THE NERVOUS COMPONENT OF THE ATRIOVENTRICULAR BUNDLE

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In his monograph *Das Reizleitungssystem des Säugetierherzens* Tawara (1906) described numerous nerve fibres accompanying the atrioventricular bundle and its branches. He spoke of 'außerordentlich zahlreichen Nervenbündel' in the left branch of the bundle (calf) some of which when traced distally '...den linken Schenkel verlassen und sind entweder subendokardial oder intermuskular nach anderen Richtungen gezogen' (p. 107 loc. cit.). It would appear from this description and from the beautiful illustrations given by Wolhynski (1928) that a fully fledged alternative conducting system between atria and ventricles exists. Wilson (1909), Engel (1910), Meiklejohn (1914) and Scaglia (1927) all found nerves within the bundle but considerable species differences were reported. Woollard (1926) claimed that very fine fibres of the intracardiac network actually penetrated the substance of individual heart-muscle fibres and ran therein for considerable distances giving off at intervals small terminal loops and swellings. Much the same appearances were recorded, too, by Boeke (1932). These anatomical findings have, however, received scant recognition in current views of the mechanism of the heart beat, though strong criticism has come recently from Glomset and his co-workers (1940, 45, 48). In view of the importance of anatomical structure as a sound basis for physiological theory, it was decided to examine the nervous component of the atrioventricular bundle in a variety of animals.

MATERIAL AND METHODS

The animals examined were sheep (foetal and adult), rabbit, guinea-pig, rat, cat, dog, macaque, chimpanzee, gorilla and man. From each heart a block of tissue was cut comprising the interatrial septum and the upper part of the interventricular septum. Fixation was in 10% neutral formalin and frozen sections at 40μ were impregnated by the method of Bielschowsky-Gros. In the case of the gorilla heart and in one human heart paraffin sections (10μ) were prepared and stained by Bodian's method. Methylene blue was tried initially with rabbit material, and although some satisfactory preparations were made they did not compare in clarity with the silver method. Difficulties of interpretation as between nerve fibres and connective tissue strands have been remarkably few with the silver method—fewer than with methylene blue. One or two technical points may be mentioned. The initial silver bath (20% silver nitrate) should not be prolonged beyond 1 hr., 30–35 min. is quite satisfactory. In making up the ammoniacal silver solution, whilst no definite rule can be given as to the quantity of ammonia which should be incorporated, it does seem important to add the ammonia a few drops at a time and

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to shake well immediately after each addition. It is not satisfactory to add in one stage the approximate amount of ammonia required and then finish off by adding drops.

OBSERVATIONS

Sheep. Numerous bundles of nerve fibres are embedded in the substance of the atrioventricular bundle. Many appear to originate in scattered masses of ganglion cells in the lower part of the interatrial septum in and around the atrioventricular node. At the bifurcation of the bundle nerves pass into both right and left branches (Pl. 1, fig. 1). These nerves may leave a branch and pass for considerable distances subendocardially (Pl. 1, fig. 2) before turning into the myocardium. The further fate of these nerves is difficult to follow. Nerve fibres also accompany the larger blood vessels, though endings within the media were never seen. It is interesting to recall that Stöhr (1928) never found nerve endings stainable with silver within the media of vessels, though Blair & Davies (1935) claim to have demonstrated them. Within the myocardium there is a beautiful network of capillaries elongated in the direction of the heart muscle fibres and so rich that fibres and capillaries alternate. In more or less close relation to these capillaries fine non-myelinated nerve fibres twist and turn but never, apparently, form nerve endings on capillary walls. The appearances suggest a closed network of nerve fibres as described by Stöhr (1928). Many of the fine nerve fibres pass very close to muscle fibres and some even seem to pass through their substance, though it is surprisingly difficult to be certain of the relation of nerve fibres to muscle cells even at high magnification with stereoscopic eyepieces. Certainly no nerve terminations of the type depicted by Boeke (1932) were found, though admittedly he employed a slightly different staining technique. It seems probable that there is continuity between the nerve fibres leaving the bundle branches and the intramural network, for the origin of which it would be difficult to account; but in the present material this continuity could not be established with any degree of certainty. An origin from the nerve plexus accompanying the coronary vessels is conceivable, for there is undoubtedly a rich plexus surrounding the larger vessels. In spite of numerous attempts, however, it has not been found possible to demonstrate more than a few nerve fibres in association with the smaller coronary vessels, and certainly not sufficient to account for the rich plexus within the myocardium.

