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Arachnoid granulations in sheep

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Arachnoid granulations and arachnoid villi are herniations of the arachnoid membrane and its contained subarachnoid tissue into venous channels. The term 'granulation' has been used to denote structures which are visible by the unaided eye while structures very similar in morphology but only observed with the aid of a microscope are called 'villi'.

Ever since Pacchioni's classical description of arachnoid granulations in 1705, many workers have evinced much interest in their structure and function. Following on the work of Key & Retzius (1875), who postulated a filtration function to the granulations, Weed (1914*a*, *b*) injected potassium ferrocyanide and iron ammonium citrate into the subarachnoid space of anaesthetized cats and observed the presence of Prussian blue granules in the superior sagittal sinus. He concluded that arachnoid villi were the channels of cerebrospinal fluid filtration into the venous sinus, the granulations being merely hypertrophied villi. The absence of granulations in human infants and in some mammals seemed to support his contention.

Following these experiments of Weed, Cushing (1914) agreed that granulations and villi played a rôle in the passage of cerebrospinal fluid into blood by filtration, but in 1902, in common with the more recent results of Welch & Friedman (1959, 1960) and Welch & Pollay (1961), he postulated that an open communication existed between the subarachnoid space and the venous system. Welch & Pollay (1961) demonstrated that colloidal gold particles, polystyrene spheres, yeast and erythrocytes injected into the subarachnoid space passed through tubes in the villi of monkeys, although there was no evidence of rupture of the villi either due to the pressure of injection or from any other cause. The tubes were shown to open into the subarachnoid space at one end and at the other into the venous sinus. Welch & Friedman (1959, 1960) believed that, although a direct communication did exist between the venous sinus and cerebrospinal fluid systems, the flow of fluid was only from the subarachnoid space to the venous sinus, and not vice versa, a feature resulting from the physiological valvular mechanism of the arachnoid villi. They clearly demonstrated, in the monkey, that increase in the pressure in the subarachnoid space above a critical pressure caused the villi to balloon out and the tubes within them to dilate. On increasing the pressure in the venous sinus, the villi were flattened and the tubes obliterated.

Trolard (1870) and Schaltenbrand (1955) described cavernous spaces in the arachnoid granulations of man. The former stated that they communicated with the venous sinus, while the latter was uncertain whether these cavities, lined with endothelium, had any communication with the venous sinus. It is possible, however, that these two workers may have been referring to the blood vessels described in

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granulations by Pacchioni (1705), Le Gros Clark (1920) and Kolesnikov (1940), though Turner (1961) stated that the blood vessels seen by the previous workers were those in dural tissue found between adjacent granulations.

A survey of the occurrence and structure of granulations and villi in a series of mammals led to the sheep being chosen for this present study. The objective was to determine whether or not there was a direct communication between the venous sinus and the subarachnoid space through arachnoid granulations.

MATERIALS AND METHODS

A. *Morphological study*

(1) *Paraffin sections*

Nine adult sheep were used. The sheep were killed by decapitation using a guillotine method. The cranial vault was removed within 10 min. of death and the whole head immersed in 10 % formol saline. After 3 days, the brain together with its coverings was carefully removed and re-immersed in the same fixative for a further 24 hr. The granulations were removed as small blocks of tissue together with surrounding dura mater, a portion of the superior sagittal sinus, the parasagittal membranes and the adjacent portions of cerebral cortex.

The tissues were then dehydrated in graded alcohols and doubly embedded, using either Peterfi's technique (Carleton & Drury, 1957) or the method of Brain (1949). Blocks of tissue were serially sectioned at either 10 or 15 μ and the sections routinely stained by (*a*) Harris's haematoxylin and eosin, as a general stain, or by (*b*) Peters (1958) silver proteinate method for nerve fibres.

Details of the structure were not very clear in some of the paraffin sections, because of the thickness, distortion and shrinkage produced by this method on the hard dural tissues. For this reason, methacrylate and Araldite were also used as embedding media for light microscopy.

(2) *Methacrylate sections*

Four adult sheep were used. Small blocks of tissue containing arachnoid granulations and the dura forming the sinus wall were fixed in 10 % formol saline for 1 hr. and then placed for 2 hr. in fixative containing 2 % osmium tetroxide (Dalton, 1955). Next the tissue was washed in 10 % alcohol and treated with three, half hourly changes of absolute alcohol (over silica gel) and embedded in methacrylate in gelatine capsules at 60° C. Sections were cut at 1 μ on a Porter–Blum microtome and stained with 1 % toluidine blue in 1 % borax solution or by the method of Jennings, Farquhar & Moon (1959).

