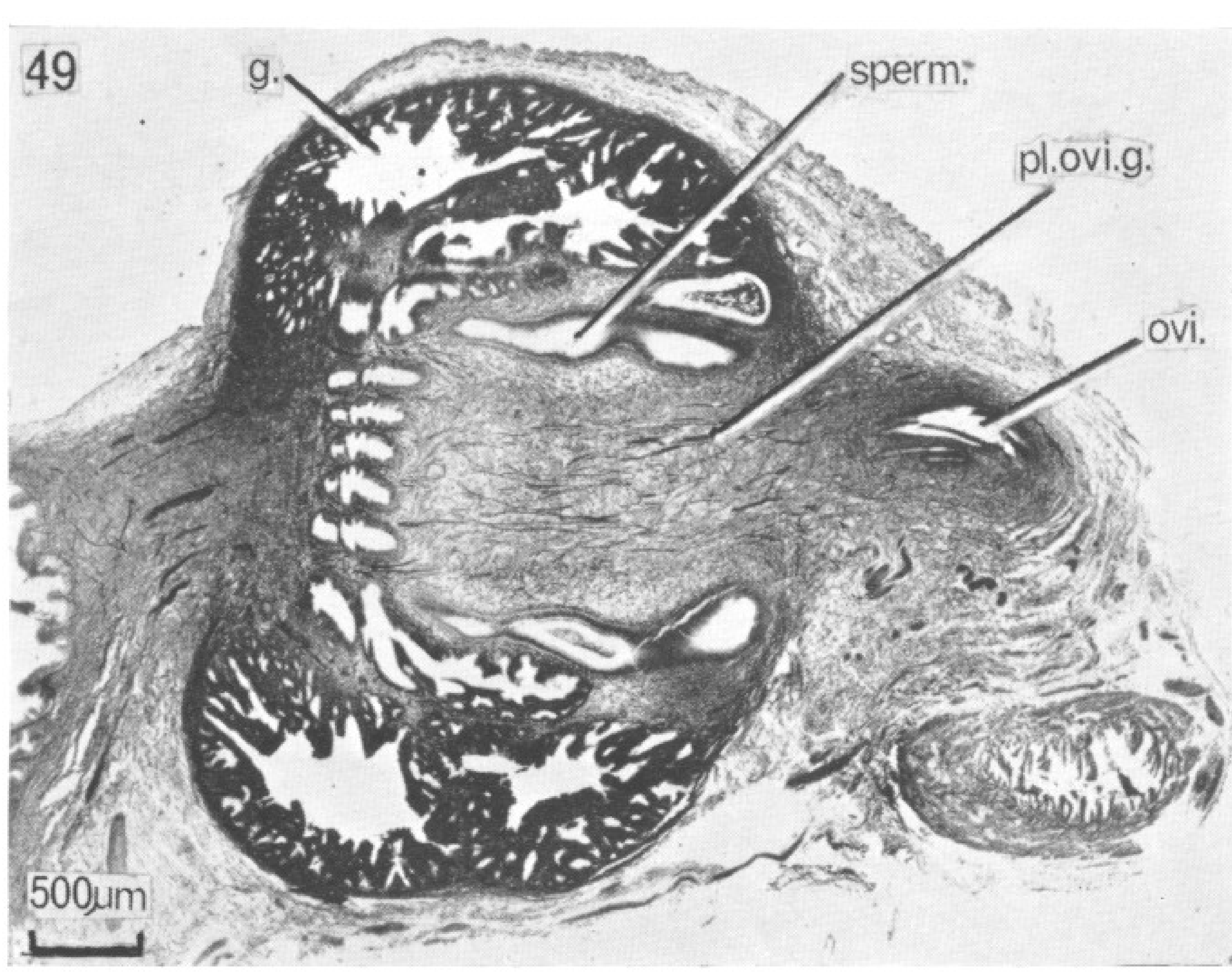

44
200μm

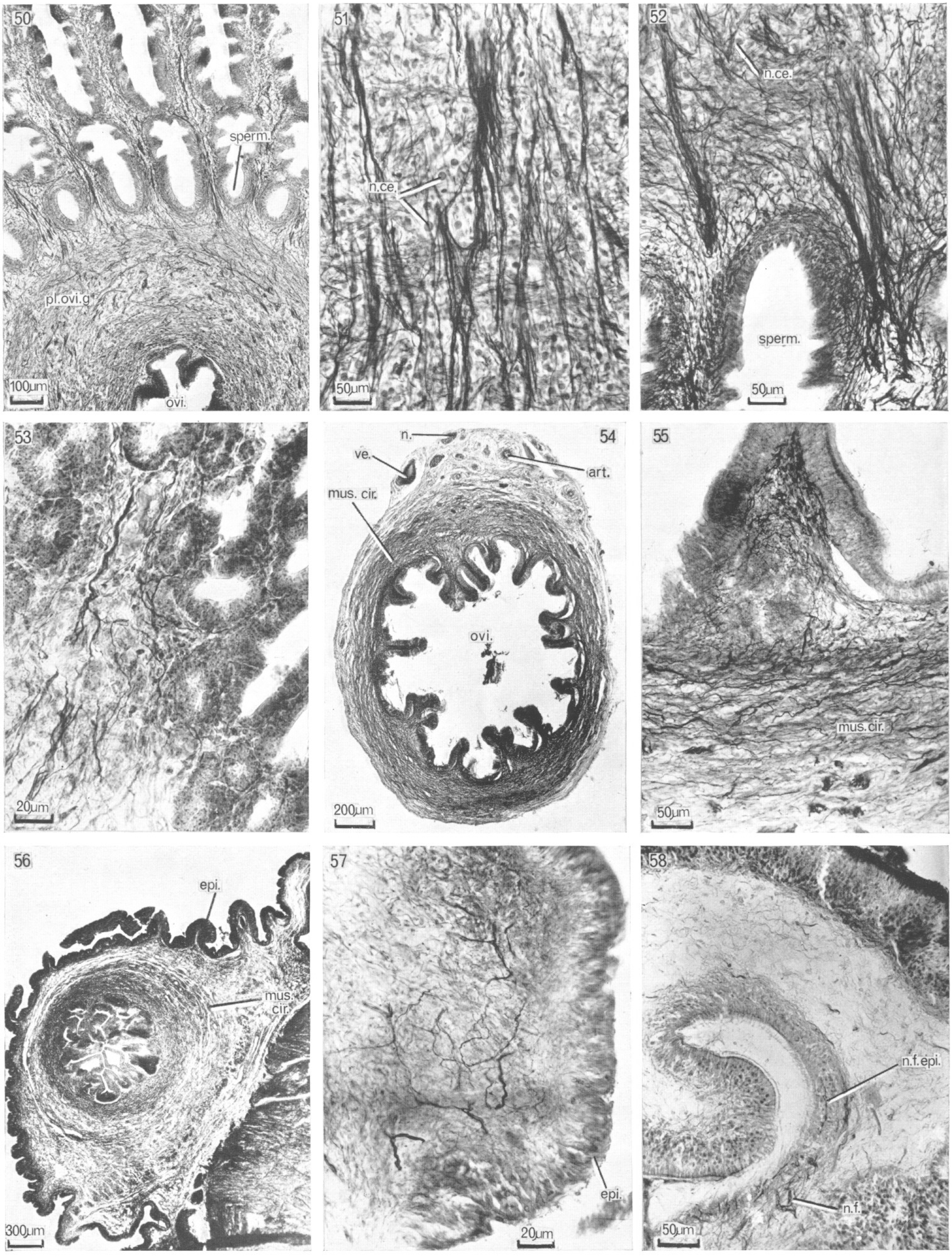

45
n.
ovi.
gen.–peri.
50μm

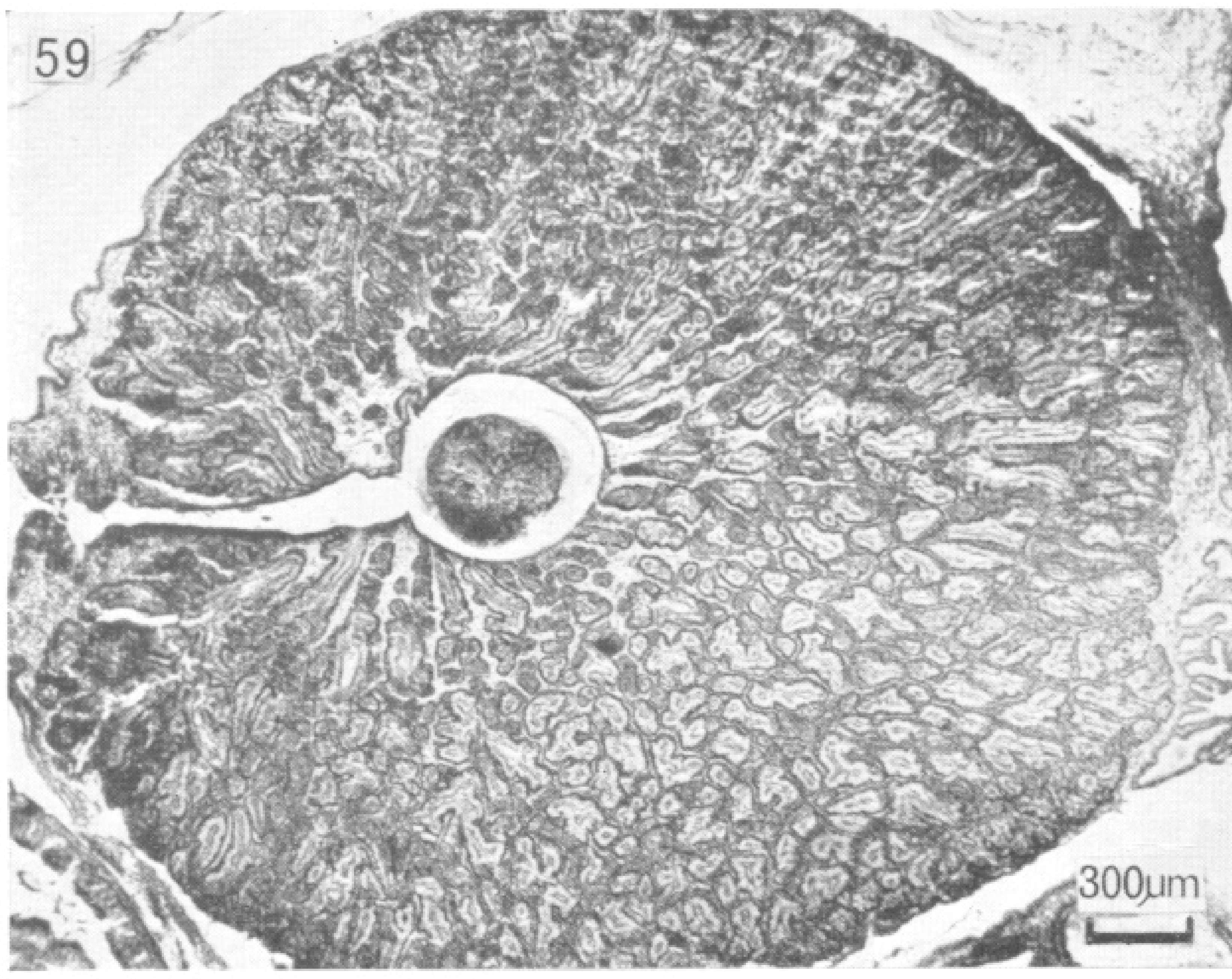

46
10μm

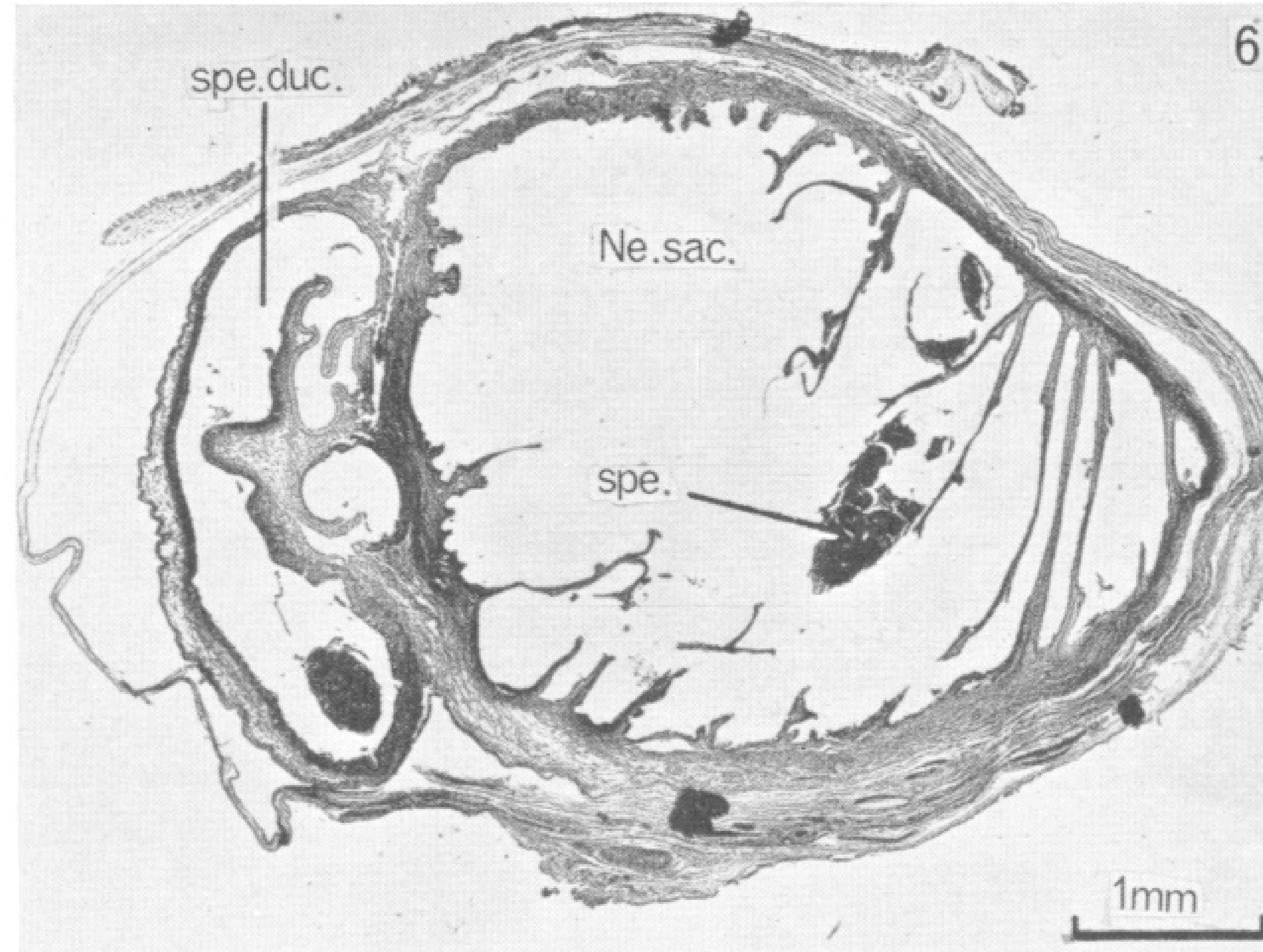