Rabbit. Numerous non-myelinated fine nerve fibres pass amongst the cells of the atrioventricular node, coming into intimate contact with muscle cells (Pl. 1, fig. 3). The bundle and its branches are poorly developed and the latter can be followed for only a short distance on each side of the upper part of the interventricular septum. The nerve fibres of the node do not become massed into definite strands within the bundle, but individual fibres interlace with muscle cells. Moreover, many nerve fibres surround the bundle and are not actually within its substance. Once the bundle reaches the upper part of the interventricular septum considerable numbers of nerve fibres pass off into the septum. Biggs (1908), working with the isolated perfused rabbit heart, found it impossible to produce marked or permanent dissociation between atria and ventricles by extensive lesions of right and left bundle branches in the interventricular septum. He came to the conclusion that there must be some other path of conduction which could only be divided by an incision at, or before, the bifurcation of the atrioventricular bundle. It has been claimed that such results may be due to the existence of aberrant conducting fibres which leave the main atrioventricular bundle to pass independently through the fibrous skeleton of the heart. In two rabbit hearts examination of complete serial sections of the bundle and its division failed to show any such aberrant fibres. The arrangement of the nervous component of the bundle as described above is such that only wide incisions in the upper part of the interventricular system are likely to divide it completely. If the nerves of the bundle do indeed play an important part in conduction of the heart beat, then their arrangement might well explain the extensive nature of the lesions which Biggs found necessary to produce dissociation. This finding has recently been confirmed in unpublished work by Field & A. F. Rogers.

Rat. The bundle and its branches are poorly defined histologically in this animal. Numerous fine non-myelinated fibres pass through the atria to the ventricles in the neighbourhood of the bundle rather than within its substance (Pl. 1, fig. 4). Many show well-marked beading (Pl. 1, fig. 5). Having reached the interventricular septum the nerves quickly become lost within it.

Guinea-pig. In this animal the nervous component of the bundle is more compact than in the rabbit or rat, its arrangement resembling rather that obtaining in the sheep. The bundle itself is somewhat more easily made out than in the rat, and once again the nerve fibres within it pass off into the upper septal musculature (Pl. 2, fig. 6).

Dog. The atrioventricular node in this animal is permeated through and through with a remarkable network of fine non-myelinated nerve fibres (Pl. 2, fig. 7). The photograph hardly gives an adequate impression of the richness of fibres within the node. As examination is made under high magnification with the fine adjustment of the microscope more and more nerve fibres come into view intimately related to muscle cells. Nerve endings are, however, conspicuously absent. Within and around the bundle are more or less compact nerve fascicles; occasional fibres appear to have a myelin sheath (Pl. 2, fig. 8). In the upper part of the interventricular septum many nerve bundles forsake the conducting system and pass into the myocardium. At intervals individual fibres separate from these bundles. The richness of the nervous component of the conducting system in the dog is striking, and is of especial interest as this animal has been so widely used experimentally in work on the conduction of the cardiac impulse.

In the lowest part of the interatrial septum, in and around the region of the atrioventricular node, there are many islands of ganglion cells from which the nerves of the bundle take origin (Pl. 2, fig. 9).

Macaque and Chimpanzee. Ganglion cells are frequently met with in clusters in the lower part of the interatrial septum of these animals, and in the macaque they are occasionally binucleated and lobulated. Within the conducting system of these animals—not at all well developed histologically—there are relatively few nerve fibres as compared with the previous animals described, and the few there are appear as isolated fibres (Pl. 2, fig. 10). On two occasions, in some fifty sections, the writer has come across what appear to be nerve endings in relation to muscle cells in the bundle of the macaque. These endings are very minute but they do bear some resemblance to those described in the general myocardium of the sheep

(Boeke, 1932). If these be true nerve endings they must be very rare or very difficult of impregnation. They appear to be of digitate type and on focusing up and down a suggestion of a periterminal network may be made out.

