

New observations upon the structure and formation of certain nervous centres : tending to prove that the cells and fibres of every nervous apparatus form an uninterrupted circuit / by Lionel S. Beale.

Contributors

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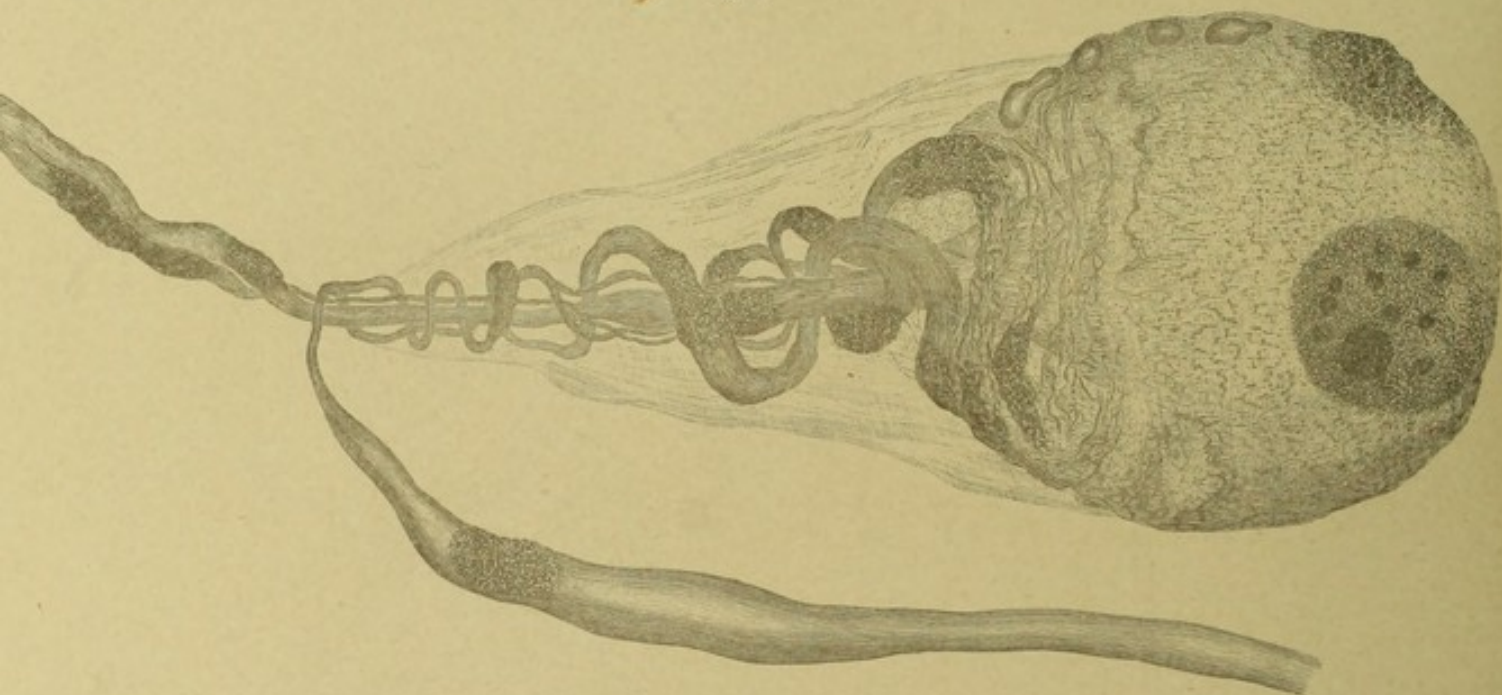
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Fig. 1.



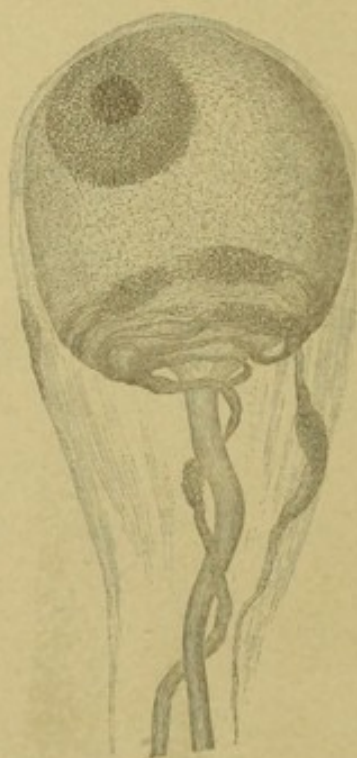
One of the ganglion cells embedded in the trunk of a nerve near the lumbar nerves of the Green Tree-Frog (*Hyla arborea*). The cell was isolated by dissection and pressure in glycerine. A *straight fibre* is seen to be continuous with the central part of the cell, and a *spiral fibre or fibres* with its circumference. The matter of which the body of the cell is composed passes into the fibres. The germinal matter was coloured with carmalum. The broad fibre forming the continuation of the nucleated spiral fibre is a true 'dark bordered fibre.' $\times 1800$. Jan., 1863.

Fig. 2.



Young ganglion cell.
 $\times 700$.

Fig. 3.




Fully-formed ganglion cell.
 $\times 700$.

Fig. 4.



Old ganglion cell.
 $\times 700$.

Three ganglion cells from a ganglion near the aorta of the Common Frog (*Rana temporaria*). In the youngest cell the second fibre does not coil spirally round the first. In Fig. 3, several coils are observed; and in Fig. 4 the coils are very numerous. The spiral increases in extent as the cell advances in age.

1000th of an inch  $\times 700$.

1000th of an inch  $\times 1800$.

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NEW OBSERVATIONS

UPON

THE STRUCTURE AND FORMATION

OF

CERTAIN NERVOUS CENTRES,

TENDING TO PROVE

THAT THE CELLS AND FIBRES OF EVERY NERVOUS APPARATUS
FORM AN UNINTERRUPTED CIRCUIT.

BY

LIONEL S. BEALE, M.B., F.R.S.,

FELLOW OF THE ROYAL COLLEGE OF PHYSICIANS,

PROFESSOR OF PHYSIOLOGY AND OF GENERAL AND MORBID ANATOMY IN KING'S COLLEGE,

PHYSICIAN TO KING'S COLLEGE HOSPITAL,

AND HONORARY FELLOW OF KING'S COLLEGE, LONDON.



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“ La médecine est un art dont les progrès sont en grande partie dépendants de ceux de la physiologie.”

MILNE-EDWARDS.

P R E F A C E .

THIS Memoir, which has been printed in Part II. of the Philosophical Transactions for 1863, is devoted to the consideration of a peculiar and special arrangement, now demonstrated for the first time, in connexion with certain nerve-cells; but as the conclusions arrived at bear in a very important manner upon several fundamental questions relating to the typical anatomy of every nervous apparatus, the Author has ventured to publish it in a separate form. By the kind permission of the Council of the Royal Society to use the type already set up, he has been enabled to produce the Memoir at very small cost.

61 *Grosvenor Street, London,*

May 1864.

NEW OBSERVATIONS
UPON
THE STRUCTURE AND FORMATION
OF
CERTAIN NERVOUS CENTRES.

IT is an opinion now very generally entertained by anatomists that in vertebrate and in certain invertebrate animals, there are in connexion with the nervous system apolar, unipolar, and multipolar, including bipolar cells.

It is easy to demonstrate the presence of multipolar cells, but it is another matter altogether to prove that certain cells which seem to be *apolar* or *unipolar* are really of this nature. An observer is justified in asserting very positively the existence of that which he has himself distinctly seen and has shown to others; but it does not follow that he is correct in concluding that, because a fibre or other structure has not been seen by him in certain specimens, it therefore does not exist, for the actual existence of a structure and its demonstration are two very different questions in minute anatomical inquiry. The one is a question of fact, no matter how it may be explained, or how many different interpretations may be offered of it. The other is but an inference arrived at in the absence of evidence, and may result from imperfect means of observation, or want of due care on the part of the observer in preparing the specimen.

A new fact, if capable of being demonstrated to others, will be received at once as true, but negative assertions, although supported by the authority of the most experienced, ought in matters of observation to be received with the greatest caution.

It is one thing to assert that a cell *has* no fibre proceeding from it, or that a cell has but one fibre, and another to state that no fibre or but one fibre has *been demonstrated*. Although many general facts are opposed to the notion of the presence of apolar and unipolar cells, the existence of such cells is generally admitted and taught. If apolar and unipolar cells exist at all, they are certainly less numerous than the multipolar cells; and it is clear that the arrangement and action of the three classes of cells, *apolar*, *unipolar*, and *multipolar*, must be very different. Indeed it almost follows, if the three classes of cells do exist, that there must be as many distinct kinds of principles of action. Nerve-cells, which bear such different relations to nerve-fibres as must exist in the case of the cell unconnected with any fibre at all, the cell connected with one, and that connected with more than one fibre, cannot possibly influence the fibres in precisely the

same manner. The supposition of such an anatomical arrangement involves the existence of different principles of action.

There are, however, authorities who consider it consistent with many facts they have themselves observed, or accepted as having been demonstrated by others, that the arrangement of different parts of the nervous system may be upon a totally different type—that, for example, in some central parts nerves may be in bodily connexion with the cells that influence them, while in other cases a fibre may be influenced by a cell with which it is not structurally connected, and that in some tissues nerves may terminate in distinct ends, while in others they form networks, and in others again terminate in “cells.” A high authority, Professor KÖLLIKER, only last year suggested to me that, although it might be true that nerve-fibres formed plexuses or networks in the muscles of the mouse, it did not *therefore* follow that they did not terminate in free ends in the muscles of the frog, although no essential difference in minute structure, or different principle of action, is known to exist in the muscular tissue of these animals.