47
pl.ovi.g.
ovi.
sperm.
g.
500μm

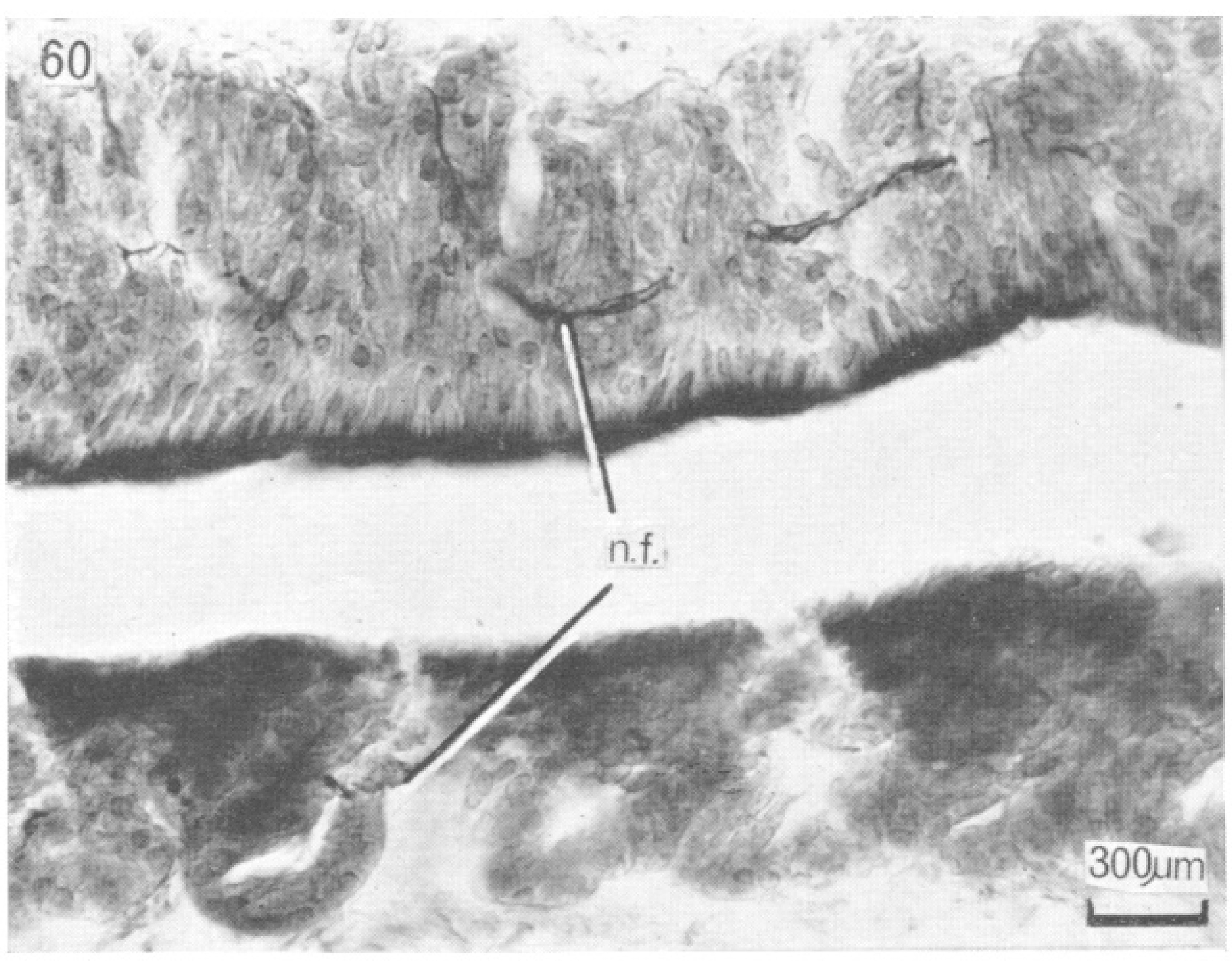

48
g.
pl.ovi.g.
ovi.
ovi.
sperm.
500μm

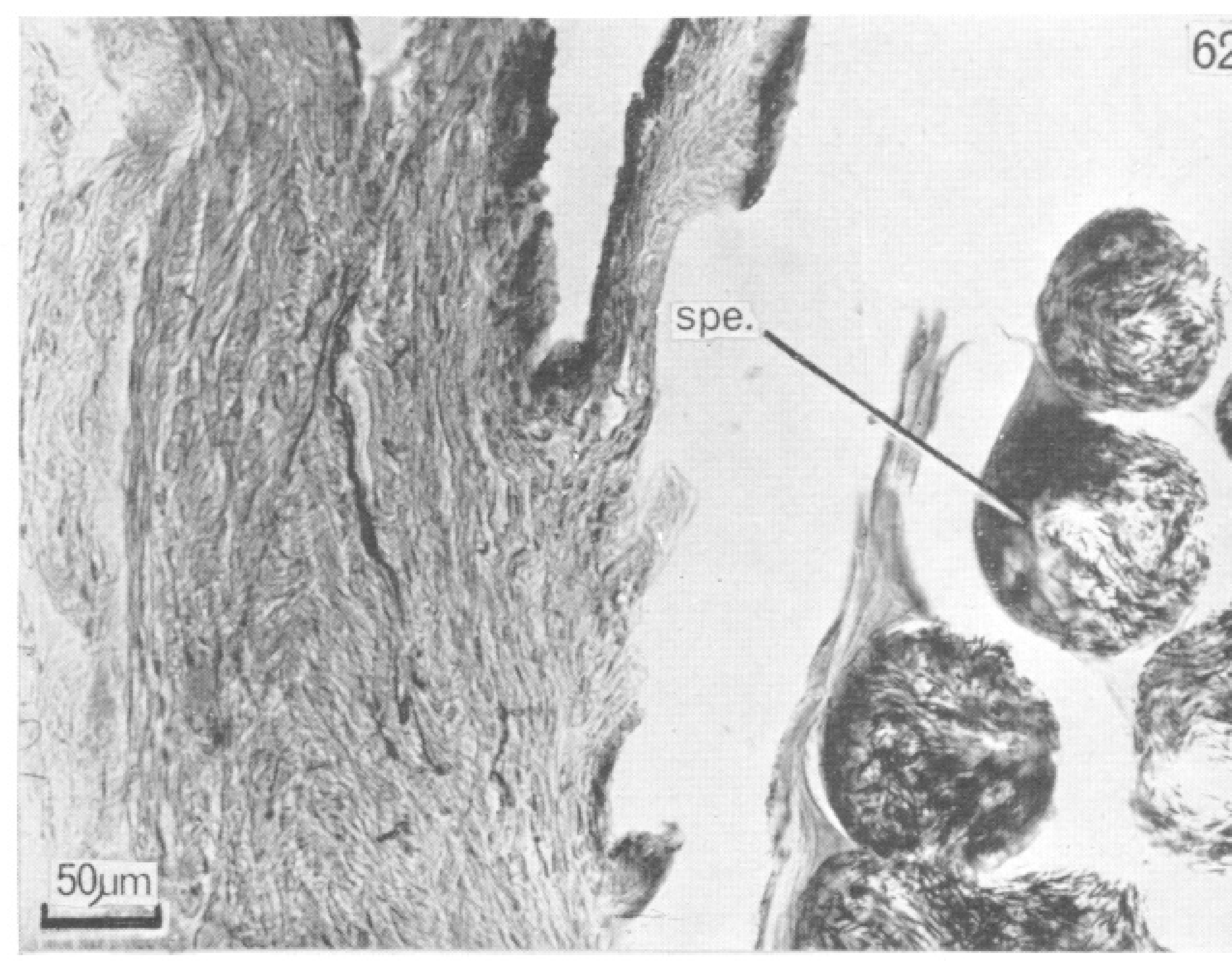

49
g.
sperm.
pl.ovi.g.
ovi.
500μm