In the subendocardium of the interventricular septum fine beaded nerve fibres were found in the chimpanzee (Pl. 3, fig. 11). Many end in small terminal enlargements immediately beneath the endocardium. It was not possible in the sections prepared to determine whether these fibres were in continuity with those of the atrioventricular bundle. The intramural nerve plexus described above in the sheep heart was particularly well impregnated in the chimpanzee myocardium and appeared to be of the same character (Pl. 3, fig. 12).

Gorilla. The atrioventricular bundle in this animal contains no discrete nerve fascicles. The bundle was sectioned transversely—an unfavourable plane for picking out longitudinally running nerve fibres, but there do seem to be some fine non-myelinated, beaded fibres associated with it, especially near its periphery (Pl. 3, fig. 13). These fibres are gathered together into more compact bundles on reaching the interventricular septum and can be found coursing within the myocardium (Pl. 3, fig. 14). Their mode of termination could not be discovered.

Man. In relation to the atrioventricular node and bundle there are considerable numbers of fine nerve fibres, more especially around the bundle than in it (Pl. 3, fig. 15). Some of the nerve fibres leave the vicinity of the bundle to pass through the fibrous tissue surmounting the interventricular septum.

DISCUSSION

In or associated closely with all the atrioventricular bundles examined considerable numbers of nerve fibres were found. These fibres in some animals (sheep) are gathered together into discrete fascicles whilst in others with less well developed bundles they tend to run singly in a tortuous fashion. It would seem that when the bundle is well developed it acts as a great high-road from atria to ventricles and many nerve fibres pass within it. It may be that the general looseness of texture of the bundle and the fact that it develops in a region of relative quiescence (Field, 1950) make it a particularly favourable stroma for nerve fibres. When the nerve fibres are less numerous they tend to travel singly and often pass in the general neighbourhood of the bundle rather than within its confines. Lawrentjew & Gurwitsch-Lasowskaja (1930) studied the nerves of the atrioventricular bundle in the rat. They were struck by the 'erstaunliche Reichtum des Atrioventrikularbündels an Nervenelementen' (p. 591), and described the nerve fibres as forming a superficial plexus on the surface of the bundle and a deeper one within it. This latter, they claimed, consisted of fine non-myelinated fibres, whilst the former contained some myelinated fibres also. They found small ganglion cells (6–10 μ) scattered in the superficial plexus and noted their poorly argentophil character, it being necessary to overstain the preparation in order to render them at all visible. Deliberate overstaining brings in difficulties of interpretation because of connective tissue impregnation, and all preparations in the present work which showed connective tissue staining have been rejected. Lawrentjew & Gurwitsch-Lasowskaja were never able to see fibres leaving the neighbourhood of the bundle to pass off into the general myocardium. The present material, however, affords many instances of such an occurrence both in lower animals (Pl. 2, fig. 6) and in man.

It must be recognized, therefore, that a nervous atrioventricular pathway exists in and around the atrioventricular bundle. Moreover, this nervous pathway is so intimately related to the bundle that lesions, pathological (e.g. Perry & Rogers, (1934), or experimental, must necessarily involve both the muscular and the nervous component. This fact, of outstanding importance, was clearly recognized by Cohn & Trendelenburg as long ago as 1910. They wrote: 'Man wird also immer im Auge behalten müssen, daß selbst bei einem Schnitte, der auf das genaueste die Grenzen der muskulären Bündelfaserung einhält, eine Unzahl feinster Nervenfasern durchschnitten wird so daß eine funktionelle Ausschaltung lediglich der Muskelfasern des Bündels ein Ding der Unmöglichkeit ist' (p. 84). From their careful and detailed study of the effects of lesions produced in the course of the atrioventricular bundle these authors cautiously drew the conclusion that 'Es kann nunmehr mit Sicherheit gesagt werden, daß dieser Weg auf das Engste mit dem Übergangbündel (worunter in diesem allgemeinen Sinne stets Muskulatur mit Nervengespinnst verstanden ist) zusammenfällt' (p. 84). Nevertheless, since that time attention—particularly from the clinical standpoint—has been fixed almost exclusively on the muscular component. It is difficult to establish the origins of such an unbalanced outlook, particularly as Wilson (1909) was driven to the conclusion that 'The neurologist might well refuse to recognize in...(the atrioventricular bundle)...a muscle bundle; to him it might become conspicuously a nerve pathway of very intricate structure' (p. 157). It may be that emphasis has fallen mainly on the muscle of the bundle because of the relative ease with which it can be examined histologically as opposed to the more complicated methods, often difficult of interpretation, necessary for the demonstration of the nervous component.

