The Nerves of the Atrio-ventricular Bundle.

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[Plates 4—6.]

Physiologists, in explaining the transmission of the wave of contraction in the heart from atrium to ventricle, have alternately leaned towards either the myogenic or the neurogenic hypothesis. Many of the discussions on this subject have been useless and many of the deductions false, because of the misconception of the anatomical facts. For long it was held that though in cold-blooded vertebrates the experiments of Gaskell had settled the question in favour of the myogenic theory, yet in mammals there existed an interruption between the atrial muscle and the ventricular muscle at the atrio-ventricular groove, and that this was opposed to a general acceptance of the myogenic theory. Later anatomical investigation, however, has definitely shown that there exists in all mammals, between the atria and the ventricles, a pathway of modified muscle fibres along which the contraction wave appears to go. This is the atrio-ventricular (auriculo-ventricular) bundle, or bundle of His. The discovery of this muscular connection gave very decided support to the myogenic hypothesis, and at present it would appear that prevailing opinion favours this theory. It receives additional support in so far that in this bundle only a few nerve fibres have as yet been recognised by one or two observers; some assert that nerves are not present, or, if so, are too few in number to be of any moment. More definite statements have been made by Tawara and Retzer. Tawara (1) found that "in the heart of the calf the atrio-ventricular bundle is accompanied by a very considerable nerve bundle, which runs with the muscle bundle, and in the left ventricular septum nerve cells are present 1·2 cm. below the aortic valve." In the atrio-ventricular bundle of the sheep only a few nerve bundles were seen, but in the dog, cat, and in man he could find none, though he expressly states that these cannot be excluded, since fine nerve fibres accompany the bundle. Retzer (2) has pointed out that the first ganglion cells that appear in the embryonic heart lie in the atrial septum, immediately above the beginning of the conductive system; further, that the Purkinje fibres are surrounded by a plexus of non-medullated nerves.

Such is the present position of our knowledge of the nerve constituents of

the atrio-ventricular bundle. Although a vast amount of work has been done on the nerves of the heart generally, yet, so far, but little attention has been directed to this particular and definite strand. In this preliminary paper I have limited the report to the muscle band as it passes from the atrium to the ventricle, and shall not discuss the nerve constituents in the connections of the atrio-ventricular bundle with the ordinary muscle of the atrium or of the ventricle; that is, I limited the investigation to that part which extends from a point in the bundle towards the coronary sinus over the bifurcation into right and left branches and down these into the right and left ventricles. These parts are represented in figs. 1 and 2 (Plate 4).

Historical.—The first specific demonstration of the presence of a muscular connection between the atrium and ventricle was given by Gaskell in 1883. Previous to that time many writers had declared that such a connection existed, but their statements were indefinite. For instance, Paladino (3) is referred to by Bardeleben as having found that "die Vorhofsmuskulatur endet nicht an den Annuli fibro-cartilaginosi, sondern geht grossentheils in die Ventrikelwand und die Papillarmuskeln weiter." It was Gaskell (4) who first definitely showed that in the tortoise the contraction wave spreads from the sinus over the auricle to the ventricle by means of the muscular connection which exists between the three parts of the heart at the sino-auricular and auriculo-ventricular grooves. He found that at the sino-auricular junction the fibres of the sinus form a circular muscle-ring from which the fibres of the auricle take origin. From this origin the fibres of the auricle, after ramifying in all directions, approach and get attached to the upper and middle part of the auriculo-ventricular groove, forming a ring of muscle fibres from which in turn the fibres of the ventricle take origin. By experimentally sectioning between the two auricles, and by removal of the visceral pericardium, he was able to show that the "ventricle contracts in due sequence with the auricle, because a wave of contraction passes along the auricular muscle and induces a ventricular contraction when it reaches the auriculo-ventricular groove." The integrity of the whole muscle at the auriculo-ventricular groove is unnecessary for this sequence, for there exists a definite track along which the wave of contraction passes. Histologically he found that the muscle fibres present in the auriculo-ventricular muscle-ring differed from the muscle cells of the auricle and ventricle both in the size of the nucleus and the character of their striation.

In spite of Gaskell's work, the hypothesis generally accepted was that the contraction wave cannot be myogenic because in mammals there occurred a distinct break between the muscle of the atria and the muscle of the ventricles. It was held that the atrial fibres and the ventricular fibres

belonged to independent systems, and were separated by a considerable amount of connective tissue at the atrio-ventricular junction. In 1893, ten years after Gaskell's work appeared, Stanley Kent (5) showed that muscular connection did exist in the mammalian heart. He found in young rats that there was at birth a well-defined continuity of atrial and ventricular muscles. As age advanced there took place a considerable development of connective tissue in the atrio-ventricular groove; nevertheless, in adults there still persisted well-marked bands of muscle tissue between the two chambers over a considerable area of the atrio-ventricular groove, and in particular at the junction of the atrio-ventricular septum. This muscular connection varied in amount in different animals, yet could be demonstrated in all; but the exact location of these bands he did not definitely determine.

In the same year there appeared the work of Wilhelm His, junior (6), "Die Tätigkeit des embryonalen Herzens und deren Bedeutung für die Lehre von der Herzbewegung beim Erwachsenen." Here for the first time was given the definite location of the atrio-ventricular bundle. His demonstrated that in the earliest stages of development of the mammalian heart there exists a continuous muscle union between the heart segments, and that the primitive contraction goes on without the presence of ganglion cells. Further, it was erroneous to suppose that this primitive continuity of muscles was completely interrupted in the adult by connective tissue at the atrio-ventricular groove; that while a break did occur it was by no means complete, for at a particular place in the atrio-ventricular septum muscular union persists. This union is brought about by a strand of muscle fibres which springs from the posterior wall of the right atrium, passes forward to the atrio-ventricular groove lying in the upper part of the ventricular septum, soon forking into right and left branches. The presence of this bundle of His has been confirmed by many subsequent writers.

The most important work on the atrio-ventricular bundle is that of Tawara (1), "Das Reizleitungssystem des Säugetierherzens." This Japanese investigator, working in Aschoff's laboratory in Marburg, published, in 1906, a careful and exhaustive monograph on the macroscopic and microscopic appearances of the bundle in a series of mammals. In it he demonstrated the connections of the fibres of the bundle with the ordinary cardiac muscle and the relation of the Purkinje fibres throughout the heart to the atrio-ventricular fasciculus. His findings (7) may be summarised as follows:—

(1) In man and all the animals examined, the Purkinje fibres or their equivalents form the outspreading of a muscular system which unites the atrial muscle to the ventricular muscle. This muscular system constitutes the atrio-ventricular bundle.

(2) This muscular system has a uniform arrangement in all mammals, though slight individual differences appear. It runs from the atrial wall through the atrio-ventricular fibrous septum to the point where it spreads out in the ventricular wall, at first as a bundle enclosed in connective tissue, then spreading out into tree-like end branches. The closed strand never enters into relation with the ventricular muscle, but the end branches fuse with the usual ventricular muscle.

(3) This uniting system is early developed in the embryo. From this time on, leaving growth out of consideration, it remains unchanged during life. It is *not* affected by hypertrophic and atrophic processes in the heart in the same way as the ordinary cardiac muscle.

(4) The topographical, histological, and biological peculiarities of this system are opposed to the suggestion that its function is that of a heart pump, like the ordinary cardiac muscle. Moreover, the physiological experiments of Gaskell, Engelmann, Herring, and others suggest that in this system can be found a conducting path for the co-ordination of the heart muscle.

Macroscopic Description of the Bundle.—To dissect out rapidly the atrio-ventricular bundle, I have found it best first to identify the pale pink muscle fibres of the right and left branches. These are more or less subendocardial. The left is readily observed at a varying distance beneath the junction of the posterior semilunar (non-coronary) with the right semilunar valve. The right branch, less readily found in some mammals because covered by a thin layer of ventricular muscle, can be found lying near the line which joins the moderator band to a point under the medial (septal) cusp, adjacent to its junction with the anterior (infundibular) cusp of the tricuspid valve. From either of these points the entire atrio-ventricular band can be dissected out.