(3) *Araldite sections*

Four adult sheep were used. The procedure employed was almost the same as for methacrylate sections. Following final dehydration in absolute alcohol, the tissue was embedded in Araldite using the method of Glauert & Glauert (1958). Sections were stained with 1 % toluidine blue in 1 % borax solution or in 1:4 pyronin–toluidine blue stain (Ito & Winchester, 1963).

Electron microscopic studies were also carried out on sheep arachnoid granulations, and these results are to be published later.

B. *Injection of indian ink*

During the course of this investigation, two sets of channels lined by flattened endothelial cells were observed (*vide* Results) in the arachnoid granulations of sheep. One set appeared to arise from the blood vessels of the dura, while the other, which formed continuous channels, appeared to connect the subarachnoid space to the venous sinus. In order to confirm this observation and to assess whether the two systems are separate or linked, the following experiments were carried out.

If the arterial system was injected with indian ink, only those channels arising from arteries would contain the dye, and no other; conversely, if the subarachnoid space was injected any channels joining the subarachnoid space to the venous sinus should show the ink, but not those arising from the blood vessels.

(1) *Intra-arterial injection*

Three adult sheep were used. The animals were killed by decapitation and the arteries washed out by perfusion with 3·8 % sodium citrate through both common carotid arteries. The superior cerebral veins opening into the superior sagittal sinus were ligated. This was done in order to prevent indian ink from flowing through the capillaries and veins into the sinus, from which it might enter any tubules (*vide* Results) traversing the granulation. As a further precaution, that part of the sinus containing the granulations was isolated by ligatures and severed from the rest of the sinus. The sinus was then thoroughly washed with 1 N saline after which 125 ml. of a solution of indian ink (containing 1 part of 'Higgins' indian ink in 5 parts of 1 N saline) were injected into each common carotid artery by gravitational flow. The column of injection fluid measured approximately 1 m. As it was impossible to ligate all the venules, and to prevent the leakage of some indian ink into the opened sinus, the sinus surface of the granulations was continuously washed with 1 N saline during the period of injection. Thus, India ink in any channel could only have reached it via the arteries, and not from the venous sinus. After injection the brain was fixed *in situ* in 10 % formol saline for double embedding in paraffin and for embedding in methacrylate and Araldite.

(2) *Subarachnoid injection*

Three adult sheep were used. After decapitation the vascular system was again washed out with sodium citrate. A small bore polythene tube was then passed along the dorsal aspect of the spinal medulla between the pia and arachnoid membranes, towards the cisterna magna of the brain. The cut edges of the spinal medulla and the polythene tube were tightly tied together to prevent any back flow of fluid between the pia and arachnoid membranes. 50 ml. of indian ink solution were injected through the polythene tube by gravitational flow (similar to the intra-arterial injection). 50 ml. of indian ink solution was used to replace approximately some of the cerebro-spinal fluid that was lost from the cut end of the cervical spinal cord. This technique was employed as there was no appreciable difference in the histological structure between the injected and uninjected material. Blocks of tissue were excised for double embedding in paraffin and also for embedding in methacrylate and Araldite.

RESULTS

Arachnoid granulations are present in all the specimens of adult sheep examined. The minimum number present is three and the maximum number is eight. The granulations are usually situated in the caudal part of the superior sagittal sinus near the commencement of the transverse sinus (Pl. 1, fig. 1). These arachnoid granulations are cauliflower-like bodies which project freely into the sinus and are found at or near the opening of cerebral veins into the superior sagittal sinus.

Arachnoid granulations are seen as herniations of the arachnoid membrane and subarachnoid tissue into the venous sinus, through gaps in the dura mater forming the walls of the sinuses. A granulation possesses a body, and a neck, through which the core of the granulation communicates with the main part of the subarachnoid space (Pl. 1, fig. 2).

At this stage it may be useful to define the following terms. Surface epithelial cells are those covering the arachnoid granulations where they form part of the walls of blood vessels (endothelial). Mesothelial cells are those that form incomplete linings of the spaces between the collagen bundles of the fibrous tissue trabeculae which surround the endothelially lined channels in the core of the granulation. Arachnoid epithelial cells are defined as those of the arachnoid membrane lining the subdural space.

Surface epithelium of arachnoid granulations

The surface epithelium of arachnoid granulations is composed of a layer of cells, continuous with that lining the lumina of intra-dural venous sinuses (Pl. 1, fig. 2). Most commonly these cells of a granulation are flattened, containing dense basophilic nuclei, but sometimes the cells are rounded with spherical nuclei. These cells are similar to the arachnoid epithelial cells and the mesothelial cells and are all morphologically indistinguishable. Since the surface epithelial cells form part of the wall of the venous sinus, they are regarded as endothelial cells.