Some authors have described ganglion cells in the atrioventricular bundle at its bifurcation and in the proximal parts of the bundle branches, Tawara (1906), Lawrentjew & Gurwitsch-Lasowskaja (1930). The latter authors draw attention to the difficulty of demonstrating such cells, for even when the nerve fibres are adequately impregnated they appear very pale. In the present material nerve cells could not be identified with certainty within the atrioventricular bundle or its branches, though they were numerous in the region of the atrioventricular node. Engel (1910), using a methylene-blue technique on the calf heart, was unable to demonstrate the rich pericellular plexus described by Wilson (1909) within the bundle, but claimed that its innervation did not differ materially from that of the general myocardium. For him the thing which distinguished the bundle was the presence of the large nerve trunks which passed within it and divided to pass into its right and left divisions. Engel estimated that in the calf bundle there were about twice as many non-myelinated as myelinated fibres. Fukutake (1925), again using a methylene-blue method, described a fine nerve plexus in association with the fibres of the general myocardium and encompassing also the Purkinje system. From his description and illustrations, however, it is probable that he was dealing, to some extent at all events, with connective tissue fibres. Vitali (1937) has described a very rich network of delicate nerve fibres surrounding each Purkinje cell and penetrating within the cytoplasm to end in the neighbourhood of the nuclei. He is inclined to regard the pericellular network as sensory in function, and is of the opinion that in its varying stimulation during different phases of the cardiac cycle it may aid in the regulation of the heart beat. Nonidez (1943), however, is of the opinion that the fibres described by Vitali are part of the argyrophil reticulum present everywhere in the myocardium. Scaglia (1927) found such large numbers of nerve fibres within the atrioventricular bundle that he came to the conclusion that they were not expended solely in the innervation of Purkinje tissue, but passed also to other parts of the heart. Mingled with these nerve fibres Scaglia found nerve cells either singly or in small groups. These findings were limited to the heart of *Bos taurus*, but the author expressed the opinion that fundamental species differences were unlikely.

FUNCTION OF THE NERVOUS COMPONENT OF THE ATRIOVENTRICULAR BUNDLE

It is generally accepted that the vagus nerves depress the activity of the conducting system, though the mechanism of such action remains obscure. The nerve fibres within the atrioventricular bundle are regarded for the most part as postganglionic autonomic fibres regulating conduction of the cardiac impulse carried by the specialized muscle of the bundle. Whilst it is not proposed to re-open here the question of myogenic as against neurogenic conduction of the heart beat, it should be emphasized that there exists between atria and ventricles a considerable nervous pathway, intimately related to the muscular bridge so widely accepted as the true conductor of the cardiac impulse. It must further be noted that the relation between the nervous and muscular components of the bundle is so close that it is impossible by experimental means to destroy one without the other (Cohn & Trendelenburg, 1910). The numerous experiments of this type only show that the path of atrioventricular conduction resides in the bundle, but cannot testify as to the relative parts played by the muscle and nerve components. Some evidence in this respect is, however, afforded by the work of Agduhr (1933) and Agduhr & Stenström (1928). They showed that cod-liver oil in certain dosages produced focal areas of degeneration in the myocardium. In the course of large numbers of experiments on mice it might occasionally happen that such lesions involved the atrioventricular bundle without necessarily producing a complete heart block. In one such heart Agduhr (1933) was able to find seemingly intact nerve fibres in the vicinity of the atrioventricular bundle. On the basis of his observations he raised the question whether it might not be the nerve fibres rather than the specific muscle tissue which were the conducting elements in the bundle. Wahlin (1935) was able to confirm Agduhr's observations. He found that sclerotic patches developing in the course of the atrioventricular bundle might be associated with a normal prolonged P-R interval but did not necessarily entail atrioventricular dissociation. Such cases showed intact nerve fibres passing from atria to ventricles in the vicinity of the bundle. These observations he regarded as 'eine Stütze fur die neurogene Auffassung daß die Nerven und nicht die muskuläre Komponente des His'schen Bündels das Substrat der Reizleitung zwischen Vorhof und Kammer darstellen' (p. 86).