Now I submit that such arguments are utterly untenable unless the supposed difference in the arrangement of the particular structure be associated with a fundamental difference in the tissues under its immediate influence or holding a fixed relation to it. I venture to assert that if the nerve-fibres terminate in ends upon the sarcolemma of the muscles of the frog, they terminate in ends upon the sarcolemma of the muscles of the mouse. That in one case there may be more ends than in another, that there may be all sorts of modes of branching, that fibres may pass off from the trunks at different angles, and that an infinite number of variations in detail may exist, is consistent with all that has been observed in nature; but I submit that there is no reason for supposing that any typical or fundamental difference exists with regard to the arrangement of nerve-fibres in corresponding tissues in different animals. So, admitting as we must that by far the majority of ganglion-cells in different nervous centres have more than one fibre in connexion with them, it seems more reasonable to conclude that those cells which *appear* to have but one, and those in connexion with which no fibres whatever have been demonstrated, have really two or more fibres connected with them—but too fine to be demonstrated by ordinary means,—than to accept the necessary inference, *that there are in the very same part or organ three distinct classes of nerve-cells exhibiting as many fundamental differences of relation to the fibres which they are supposed to influence.*

I have been compelled to conclude, from anatomical observation, that although many ganglion-cells exist which appear to be destitute of fibres, none do really exist without them. I have studied this question in various parts of the nervous system and in different animals, from mammalia down to the annelida, and, with regard to the arrangement of the nerve-fibres in nerve-centres, I feel justified in drawing the following general conclusions:—

1. That in all cases the fibres are in bodily connexion with the cell or cells which influence them, and this from the earliest period of their formation.

2. That there are no apolar cells, and no unipolar cells, in any part of any nervous system.

3. That every nerve-cell, central or peripheral, has at least two fibres in connexion with it.

Now, in the ganglia connected with many of the nerves distributed to the internal organs of the frog, there are many apparently *unipolar* and *apolar* cells; but one object of this memoir is to prove that all these nerve-cells have at least two fibres proceeding from them.

Although the present inquiry will be limited to the particular cells connected with the ganglia in different parts of the body of the frog, it necessarily involves the consideration of many fundamental principles of the utmost interest with regard to the intimate structure of the highest tissue existing in living animals. Nor must it be supposed, because I only describe the structure of certain special cells, that my observations have been limited to these cells alone. I have studied the arrangement of nerve-cells and fibres, in the centres and also in peripheral parts, in many different animals.

Upon examining some specimens of the ganglia near the branches of the large arteries distributed to the viscera of the frog, more than two years ago, I was surprised to find that from many of the pear-shaped cells two fibres proceeded—not from either pole, as delineated by WAGNER in the nerves of the pike, but the fibres emerged apparently pretty close together, from the narrowest extremity of the cell, although they did not appear to originate from the same part of the cell.

My specimens have all been prepared in precisely the same manner, and my observations have been made with the aid of powers magnifying more highly than those generally employed in such researches. All the drawings illustrating the subject are magnified from 700 to 1800 diameters, and a few are magnified to the extent of 2800. Many of the preparations have been preserved for two years, and will probably retain their characters for a considerable time longer.

I have arranged the questions considered in this communication under the following heads:—

1. General description of the ganglion-cells connected with the sympathetic and other nerves of the frog.

2. On the formation of ganglion-cells.

a. Ganglion-cells developed from a nucleated granular mass like that which forms the early condition of all tissues.

b. Formation of ganglion-cells by the division or splitting up of a mass like a single ganglion-cell.

c. Formation of ganglion-cells by changes occurring in what appears to be a nucleus of a nerve-fibre.

3. Further changes in the ganglion-cell after its formation.

4. Of the spiral fibres of the fully formed ganglion-cell, and of ganglion-cells at different ages.

5. Of the essential nature of the changes occurring during the formation of all nerve-cells, and of the formation of the spiral fibres.
6. The sense in which the term "nucleus" is employed in this paper.
7. Of the fibres in the nerve-trunks continuous with the straight and spiral fibres of the ganglion-cells.
8. Of the ganglion-cells of the heart.
9. Of the ganglion-cells and nerve-fibres of the arteries.
10. Of the connexion of the ganglion-cells with each other.
11. Of the capsule of the ganglion-cell, and of the connective tissue and its corpuscles.

1. *General description of the ganglion-cells connected with the Sympathetic and other nerves of the Frog.*

All the ganglion-cells from which nerve-fibres proceed to the vessels and other parts in the submucous areolar tissue of the palate, to the tongue, lungs, and neighbouring organs, those from which nerves distributed to the viscera are derived, as well as the cells connected with the pneumogastric, those forming the ganglia upon the posterior roots of the spinal nerves, and some others, exhibit the same general structure—although there are many special peculiarities, and great differences in size, observed in the cells of which some of these ganglia are composed.

The general form of these cells is oval or spherical; but upon closer examination it is found that the most perfectly formed ganglion-cell is more or less pear- or balloon-shaped in its general outline, and by its narrow extremity it is continuous with nerve-fibres which may be followed into nerve-trunks.

In Plate I. fig. 1, a well-formed ganglion-cell from a ganglion close to one of the large lumbar nerves of the little green tree-frog (*Hyla arborea*) is represented. The substance of the cell consists of a more or less granular material, which by the slow and prolonged action of acetic acid becomes decomposed, oil-globules being gradually set free. Near the fundus or rounded end is seen the very large circular nucleus with its nucleolus. In some of these cells, at about the central part or a little higher, are observed a number of small oval nuclei, fig. 20, *c*. These oval nuclei are arranged transversely to the long axis of the cell, and several follow each other in lines which pass in a direction more or less obliquely downwards towards the lower narrow part of the cell. In fig. 1 very few of these nuclei are seen, but in figs. 20 & 26 many exist. The matter of which the mass of the cell consists gradually diminishes in diameter, and contracts so as to form a fibre, in which a nucleus is often seen. At the circumference of the cell, about its centre, the material gradually seems to assume the form of fibres, which contain numerous nuclei, and these pass around the first fibre in a spiral manner. Thus a fibre comes from the centre of the cell (*straight fibre*), and one or many fibres (*spiral fibres*, figs. 1, 3, 4, & 22 to 28, 31 to 38, & fig. 42) proceed from its surface. Neither of the fibres can be traced to the large "nucleus" of the cell.

2. *On the formation of the ganglion-cell.*

I now proceed to describe the changes which I believe take place in the structure of these ganglion-cells during their development, growth, and decay. The drawings which illustrate these observations, although arranged so as to form as far as possible a connected series, are actual copies from nature, made from very many different specimens at intervals during the last two years and a half. The clearest as well as the least uninteresting manner of describing the points of anatomical detail will probably be to arrange the facts of observation so as to construct, as far as may be possible, a connected history of the structural alterations occurring during the life of these elaborate organs. But it is not pretended that the sketch can amount to more than a rough and imperfect outline of the process which actually occurs; for the nature of the inquiry is such that it is absolutely impossible to observe the same cell at different periods of its life, so that the history is made up of fragmentary details obtained at intervals during a long course of investigation.

The development of these, as of most other structures, may be studied *in the fully formed animal as well as in the embryo*, and the various changes occurring may be observed with greater precision and distinctness in the former than in the latter. I shall not enter into the question of the origin of the "nucleated blastema" or of the "granular matter" observed in such quantity in all developing structures. The word "cell" I shall use in a general sense, because it is shorter than "elementary part."

The nerve-cell does not at all ages possess the well-defined structure (cell-wall, cell-contents, and nucleus) usually accorded to it by anatomists, but always consists of *matter that is living*, and *matter that has lived*. The first is coloured by an ammoniacal solution of carmine, the last is not so coloured. A reference to any of my drawings will enable the reader to see at a glance what I understand by a cell or elementary part, and will render further description needless*. In the very young animals these ganglion-cells gradually form from "nuclei" which appear to be imbedded in very soft granular matter. The fibres extend from the collection in at least two directions, and exist as granular nucleated bands, the course of which cannot be followed for any great distance, partly in consequence of their extreme transparency and tenuity, and partly because they ramify amongst the "nuclei," of which all the different tissues at this early period are in great part composed. The fibres do not *grow out from the cells*, but are formed as two masses of germinal matter gradually separate from each other. But new ganglion-cells, nerve-fibres, and nuclei are being constantly produced, not only in fully developed young animals, and in the adult, but certainly for a considerable time after the animal has arrived at maturity, and I believe almost to the close of the ordinary period of life. A young cell, a fully formed cell, and an old cell are represented in figs. 2, 3, & 4, magnified 700 diameters.

* This question has been fully considered in my lecture "On the Structure and Growth of the Simple Tissues," delivered at the Royal College of Physicians in 1860; and the general conclusions then arrived at, and since confirmed by other observations, will be found to be strongly supported by facts recounted in this paper.

In the fully developed frog, ganglia are formed,

1. From a nucleated granular mass like that seen in the embryo, but continuous with nerve-fibres.
2. By the division and splitting up of a mass like a ganglion-cell.
3. By changes occurring in what appears to be an ordinary(?) nucleus of a nerve-fibre.

a. *Ganglion-cells developed from a nucleated granular mass like that which forms the early condition of all structures.*

At first an elongated delicately granular mass is observed in connexion with nerve-fibres, more or less of an oval form, tapering into a tolerably broad granular band or fibre at either extremity. This band often appears to consist of but one broad fibre, but it may generally be resolved into several finer fibres. It cannot be said that nuclei as distinct and separate and *isolable* bodies are imbedded in this; but by the action of carmine numerous rounded portions of matter are darkly coloured, and these may be seen to pass gradually into the surrounding substance, which is only slightly tinted by the red solution. In the small ganglion represented in Plate II. fig. 5, several such nuclei gradually passing into the surrounding uncoloured matter may be observed. These nuclei divide and subdivide; and at a more advanced period of development, the whole mass having increased in size, indications of its division into several lobes or portions may be seen (*b, c, d*). These divisions become more and more distinct, until a number of masses, all exhibiting the same structure, but still intimately connected with each other, result. At *b* several of the cells distinctly separated from each other, and beginning to assume a pear shape, are seen. As the cells approach their fully developed form they *move away from the point where they were first developed*, as represented in fig. 6. In this figure the cells that project furthest and have the longest stems are the *oldest*. From the mode of formation, it is obvious that, at least for a certain time, the cells are continuous with each other (fig. 5, *a, b, c, d, e*), while it is also clear that the very matter of which at first the substance of a cell is formed may subsequently be drawn out so as to form a fibre. It appears, however, that as the ganglion-cells grow and separate from each other they change their relative positions, so that it is impossible to trace any one fibre for more than a comparatively short distance. The connexions of the ganglion-cells will be considered separately.