Crypts and tubules

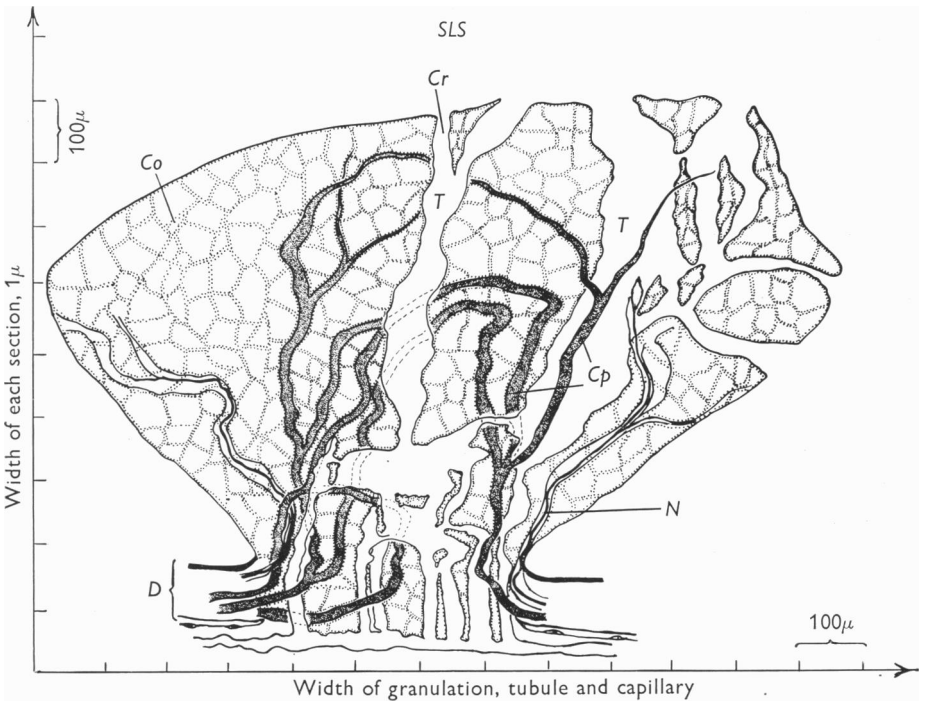
The surface epithelium of arachnoid granulations in sheep is invaginated into the core of each granulation at many points. Such invaginations give the appearance of crypts in sections cut along the long axis of the granulation (Pl. 1, fig. 3). The cells lining these crypts are similar to those of the surface epithelium of the granulation. The diameters of the crypts vary from 100 to 300 μ, and, in serial sections cut transverse to the vertical axis of granulations embedded in plastic material, the crypts are seen to be in continuity with tubules within the body of the granulation. Both tubules and crypts are lined by endothelial cells (Pl. 1, figs. 4, 5). The mean diameter of these tubules is about 60 μ, but they vary from 45 to 150 μ.

There are, however, other channels lined by endothelial cells in the core of the arachnoid granulations of sheep. They measure from 6 to 15 μ in diameter, usually contain red cells in their lumina, and have the characteristic appearance of blood capillaries (Pl. 2, fig. 6). Differentiation between the tubules and the narrower vascular channels is only possible when indian ink is injected separately either into the carotid arteries, or into the subarachnoid space.

Intra-arterial injection

Macroscopically, the dural blood vessels contain particles of the injected indian ink, and so do the cerebral veins up to the point of their ligation. No indian ink particles are observed in the sinus.

Microscopically, in both paraffin and methacrylate sections, indian ink is observed in the narrow channels arising from dural blood vessels but not in the tubules



Text-fig. 1. Graphic reconstruction of sheep arachnoid granulation. *SLS* = superior sagittal sinus, *T* = tubule, *Cp* = capillary, *N* = nerve fibres, *D* = dura, *Co* = core of granulation, *Cr* = crypt.

(Pl. 2, fig. 8). These indian ink-filled channels must be the capillaries as they connect with the dural blood vessels.

Two graphic reconstructions have been made from serial transverse sections of the intravascularly injected granulations embedded in methacrylate, by plotting the width of granulations, diameters of tubules and capillaries as abscissae and the thickness of the sections as ordinates (the thickness of each section is 1 μ and every tenth section has been taken). One of these reconstructions is shown in Text-fig. 1. It is possible to demonstrate the relative positions of blood vessels and the arachnoid tubules.