It is interesting to find that Glomset and his co-workers (1940–8), from their extensive review of the literature and examination of clinico-pathological material, are also inclined to afford the intrinsic nervous system of the heart an important role in cardiac action. Indeed they reach the conclusion that 'an atrioventricular muscular conduction system does not exist in any of the species studied. Therefore, the present concept of cardiac conduction is as inaccurate as was the concept of the circulation in preharveian days' (1948, p. 170).

SUMMARY

The nervous component of the atrioventricular bundle has been described in sheep, rabbit, guinea-pig, rat, cat, dog, macaque, chimpanzee, gorilla and man. The possible significance of these fibres is briefly discussed.

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EXPLANATION OF PLATES

PLATE 1

Fig. 1. Coronal section through the upper interventricular septum of a 38 cm. sheep embryo. The bifurcation of the atrioventricular bundle is seen straddling the septum and bundles of nerve fibres are present within the right and left branches. ×110.

Fig. 2. Right face of interventricular septum showing subendocardial nerve bundles derived from the right branch of the His bundle. 38 cm. sheep embryo. ×110.

Fig. 3. Atrioventricular node of rabbit heart. Numerous fine beaded nerve fibres are seen intertwining with pale muscle cells. ×780.

Fig. 4. Coronal section through rat heart. Numerous nerve fibres are seen in association with the atrioventricular bundle. ×110.

Fig. 5. High power view of fig. 4. Beaded character of the atrioventricular nerve fibres is apparent. ×850.

PLATE 2

Fig. 6. Coronal section through upper part of interventricular septum of guinea-pig. To the right is the left branch of the atrioventricular bundle accompanied by a nerve bundle. A single nerve fibre is seen leaving this bundle and passing off with the septal musculature. ×350.

Fig. 7. Atrioventricular node of dog heart. A very rich plexus of fine nerve fibres is seen intermingled with the tangled and rather poorly staining muscle fibres of the node. ×700.

Fig. 8. Small bundle of nerve fibres accompanying the atrioventricular bundle of the dog. One fibre shows a distinct myelin sheath.

Fig. 9. Group of ganglion cells in the lowest part of the interatrial septum; giving origin to some of the nerve fibres of the His bundle. Dog heart. ×400.

Fig. 10. Macaque atrioventricular bundle. Single nerve fibre coursing between poorly differentiated muscle cells. ×1000.