b. *Formation of ganglion-cells by the division or splitting up of a mass like a single ganglion-cell.*

One of the masses (cells) just described (*b, d*, fig. 5) having reached a considerable size may divide and subdivide, and thus new cells may be developed from it. The stem by which the cell is connected with the rest of the ganglion divides and subdivides into numerous fibres, and in this manner it seems that a number of separate ganglion-cells may be formed by the division of one. The fibres proceeding from each of the new cells

are arranged in a bundle which corresponds to the stem of the original cell. The changes just described are well seen in figs. 7 & 8 from a sympathetic ganglion, and in figs. 11 & 12 from the intervertebral ganglia*. This mode of multiplication generally occurs before the cell has assumed its complete and perfect form (figs. 1, 3, & 4). Although I have examined hundreds of ganglia, I have only seen on very few occasions such a change occurring in a cell which exhibits a distinct spiral fibre, and I have not been able to study it. The greater part of the old spiral fibres would probably waste and disappear, and new ones would be developed from a new germinal mass, resulting from the growth and multiplication of the "nuclei" of the old fibres. The fibres connected with a mass undergoing development into several ganglion-cells often exist in considerable number, but sometimes are so fine as only to be just visible under a power of 3000, and I believe others exist which are too fine and delicate to be seen by means at present at our disposal. In fig. 6 several fully formed ganglion-cells are observed; and here and there are oval masses of about the same size, but containing numerous nuclei, and connected with the ganglion by very fine fibres (fig. 6, at *a* & *b*).

In fig. 7 one of these is represented much more highly magnified; and in fig. 8 another which has increased greatly in size, and contains numerous separate ganglion-masses is magnified 1800 linear. These cells are dividing and subdividing, and from the whole mass would have been formed a new *ganglion* composed of upwards of *thirty cells*.

c. Formation of ganglion-cells by changes occurring in what appears to be a nucleus of a nerve-fibre.

I have several specimens which exhibit a single ganglion-cell in connexion with a very fine nerve-fibre. Not that the fibre is actually single, for it consists of at least three or four very fine fibres; but it runs by itself at a distance from any other fibres or ganglia, and is imbedded in transparent cord-like connective tissue.

The changes occurring during the formation of a single ganglion-cell, in connexion with what is undoubtedly at first a single granular fibre, are of the utmost interest. I cannot be perfectly confident that the history I give of these changes is absolutely true in all points of detail; for, as may be easily imagined, to isolate fine fibres with nuclei exhibiting the different stages of change is a difficulty of no ordinary character, while

* My friend Mr. LOCKHART CLARKE has not observed this division of the cells which enter into the formation of the ganglia on the posterior roots of the nerves of mammalia. He describes the gradual increase in size and the alteration in structure and form of the cells as development advances, but says nothing about their *increase in number*. It is true that Mr. CLARKE's observations were made upon mammalia, while the statements in my paper refer only to the frog; but it is almost certain—I think indeed that it is quite certain—that if the cells do not multiply by division in mammalia they do not do so in the frog. Upon this question of fact, therefore, I regret to say that Mr. CLARKE and myself are at issue. The specimens from which my figures 11 & 12, which show this division most distinctly, have been copied, may be examined by any one who desires to see them. This question shall be further investigated by me. Mr. LOCKHART CLARKE's observations will be found on page 927 of the Philosophical Transactions for 1862, Part II.

hundreds of specimens may be examined without finding one in which such fibres are observed.

The drawings represented in figs. 9, 10, 13, 14, 15, 16, 17, & 18 show the points I have observed in connexion with this question.

A nucleus which cannot at first be distinguished from the ordinary nuclei in connexion with the nerve-fibres, grows somewhat larger than the rest (figs. 9 & 14). I am not prepared to say that *any* nucleus connected with the fibres could or could not undergo the changes about to be described; but the nuclei from which the ganglion-cells are formed exhibit at first nothing peculiar. Sometimes several in different parts of a fibre may enlarge to some extent; but for the most part only one in the course of a long distance will be developed into a ganglion-cell. Of course the opinion that a ganglion-cell may be developed from *any nucleus* up to a certain period of its life is quite tenable, and it may be that the actual change is determined by the presence or absence of certain conditions, but this speculation I will not pursue. The enlarged nucleus which is about to become developed into a ganglion-cell soon exhibits a transparent portion at its circumference.

From what has been stated, it is clear that every ganglion-cell developed in the course of a nerve-fibre must have a fibre proceeding, as it were, from either pole (bipolar cells); but the difficulty of defining the changes with the utmost certainty arises from the rarity with which single fibres emanating from either end of the cell, like those represented by authors, occur. The only cells exhibiting these characters in the frog that I have seen are, in my opinion, young and imperfectly formed cells. Such an *appearance* is not uncommon in fully formed cells in ganglia; but in all cases in which I have observed it in the frog, more careful investigation has satisfied me that it was fallacious, and depended upon a fibre really passing close to the cell, without being connected with it, although it appeared at first to emanate from the end opposite to that which certainly terminated in a straight fibre. In the frog I feel almost certain that fully formed cells, with a nerve-fibre coming from the opposite poles, as delineated by WAGNER and KÖLLIKER in the pike, do not exist; and I have failed to find examples of the cells represented by KÖLLIKER in three specimens of the pike which I have examined. My want of success, however, probably depends upon imperfect investigation, as such fibres undoubtedly exist in the skate. In the posterior roots of the spinal nerves of the common skate such cells are easily found; but there is a difference in the arrangement of the two fibres, and their relation to the mass of the cell corresponding to that already described in the frog, which deserves more attentive examination. I shall describe the peculiar structure of these cells in another communication.

The cells which are not fully developed, delineated in figs. 9, 14, 15, & 16, have a fibre coming from either extremity, but, as will presently be shown, there is reason to believe that as the cell grows the arrangement of these fibres soon becomes altered. The appearances represented in fig. 18, when examined by a low power, would be considered to be due to the presence of fibres emanating from either end of the cell, but under a higher power the true arrangement, which is very different, can be clearly demonstrated.

3. *Further changes in the ganglion-cell after its formation.*

The ganglion-cell having assumed such forms as represented in figs. 9 & 14, now undergoes further changes. It becomes separated more and more from the point where its formation commenced (figs. 32 & 33, Plate VII.). The two opposite extremities of the cell are drawn down (fig. 34). The fibres increase in length and lie parallel to each other, and the form of the cell becomes much altered. If formed in connexion with one of a bundle composed of numerous fibres, the cell seems to grow away, as it were, from the bundle, and sometimes is found at some distance from it, as represented in fig. 41 *d*; but more commonly its long axis corresponds to the direction in which the fibres of the bundle run (figs. 17 & 21). This is constantly observed in the cells in connexion with bundles of fibres running close to the large arteries in the abdomen; and they may easily be mistaken for cells having a fibre springing from each end. But in this case also the ganglion-cell is some distance from the spot where its first formation commenced, and the two fibres which now extend from it may lie parallel to each other for the distance of four or five thousandths of an inch from the cell, and then take opposite courses in the bundle of nerve-fibres.

The ganglion-cell, when fully formed, may lie on the outside of a bundle of nerve-fibres, while the fibre or fibres with which it is connected may run in the central part of the bundle. The two fibres passing from the cell run amongst the bundle of nerve-fibres, to which their course is at first more or less at right angles. Sometimes the fibres from a ganglion-cell pass partly round the circumference of a bundle of nerve-fibres, and then run amongst them. Often the fibres appear to pass quite to the centre of the bundle. At this point, in fortunate specimens, the two fibres may be seen to alter their course and run with other fibres of the bundle, but in opposite directions (see figs. 32 to 37; also figs. 1, 20 *a* & *c*, and fig. 25). As these fibres are often less than the $\frac{1}{60,000}$ th of an inch in diameter, it is very difficult to follow them in the bundle for any great distance; and in ordinary specimens, in endeavouring to unravel the bundle of nerve-fibres, they are inevitably broken. Often they break close to the ganglion-cell; in which case the cell itself, especially if examined in water, appears as a round *apolar cell*, while the fibres which were continuous with it might be easily mistaken for fibres of connective tissue running transversely around the bundle of nerve-fibres imbedded in the neurilemma. Indeed it is probable that many authorities will still maintain not only that the spiral fibre, but that many fine fibres I have described as nerve-fibres really consist of modified connective tissue. If I had only specimens from the common frog, I might have experienced some difficulty in demonstrating that the spiral fibre was a true nerve-fibre to the satisfaction of every one; but many specimens which I have from the green tree-frog settle the question beyond dispute. The spiral fibre is as large and thick as the straight fibre, and, like it, has been traced into a dark-bordered fibre (figs. 1 & 19). Figs. 17 to 28, 31, 38, and figs. 41 & 42 represent different forms of ganglion-cells.