It is evident from the reconstruction that the tubules, which are in continuity with the crypts at the surface of the granulation, appear to communicate with similar tubules of the subarachnoid space. Each tubule does not pass through the granula-

tion independently, but joins up with others to form a network of tubules in the centre of the granulation. From this network, separate tubules arise inferiorly and pass through the neck of the granulation to join the subarachnoid space.

Subarachnoid injection

On opening the sinus, no blood is observed macroscopically, though there are particles of indian ink in it. The granulations stand out as black beads, and examination of the surface of the granulation shows the presence of darker pitted areas, probably the openings of the crypts filled with Indian ink (Pl. 2, fig. 7). The entire subarachnoid space is blackened.

Microscopically, the arachnoid tubules but not capillaries are observed to be filled with Indian ink (Pl. 2, figs. 10, 11). It is possible in most sections to identify separately the tubules and the spaces between collagen bundles in the fibrous tissue trabeculae in the core of the granulation (Pl. 2, fig. 9). In a few areas, however, where the granulation is packed with indian ink, separation between tubules and the spaces between the collagen bundles is impossible (Pl. 2, fig. 11). Indian ink is also present on the surface of the granulation as well as in the sinus (Pl. 2, fig. 11), thus indicating the patency of the tubules. Since there is no histological evidence of rupture of a membrane, i.e. lining of tubule or of surface epithelium, these findings suggest the existence of a direct communication between the subarachnoid space and the venous sinus through the tubules.

On examining the junction between granulations and subarachnoid space, indian ink is found in tubule-like spaces of the subarachnoid tissue (Pl. 3, fig. 12). Whether these spaces in the subarachnoid tissue represent a tubular system similar to that described in granulations has not been determined.

Capillaries

The capillaries in the arachnoid granulations of sheep arise from blood vessels of the dura mater and enter the granulation at the points where they pass through openings in the dura. These capillaries travel some distance into the neck of the granulation and then course vertically upwards into the core. By joining with others, most of the capillaries form loops while a small number appear to end blindly some distance below the surface epithelium of the granulation (see Text-fig. 1). The diameters of the capillaries vary; the larger ones resemble the endothelially lined tubules. No communications were found either between the capillaries and the tubules or between the capillaries and the venous sinus.

Core of arachnoid granulations

The core of an arachnoid granulation is formed of collagen bundles between which are spaces often surrounding the capillaries, tubules, nerves and a variety of cells. The bulk of the granulation is composed of a network of these collagen bundles, similar to that found in the subarachnoid space (Pl. 1, fig. 2). The collagen bundles are sometimes covered by mesothelial cells, and are more tightly packed at the periphery of the granulation than at the centre. The spaces between the collagen bundles communicate with one another and with similar spaces found in the subarachnoid space (Pl. 1, fig. 2). On section, some of these spaces give the appearance

of tubes, an appearance which probably has led Welch & Friedman (1959) to term them 'coapted tubes'. These spaces are quite distinct from the tubules described earlier. The mesothelial cells that cover the collagen bundles have been shown in electron micrographs to form incomplete linings to the spaces, while the tubules on the other hand are completely lined by endothelial cells (Jayatilaka, 1964).

Nerve fibres

In silver-impregnated sections, it is difficult to differentiate between nerve fibres and collagen bundles, but, by increasing the pH of the silver proteinate mixture in Peters's method, the nerve fibres stand out more prominently (Pl. 3, fig. 13). In osmium-fixed material the myelin sheaths of the nerve fibres are observed (Pl. 3, fig. 14). On tracing nerve fibres in serial sections, they are found in bundles with little branching, except towards their terminations (Text-fig. 1). The course of the nerve fibres bears no relationship to that of blood vessels of the granulation and no specialized nerve endings have been observed.

DISCUSSION

This study confirms the observations of Turner (1958) that arachnoid granulations are herniations of the arachnoid membrane and subarachnoid tissue into venous sinuses. This is supported by developmental anatomy, the granulations appearing to arise by proliferation of the arachnoid cells surrounding the cerebral veins at their entry into venous sinuses (Jayatilaka, 1964).

The injection of indian ink into the vascular system clearly demonstrates that blood vessels are present in granulations and that they arise from dural blood vessels. The demonstration of these blood vessels separately from the tubules (connecting subarachnoid space to venous sinus), both of which are lined by endothelial cells, allows of a clear indication of the presence of two such separate systems.

The patency of the tubules has been demonstrated by the fact that, following the injection of indian ink into the subarachnoid space, the dye is found both in the tubules and in the venous sinus, with no evidence of rupture of the granulation, as shown by the unbroken surface of the epithelial cells lining the tubules with the surface epithelial cells covering the granulation. This is also seen in the graphic reconstruction (Text-fig. 1). Thus, these findings support the views of Cushing (1902), Welch & Friedman (1959, 1960) and Welch & Pollay (1961) that there exists an open communication between the subarachnoid space and the venous sinus.