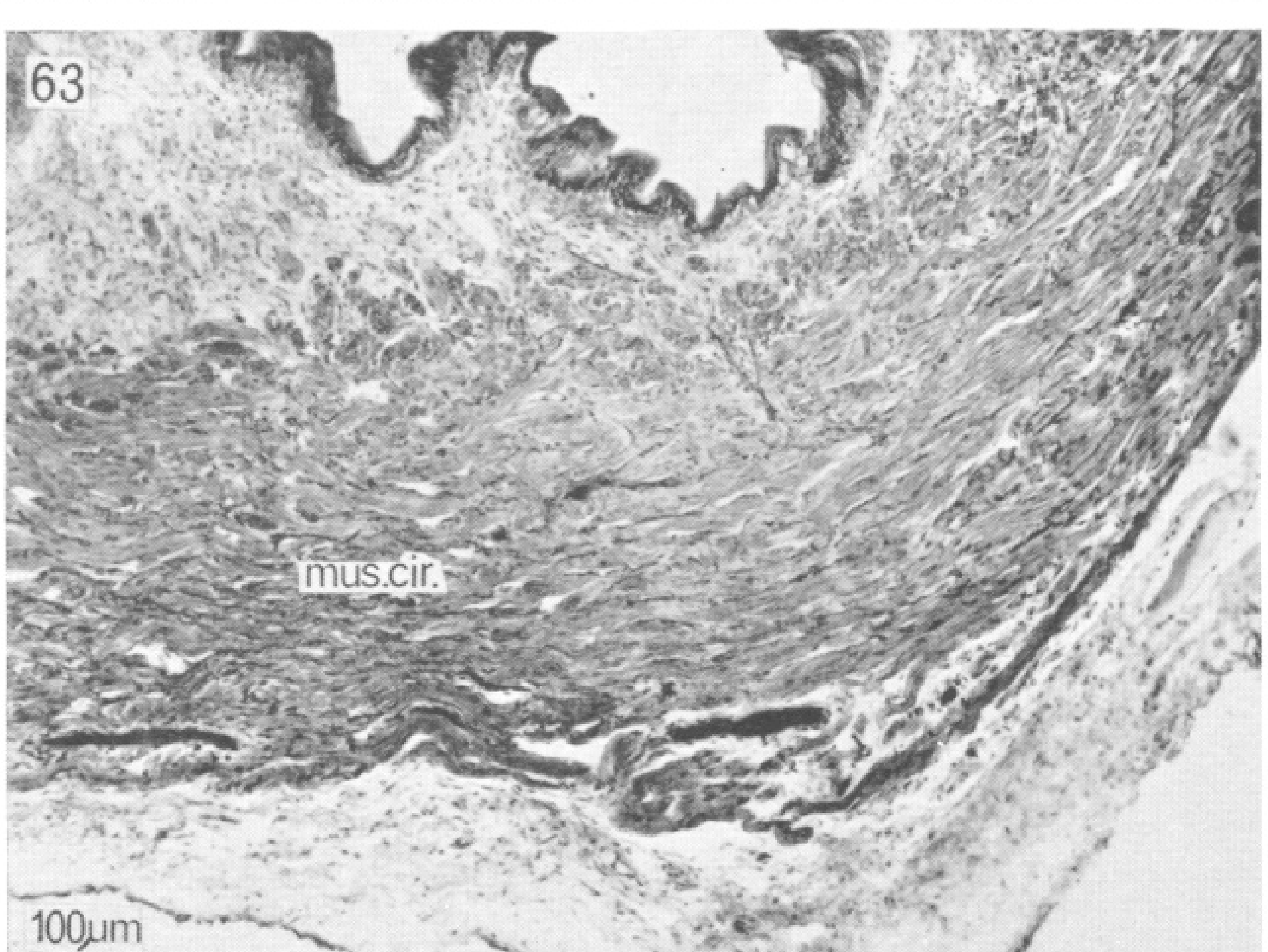

50
sperm.
pl.ovi.g
100µm
ovi.
51
n.ce.
50µm
52
n.ce.
sperm.
50µm
53
20µm
54
n.
ve.
art.
mus. cir.
ovi.
200µm
55
mus.cir.
50µm
56
epi.
mus.
cir.
300µm
57
epi.
20µm
58
n.f.epi.
n.f.
50µm