As seen in the calf, where it is very large, the bundle originates in the posterior wall of the right auricle in the region of the sinus coronarius (Plate 4, figs. 1 and 2). At this point there is a mass of pink fibres—not red like the ordinary cardiac fibres, and less pale than the main continuation of the band. It is cone-shaped in appearance, with an ill-defined base merging into the auricular muscle and a well-marked apex passing into the narrow band of white tissue which goes forward into the atrio-ventricular septum in a groove on the under surface of the cardiac cartilage. Reaching the upper part of the interventricular septum, it divides into a right and a left branch. The right branch passes downward on the septal wall of the right ventricle more or less superficial towards the septal attachment of the moderator band. Here it begins to separate out and send branches into the septum. If a transverse section be made of the moderator band, Purkinje fibres are seen in

small bundles isolated by more or less definite connective tissue sheaths. Through the moderator band it reaches the lateral wall of the ventricle and the papillary muscles. The left branch appears under the endocardium of the septal wall of the left ventricle about 1·5 cm. below the junction of the posterior with the right semilunar valve. Immediately under the aortic opening it is covered with cardiac muscle. On reaching the surface of the heart it spreads out and sends branches downwards and outwards to the septal and lateral walls of the ventricle.

In mammals generally, the course of the atrio-ventricular bundle agrees in the main with this, but some slight differences are observed. Thus in the sheep the band is smaller and less distinct. The right septal branch is covered by cardiac muscle from the atrio-ventricular septum to the moderate band; the left branch appears under the endocardium 1·2 cm. beneath the junction of the right and posterior aortic valves. In the pig there is a close resemblance to this. It is interesting here to note how in all mammals the bundle is in close apposition to the insertion of the aorta, behind its posterior valve.

Microscopically, as Tawara pointed out, one must also distinguish an atrial and ventricular part. The atrial part begins as a complicated network of branching fibres smaller than the atrial muscle cells with a nucleus lying in undifferentiated protoplasm and with fibrillæ less well developed and more irregular than in the ordinary cardiac cell. Within this network lie connective tissue with fat, blood-vessels, and nerves. From it emerges a series of more or less parallel muscle fibres similar to those of the network surrounded by a well-marked connective tissue sheath. The appearance of these cells and the amount of connective tissue between them readily distinguish them from the ordinary cardiac muscle.

The ventricular section begins immediately where the atrio-ventricular bundle breaks through the fibrous septum of the atrio-ventricular groove. It consists of an irregular network of muscle cells surrounded by connective tissue. Histologically it has no similarity with the atrial portion of the band nor with the ordinary cardiac muscle cell. One, two or more of the cells of the atrial strand pass into a much larger cell of irregular size and shape which possesses many features in common with a Purkinje cell. As the ventricular strand passes down the septum, these initial cells gradually pass into typical Purkinje fibres which constitute the muscle cell component of the two arms and their outspreading branches.

Technique.—As a first step, it is necessary to be able rapidly to cut out the bundle either after staining or in the fresh condition. This can be done after a series of preliminary dissections. For the purpose of this research I limited

my observations to the main bundle surrounded by its connective tissue sheath, including the part directed to the coronary sinus and the two arms running into the septal walls of the right and left ventricles (figs. 1 and 2). My results have been obtained by the methylene blue "vital" method. Occasionally the Cajal method or gold impregnation was used, but with results less satisfactory, chiefly, I believe, because the methylene blue gave such definite results that it was not felt necessary in this preliminary report to ascertain experimentally the modifications which appeared necessary to apply either of these methods, especially the Cajal, to the heart muscle.

The strength of the solution injected was :—

Methylene blue, $\frac{1}{2}$-per-cent. solution	10 c.c.
Salt solution, 0·9-per-cent. solution	90 „

The coronary arteries were injected with the solution either directly or indirectly from the aorta. When the heart was well injected the bundle was rapidly dissected out, placed on a slide and examined in the usual way; or the bundle was cut out from the fresh heart, partly immersed in a methylene blue solution slightly weaker than the above, and kept in a hot chamber at a temperature of 37° or 38° C. The full description of the technique in use has been so often presented in previous papers, Wilson (8), that it seems unnecessary to repeat it here. Fixation was always done in 8-per-cent. ammonium molybdate and sections cut in paraffin.

The limitations of the methylene blue technique are well known. This dye, though neurotropic, is not monotropic. A difficulty encountered in the atrio-ventricular bundle is the affinity of the methylene blue for the elastic fibres—a tissue sufficiently abundant in the bundle to give trouble at first. Recognising this possible source of error, one readily gets accustomed to distinguish between the relatively coarse wavy fibres of the elastic tissue and the fine varicose fibres of the nervous strands branching and anastomosing irregularly.

The nerve fibres are in the main non-myelinated. A few medullated fibres are to be seen, especially in the calf: these appear usually as isolated fibres and do not enter as a rule into the strands of fibres which pass directly through the bundle.

The staining of all the nerve elements in the bundle in one and the same preparation is unusual. Thus it is not common to get in the same preparation the finer network together with the ganglion cells and their processes. If one gets good ganglion cells with processes, the finer varicose fibres distributed through the muscle are usually poorly stained. This agrees with the observations which I have satisfied myself with time and again, that the

dye will at one time select motor endings in preference to sensory or vasomotor; at another time, under the same external conditions, the sensory or the vasomotor are the better, and may be the only ones stained well. This appears to me to be due to the particular chemical state of the nerve ending at the moment the dye reaches it.

The animals used in the investigation have been the calf, sheep, and pig, and to a less extent the dog. Tissue was also obtained from the human heart. I am not prepared at this time to report on the results of the investigation on human material or in the dog, but so far as these have gone I have no reason to believe that they will not bear out the results reported in this paper on the three first-mentioned animals.

The examination was confined to the part of the bundle extending from near the coronary sinus through the fibrous septum and down both arms. Though this constitutes but a part of the entire bundle, it forms an important section; it is a well-defined structure and includes the path across the atrio-ventricular septum. To avoid confusion, it is referred to in this paper as the atrio-ventricular bundle.

Even a very superficial examination convinces one of the important part taken in its composition by nerve elements. Nerve cells are scattered in profusion along its course, and nerve fibres pass in strands along with its muscular elements or intricately interlace around its cells. There is no part of it, from the coronary sinus to the end of its right or left arm, bereft of groups of ganglion cells or devoid of nerve fibres. The neurologist might well refuse to recognise in it a muscle bundle; to him it might become conspicuously a nerve pathway of very intricate structure.

In the bundle the nerve elements divide themselves for descriptive purposes into three groups:

I. Ganglion cells.
II. Nerve fibres and plexuses.
III. Nerves directly associated with the blood-vessels.

I. The ganglion cells are naturally first described, for they are the most conspicuous nerve structures present, both from their abundance and their size. They are found usually in groups of varying number; some of these in the calf have as many as 16 nerve cells, but more may easily be present. Individual cells, scattered either in the course of the nerve strands or isolated in the fibrous tissue around the bundle, are frequently seen.

Nerve cells are abundant in the atrio-ventricular bundle of all the animals studied, but I have examined them chiefly in the calf, where, from their large size and from the facility with which they stain, they are especially suitable

for investigation. All three varieties of cells are found (see Plate 5) unipolar (fig. 3), bipolar (fig. 4), and multipolar (fig. 5). Ganglionic groups are scattered in the connective tissue not only around the muscle band but also in the interstices between the muscle fibres (fig. 4). They are not especially located in the subendocardial area; when the bundle reaches the surface of the heart, they are seen not only between its tissue and the endocardium, but are also equally conspicuous within the bundle and in the fibrous tissue on the side remote from the endocardium.

They can be seen all the way from the coronary sinus to the distribution in the right and left walls of the ventricular septum. In the particular part examined they appear to be most abundant near the point of bifurcation and in the course of the right and left ventricular divisions. Their abundance may be roughly estimated by saying that in a series of sections of one of these arms, especially the left, cut 50 microns thick, it is no unusual thing to find in a section three or four ganglionic masses containing from five to nine nerve cells. Were one roughly to indicate any one area more than another where they are conspicuous, one might select the upper border of the bundle just before its division into right and left limbs. Here there is a large group, easily seen in the calf and sheep, lying in the fibrous tissue outside the bundle whose processes pass into the muscular pathway.