On the basis of an open communication between the subarachnoid space and venous sinus, the results of some previous workers can be explained. In man, Key & Retzius (1875) found particulate matter in the venous sinus after subarachnoid injection of 'cinnabar ground in water' and explained the passage of particles through 'stomata' (between cells of the surface epithelium) instead of through tubules, of which they had no knowledge. Further, in the cat, Weed (1914*a*, *b*) observed Prussian blue granules in the venous sinus after introducing potassium ferrocyanide and iron ammonium citrate into the subarachnoid space and subsequently fixing the animal with acidified formalin. He concluded that the ferrocyanide–citrate mixture had filtered through the surface epithelium of villi and was

precipitated by the acidified formalin in the sinus. The Prussian blue forms even without the presence of hydrogen ions (hydrogen ions only render the Prussian blue granules insoluble). The presence of the Prussian blue in the sinus could also be explained by the open communication through the tubules into the venous sinus. These results, together with the findings in the present investigation, suggest that the passage of cerebrospinal fluid from the subarachnoid space to the venous sinus could also occur by direct flow through the tubules, rather than by ultra-filtration alone, across the plasma membranes of the surface epithelial cells of the granulation.

Although nerve fibres are present in the arachnoid granulations of sheep, the absence of specialized nerve endings, and the fact that they bear no relationship to blood vessels of the granulation, make their function obscure.

SUMMARY AND CONCLUSIONS

1. Arachnoid granulations in sheep are herniations of the arachnoid membrane and subarachnoid tissue into venous channels.

2. Two sets of channels lined by endothelium are observed in the core of arachnoid granulations. One set arises from the dural blood vessels while the other (tubules) connect the subarachnoid space to the venous sinus. Differentiation between the two is possible when indian ink is injected either intravascularly or into the subarachnoid space.

3. The patency of the tubules is demonstrated by the fact that, following injection of indian ink into the subarachnoid space, the dye is found in the tubules and on the sinus surface of the granulation. There is no histological evidence of rupture of the granulation due to the pressure of the injection. These findings suggest that there is a direct communication between the subarachnoid space and the venous sinus.

4. On the basis of an open communication, the results of previous workers are explained. The flow of cerebrospinal fluid from the subarachnoid space could occur both by direct flow through tubules as well as by filtration across a cell membrane.

5. Though nerve fibres are present, their function is obscure.

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EXPLANATION OF PLATES

PLATE 1

Fig. 1. Photograph of a sheep superior sagittal sinus (*LS*) showing arachnoid granulations (*AG*) at the opening of cerebral veins (*CV*). *TS* is transverse sinus. × 2.

Fig. 2. Section cut in long axis of sheep granulation in venous sinus. Paraffin embedded, H. & E. × 54. *EL* = endothelial layer, *AG* = arachnoid granulation, *LS* = superior sagittal sinus, *D* = dura, *CV* = cerebral vein, *AS* = subarachnoid space and *DS* = subdural space.

Fig. 3. Section cut along long axis of arachnoid granulation (*AG*) showing crypt (*Cr*) opening into the venous sinus (*LS*). Araldite embedded, toluidine blue. × 500.

Fig. 4. Transverse section of a granulation showing tubules (*T*). Methacrylate embedded, H. & E. × 350.

Fig. 5. Same as fig. 4. Methacrylate embedded, H. & E. × 600.

PLATE 2

Fig. 6. Transverse section of arachnoid granulation showing capillaries (*Cp*). Paraffin embedded, H. & E. × 530.

Fig. 7. Photograph of arachnoid granulation after subarachnoid injection with indian ink, showing openings of crypts (*o.Cr*) and indian ink (*I*) in sinus. × 3.

Fig. 8. Transverse section of sheep granulation after intra-arterial injection with indian ink. Arrow shows capillary filled with the ink while the tubule (*T*) is empty. Araldite embedded, toluidine blue. × 530.

Fig. 9. Transverse section of granulation following injection of indian ink into the subarachnoid space. Arrow shows indian ink in tubule. Indian ink is also seen in the spaces between collagen bundles. Methacrylate embedded, H. & E. × 530.

Fig. 10. Transverse section of arachnoid granulation after subarachnoid injection with indian ink. Arrow shows tubules filled with indian ink while capillaries (*Cp*) are empty. Paraffin embedded, H. & E. × 54.