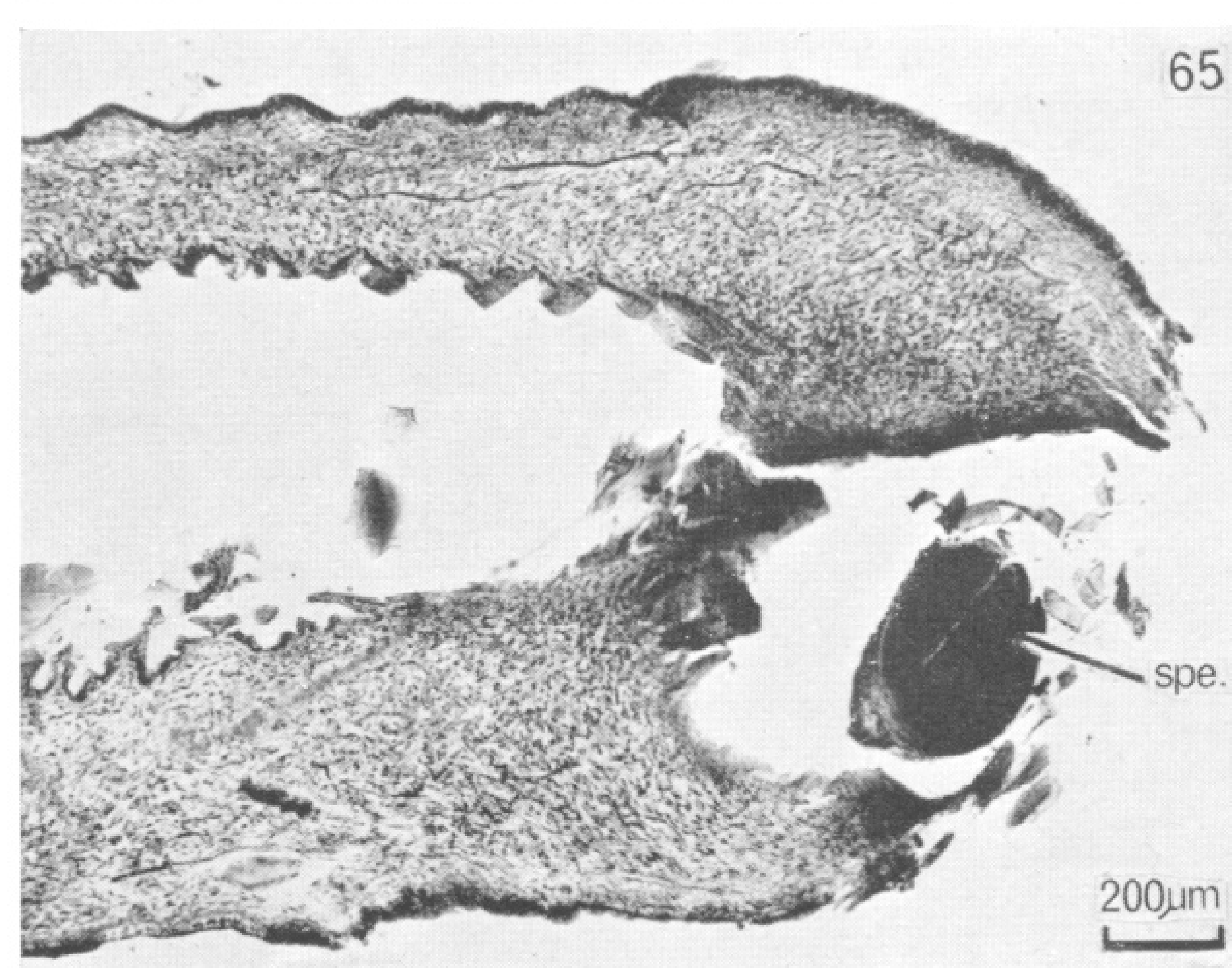

59
300µm

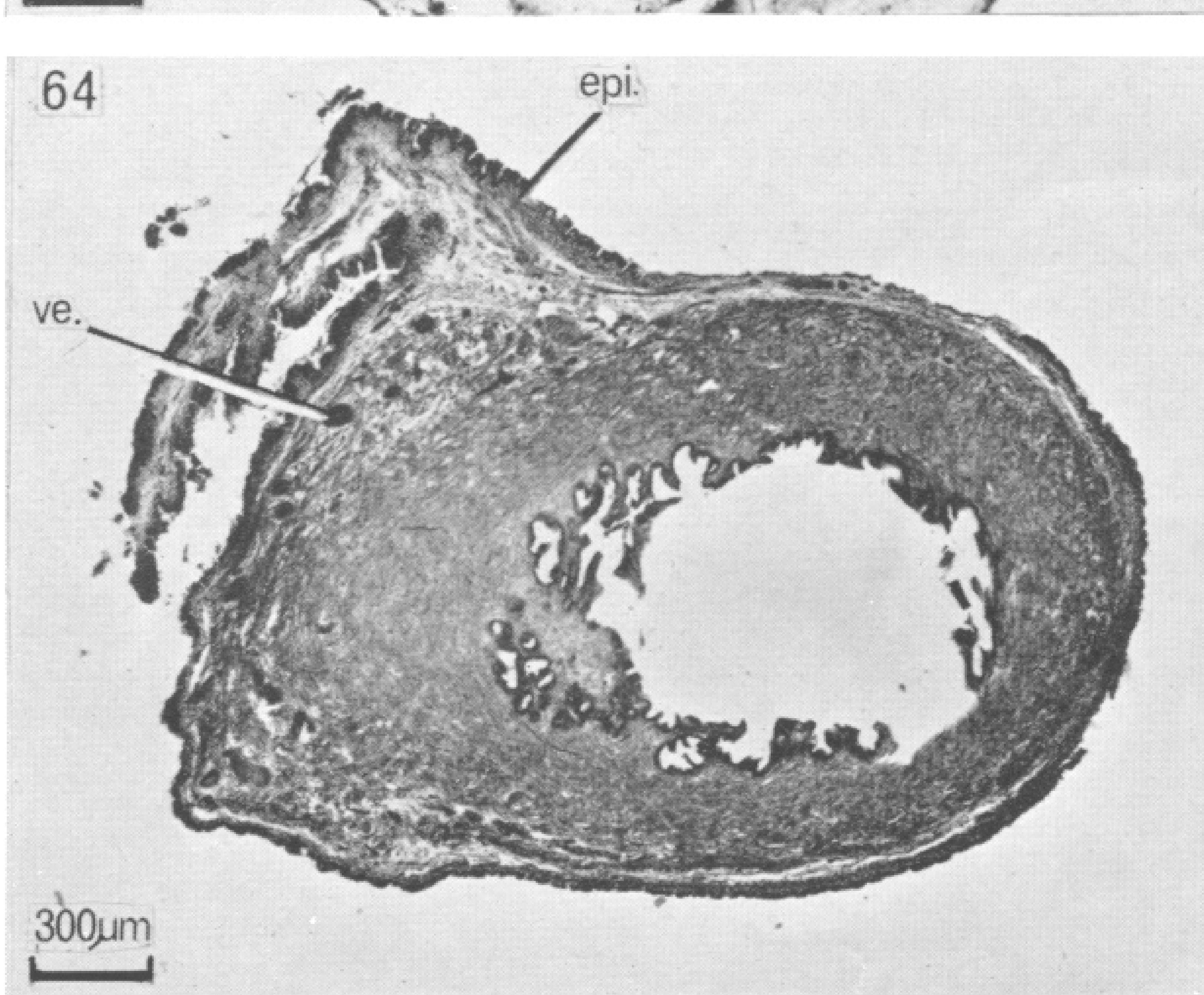

61
spe.duc.
Ne.sac.
spe.
1mm

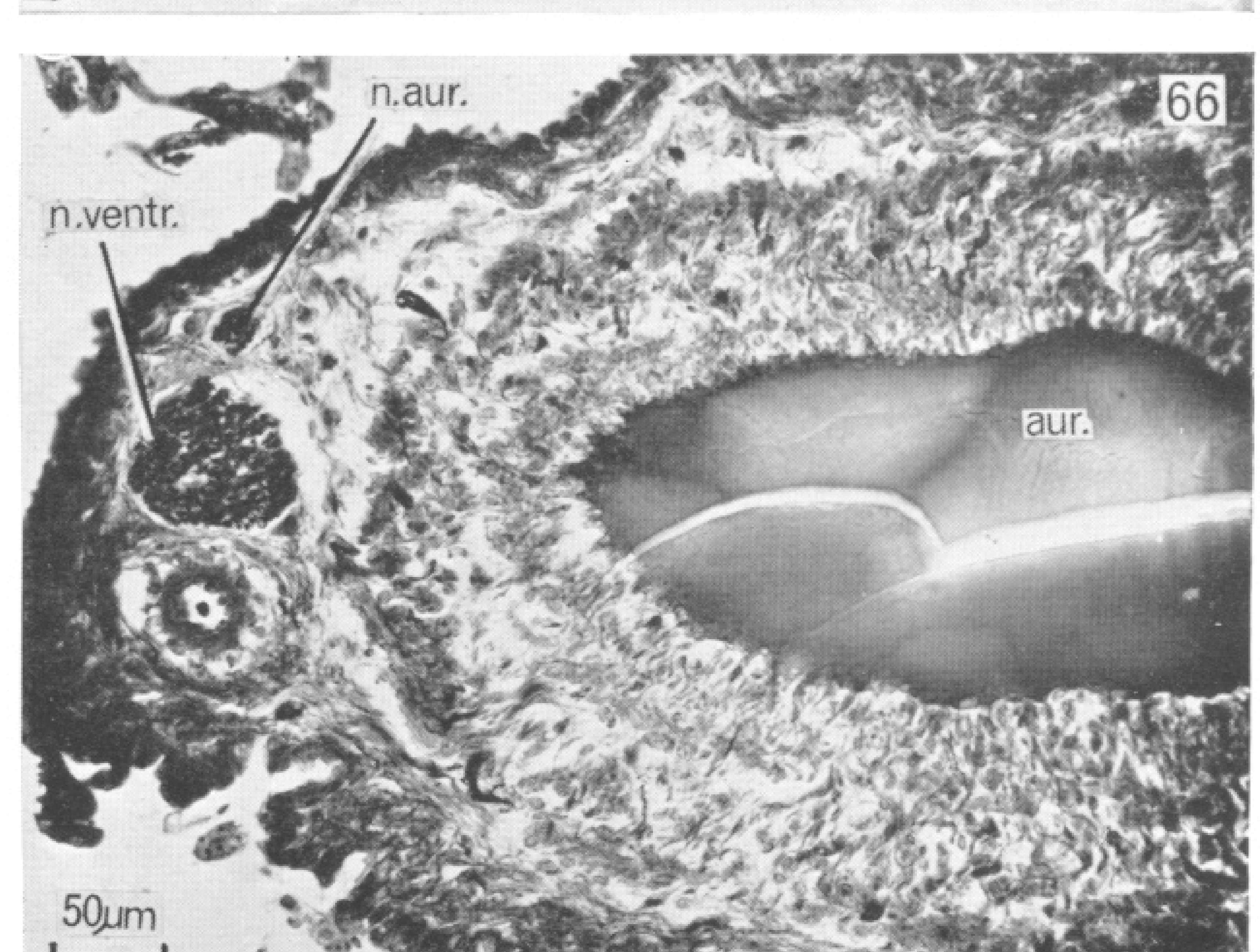

60
n.f.
300µm