The processes of these nerve cells can often be traced for a long distance gradually dividing in their course (fig. 3). Many of them ultimately become varicose fibres, and some at least go into the nerve plexus around the muscle cells. But the mode of termination of the majority, from the distance they traverse and from the failure to stain referred to above, I have so far been unable to determine. Fig. 6 shows a large nerve cell in some respects akin to Dogiel's type I. It has one long process and several smaller ones, which latter project only a short distance from the cell-like sharp prickles. The long process can be traced for a very considerable distance; it frequently divides and ultimately ends as very fine varicose fibrils which enter into the plexus around the muscle bundle. Fig. 5 shows the interlacing of the processes of several nerve cells in one pericellular plexus. Here a multipolar cell, $G._1$, gives off a branch, one of whose rami enters into the pericellular nest of cell $G._2$, into which also enter twigs from two other more distant nerve cells by fibres C and D.

II. In the atrio-ventricular bundle the nerves present themselves

(*a*) as strands of fibres;

(*b*) as plexuses of fibrils.

(*a*) The nerve strands have a general course along the length of the bundle. In preparations of the entire bundle they are seen to break into the fibrous

tissue around it at various parts of its course, but chiefly prior to or near the point of division into the right and left arms. Thus several strands appear towards the coronary side of the division, corresponding to the position of the ganglionic group referred to above. The question of the source of the fibres lies outside the field of the present investigation, but their course indicates an origin near the insertion of the aorta and the lower part of the atrial septum. Sections of the bundle bring out more clearly the relation of these strands to the ganglion cells. Throughout their course nerve cells are scattered individually or in groups and the processes of these cells enter into the nerve strand (fig. 4). The fibres of these strands are not in close apposition. This is especially observed in the left septal part (fig. 4). They are found in the connective tissue both around the bundle and between the muscle cells. They have irregular connection with each other. Often one can see a strand send off a single fibre or a group of three or four fibres which pass across the intervening muscle cells to an adjacent strand and then continue their course along this. Occasionally a fibre may be observed to turn backwards; however, the general tendency is for the strands to pass downwards in the direction of the atrio-ventricular bundle. The fibres are as a rule non-medullated, most of them with varicosities. These varicosities occur at less frequent intervals than in group (*b*). The medullated nerves seen have been chiefly in the cow. It is with fibres of this group that at first the elastic tissue is apt to be confounded, but enough has been said to show how they may be easily differentiated.

It is difficult to tell what becomes of these strands. Many of them pass through that part of the bundle I have examined. Some, however, may be seen to break up into very fine varicose fibrils which enter into plexus (*b*) (fig. 4, A.).

(*b*) The nerve plexuses are composed of very fine fibrils with varicosities at frequent intervals. They can be seen with the 8-mm. objective and 4 ocular, but require a higher power for distinct observation. The fine branches lie in close apposition to the muscle cells and have absolutely no resemblance to elastic tissue. In well-stained preparations they are so dense and intricate from frequent branchings and anastomoses that it is impossible to trace individual fibres for any distance. I have chiefly studied these plexuses in the pig and sheep. Here they form a continuous network which can be traced for long distances over a series of sections and appear to extend the whole length of the atrio-ventricular bundle. Their general characters can be well seen in figs. 7 and 8. As will be noted, it is not a case of a nerve breaking up and surrounding individual muscle cells, but of a complicated network lying around both single cells and groups of cells.

The source of the plexuses is not easy to determine. The difficulty is due partly to the length of the varicose fibrils before they enter intimately into the plexus, and partly to the difficulty of staining at the same time sufficiently well ganglion cells and muscle plexuses. Occasionally, however, a non-medullated fibre can be seen to pass out from the strand and break up into fine twigs, which ultimately become very fine varicose fibrils and enter into direct relation with the muscle plexus. (See Plate 6.)

III. Nerves related directly to the blood-vessels of the atrio-ventricular bundle. These have no special significance in this locality and differ in no way from nerves found in arteries elsewhere, so well described by Dogiel and others. Two distinct varieties present themselves:—

(1) A vasomotor plexus of fine non-medullated varicose fibrils (fig. 9). These are most abundant in the large vessels and gradually get fewer as the smaller arterioles are reached. At the point where a vessel divides or a branch is given off, the plexus becomes more dense; it is as if the fibres became concentrated at the point of division. Then the plexus divides or sends offshoots along the arterial ramus, the amount sent off varying with the size of the branch. The main plexus runs in the adventitia, but a part of it passes into the tunica media to form anastomosing branches directly related to the muscle fibres. These do not appear to me to form definite endings; the knob-like endings on the muscle cell sometimes described appear to be artefacts due to a stoppage of the dye. This appears to be confirmed by relatively few appearing in well-stained preparations and their abundance in badly-stained tissue.

(2) Distinct from these are the so-called sensory endings. These are definite end organs situated in the fibrous coat around the vessel, and differ from the above described anastomosing plexus formations. They are so called because of their resemblance to sensory endings elsewhere. A nerve fibre thicker and less varicose than the ordinary vasomotor nerve and at times faintly medullated is seen to break up in the tunica adventitia into a more or less complex arborisation which is non-capsulated. In the smaller arterioles they are very simple (fig. 9, S.), in the larger arteries of the bundle they become extremely complex (fig. 10).

Conclusions.

I. Anatomically the atrio-ventricular bundle contains not only a special form of muscle fibre distinct from the ordinary muscle of the atrium or the ventricle, but, as I have shown, is an important and intricate nerve pathway in which we find:—

(1) Numerous ganglion cells—monopolar, bipolar, and multipolar—whose processes may pass—

(*a*) To adjacent ganglion cells in the bundle;
(*b*) To the muscle fibres in the bundle;
(*c*) Through the muscle bundle so far as it was examined.

(2) Abundant nerve fibres running through it in strands, the processes of which may end (*a*) in ganglion cells in the bundle; (*b*) in the muscle plexus, or may pass through the part examined.

(3) An intricate plexus of varicose fibrils around and in close relation to the muscle fibres of the bundle.

(4) An abundant vascular supply with well-marked vasomotor nerves and sensory endings.

II. Physiologically it has been shown that the atrio-ventricular band constitutes the pathway which assures the communication of the atrio-ventricular rhythm. When the bundle is sectioned or crushed the ventricles cease momentarily to beat, though they soon regain pulsation, but with a rhythm much more slow than that of the atrium. Pathological anatomy supports this view; the allorythmia or Stokes-Adams disease can be explained satisfactorily by lesions involving this pathway. As a result of these physiological experiments and from these pathological conditions, it has been asserted that the contraction wave must be myogenic. To such a deduction my anatomical findings are opposed. They demonstrate that in these experiments and pathological conditions an important nerve pathway is equally involved with the muscle bundle. Considering the neurogenic as opposed to the myogenic hypothesis from the anatomical standpoint, one must acknowledge that the very complex nerve constituents of the bundle indicate an important nerve pathway and are very suggestive of an intricate nerve mechanism.

Can the atrio-ventricular bundle be regarded as a neuro-muscular spindle?

It has recently been stated that "the conclusion derived from the study of the development and cytological structure of the conductive system is that it is a neuro-muscular apparatus akin to the neuro-muscular spindle of voluntary muscle" (Retzer (9)). Similar suggestions have been made by others, and readily present themselves as a possible explanation of the position and structure of the atrio-ventricular bundle. But have we anatomical data on which to base such a conclusion? To answer this it is necessary to consider the structure of the neuro-muscular spindle.

Were one to accept Golgi's definition, made in 1880, that it is "a bundle of incompletely developed muscle fibres surrounded by a special sheath," one

might be tempted to acquiesce in the above view, at any rate provisionally. But the work since then, especially of Ruffini (11) and Sherrington (12), has so widened our knowledge of the neuro-muscular spindle that Golgi's definition is now inadequate, and it is with the complex nerve ending which they describe that the atrio-ventricular bundle must be compared.