4. *Of the spiral fibres of the fully formed ganglion-cell, and of the ganglion-cells of different ages.*

In all but very young ganglion-cells the remarkable spiral fibres already alluded to exist. In fig. 1, which represents a fully formed cell, the beautiful spiral arrangement of one of the fibres is observed, and in figs. 21, 22, 27, & 28 several fibres are seen to proceed from one ganglion-cell. Close to the cell in which there is a considerable extent of spiral, the course of the fibres is almost transverse. The fibres seem to be coiled around the lower thinner portion of the ganglion-cell (figs. 1, 3, 4, 20, 25, 31). Then the fibres pass spirally round the straight fibre away from the cell, and each turn becomes more oblique than the one above it, until at last the fibre (or fibres) lies parallel with the other fibre which leaves the cell. The spiral fibres are necessarily longer than the straight fibre. The spiral fibre eventually takes a course in the compound nerve-trunk to which the fibres may be traced, the very opposite of that taken by the straight fibre; so that, although the two fibres run parallel to each other for some distance from the ganglion-cell, as STANNIUS observed was the case in the bipolar cells of the calf, it is certain that, at least in many instances, they at length pass in opposite directions (fig. 1). KÖLLIKER thinks that "by far the greater part, perhaps all," of the fibres from the ganglion-cells of the spinal nerves pass in a "*peripheral direction*;" but I believe this statement is erroneous, both as regards the existence of but one fibre, and its course. I have never been able to find any ganglion, large or small, the fibres of which passed in but one direction. Even when a ganglion consists of only three or four cells, *compound fibres pass from it in different directions*. I doubt if a nerve-cell anywhere exists whose fibres pass to their destination in the same direction. In connexion with this question I may revert to the fact I have already stated*, that whenever any compound nerve-trunk, large or small, composed of any form or number of nerve-fibres in any part of the organism of man or animals, passes into another trunk running at, or nearly at, right angles to it, its component fibres divide into branches which pass in *opposite directions*. This general fact is most important; and I have never seen anything to make me believe that the disposition is not universal, and therefore essential even to the simplest nervous apparatus. As the disposition exists in bundles of fibres which there is reason to believe are purely sensitive, as well as in the case of those which are purely motor, it looks as if fibres invariably passed in two directions, whether they be traced from their peripheral distribution or from their central origin. The arrangement spoken of is represented in fig. 40, which is from the submucous areolar tissue of the palate of the frog †.

The spiral fibres can be shown to be continuous with the material of which the body of the cell is composed as well as the straight fibre; but the former are connected with its surface, while the latter proceeds from the more central part; so that, in the most

* Philosophical Transactions for 1862, page 894.

† See a paper in my 'Archives,' "On the Branching of Nerve-trunks, and of the subdivision of the individual fibres composing them," vol. iv. p. 127.

perfect of these cells, the straight fibre forms a stem around which the spiral fibres are coiled (figs. 1, 3, 19, 20, 25, 38, &c.).

The nuclei in connexion with the spiral fibres are well represented in figs. 1, 19, 20, 26. Sometimes they are still more numerous, and I have seen as many as twelve nuclei in the lower part of one of these cells. Several are imbedded in the very substance of the matter of which the cell is composed, but they lie for the most part near the surface. They vary a little in size, and divide longitudinally and transversely. By the division of a nucleus, and the subsequent formation of a fibre from each of the two resulting nuclei, a single spiral fibre is continued onwards from a certain point as two fibres; but it is, I think, probable that in some cases the fibre itself may divide into two, quite irrespective of the nuclei in connexion with it. I have seen instances in which the straight fibre passes through a fissure in the spiral fibre. The connexion of the spiral fibres with the surface of the body of the cell is well seen in figs. 1, 3, 19, 22, 26, 31, & 42.

If figs. 3, 20 *a, b*, 24, 25, & 31 be compared with figs. 1, 4, 20 *c*, 23, & 25, a great difference in the extent of the spiral portion of the fibre will be noticed; and it has been already shown that at an early period there is no spiral fibre at all, but that the part of the fibre which is to become spiral pursues a course at first opposite, then perhaps at right angles to, and afterwards parallel with the other fibre (figs. 10, 13, 16, 19, 20, & 24). It has also been shown that, as a general rule, those ganglion-cells which have the longest stems, or are separated by the greatest distance from the general mass of the ganglion (fig. 6), are the oldest cells. Now these are the very cells in which the spiral exhibits the greatest number of coils; and from numerous observations I am convinced that the number of coils increases as the fibre advances in age (figs. 2, 3, & 4).

Moreover numerous observations prove that the quantity of matter constituting the body of the cell varies greatly in different cases; and it is almost certain that as these cells advance in age they diminish in bulk, while the so-called nucleus is absolutely, as well as relatively, smaller in the oldest cells. The fundus of the cell, with its large nucleus, exhibits the same characters for a long period; but at the lower, narrow portion of the cell great alterations are observed. In some cells scarcely anything is left except the large nucleus, external to which is a little "formed matter," from which several fibres proceed. Old ganglion-cells are represented in figs. 4 & 25.

Now, as has been shown (figs. 9, 10, 11, 12, 13, 14, & 17), there is only one large nucleus at an early period of development of the cell; while in a fully formed cell there may be from ten to twenty smaller oval nuclei at the lower part of the cell, some of which are connected with the spiral fibres, as well as the large circular one at the fundus of the cell. There is also very frequently a nucleus in the straight fibre near its origin (figs. 1 & 19). It seems pretty certain that all these smaller nuclei are developed from the larger one; but this question will receive further consideration in the sequel.

There are then, in the fully developed ganglion-cell, "nuclei" connected with the *straight fibre* as well as with the *spiral fibre or fibres*; and it must be borne in mind

that there are nuclei connected with the dark-bordered fibres, near their origin in some instances, and near their distribution in all tissues, as well as in connexion with the pale fibres distributed with them. And there is also the very large nucleus with nucleoli at the fundus of the cell.

5. *Of the essential nature of the changes occurring during the formation of all nerve-cells, and of the formation of the spiral fibres.*

Although ganglion-cells are formed according to the three different processes just described, it will be found, upon careful consideration, that the changes which occur are, in their essential nature, the same in all. In every case it has been shown that what is commonly called the "nucleus" takes an important part in the process; and in the drawings (figs. 5, 9, 15, & 38) the large size of the "nucleus" in the young cells cannot fail to be noticed.

In considering the actual changes which occur, it will be better to call the matter which is coloured red by an ammoniacal solution of carmine "*germinal matter*," and the colourless matter around it and continuous with it "*formed material*." In young specimens the germinal matter is sometimes seen to gradually pass into the formed material; but in fully formed cells of all kinds there appears a line of demarcation.

Neither ganglion-cell, nor nerve-fibre, nor indeed any *living* tissue exists without there being *living germinal matter* in connexion with it. On the other hand, masses of germinal matter exist before either ganglion-cells or distinct *fibres* are formed. If figs. 5, 9, 14, 15, 16, & 38, which represent young ganglion-cells, be contrasted with figs. 1, 3, 4, 20, & 27, which are taken from fully formed or old cells, the different proportion of "*germinal matter*" to the "*formed material*" at different ages will be observed; and it is to be noticed that the youngest cells (fig. 9) consist almost entirely of germinal matter, while in the fully formed cell there is at least from ten to twenty times as much "*formed material*" as there is of "*germinal matter*" (fig. 1).

In the fully formed cell the germinal matter (nucleus) exhibits a line around it, but there is no cell-wall or other structure between it and the granular material which surrounds it. In fact, by the use of high powers, an actual *continuity of structure* may usually be demonstrated. The smaller centres (nucleoli) also seem to be distinct from the germinal matter in which they lie. Even in these so-called "nucleoli" still smaller spherical bodies, to the number of three or four (nucleoluli), are sometimes to be seen distinctly (figs. 26 & 27). These centres are evidently formed one within the other.

The last or smallest centres are most darkly coloured. In the "nucleoli" the colour is not so intense. The "nuclei" again are still paler, but nevertheless the colour is very decided indeed. The matter more external is very faintly coloured, or it remains perfectly colourless. So that in this, as in many other instances elsewhere, it is to be noticed that the outer part of each cell, or that in *actual contact with the colouring solution*, is not coloured, while the intensity of the colour gradually increases as we

pass towards the *innermost part* of the germinal matter, although this may be situated at the greatest distance from the colouring solution. To reach the *nucleus* and *nucleolus*, it is obvious the solution must pass *through a considerable thickness of tissue*. *The colour is, however, deposited here in greatest quantity.*

Again, it is to be noticed that in the younger cells (figs. 9 & 38), which are more or less darkly *coloured* over their whole extent, the one or two distinct nuclei seen in the fully formed cells are not to be demonstrated, although it often happens that a vast number of very darkly coloured spots are to be discerned, each being imbedded in matter more faintly coloured than itself. In the young cell every part of the germinal matter, or, in ordinary phraseology, the "entire cell," possesses equal power, and, as we have seen, may divide and give rise to the production of several separate cells; but when the formed matter is produced on the surface; the cell, as a whole, no longer possesses this power, which is restricted to the so-called "*nucleus*" or "*nucleolus*," which may divide and give rise to the formation of new cells.

Suppose new cells are to be developed from a fully formed cell: the outer colourless or formed material, the cell-wall, if present, and the surrounding connective tissue *take no part in the process*; but the active changes are effected by the "*living germinal matter*" ("*nucleus*") alone.

How, then, is the formed material of the cell produced? The observations just made seem to me to lead to but one conclusion—that the *formed material* results from changes occurring in the *germinal matter*. I hold that all the formed material was once in the state of germinal matter, and that whenever the ganglion-cell increases in size, or the fibres in connexion with it increase in length, except of course when artificially stretched, a certain amount of *germinal matter undergoes conversion into formed material*. The changes which take place in the formation of nerve-fibres occur in a similar order; but as the relations of structure produced are more simple, the alterations may be studied more readily and described more clearly.

Figs. 29 & 30 represent a portion of a dark-bordered fibre in course of development. It consists of nuclei in connexion with fibres. The fibre is seen to be thinnest about midway between the respective nuclei (*b*). The fibre grows at the points marked *a*, and at these points only. The oldest parts of the fibre are the narrowest portions, marked *b*. These are narrow because at the time of their formation the masses of germinal matter were so much smaller than they are now (fig. 30). The nuclei in connexion with these fibres may divide, and other new fibres may be produced; and a similar process occurs in the nuclei of the ganglion-cell which are connected with the formation of the spiral fibres.

Fig. 29 gives the appearance which this fibre would have presented if examined at an earlier period. Now, although this figure literally represents but my own view of the matter, it is only just that I should state that fibres presenting every degree of change have been actually observed in the same specimen, so that there can be little doubt as to the general truth of the facts brought forward, although differences of

opinion may be entertained with reference to some of the explanations I have ventured to offer.

My observations upon various tissues in different stages of development have convinced me that the growth of the cells or elementary parts is a much more simple process than is generally supposed, and consists merely in a certain proportion of germinal matter undergoing conversion into formed material, while at the same time pabulum passes into the germinal matter, and the wonderful properties or powers possessed by this substance are communicated to it. By this formation of new germinal matter the proportion of the latter converted into formed material, and the formed material which is destroyed and removed, may be completely compensated for.