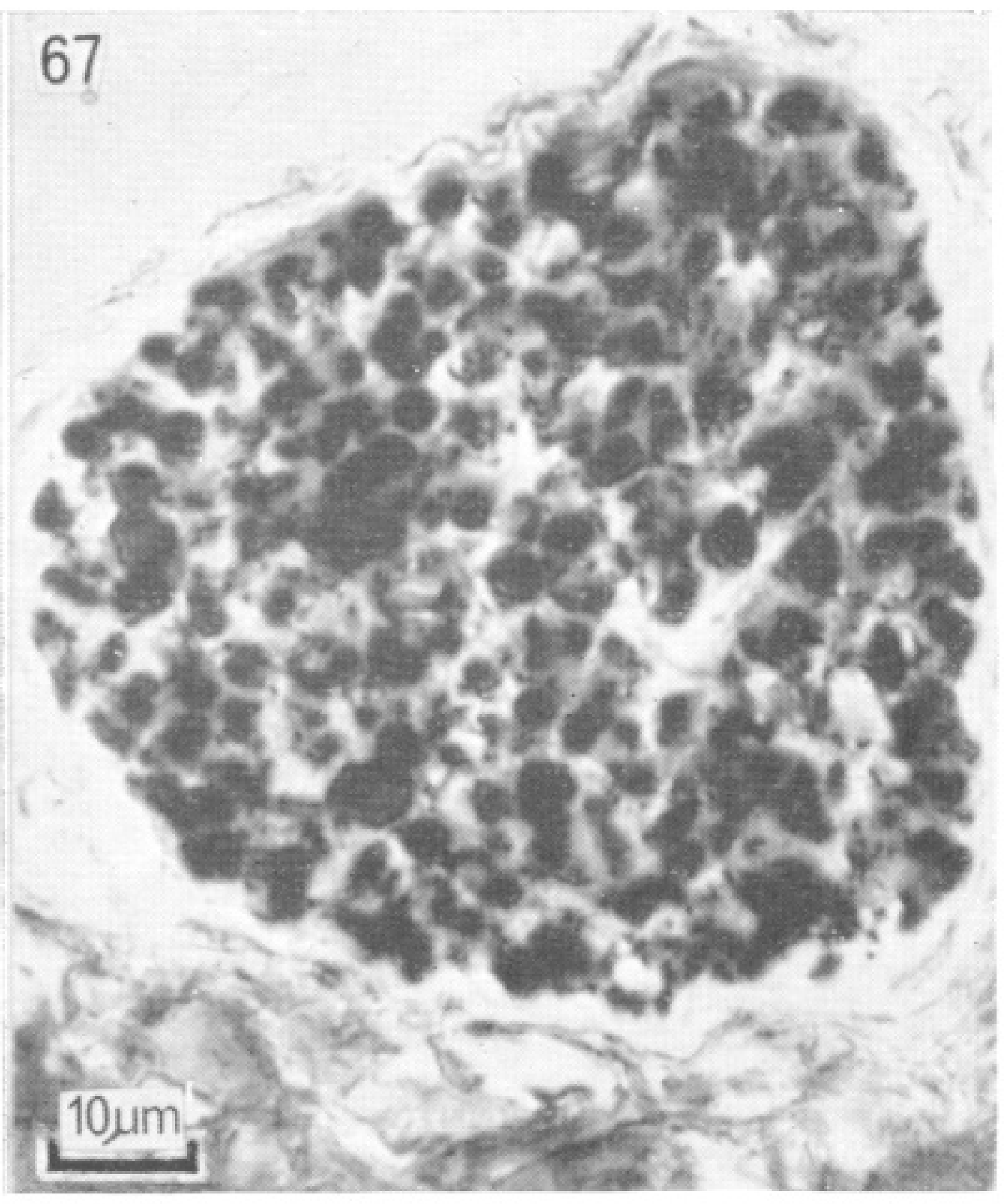

62
spe.
50µm

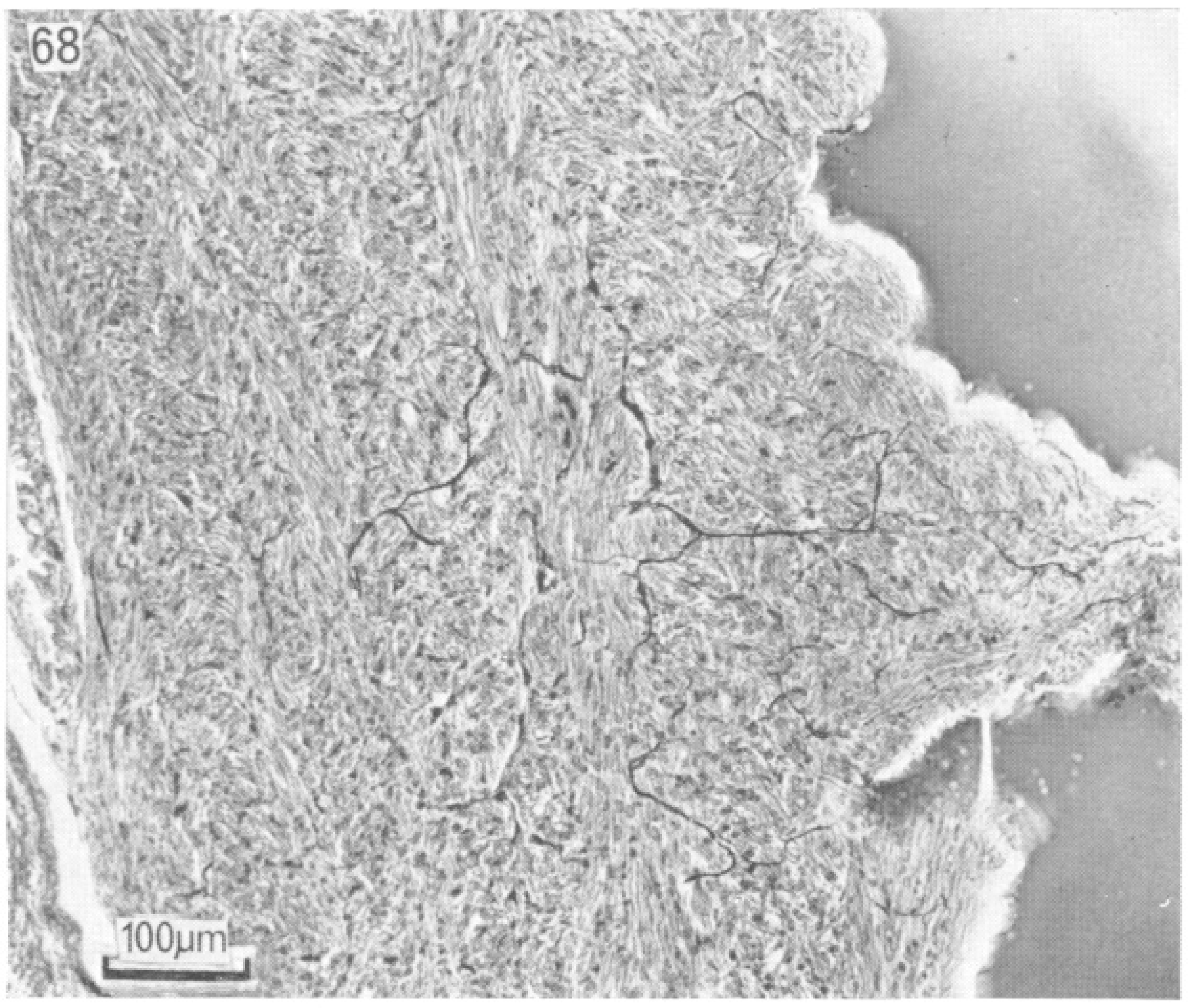

63
mus.cir.
100µm

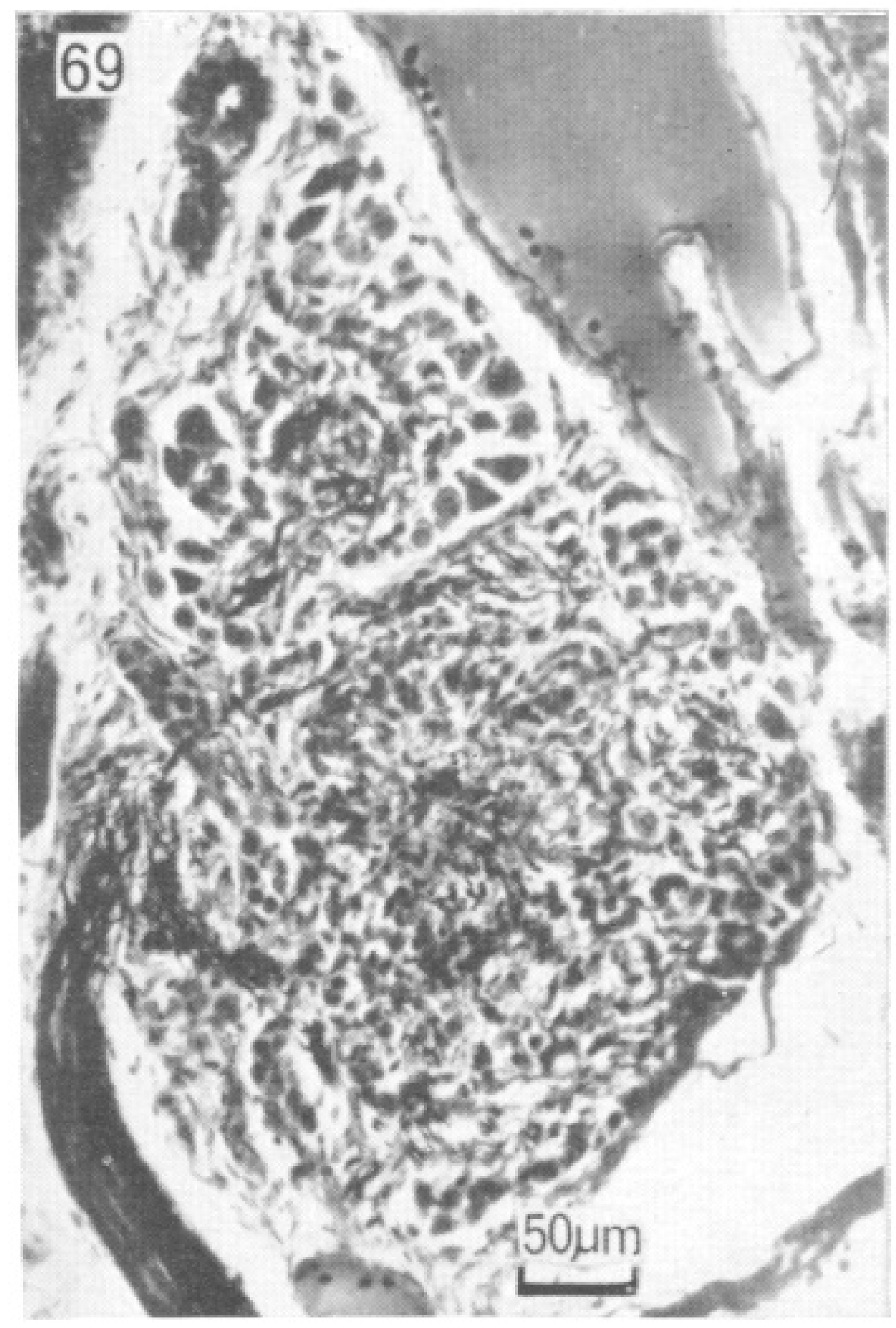

65
spe.
200µm