The essential anatomical points in the structure of the neuro-muscular spindle may be summed up as follows:—

(1) The fibres which go to form the muscle bundle (Weissmann's bundle) in the neuro-muscular spindle have a diameter less than that of the ordinary muscle fibre. The fibres are directly in apposition, and no connective tissue lies between them, though connective tissue lies around Weissmann's bundle and constitutes the axial sheath of Sherrington. The striation of the fibre is usually only marked in the marginal area, and so on transverse section it looks like a Purkinje fibre. Regarding the two ends of Weissmann's bundle, one, the wider end, is muscular; the other tendinous where the axial fibres of the bundle are attached to the fibrous tissue of the capsule or to the tendon of the muscle.

(2) Around it lies a lymphatic space.

(3) There is a distinct capsule of concentric superposed lamellæ of connective tissue. At the tendinous end of the muscle bundle it is thin and adheres to the tendinous portion of the spindle; at the muscular end it is thin and may be absent.

(4) In the vast majority of cases it is fusiform in shape.

Contrast this with the anatomical description given of the atrio-ventricular bundle in this paper, and it will be seen that, apart from the muscle cells being similar to Purkinje fibres, they have nothing in common. This lack of agreement is further emphasised when we compare the nerve constituents of each:—

(5) To the distribution and termination of the nerves in the neuro-muscular spindle, with its three distinct kinds of endings described by Ruffini, there is nothing comparable in the atrio-ventricular bundle.

(6) Ganglion cells are not present in the neuro-muscular spindle, whereas they are a marked feature in the atrio-ventricular bundle.

From the above, one must conclude that, whatever the physiological significance of this bundle may be, it has anatomically nothing in common with the neuro-muscular spindle.

In conclusion, I wish to express my great indebtedness to Dr. Mott for allowing me to carry out a considerable part of this investigation at the Pathological Laboratory at Claybury, and for his kindness in assisting me to procure a large part of the material which has been used.

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EXPLANATION OF PLATES.

A.V.B. = atrio-ventricular bundle.
R.B. = right branch of A.V.B.
L.B. = left branch of A.V.B.
B. = bifurcation.
C.S. = coronary sinus.
M. = muscle.
G. = ganglion cell.

PLATE 4.

FIG. 1.—Dissection of right atrium and ventricle of calf to show A.V.B. The band is seen passing from under atrial muscle near C.S. to B., then continued under medial cusp over right ventricular septum at R.B. towards the insertion of moderator band (M.B.).

V.C.I. = inferior vena cava.
A. = auricle.
M.C. = medial cusp.
A.C. = anterior cusp.

FIG. 2.—A.V.B. of calf looking down from above. The great portion of atrium has been removed to show bifurcation in the upper part of ventricular septum.

R.V.S. = right ventricular septum.
L.V.S. = left ventricular septum.

PLATE 5.

FIG. 3.—Monopolar ganglion cell; one of six lying among muscle fibres of A.V.B. on septal wall of calf. Zeiss comp. oc. 4, obj. 8 mm.

FIG. 4.—Group of ganglion cells lying among nerve fibres in A.V.B. on left septal wall of calf.

A. = nerve fibre breaking up near muscle fibre and entering into muscle plexus (not distinguishable with this low power). Zeiss oc. 6, obj. AA.

FIG. 5.—Ganglion group in A.V.B. of calf, showing pericellular plexus around ganglion cell ($G._2$) containing fibres from three nerve cells.

$G._1$ = nerve cell which sends off process (dendrite) B, which branches repeatedly within ganglionic group. One of these branches breaks up into a network which embraces the adjacent ganglion cell $G._2$.

C. = nerve fibre from an adjacent ganglion—not shown—which breaks up into two branches: from these, twigs pass into plexus around $G._2$, others into plexus around $G._1$.

D. = nerve fibre from nerve cell in same group as C, which breaks into plexus around $G._2$.

E. = varicose fibril clinging to A—neuraxis of $G._1$.

FIG. 6.—Nerve cell in A.V.B. calf, containing a well-marked nucleus with halo. The cell has several small processes which project, like sharp prickles. It has one long process, A, which divides frequently; its ultimate branches become varicose and lie in close proximity to muscle fibres of A.V.B. Zeiss comp. oc. 4, obj. 2 mm.

PLATE 6.

FIG. 7.—Plexus around and adjacent to muscle fibres of A.V.B. of pig, immediately to coronary side of its division into right and left septal branches. Zeiss oc. 4, obj. 8 mm.

FIG. 8.—Plexus around muscle fibres of left septal branch of A.V.B. of pig. Zeiss comp. oc. 4, obj. 2 mm.

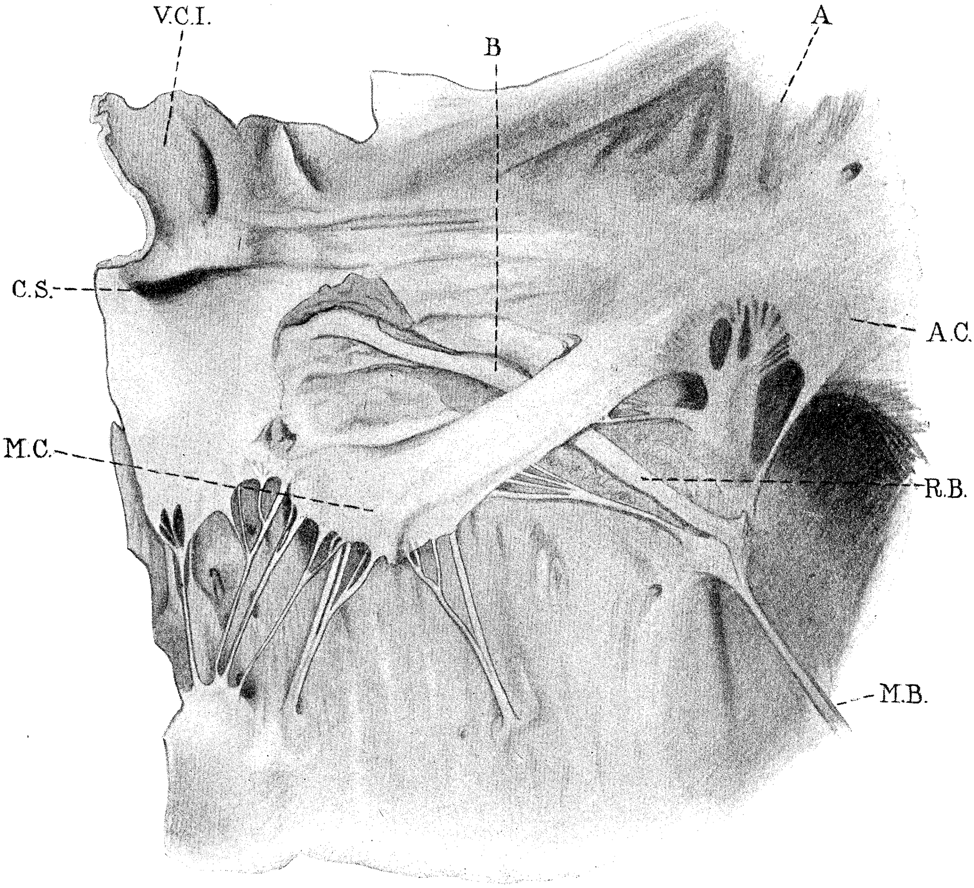
FIG. 9.—Vasomotor fibres in small artery in A.V.B. of pig.

S.N. = sensory nerve, S. = sensory ending, V.M.P. = plexus of fibres at bifurcation of artery.

FIG. 10.—Sensory ending in wall of artery in A.V.B. of cow.

A. = nerve which breaks up into complex ending.

FIG. 1.



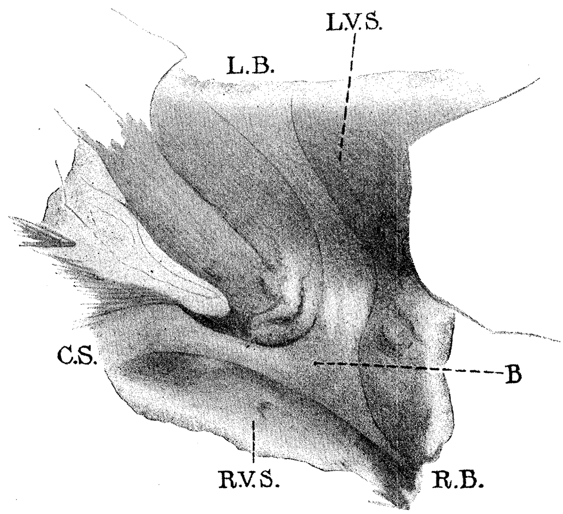


FIG. 2.