There is a certain relation between the proportion of germinal matter and formed material of the cell, which varies at different ages and under different circumstances, as I have shown. The rate at which pabulum undergoes conversion into germinal matter varies according to the facility with which it comes into contact with the living matter. The formed material offers a greater impediment to its passage in old than in young cells, so that under normal conditions, the process of growth occurs more and more slowly as the cell advances in age. In the young cell, more inanimate pabulum becomes *living* matter, and more *living* matter becomes *formed material* than in the adult, and in the latter, more than in the old cell.

Next, then, for consideration is the question of the mode of formation of the spiral fibre. Now it must, I think, be admitted that there is a great accumulation of evidence in favour of the general conclusion that *all living matter possesses a power of movement*. It seems to me that not one step in growth can be explained unless the particles of living matter move by virtue of some inherent force or power which acts independently of, and is capable of overcoming, the force of gravitation. The movements of living matter have been observed in many of the lower forms of living structures. I have described the phenomenon as it may be seen in the mucous corpuscles and young epithelial cells of the nasal and bronchial mucous membranes; and although I have not seen the movements in the living matter of the tissues generally, there seems to me the strongest evidence that such movements actually occur*. In these peculiar ganglion-cells we have, I think, very convincing evidence that movements have taken place uninterruptedly since the earliest changes occurring in their formation. I have endeavoured to show that the cell, when fully formed, does not occupy the same spot as it did when its development commenced; and upon consideration it will appear that it is not possible that many of the ganglion-cells could have been developed in the position in which they are found in the fully formed state.

The spiral seems to result partly from a sort of splitting and subsequent condensation of the lower portion of the cell itself, and partly by growing from the nuclei connected with the fibres, while at the same time the fundus moves away, and spiral after spiral is

* See a paper in my 'Archives,' vol. iv. p. 150, "New Observations upon the Movements of the *living or germinal* matter of the tissues of Man and the higher animals."

left around the central fibre, which is of course gradually increasing in length also. I think it doubtful if the entire cell *rotates*, because the central fibre does not appear to be twisted; but it is obviously possible that the *outer portion* of the cell might rotate slowly round the inner portion without causing any twisting of the fibre, the mass of which the cell is composed being in the natural state very soft and plastic.

It must be borne in mind that at first the two fibres of the ganglion-cell are parallel to each other, and that the cell while altering its position continues to grow. As the cell moves away, its fundus or large extremity preceding, the fibres projecting from it increase in length—are drawn out, as it were.

There is a fact in favour of rotation which I have observed so often that it may be regarded as constant—that, in peripheral parts where a dark-bordered fibre is being developed, a fine fibre passes spirally around it; and this may be accounted for in precisely the same way as I have attempted to explain the production of the spiral fibre of the ganglion-cells. The arrangement described is represented in figs. 29 & 30. It is constant, but can only be demonstrated positively at an early period of development of the dark-bordered fibre. The frequent crossing and twisting of fibres around one another amongst ganglion-cells, and the strange crossing over and under observed in the case of all fibres in the trunks of nerves, must also be due to a corresponding change of position between contiguous fibres after they have been formed, but at an early period of their life's history. The arrangement of the fine fibre, represented in figs. 29 & 30, is very remarkable; and I have seen very many specimens exhibiting the same points. It must also be noticed that the nuclei of the dark-bordered fibre are *much nearer together than the nuclei of the fine fibre*. This fact is also constant in the case of such nerves near their ultimate distribution. I am not yet able to give a satisfactory explanation of the fact, but it would seem to show either that the fine fibre has grown very much faster than the dark-bordered fibre, or that the fine fibre was developed, and perhaps in an active state, at a period anterior to the development of the dark-bordered fibre. These points are of the utmost interest, and well deserve the most searching and minute investigation; for it is certain that the settlement of many of the questions raised, and but very imperfectly considered here, must lead to the establishment of new general principles of wide application.

6. *The sense in which the term "nucleus" is employed in this paper.*

Although I have for convenience made use of the ordinary word "*nucleus*," it must be understood that it is used only in a general sense; for I maintain that the matter around the nucleus differs from that of the nucleus itself only in having reached a further stage of existence. My meaning will be readily understood by the following statement, which is supported by evidence already adduced (pages 6, 7). The whole of the germinal matter, of which the young cell is almost entirely composed, may divide and subdivide, and from it any number of new cells may be produced. Nor is it necessary that a "*nucleus*" should be present in the detached portion. The "*nucleus*" is often

not to be distinguished until *some time afterwards*. This fact may be observed in the germination of pus and mucus. Neither "nucleus" nor "nucleolus," therefore, are bodies possessing *peculiar powers or actions upon matter around them*, nor is the "nucleus" essential to the being or to the *multiplication of a "cell" or elementary part*. Nuclei are but new centres which appear in preexisting germinal matter; and in these again new centres may arise, and so on, centre within centre. In some of the nerve-cells there is but one such centre, in others more than one. In some the "nucleus" is dividing (figs. 11 & 12). The terms *nucleus, nucleolus, nucleolulus* are arbitrary, and indicate germinal centres, which have appeared one after and one within the other. These consist of living matter in different phases of existence.

After a time the germinal matter of which a young "cell" is composed, at its outer part undergoes conversion into formed material. *This formed material cannot produce new formed material*. It may undergo *physical and chemical* changes, but it is no longer the seat of *vital changes*. The germinal matter which remains (nucleus) may still, up to a certain period, give rise to the production of *new cells*. The more the formed material around it increases the greater is the impediment to the passage of nutrient matter, and the more slowly it lives; so that, instead of new cells being produced, the germinal matter that remains gradually undergoes conversion into formed material; and it is doubtful if the germinal matter, at its outer part, where this conversion is actually occurring, could under any circumstances give rise to the production of new cells. It has reached a later stage of being, and has lost this power. Such *vital power*, however, undoubtedly still exists in that part of the germinal matter which in these nerve-cells is known as the "nucleolus." In passing from without inwards, in the case of a fully formed cell (fig. 1) we meet with matter in different stages of existence, which exhibits a difference in power. Most externally is the formed matter, which possesses no power of *formation or reproduction* whatever; next we come to matter in which the vital powers of reproduction still exist, but to a limited degree. It may increase; but from it no defined complex structure like a ganglion-cell could be produced. It is gradually undergoing conversion into formed matter. Within this, again, is germinal matter, which possesses the power of increase, and of giving rise, under certain conditions, to the production of perfect ganglion-cells. This matter (nucleus, nucleolus) still retains the *power possessed by the entire mass, of which the embryo cell was composed*, before it exhibited the wonderful structure evident in its fully developed state; and from it new cells might be developed.

7. *Of the fibres in the nerve-trunks continuous with the straight and spiral fibres of the ganglion-cells.*

The ganglion-cells I have described are not connected with one peculiar kind of nerve-fibre only. In the frog it is probable that the bundle of very fine fibres correspond to the grey or gelatinous fibres of mammalia. I have shown that bundles of very fine fibres, many of which are destitute of dark-bordered fibres, are connected with ganglion-

cells*. Some of these very fine fibres with the ganglion-cell are represented in figs. 22 & 27, magnified 1800 diameters; and these remain as very fine fibres throughout every part of their course.

There is, however, no difficulty in proving that many of the pear-shaped ganglion-cells in the frog are connected with dark-bordered fibres. I have traced a dark-bordered fibre into the ganglion-cell, at the lower part of which it is sometimes convoluted in such a way that its actual connexion with the substance of the cell is not demonstrable. An example of this is represented in fig. 26. It will be asked in this case if the dark-bordered fibre exhibits an axis-cylinder quite up to the ganglion-cell. I have seen a distinct and very fine axis-cylinder, in the case of some old cells in the ganglia on the posterior roots of the nerves in the frog, within three thousandths of an inch of the ganglion-cell; but nearer to the cell the so-called axis-cylinder seems not to be distinct from the material of which the white substance is composed, as I have shown to be the case in all dark-bordered fibres near their distribution. In fact the distinction of a fibre into white substance and axis-cylinder is only to be demonstrated in nerve-fibres which have been developed for a very considerable period of time; and wherever this distinction is observed, we may be sure that the nerve-fibre is of considerable age.

As a general rule the straight fibre is thicker than the spiral fibres, and there is no difficulty in obtaining specimens in which the dark-bordered fibre can be traced on as the straight fibre of the ganglion-cell. The spiral fibres are often very fine, and are connected together here and there. Sometimes several unite to form one very fine fibre, which can be followed for some distance upon, and very close to, the outer part of a wide dark-bordered fibre. But I have many specimens in which both straight and spiral fibres are exceedingly thin and of equal diameter, others in which the straight is much thicker than the spiral fibre, and a few in which the diameter of the spiral fibre or fibres is even greater than that of the straight fibre.

I have traced the *spiral fibres* continuous with a *dark-bordered* fibre in several instances. A very conclusive specimen showing this fact is represented in Plate I. fig. 1, in which both straight and spiral fibre were continuous with dark-bordered fibres; also in fig. 19, in which the connexion between the spiral fibre and the dark-bordered fibre is represented.

So that, with regard to the fibres connected with these ganglion-cells in the frog, it may be remarked—

1. That in some instances very fine fibres, not more than the $\frac{1}{60,000}$ th of an inch in diameter, are alone continuous with both the straight and spiral fibres of the ganglion-cell.

2. That a dark-bordered fibre may be traced to the ganglion-cell as the straight fibre, while the spiral fibres are continued on as very fine fibres.

3. That the spiral fibres may be continued onwards as a dark-bordered fibre, which may be wider, at least for some distance, than the fibre continued from the straight fibre.

* Archives of Medicine, No. XII.

4. That both straight and spiral fibres may be continuous with dark-bordered fibres*.

There is no reason for assuming that the fine fibres in all cases are but an early stage of development of the dark-bordered fibres; for the two classes of fibres undoubtedly exist at every period of life of the animal, even in old age. I conclude, therefore, that these peculiar ganglion-cells in the frog are connected with both classes of fibres; and in mammalia the apparently spherical ganglion-cells, which answer to these pear-shaped cells of the frog, are connected with both grey and dark-bordered fibres.