Fig. 11. Transverse section of granulation after subarachnoid injection with indian ink. Thick arrow shows indian ink in core of granulation, which masks the tubules. Thin arrow indicates ink in isolated tubule while capillary (*Cp*) is empty. Indian ink (*I*) is also seen in the venous sinus. Paraffin embedded, H. & E. × 164.

PLATE 3

Fig. 12. Longitudinal section of junction of granulation with subarachnoid tissue. Arrows indicate indian ink particles lying in tubule-like spaces in subarachnoid tissue. Araldite embedded, toluidine blue. × 580.

Fig. 13. Longitudinal section of arachnoid granulation showing nerve fibres (*N*). Peters's silver proteinate. × 530.

Fig. 14. Transverse section of granulation showing myelinated nerve fibres (*N*). Osmium fixed, Araldite embedded, toluidine blue. × 600.


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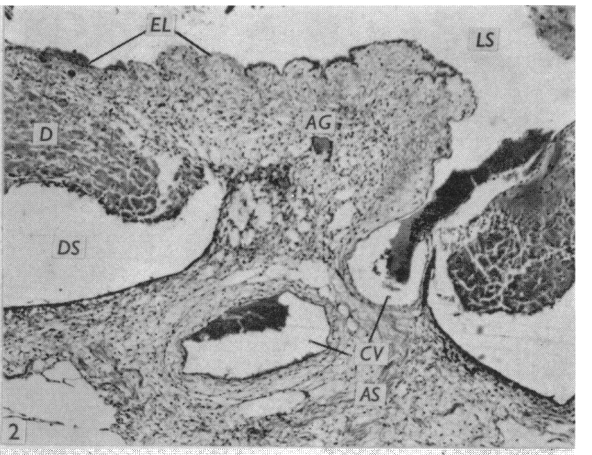
LS
AG
TS