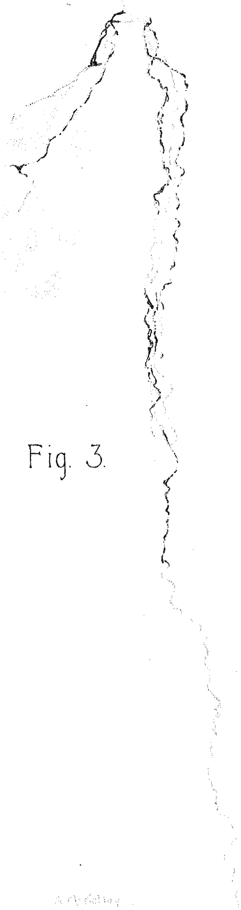
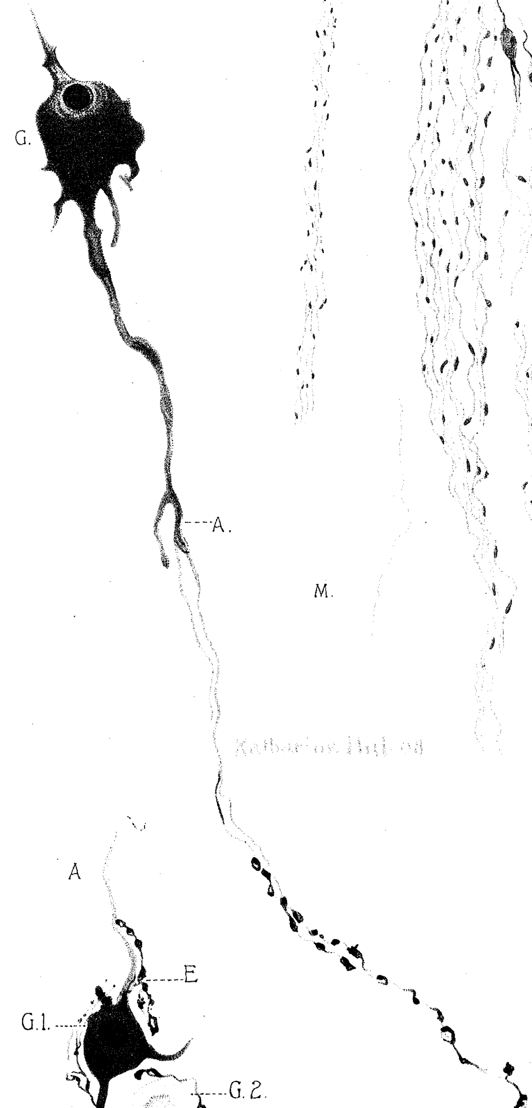


Fig. 3.



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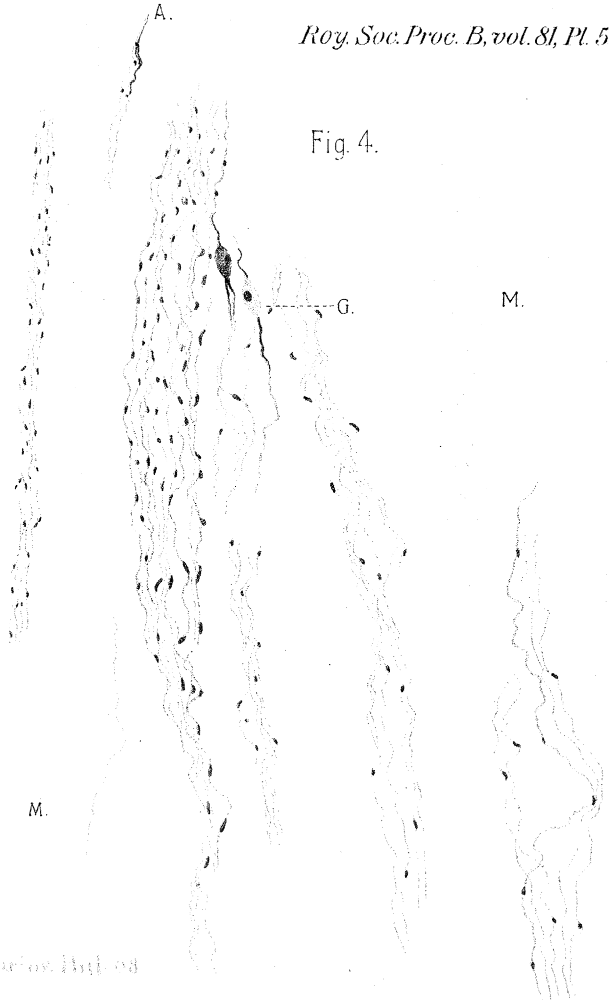

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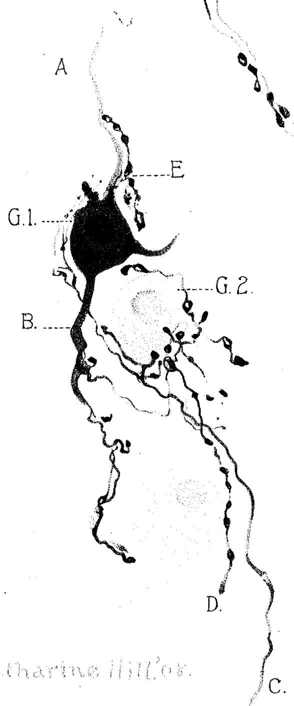


Fig. 5.

Fig. 7.

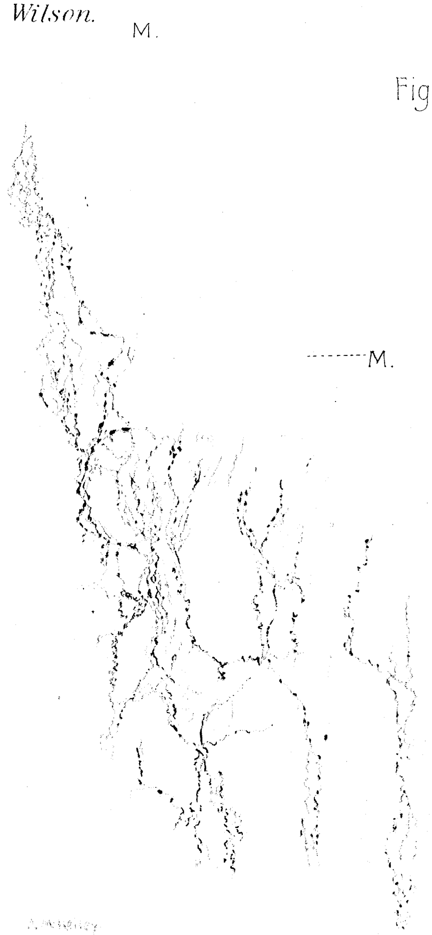


Fig. 8.

Fig. 9.