It is exceedingly difficult to follow an individual fibre for any distance in the trunk of a nerve. I have seen nerve-fibres dividing in the trunks near to ganglia, and on two or three occasions I have almost convinced myself that one of the fibres resulting from the subdivision passed to a ganglion-cell, while the other passed on in the trunk of the nerve; but I have not succeeded in preserving an undoubted specimen of such an arrangement. The difficulty of following one individual fibre is much increased by the fact that the nerves vary so much in thickness within a very short distance. Dark-bordered fibres may be very distinct, and within a distance of two thousandths of an inch may be so thin as to be scarcely demonstrable, swelling out again a little further on. This renders it necessary to isolate an individual fibre from its neighbours before its course can be traced with positive certainty for any great distance. A good example of the varying diameter of dark-bordered fibres within a short distance is represented in fig. 39.

The observations recorded in page 7 seem to show that a ganglion-cell may be developed upon a nerve-fibre already formed. Hence these ganglion-cells cannot be regarded as centres from which two nerve-fibres proceed direct to their peripheral distribution, but as *centres placed at a part of a circuit which existed as a complete circuit before the ganglion-cell was developed in connexion with it*. It is impossible to discuss this most interesting and important question without entering into the consideration of the connexion of nerve-fibres with other centres, especially with the nerve-cells in the spinal cord and parts above; so I will not pursue it further. But I would state that I have not succeeded in finding ganglia from which fibres proceed in one direction only: and, that I may not be misunderstood upon this point, let me say that I have never seen a ganglion, in connexion with the nervous system of any creature, the fibres of which proceed in but one direction only, as is now believed to be the case by many observers. From every ganglion I have ever seen, fibres proceed to their destinations in at least two different directions; and from the majority of ganglia, even in the case of those very small ones which consist only of three or four cells, fibres often pass away in three or four different directions (fig. 5). And in every case in which I have been able to obtain a separate ganglion-cell well prepared, I have seen at least two

* I do not feel quite confident that both the fibres proceeding from *one ganglion-cell*, although broad, are true dark-bordered fibres; but it would seem pretty certain that in some cases a dark-bordered fibre is connected with the cell as a spiral, and in others as a straight fibre—a fact which may hereafter be of some importance, as it may afford us a positive index of the direction in which the nerve-current circulates in these elaborate organs.

fibres; and although these may run parallel to each other for some distance, they have been so often observed to pass in opposite directions when they reach the nerve-trunk, that I believe myself justified in expressing a very positive opinion that such is always the case.

8. *Of the ganglion-cells of the heart.*

Although the description given in this paper will apply to the ganglion-cells of ganglia in different parts of the frog, including those distributed to the heart and lungs, I feel it necessary to refer particularly to the cardiac ganglia of the frog, because KÖLLIKER has recently made some very confident statements with regard to the structure, arrangement, and action of these ganglia, which my observations fail to confirm. Nor is the difference between us one of interpretation; we are at variance as to actual facts. With reference to the ganglia of the heart this observer says, "It may be particularly mentioned that the origin of nerve-fibres from unipolar cells, and the rarity of the double origin of fibres, may be especially well seen in *one* place, namely, in the septum of the heart of the frog, where also R. WAGNER admits the fact. . . . Here also we may most readily convince ourselves that there are many apolar cells without processes, as is most plainly shown in the heart-ganglia, and in the small ganglia upon the urinary bladder of the *Bombinator*, in which, as also in similar ganglia of the frog, the matter is as clear as possible"*.

But in his Croonian Lecture last year, his opinion as to apolar cells has become curiously modified. Although the existence of such cells was as "clear as possible" in 1860, great doubts are expressed upon the matter only two years afterwards:—"These cells, that is to say, all of them which are connected with nerve-fibres and whose connexions can be clearly made out, are *unipolar*, or send out *but a single fibre*, and that in a *peripheral direction*, without having any connexion with the transcurrent fibres of the *vagus*. *Bipolar or multipolar cells are not to be seen: some apparently apolar cells present themselves, but concerning these it may be doubted whether they are unipolar cells whose issuing fibre is in some way hidden from view*"†.

These positive statements are not illustrated by a single drawing, nor does Professor KÖLLIKER give any reasons for modifying his views as to the presence of apolar cells.

As the result of very numerous observations, I have to state—

1. That there are no apolar cells, either in the ganglia of the heart or in those of the bladder of the frog, although KÖLLIKER asserted that their existence was as "clear as possible."

2. The unipolar cells of KÖLLIKER really have two or more fibres proceeding from them; so that his statement, that "all the cells connected with nerve-fibres send out but a single fibre," is not a fact.

3. Some fibres certainly pass in a central direction; so that KÖLLIKER'S assertion, that all the fibres pass in a peripheral direction, is not true.

If these ganglion-cells be examined, it will be found that the fibres proceeding from

* Manual of Microscopic Anatomy, April 1860.

† Croonian Lecture, May 1st, 1862.

some pass for a certain distance in a peripheral direction, while others pursue the very opposite (Plates VII., VIII. figs. 41 & 42). Very many lying at the side of a nerve-trunk pass transversely towards the central part of the bundle of fibres. The arrangement and structure of the ganglion-cells of the heart differ in no essential particulars from those I have described in other ganglia. I have succeeded in demonstrating in several instances the straight fibre passing in one direction in the trunk of the nerve, and the continuation of the spiral fibre pursuing an opposite course. In some of these ganglion-cells the spiral is reduced to two or three coils (fig. 42), as is observed elsewhere, but I cannot but conclude that every cell has at least two fibres.

Nor can I agree with Professor KÖLLIKER in the statement that the ganglion-cells have no connexion with the "transcurrent" fibres of the vagus. Although I have not been able to demonstrate how many fibres of the vagus are connected with the ganglion-cells, nevertheless, looking generally at the course of the fibres, and at the number of the cells, and considering the facts observed in other ganglia, I regard it as very probable that many of them are connected with the cells.

9. *Of the ganglion-cells and nerve-fibres of the arteries.*

In the nerve-trunks running near the branches of the arteries of the palate of the frog are numerous ganglion-cells. These ganglion-cells are often situated at the angle of division of the nerve-trunks. Some of the fibres from the small ganglia lying near arteries may be traced to the coats of the arteries, and some fine nerve-fibres resulting from their subdivision may even be followed amongst the muscular fibre-cells of arteries not more than the $\frac{1}{1000}$ th of an inch in diameter.

Ganglia and ganglion-cells are found in considerable number in connexion with the arteries distributed to the different viscera of the abdomen, heart, and lungs, and very many are found close to the small arteries which supply the bladder of the frog. In many cases small ganglia and separate ganglion-cells are imbedded in the external or areolar coat of the artery.

In fig. 46 a small ganglion in course of development upon one of the iliac arteries of the frog is represented; and several fine branches of nerve-fibres can be followed amongst the muscular fibre-cells. I have seen very fine nerve-fibres beneath the circular muscular fibre-cells, and apparently lying just external to their lining membrane, composed of longitudinal fibres with elongated nuclei—an observation which confirms a statement of LUSCHKA'S. I have not succeeded in satisfying myself that nerve-fibres are ever distributed to the lining membrane of an artery, although, from the appearances I have observed, I cannot assert that this is not the case. In the auricle of the heart and at the commencement of the large cavæ very fine nerve-fibres are certainly distributed very near indeed to the internal surface, being separated from the blood only by a very thin layer of transparent tissue (connective tissue).

The distribution of nerve-fibres to the coats of a small artery about the $\frac{1}{800}$ th of an inch in diameter is represented in fig. 45. In all cases (and I have examined vessels in

almost all the tissues of the frog) not only are nerve-fibres distributed in considerable number upon the external surface of the artery, ramifying in the connective tissue, but I have also followed the fibres amongst the circular fibres of the arterial coat. The nerves can be as readily followed in the external coat as in the fibrous tissues generally; and the appearance of the finest nucleated nerve-fibres, already alluded to, enables one to distinguish them most positively from the fibres of connective tissue in which they ramify.

These nerves invariably form networks with wide meshes. I have demonstrated such an arrangement over and over again. A similar disposition may be seen in the auricle of the frog, in the coats of the venæ cavæ near their origin from the auricle, among the striped muscular fibres of the lymphatic hearts of the posterior extremities of the frog, and in other situations. KÖLLIKER confesses that he has not succeeded in observing distinct terminations to the nerves distributed to the vessels of muscles. This observer has made the very positive assertion that some arteries are completely destitute of nerves, and, apparently without having given much attention to the subject, says, "hence it is evident that the walls of the arteries are not in such essential need of nerves as is usually supposed." Professor KÖLLIKER seems to conclude, in too many cases, that what he has failed to see does not exist. It is easy to demonstrate nerves in considerable number on the arteries of the frog generally, though these nerves, and more especially those ramifying in the coats of the vessels of mammalia and birds, are still considered by many authorities in Germany to be fibres of connective tissue.

The nerves which supply the small arterial branches in the voluntary muscles of the frog come from the very same fibres which are distributed to the muscles. I have seen a dark-bordered fibre divide into two branches, one of which ramified upon an adjacent vessel, while the other was distributed to the elementary fibres of the muscle.

10. *Of the connexion of the ganglion-cells with each other.*

In figs. 5, 15, & 16, which represent ganglion-cells at an early period of development, several are seen connected together; in fact, the matter of which the several cells are composed is continuous. This must be the case, at least for a certain time, because a number of cells may be formed by the division of one (figs. 5, 11, 12, & 15).

After a time, as the new cells separate further and further from each other, the intervening matter which connects them becomes thinner and thinner, and forms what would be properly termed a fibre, figs. 15 & 16; and as the cells move away from the line where their formation commenced, these connecting fibres become finer and finer, and at last could not be distinguished from fibres of connective tissue. It is probable, in many instances, that all continuity of structure between some of the cells ceases; but it is to be remarked in all cases, that the nerve-fibres in the substance of a ganglion cross each other in various directions, and it is certain that fibres from several different cells run in the same bundle which leaves the ganglion. From what I have observed, I think it almost certain that, in many cases, ganglion-cells of one ganglion are connected by fibres with cells of another ganglion.