PLATE 3

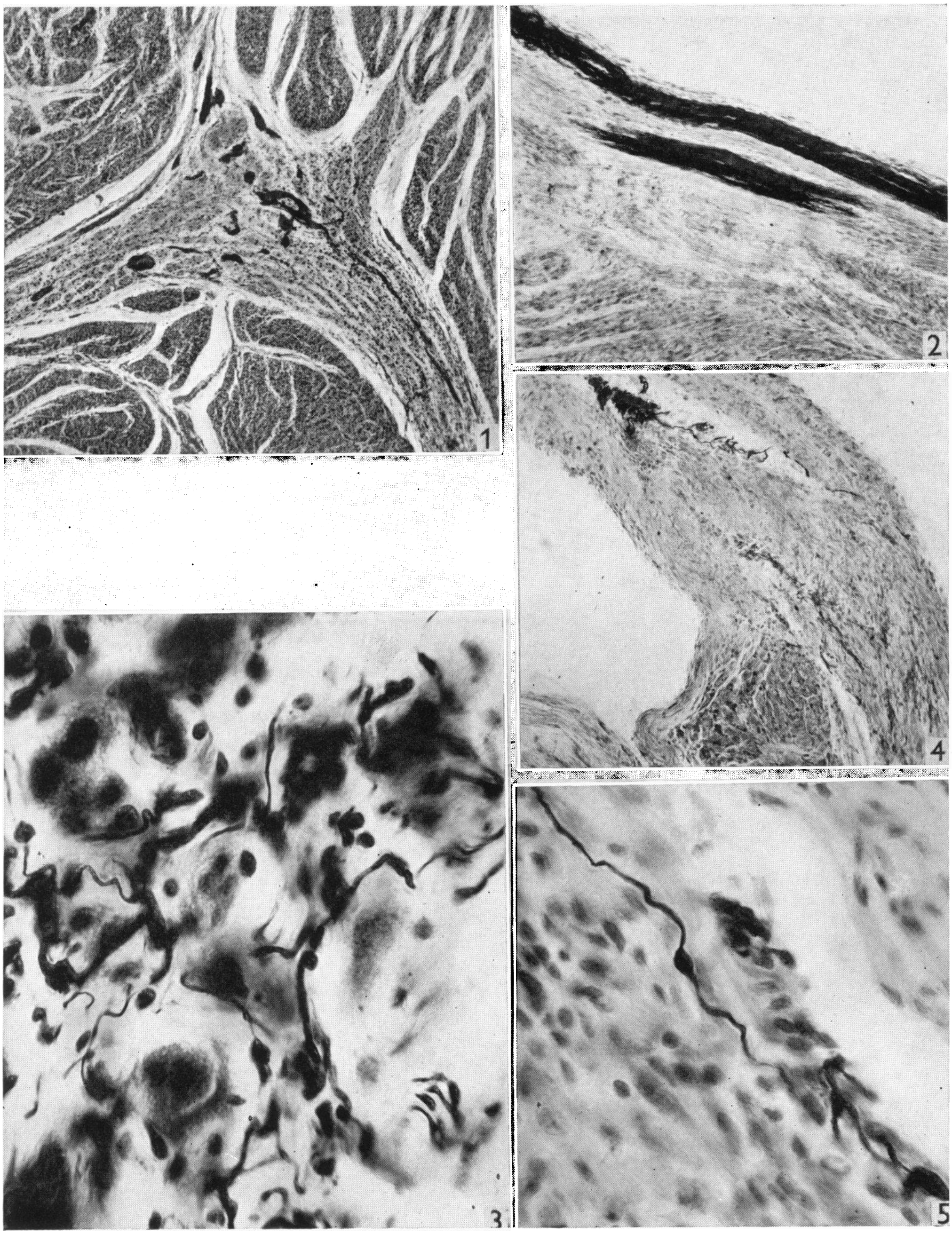
Fig. 11. Chimpanzee heart. Right face of interventricular septum showing fine beaded subendocardial nerve fibres some of which seem to end in terminal knobs beneath the endocardium itself. ×650.

Fig. 12. Chimpanzee: interventricular septum. Fine beaded nerve fibres accompanying capillaries between muscle fibres. These nerve fibres seem to be organized into a closed network. ×650.

Fig. 13. Gorilla. Transverse section through atrioventricular bundle showing fine beaded nerve fibres round its periphery. ×450.

Fig. 14. Gorilla. Interventricular septum. Strand of nerve fibres which has come through with the bundle of His ramifying in the muscle of the septum. Bodian stain. ×100.

Fig. 15. Human. Left branch of His bundle, accompanied by strand of nerve fibres. ×400.



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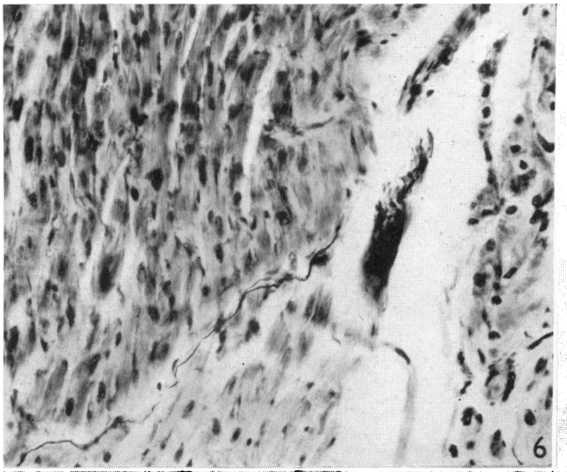