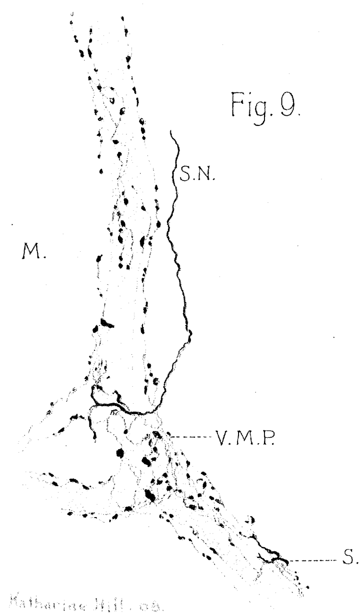
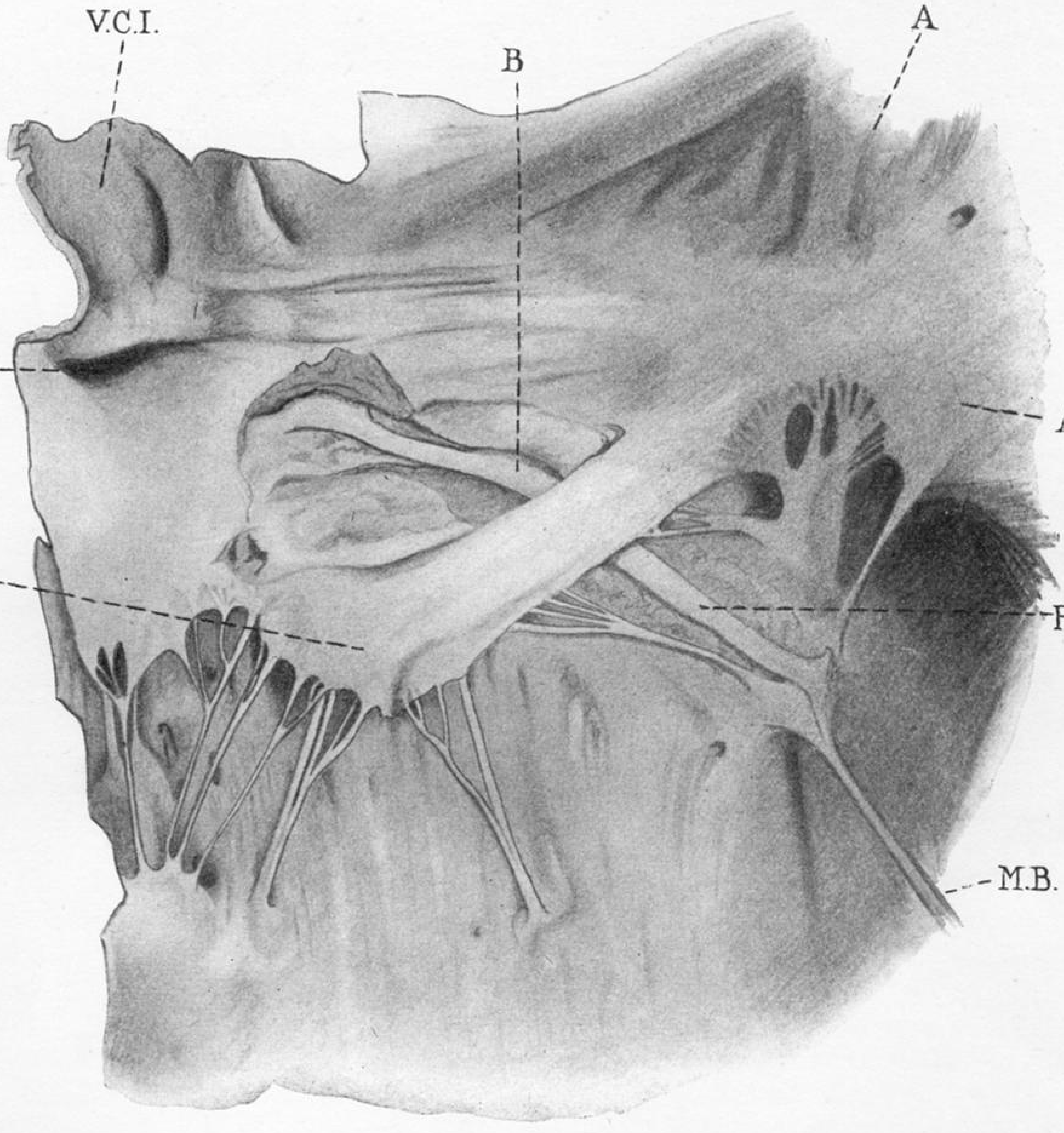


Fig. 10.

Fig. 1.



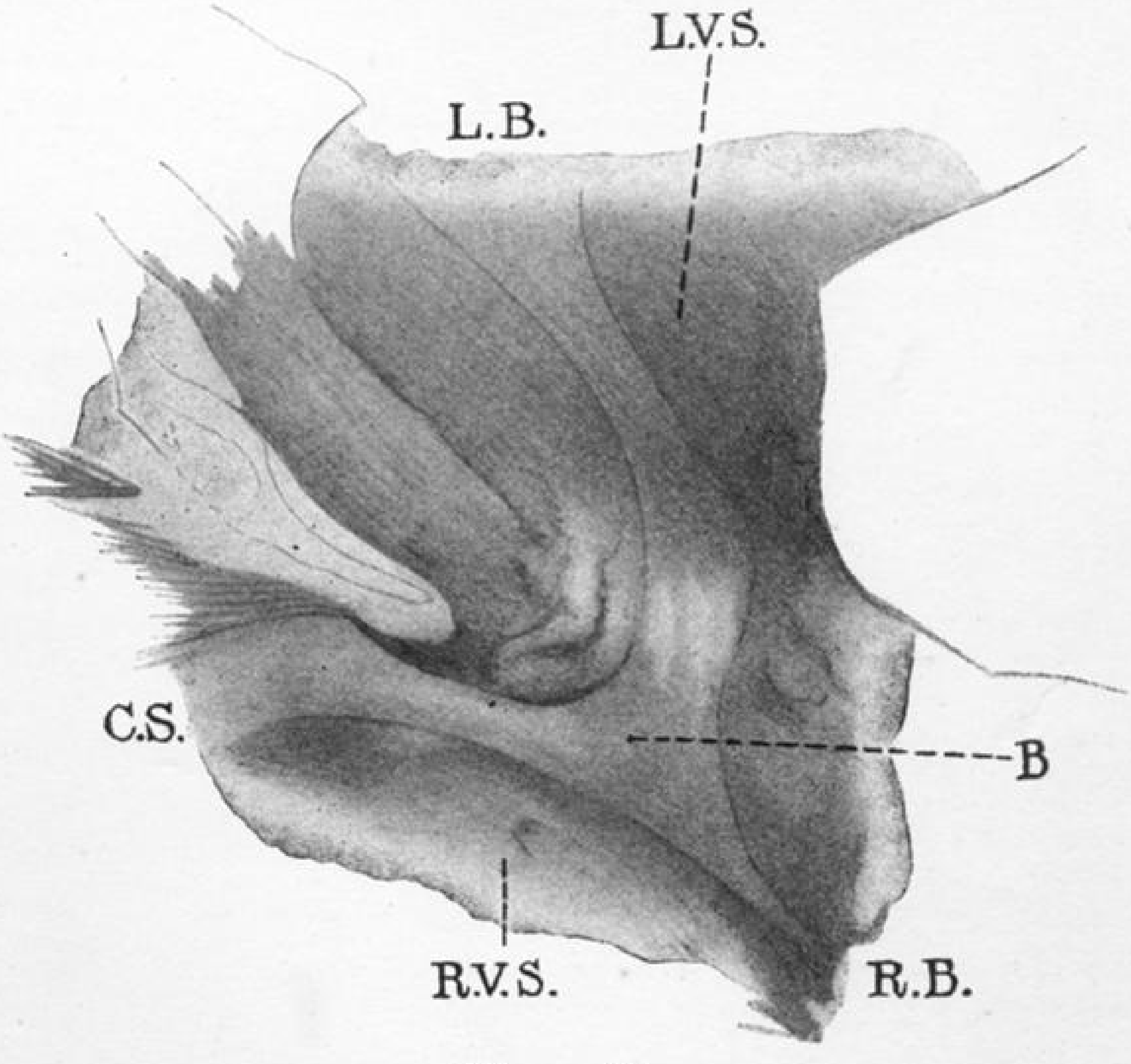


Fig. 2.