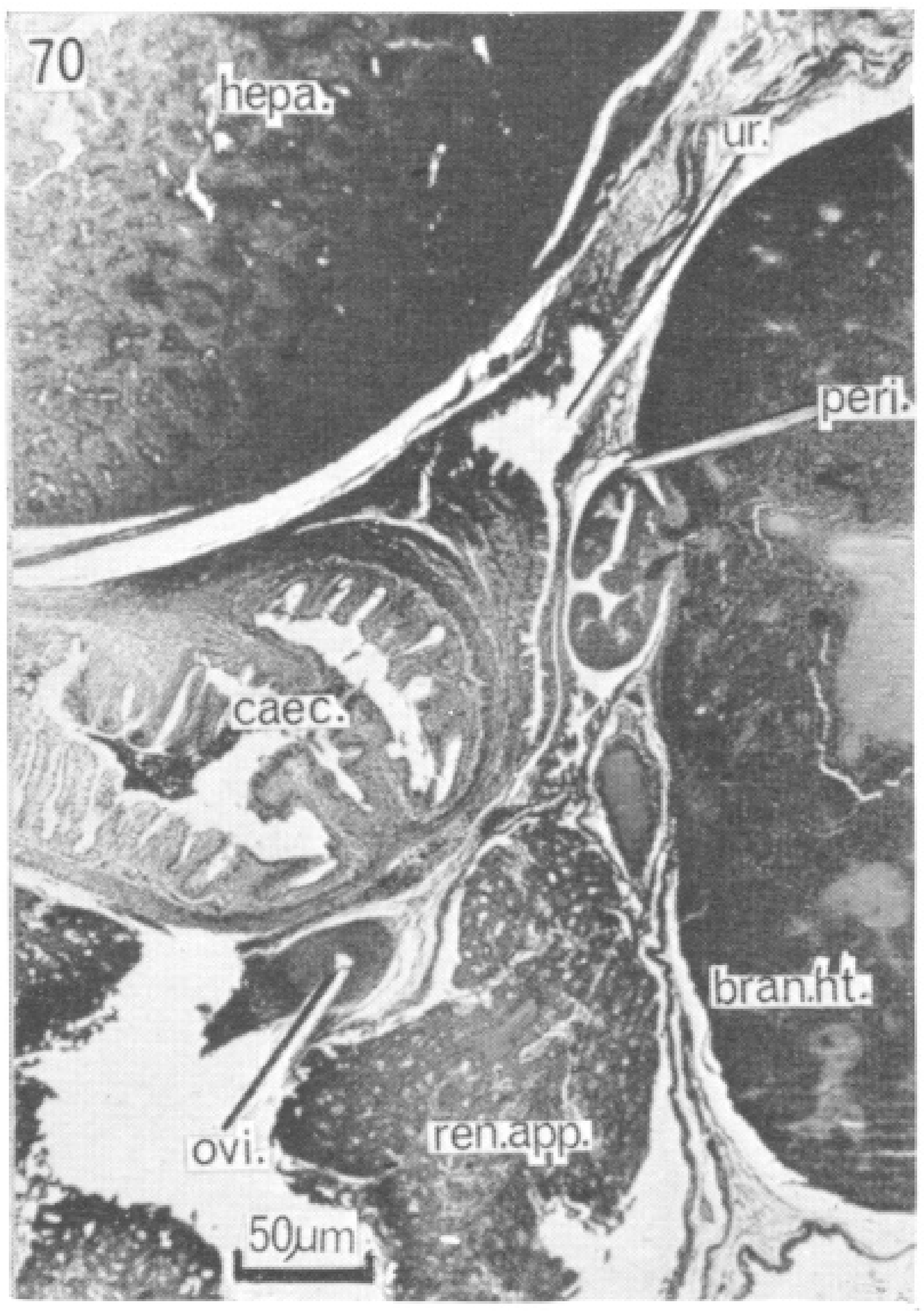

64
epi.
ve.
300µm


66
n.aur.
n.ventr.
aur.
50µm

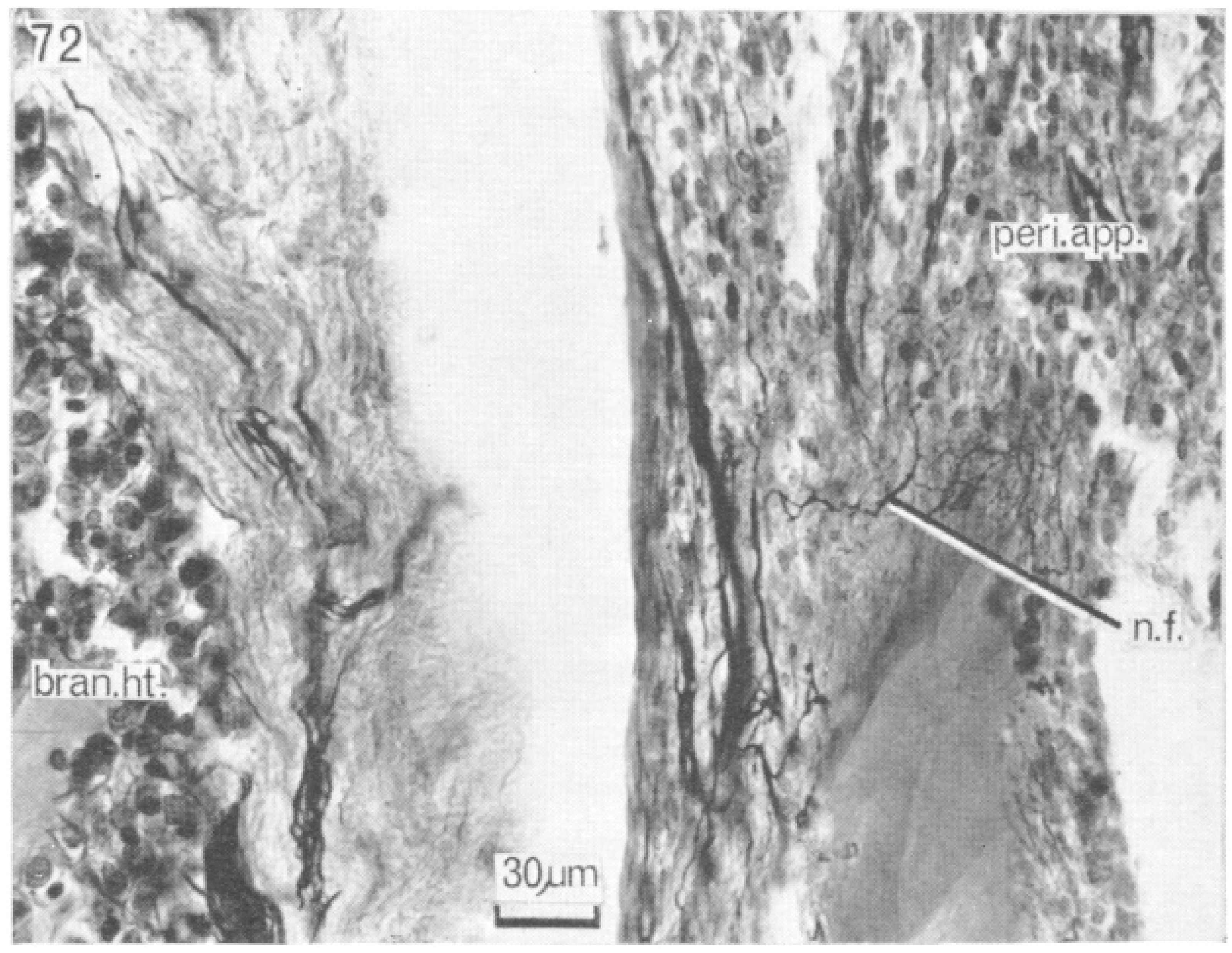

67
10μm

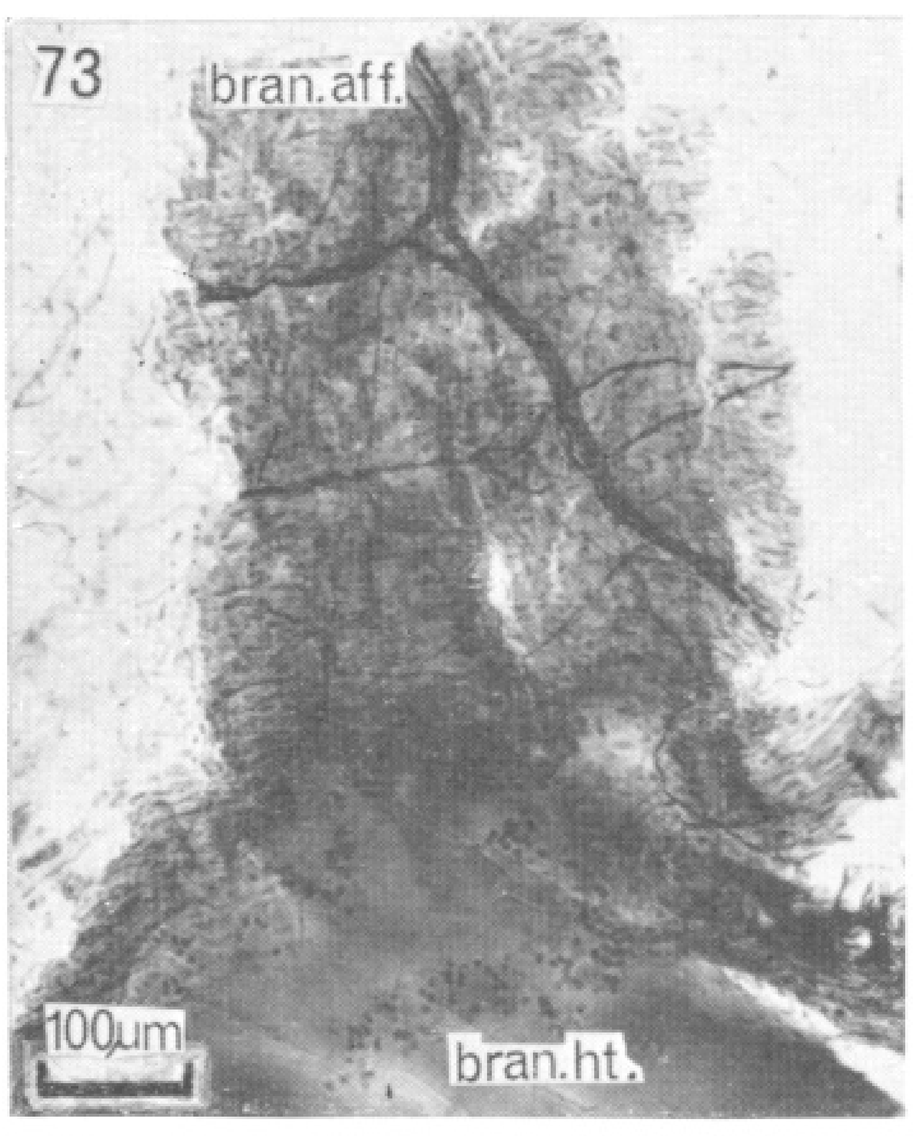

68
100μm