1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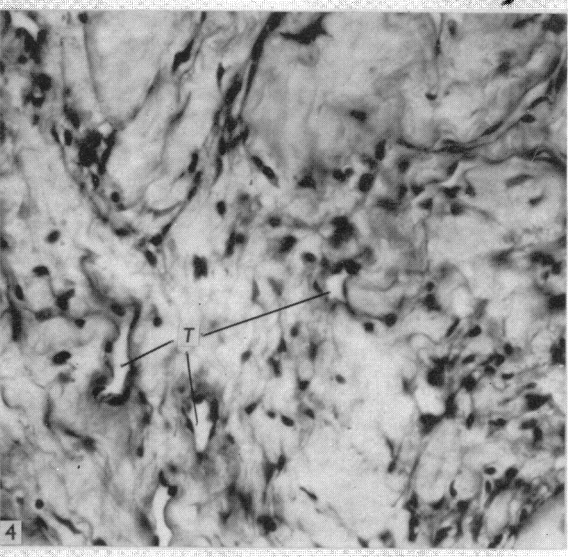
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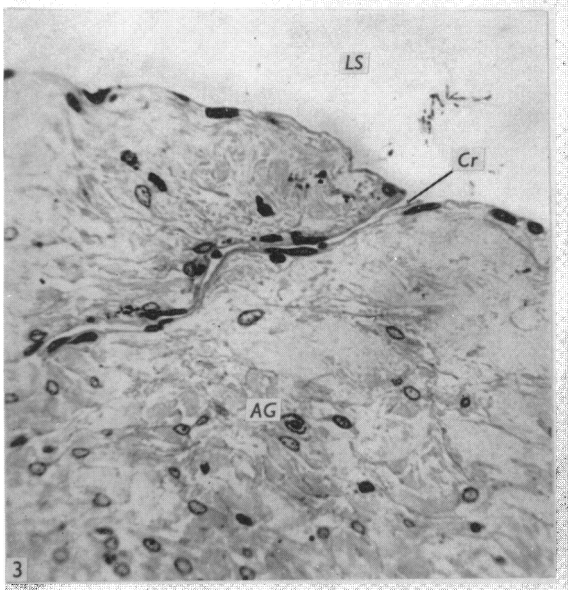
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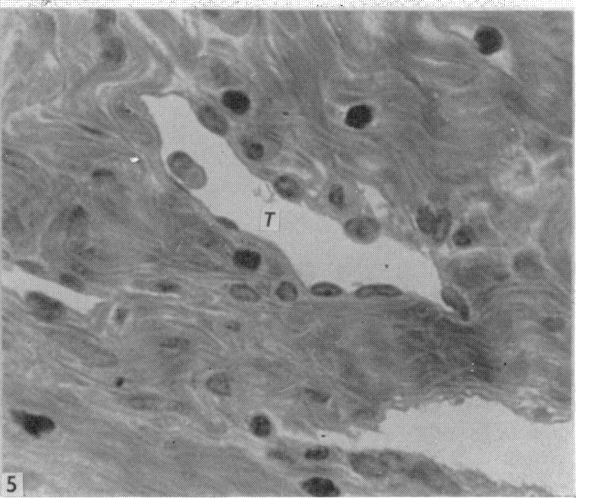
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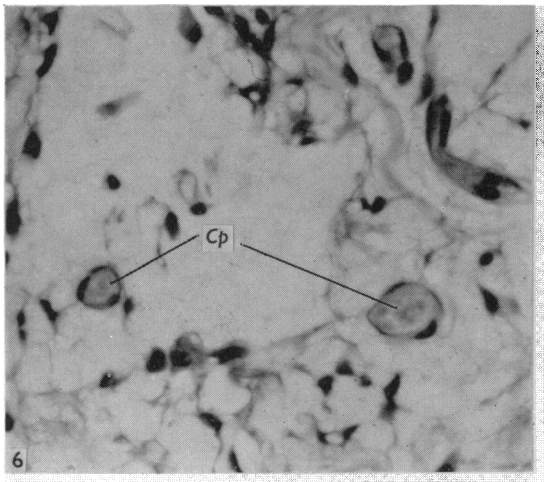
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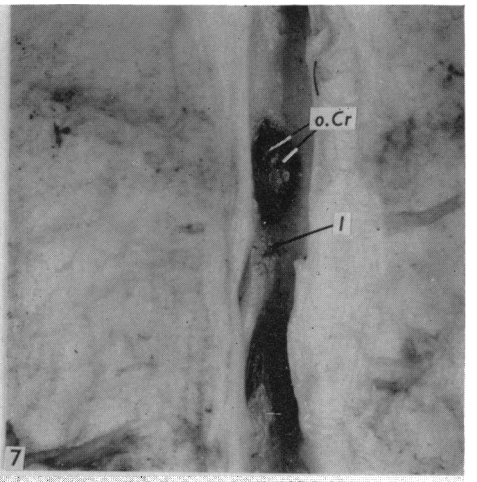
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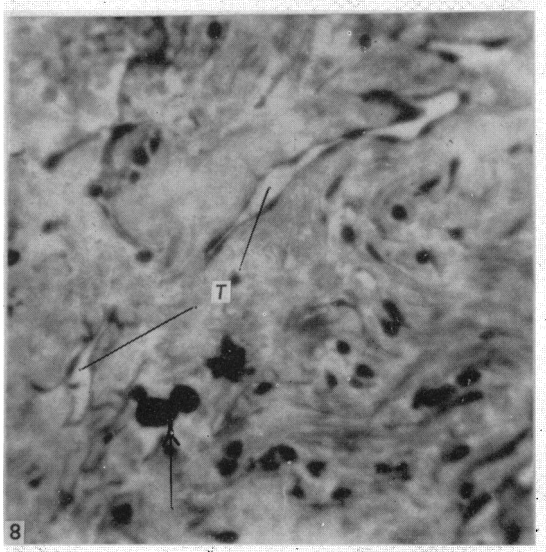
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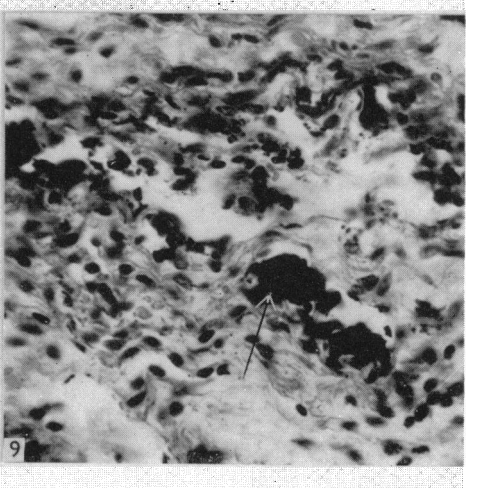
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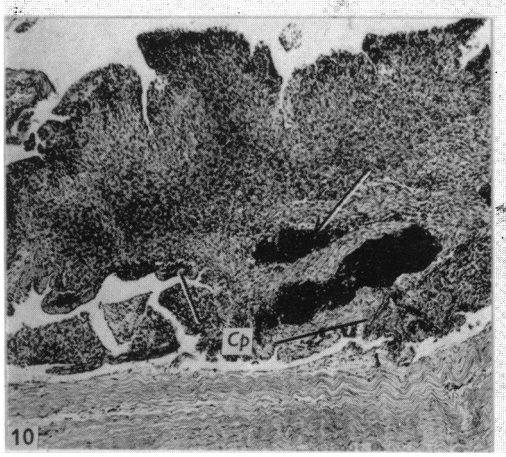
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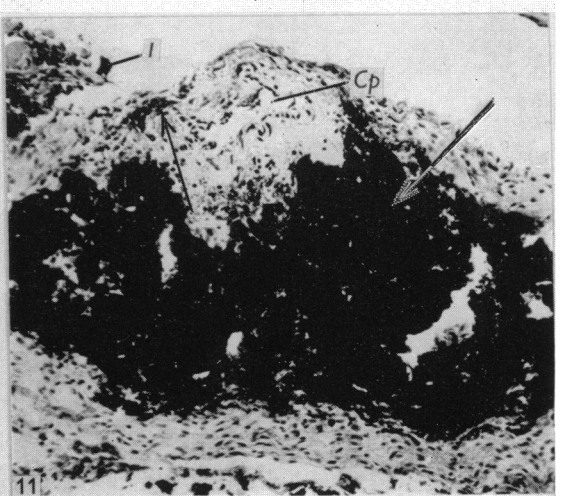
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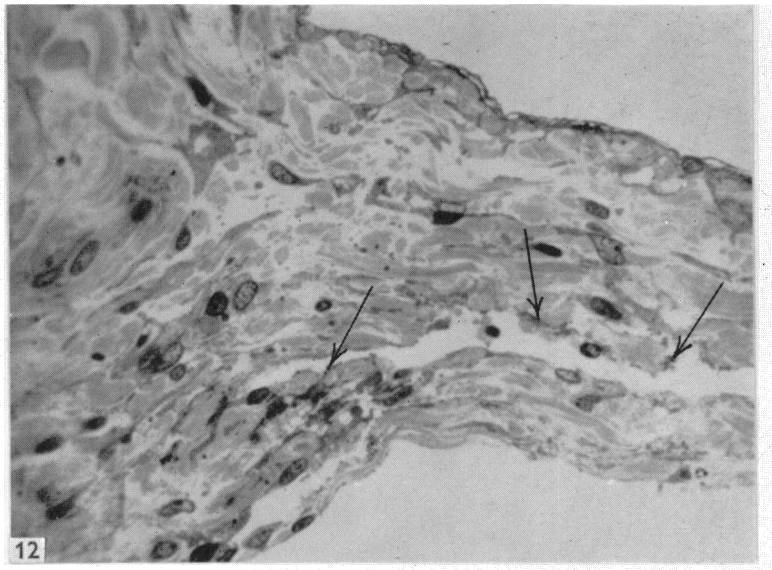