11. *Of the "capsule" of the ganglion-cell, and of the connective tissue and its corpuscles.*

From what has already been stated, it will be inferred that there is no actual cell-wall or special capsule at an early period of development of the ganglion-cell. The cell may form protrusions at various parts of its surface, like a young epithelial cell, a mucus- or a pus-corpuscle; and each offset may give rise to the formation of a new cell. After a time the cell is seen to be surrounded by, or imbedded in, a transparent substance, which in some cases exhibits a definite outline and might be termed a cell-wall (fig. 25), while in others it would be more correctly described as a matrix. In old ganglia there is a quantity of this tissue, which accumulates and becomes condensed as age advances; and it exhibits a fibrous character with nuclei imbedded in it. In consequence of the condensation of this tissue, it is often very difficult to demonstrate the anatomy of the cells in animals of mature and advanced age.

In order to understand the formation of this texture, it is necessary to examine ganglia and ganglion-cells at different ages.

Figs. 9, 14, & 15 show that at an early period the ganglion-cell consists simply of one oval mass of germinal matter, surrounded with a little formed material, from each extremity of which a fibre proceeds. The whole is imbedded in a little transparent tissue; and in similar tissue run the very fine nerve-fibres which proceed from the young ganglion-cell (figs. 10, 17, 18, 22, & 23).

Figs. 4, 27, & 28, on the other hand, show fully formed ganglion-cells which are imbedded in a tissue exhibiting striations, and a few fine fibres which resist the action of acetic acid. Around and at a short distance from the ganglion-cells there are several oval nuclei (connective-tissue corpuscles).

Figs. 4, 27, & 28 exhibit the characters of old ganglion-cells. The fibrous appearance of the matrix is more distinct, the fibres which resist the action of acetic acid are more numerous, and there are more nuclei around the ganglion-cell and around the fibres proceeding from it, but these nuclei are not connected with either.

And the important fact that the so-called connective-tissue corpuscles outside the ganglion-cells and outside the nerve-fibres are but faintly coloured with carmine, while those nuclei in connexion with the ganglion-cell and nerve-fibres, although separated from the solution by a greater distance, are more intensely coloured, must not be lost sight of. This was very distinct in the specimen represented in figs. 27 & 28.

Before any attempt is made to explain these facts, it is necessary to consider more particularly the relation of nerve-fibres and nerve-cells to the connective tissue and connective-tissue corpuscles. Although it is undoubtedly true that in preparations mounted in certain fluids it is not possible to distinguish the finest nerve-fibres from connective tissue, this distinction can be most clearly made out in some of my specimens; for example, in figs. 17 & 18 the nerve-fibre can be very readily distinguished as it runs amongst the connective tissue, and the true nature of the fibre is placed beyond question by the presence of the ganglion-cell. All fibres which can be followed for a considerable

distance, which refract like true nerve-fibres and exhibit an appearance more or less granular, especially if they can be followed into ganglion-cells, must clearly be pronounced nerves. The finest nerve-fibres may often be followed amongst the connective tissue for a long distance, and their relation to other structures most positively determined. Fig. 43 represents a portion of a very fine nerve-fibre running amongst connective-tissue corpuscles, and crossing one of the processes of a pigment-corpuscle; and it is unquestionably distinct from the last two structures. In the cornea, as I have before stated, the nerves may be followed in their numerous ramifications amongst the corneal corpuscles and their processes, and it can be seen that the latter are not connected with the nerves as KÜHNE supposes. The nerve-fibres and the corneal tissue grow together, but, although closely related, they remain structurally distinct from one another.

But although there is no structural connexion between the nuclei of a true fibrous tissue (pericardium, tendon, cornea, sclerotic, &c.) and the nerve-fibres and nerve-nuclei ramifying in it, there is some difficulty in deciding upon this question in the case of certain forms of indefinite connective tissue immediately surrounding nerve-fibres and ganglia, and it is often not very easy to decide whether a given nucleus really belongs to a nerve-fibre or should be considered as a connective-tissue corpuscle. For example: what is the nature of the nuclei near the nerve-fibre and ganglion-cell in fig. 18? These are undoubtedly, as they now appear, connective-tissue corpuscles; but how were they formed? We know that during the growth of nerves and ganglion-cells new nuclei are formed, and some of these, which lie on the surface of the fibre or cell, produce connective tissue. The nuclei under consideration are, I believe, of this nature; and I consider it probable that they belonged to a nerve-fibre at an earlier period, or at any rate resulted from the division of nuclei which were concerned in the formation of nerve-fibre. So I believe that those close to the ganglion-cell were formed by it. At the lower part of the cell may be seen three small nuclei, which are probably of the same nature. From them, up to a certain period, new nuclei might have been developed and true nerve-fibres might have proceeded; but the nuclei can now only produce a low form of connective tissue, which accumulates around the more important structures. I consider that the ganglion-cell delineated in fig. 17, from the same specimen and not very far from the part represented in fig. 18, represents an earlier stage of development than the last ganglion-cell.

But I have already shown that in many cases delicate fibres from true nerve-fibres, after gradually becoming very fine, are lost in the connective tissue. I have also shown that fibres of connective tissue result from the degeneration of nerve-fibres; and it has been proved conclusively that connective tissue results from the wasting of nerve-fibres in disease. Nor is the nervous the only tissue which by normal wasting or abnormal degeneration leaves what is termed connective tissue. A structure so special as a uriniferous tube, or a portion of the cell-containing network of the liver may waste, and all that represents it will be what is termed connective tissue and connective-tissue corpuscles.

It seems to me that the almost structureless or delicately fibrous matrix in which both nerve-fibres and nerve-cells are imbedded is the result of changes which have taken place before the nerve-fibres and cells there present have made their appearance, and if these very nerve-fibres and cells had been allowed to remain for a longer period in the living animal, they would have become surrounded with more connective tissue. Both fibres and cells might become altered and waste: all the fatty and other constituents having been absorbed, what we term "connective tissue" alone would remain. Connective tissue and connective-tissue corpuscles are produced from the very same masses of germinal matter as those from which nerve-cells and nerve-fibres are developed; and I think it must be admitted that many fibres which resist the action of acetic acid, and which are generally regarded as consisting of yellow elastic tissue, were once nerves.

Nevertheless true nerve-fibres in which the nerve-current passes do not lose themselves in the connective tissue or blend with it, nor are they connected with its corpuscles, but they form networks, as already described. A normal nerve-fibre can always be distinguished from a fibre of connective tissue.

All the structures existing in the adult ganglion were at an early period represented only by masses of germinal matter (nuclei), surrounded or separated from each other by, or imbedded in, a little soft formed material. At a very early period of development the so-called nuclei of the nerve-fibres are very close together. Nerve-centres at an early period of development bear little resemblance to the perfectly developed structure,—a remark which is illustrated in the most striking manner in the case of the particular ganglion-cells which have been described in this memoir. Nor would it be possible to prove the real nature of such a structure as that represented in figs. 5, 11, 12, & 15, if seen amongst the tissues of an embryo, imbedded as it would be in embryonic tissue almost as rich in nuclei as the structure itself. Even when nerve-tissues have reached the period of development when their essential anatomical characters are well marked, and when they perform their characteristic actions, it is often very difficult, and if the ordinary processes of preparation be employed, impossible, to demonstrate positively the arrangement of the nerve-fibres, although we may be quite positive, as for example in the case of voluntary muscles, that nerve-fibres are there. Nuclei can be seen which certainly do not belong to capillaries, and these nuclei lie transversely or obliquely across the muscular fibres, and often several may be seen following each other in lines; but only in very favourable cases can any fibre at all be made out, and with the greatest care and the highest powers a very faint and slightly granular band only can be seen. Nor can the fibres be traced to undoubted nerve-fibres: and it is even difficult to be certain of the nature of what will eventually become the large trunks consisting of dark-bordered fibres; so closely do they resemble vessels, and so numerous are the nuclei. But by using transparent injection the vessels may be made out positively, and by adopting certain precautions in preparation, which it would be tedious to refer to here, many such difficult points have been definitely settled; and I have traced the changes which occur in the minute structure of many tissues from the earliest period at which they could be recognized up to their fully developed state. In the case of ganglia and nerve-

fibres, we have at an early period what would be termed nuclei and granular matter around and between them; then we have the fully developed structure (cell-contents, spiral fibre, &c.), still bearing the same relation to the germinal matter which produced it; and lastly, when this structure has wasted, we have its remains represented by connective tissue and masses of germinal or living matter, no longer capable of producing special tissue, but only giving rise to the simple, transparent, more or less fibrous material, or connective tissue. These masses of living matter are usually known as the connective corpuscles; but in indefinite connective tissue, neither fibrous material nor corpuscles are developed as a special tissue destined for a special purpose in the economy: it is merely the remains of higher tissues, which have been in great part removed; or it is formed by germinal matter which is not capable of giving rise to any special structure. On the other hand, the so-called connective tissue of the cornea, of tendon, &c., is developed as a special tissue, and it may be said to fulfil a special purpose.

The structure of the cells in mammalia corresponding to the pear-shaped cells of the frog is a subject worthy of separate consideration; but I may mention that in several instances I have seen a fibre prolonged from the cell, corresponding to the straight fibre of the pear-shaped ganglion-cells of the frog—that the “nucleated fibres” which seem almost to encircle many of the cells correspond to the nucleated spiral fibre or fibres described in this memoir. That these nucleated fibres are true nerve-fibres, and not, as generally supposed in Germany, “nucleated connective tissue,” is rendered evident by careful observation of the changes occurring during the development of the ganglia, and, I think, clearly demonstrated by the observations recorded in this paper. I regard it as certain that if these nucleated fibres surrounding the mammalian ganglion-cells are connective tissue, both the fibres I have described in the frog’s ganglion-cell are of the same nature.

It is possible that, for many years to come, some observers will persist in terming everything in which they fail to demonstrate distinct structure, connective tissue, and all nuclei which are not seen in their specimens to be in connexion with positive vessels, positive nerve-fibres, or other well-defined tissues besides fibrous tissues, connective-tissue corpuscles; but there is little doubt that when the changes occurring during the development of special tissues shall have been patiently worked out by the use of high powers and better means of preparation, opinions on the connective-tissue question will be completely changed. The idea of the necessity for a supporting tissue or framework will be given up, and many structures now included in “connective tissue” will be isolated, just as new chemical substances year after year are being discovered in the indefinite “extractive matters.”