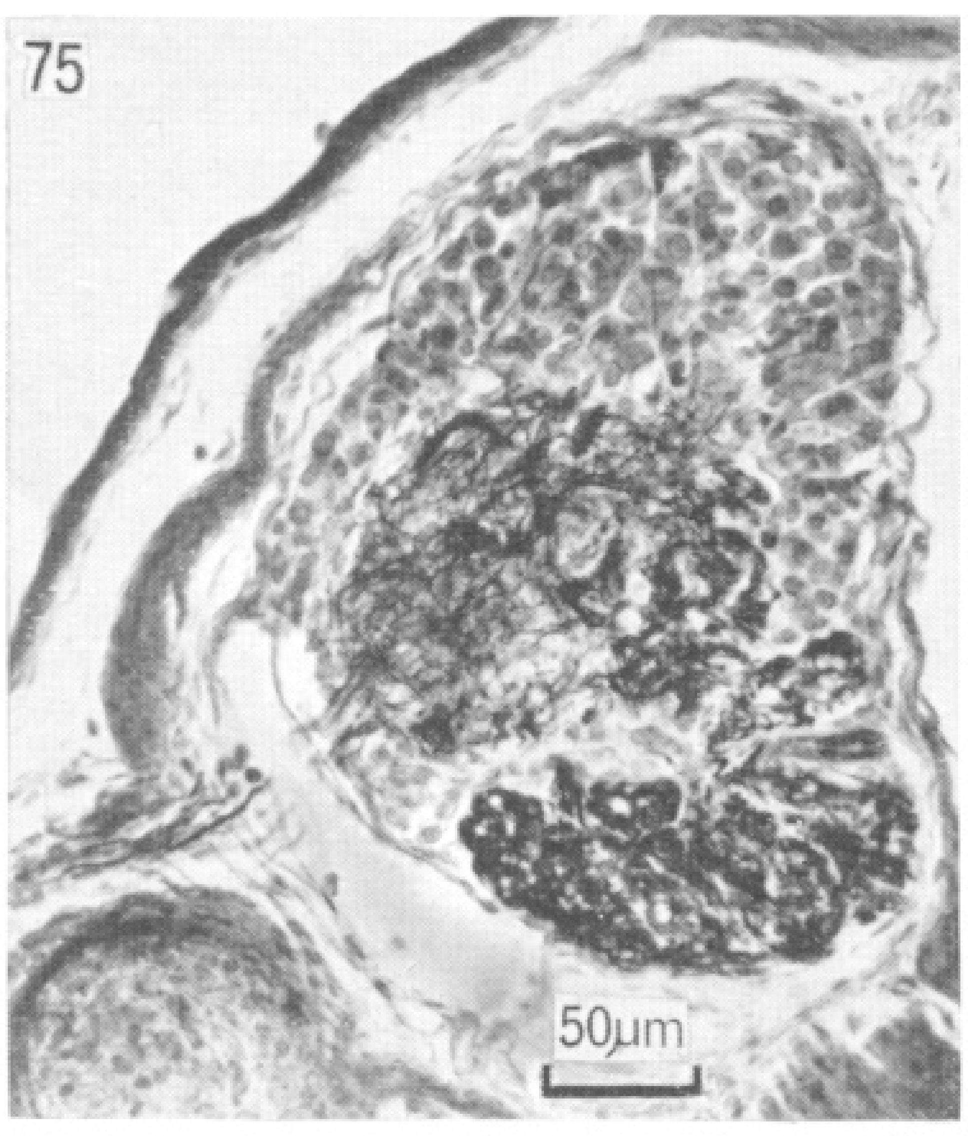

69
50μm

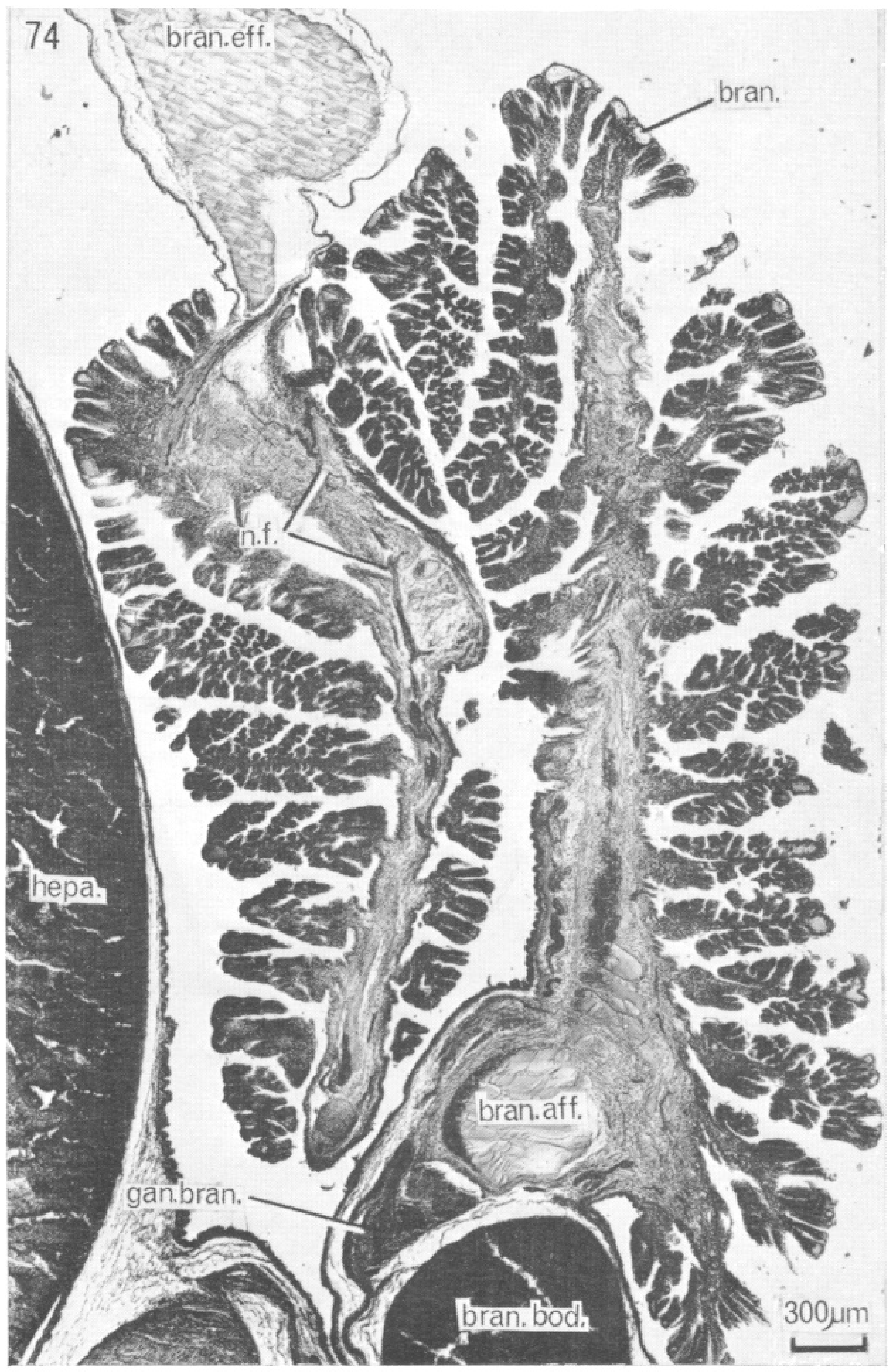

70
hepa.
ur.
peri.
caec.
bran.ht.
ovi.
ren.app.
50μm

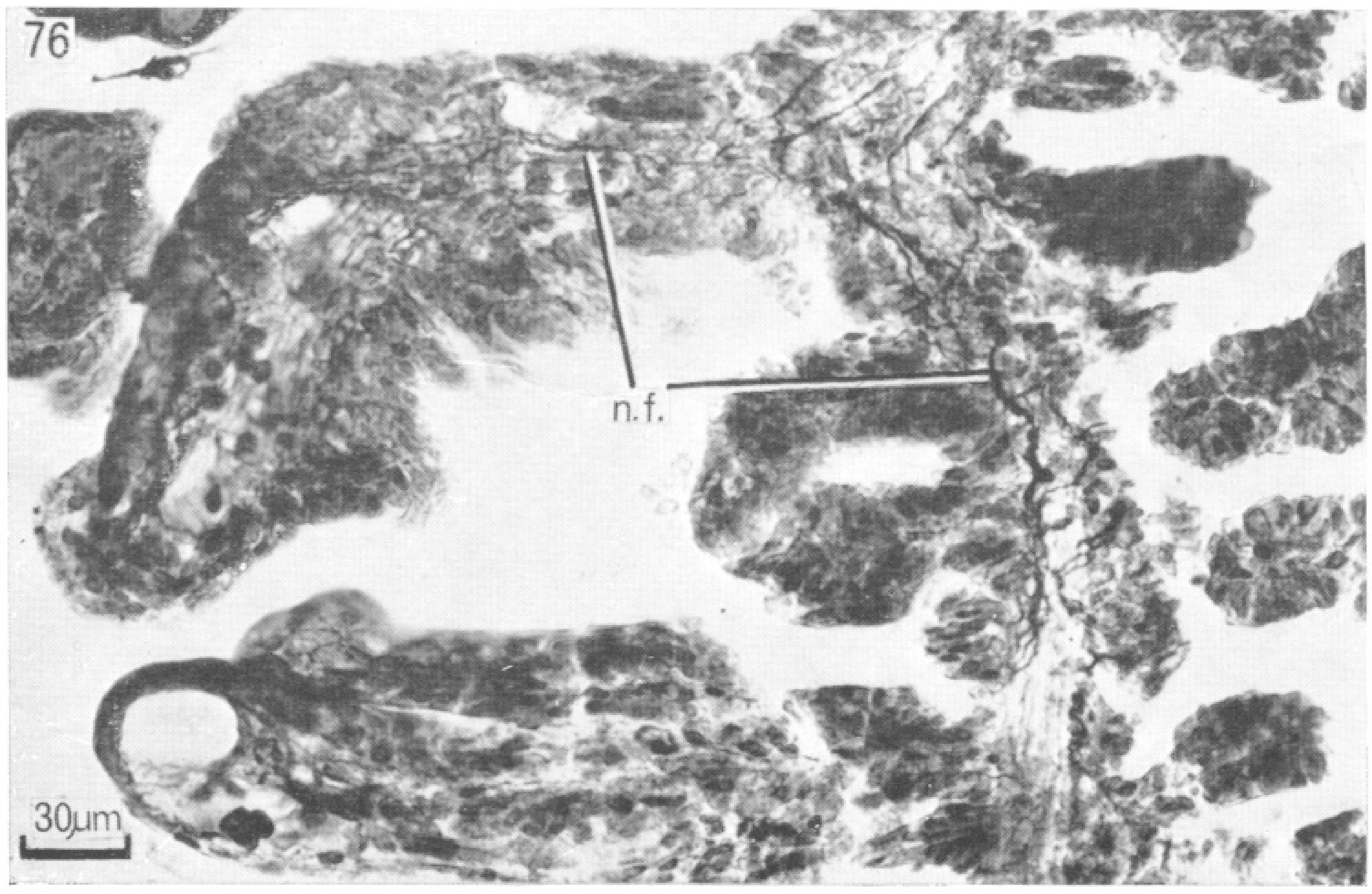

71
peri.
bran.ht.
n.f.
100μm


72
peri.app.
n.f.
bran.ht.
30μm


73
bran.aff.
100μm
bran.ht.


75
50μm


74
bran.eff.
bran.
n.f.
hepa.
bran.aff.
gan.bran.
bran. bod.
300μm


76
n.f.
30μm