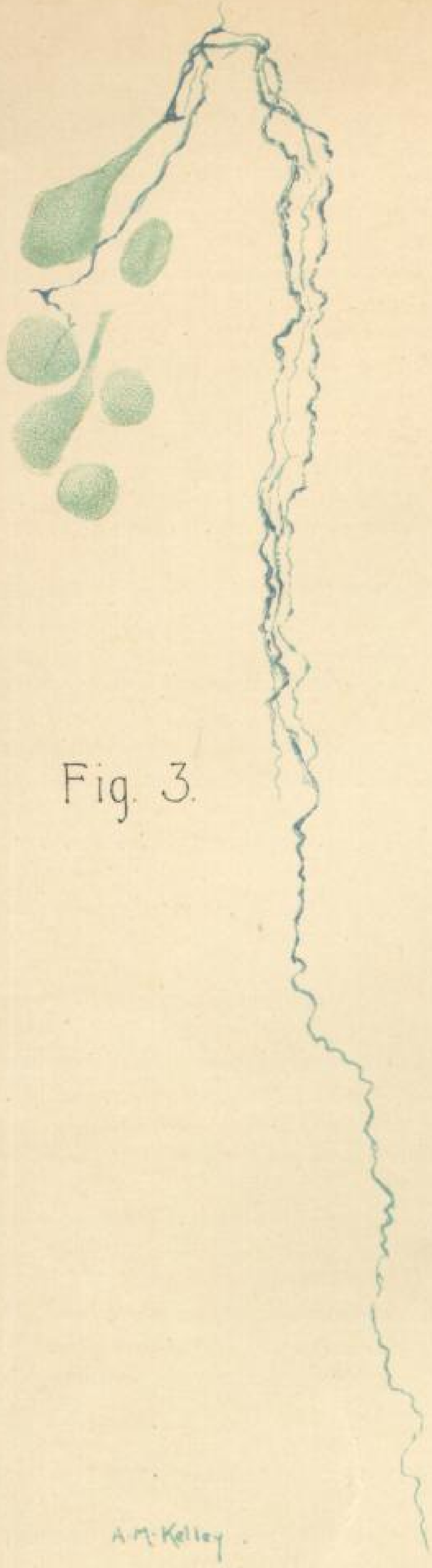
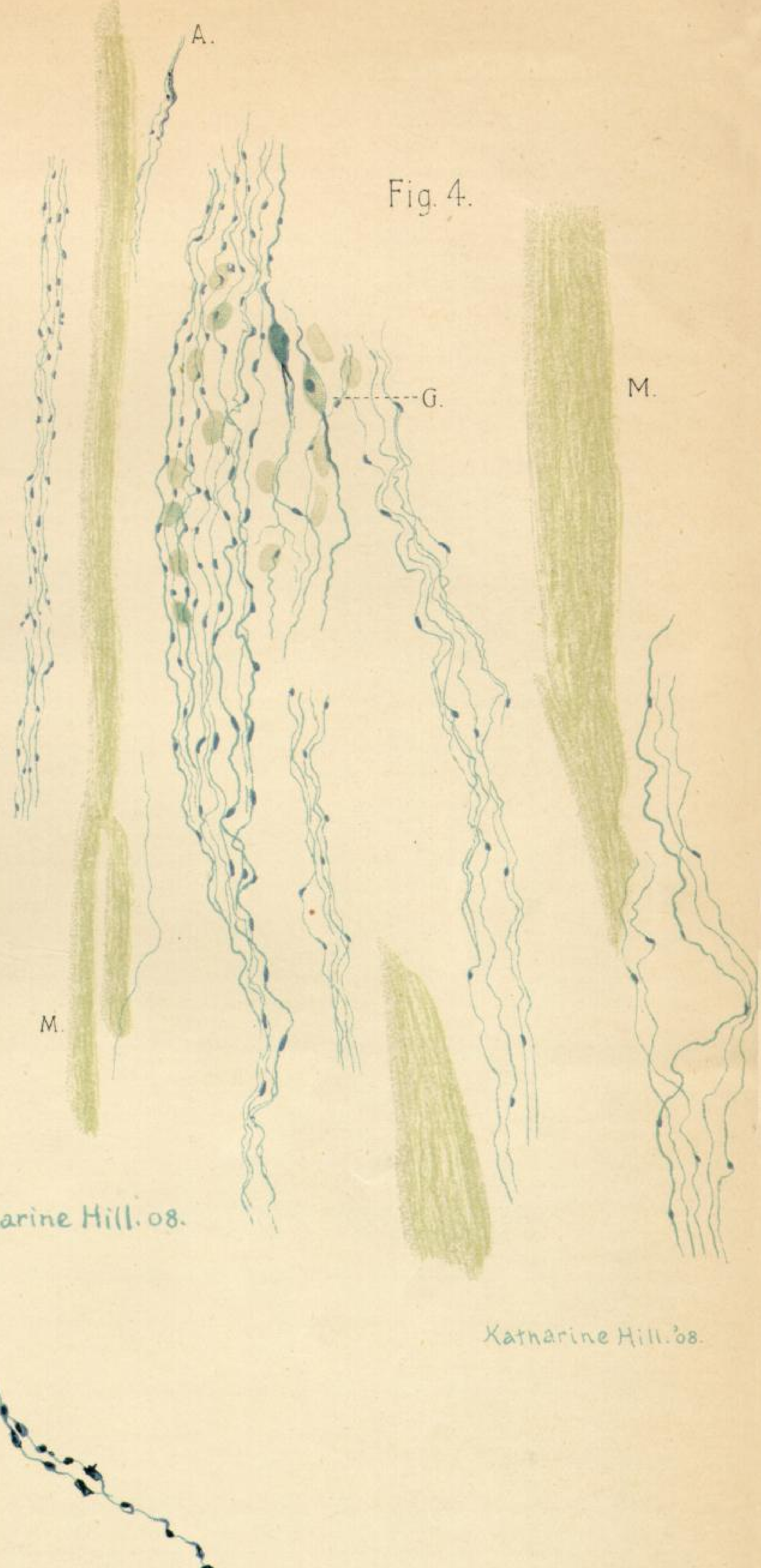


Fig. 3.

Fig. 6.



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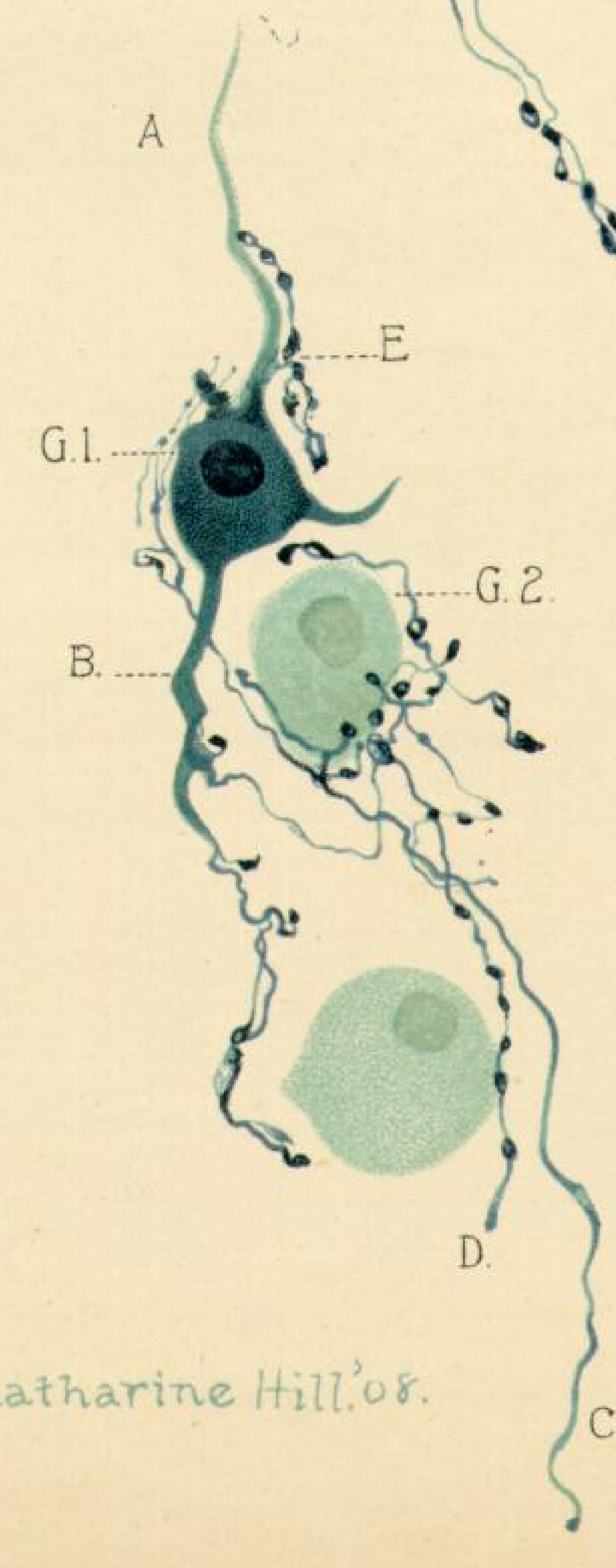

Fig. 5.