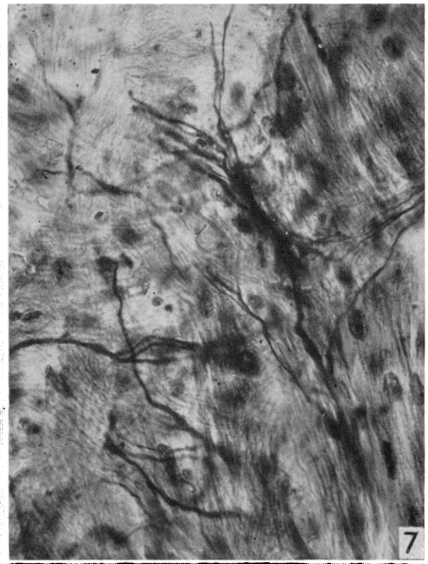

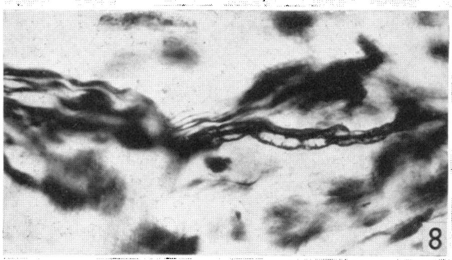

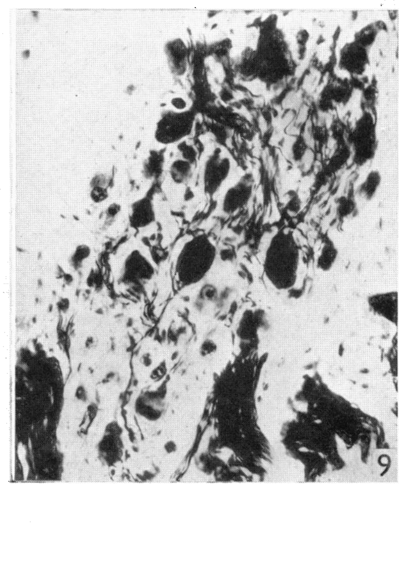

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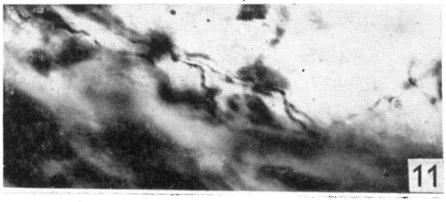

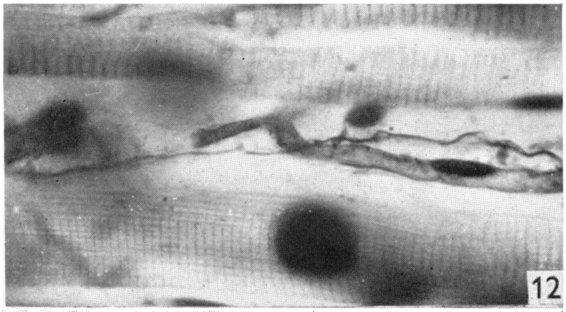

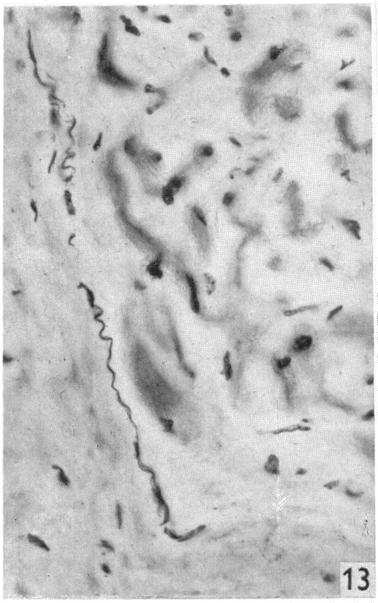

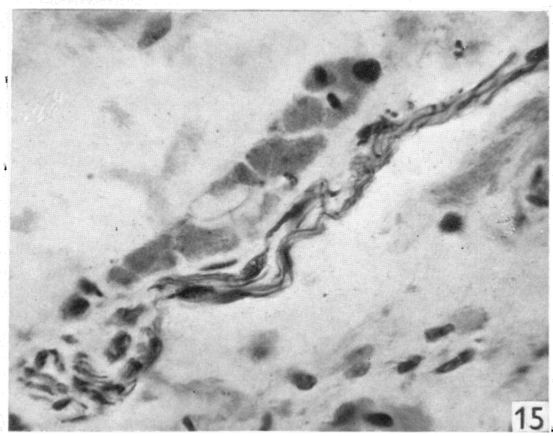

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