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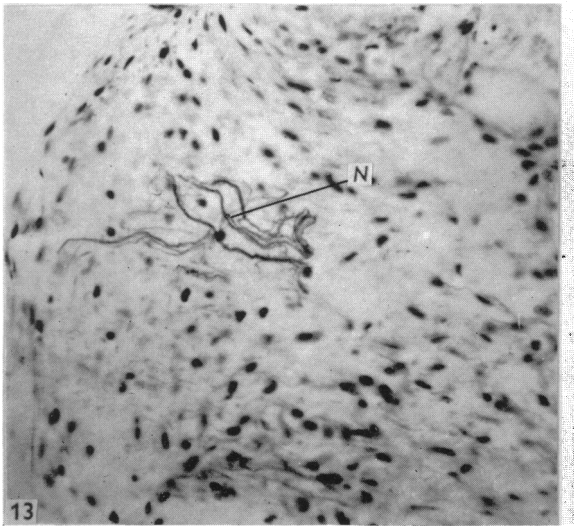

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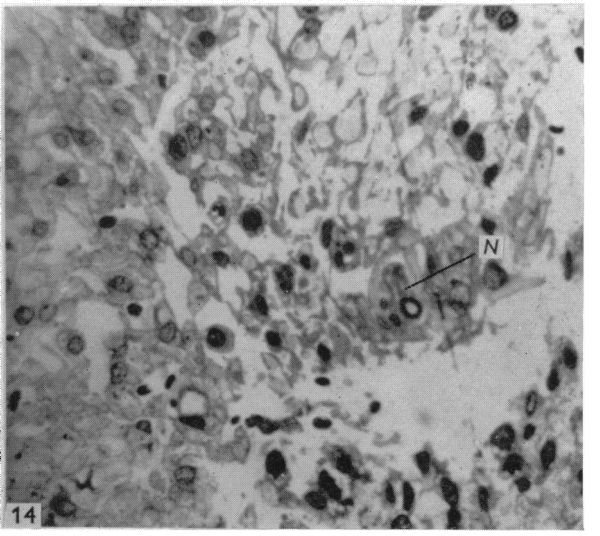

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