Fig. 7.

Fig. 8.

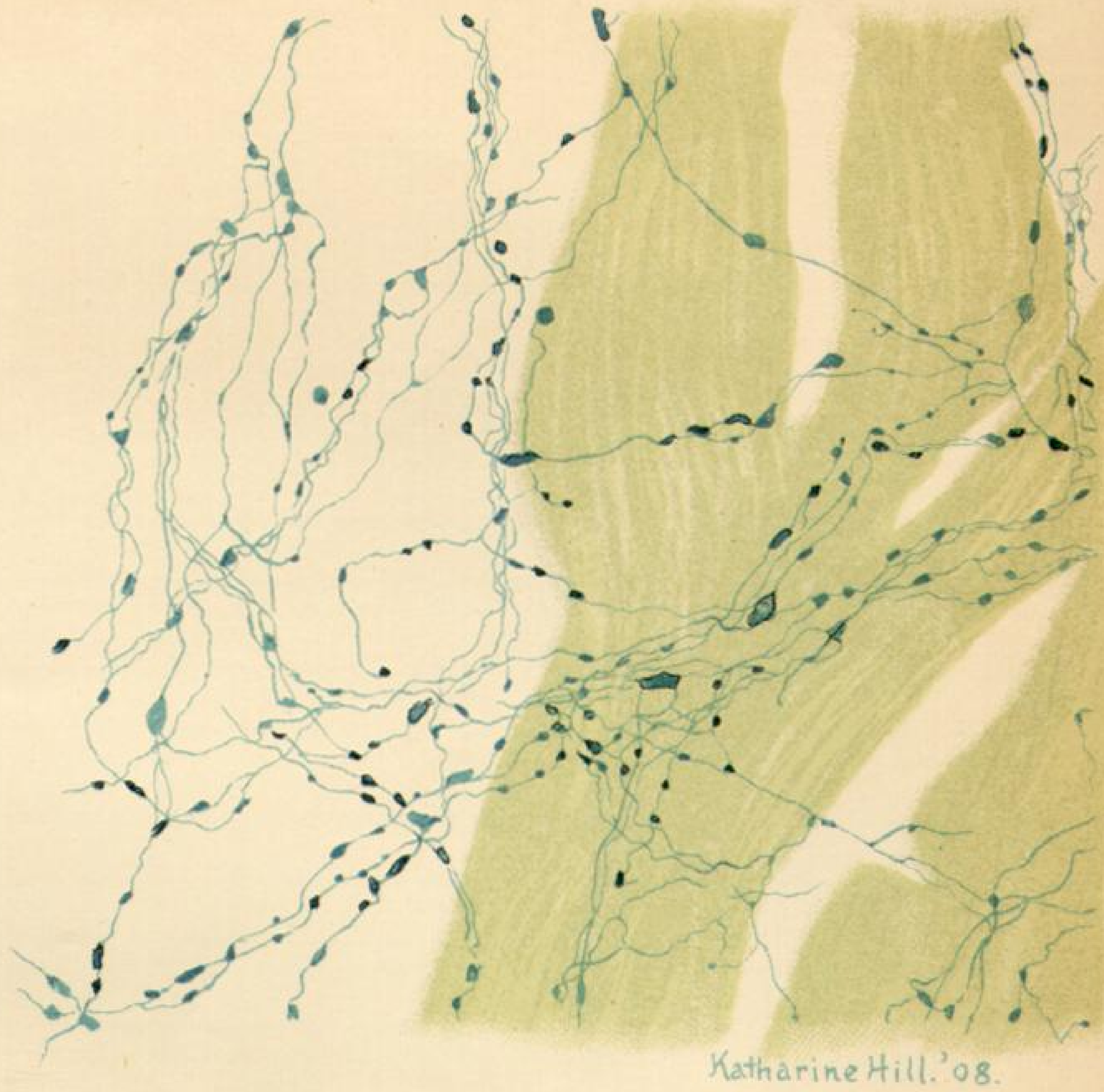

Fig. 9.

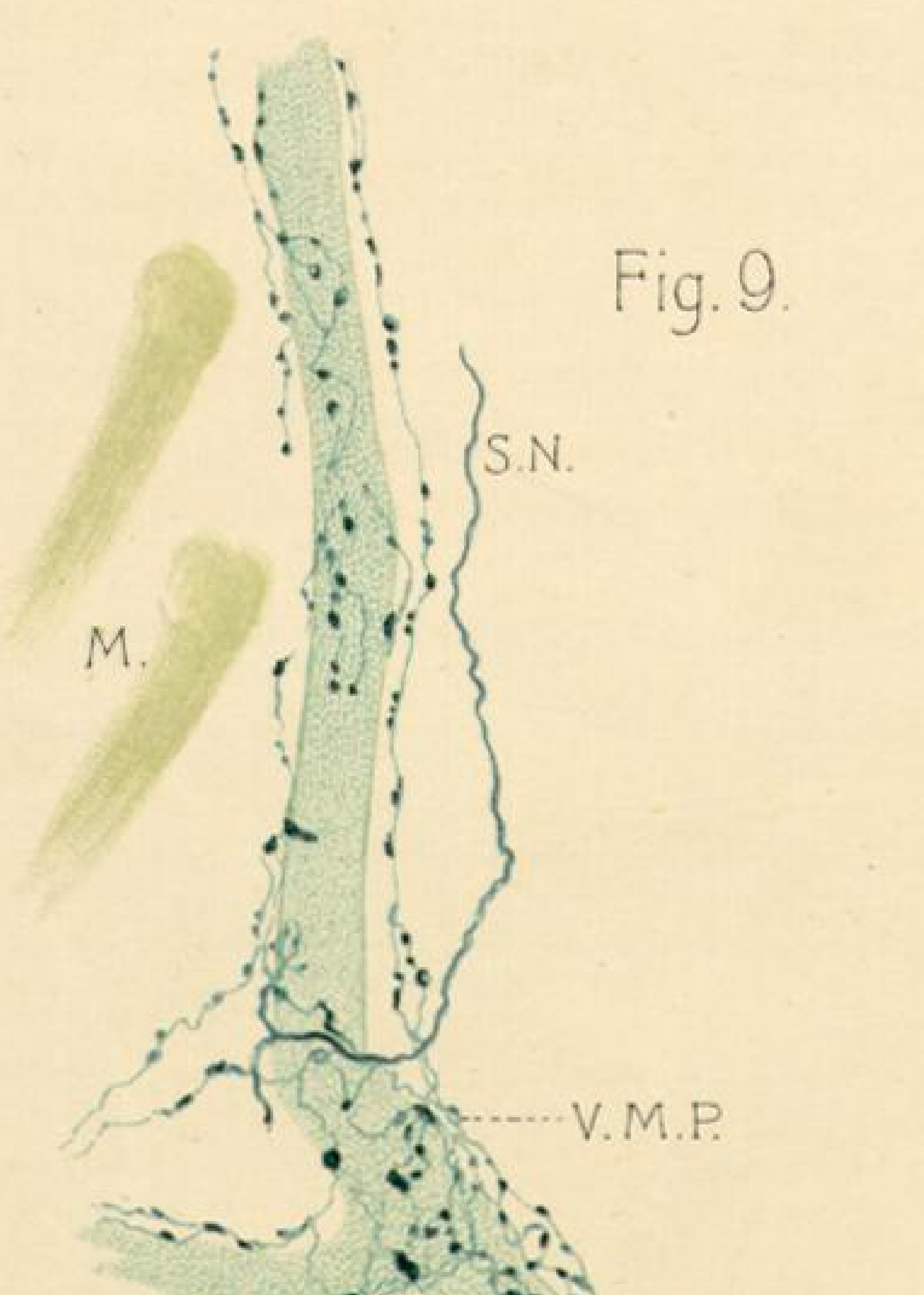

Fig. 10.