It is remarkable how positively many authorities deny the existence of structures which they have failed to demonstrate. Such a course is only justifiable on the presumption that the art of demonstrating structure has arrived at perfection; but we know, on the contrary, that it is but in its infancy. Surely it is premature to maintain that the vessels of the umbilical cord are destitute of nerve-fibres because we may have failed to

demonstrate them—that the fibres of voluntary muscle only receive nervous supply at one point, because authorities will not admit that nerve-fibres may exist which are too delicate or too fine to be demonstrated by the means they may have employed—that the spindle-shaped fibres of organic muscle generally are not supplied with nerves, because they cannot find them—that the fibres prolonged from the large cells in the cord and in the brain are not continued into fibres, because they have failed to trace them for any considerable distance.

I think I can convince any one, by positive demonstration, that the three last positions are utterly untenable; while there is every reason to believe that certain elongated nuclei and fibres, to be seen amongst the muscular fibre-cells of the umbilical arteries and on the smaller vessels of the placenta, really belong to the nervous tissue.

Moreover many observers seem to have determined in their own minds what appearance a fibre should present to be entitled to be regarded as a nerve (that it must exhibit the double contour), and then they arbitrarily assert that a fibre which does not present these characters cannot be nervous; and even if it be continuous with an undoubted nerve-fibre, it is put down as connective tissue. The alterations which are produced in undoubted nerve-fibres by stretching, pressure, and the influence of water must not be forgotten.

It is true that during the last few years pale fibres have been admitted to exist in some situations besides the Pacinian corpuscle; but few observers will be prepared to admit the existence of a very extensive distribution of delicate pale nucleated nerve-fibres in every part of the peripheral nervous system, or that the active portion of all nerve-fibres exhibits the same essential anatomical characters, and that in all cases complete circuits exist, while free ends are nowhere to be found: yet these general conclusions are justified by facts which have been demonstrated*.

Conclusions.

The following are some of the most important general conclusions I have arrived at in the course of this inquiry:—

1. That in all cases nerve-cells are connected with nerve-fibres, and that a cell probably influences only the fibres with which it is structurally continuous.

2. That *apolar* and *unipolar* nerve-cells do not exist, but that all nerve-cells have at least two fibres in connexion with them.

3. That in certain ganglia of the frog there are large pear-shaped nerve-cells, from the lower part of which two fibres proceed:—*a*, a *straight fibre* continuous with the

* I have seen numerous very fine nuclei connected together with exceedingly minute fibres in the tissues of many of the lower animals, especially insects. In this class, I am certain, nerve-fibres exist far too minute to be seen by any power yet made.

I regard very fine fibres and nuclei amongst the contractile tissue of the common Actinia as nervous, and I have seen a texture presenting similar characters ramifying in the muscular tissue of the Starfish and Sea-Urchin.

central part of the body of the cell; and *b*, a *fibre or fibres continuous* with the circumferential part of the cell, which is coiled *spirally* round the straight fibre.

4. These two fibres, after lying very near to, and in some cases, when the spiral is very lax, nearly parallel with each other, at length pass towards the periphery in opposite directions.

5. Ganglion-cells exhibit different characters according to their age. In the youngest cells neither of the fibres exhibits a spiral arrangement; in fully formed cells there is a considerable extent of spiral fibre; but in old cells the number of coils is much greater.

6. These ganglion-cells may be formed in three ways:—

a. From a granular mass like that which forms the early condition of all structures.

b. By the division or splitting up of a mass like a single ganglion-cell, but before the mass has assumed the complete and perfect form.

c. By changes occurring in what appears to be the nucleus of a nerve-fibre.

7. During the development of a ganglion-cell, there is reason to believe that the entire cell moves away from the point where its formation commenced, so that the fibres connected with it will become elongated.

8. There are “nuclei” in the body of the cell; and there are “nuclei” connected with the spiral, and also with the straight fibre. The nuclei in the cell are found upon its surface, and also in its substance.

9. The matter of which the “nucleus” is composed has been termed by me “germinal matter.” From it alone growth takes place; and in all cases the matter (formed material) of which the nerve-fibre consists was once in the state of germinal matter.

10. The “nucleolus” consists of germinal matter. It may be regarded as a new centre which originates in a preexisting centre.

11. The ganglion-cells of the frog are connected with dark-bordered fibres, and also with fine fibres.

12. Contrary to the statement of KÖLLIKER, that apolar cells and unipolar cells are to be demonstrated in the cardiac ganglia, all the cells in these ganglia have two or more fibres emanating from them.

13. The muscular coat of all arteries of the frog, and probably of other animals, is supplied with nerve-fibres.

14. Nerve-fibres are not connected with the connective-tissue corpuscles.

15. The so-called nucleated capsule of the ganglion-cells in the ganglia of mammalia usually consists of nerve-fibres, many of which are connected with the cell.

15. As nerve-fibres grow old the soluble matters are absorbed, leaving a fibrous material which is known as connective tissue. A corresponding change is observed in other textures, both in health and disease.

The first part of the book is devoted to the history of the United States from its origin to the present time. It is a comprehensive and authoritative work, and is highly recommended to all who are interested in the history of the United States.

The second part of the book is devoted to the history of the United States from the present time to the future. It is a speculative and imaginative work, and is highly recommended to all who are interested in the future of the United States.

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EXPLANATION OF THE PLATES.

The dimensions of each object delineated can be ascertained by reference to the scales at the bottom of each page, magnified by the *same power* as the object itself. These scales, however, have not been measured quite correctly; the upper one being a little too long, while the lower is a little too short.

The drawings, with the exception of figs. 32 to 37, are accurate copies of nature.

PLATE I.

Contains figures illustrating the structure of the ganglion-cells connected with the sympathetic of the frog.

PLATES II. & III.

Illustrate the changes occurring during the development of the ganglion-cells in the fully-formed frog, as observed in various ganglia of the sympathetic near the arteries supplying various internal organs of the frog, in the ganglia on the posterior roots of the nerves, the ganglia from which the heart, bladder, palate, and other organs receive their supply of nerve-fibres.

The changes occurring during the development of a granular mass of germinal matter into perfect tissues (nervous, vascular, muscular, fibrous, cartilaginous, osseous, glandular, &c.) can be studied more satisfactorily in the adult frog than in the embryo; for a complete history of the changes may be deduced from careful observations upon a small portion of an organ or structure in the same animal. For example, nerve-cells in every stage of development, from a small mass of germinal matter (nucleus) to the fully developed complex nerve-cell with its *straight and spiral fibre*, can be demonstrated even in one single microscopic ganglion (figs. 5, 6, 7, 8).

PLATE IV.

Shows the relation of ganglion-cells and nerve-fibres to connective tissue and its corpuscles (figs. 17 & 18), and illustrates the connexion between the matter of which the body of the ganglion-cell consists and that which enters into the composition of the nerve-fibre.

PLATE V.

Exhibits the structure of several different forms of ganglion-cells, all of which possess two or more fibres.

PLATE VI.

Illustrates the relation of numerous very fine fibres to a single ganglion-cell, the connexion between some of the fibres of which the bundle is formed, and the relation of the compound bundle to the cord of connective tissue in which it is imbedded. In figs. 29 & 30, the manner in which a fine nerve-fibre is coiled spirally round a dark-bordered fibre at an early period of formation of the latter is represented.

PLATE VII.

Contains—

1. Figures of ganglion-cells exhibiting particular characters (figs. 31 & 38).
2. A series of drawings showing the changes which, the author believes, take place in the production of the ganglion-cell with the spiral fibre (figs. 32 to 37).
3. A copy of a bundle of nerve-fibres in which the diameter of each fibre is greatly reduced at the point where the bundle passes through constricted apertures (fig. 39).
4. A drawing of a small compound nerve-trunk with a finer trunk coming off from it at right angles (fig. 40). It will be observed that the fine trunk is composed of fibres which pursue opposite directions in the large trunk, passing as it were towards the centre and towards the periphery.
5. A drawing of one of the pneumogastric nerves of the frog near the auricle of the heart. Numerous ganglion-cells are connected with the trunk of the nerve by very fine fibres, which are soon lost, but some pursue a direction towards the heart, while others pass towards the brain. The trunk of the nerve is at the lower part of the figure. The arrow points towards the heart. The bundle of fibres marked *b* connects the trunk of the nerve with that on the opposite side.

PLATE VIII.

Fig. 42 represents two of the ganglion-cells, and the fibres connected with them, from the pneumogastric nerve (fig. 41). The course of some of the fibres can be traced in this drawing.

The relation of a very fine nerve-fibre to the connective-tissue corpuscles, and to a portion of one of the processes of a pigment-cell, is shown in fig. 43, which is magnified nearly three thousand diameters. The distribution of nerve-fibres in the tissue external to capillary vessels is illustrated in figs. 44 & 47. The ramification of fine nerve-fibres upon the muscular coat of a small artery from the bladder of the *Hyla* is seen in fig. 45, and in fig. 46 a portion of a branch of the iliac artery, with some small ganglion-cells and nerve-fibres connected with them.



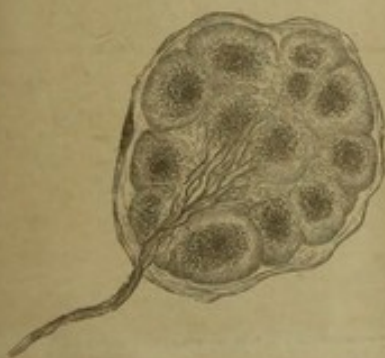
Minute ganglia in process of development, near iliac artery. Common Frog. At *a*, several cells in process of division. These cells seem to be what might be called enlarged 'nuclei' of nerve fibres. At *c*, such cells or nuclei at a still earlier period. *b*, a cell almost fully formed, with several fibres proceeding from it. *c*, masses undergoing division. At *d*, several cells and fibres are being formed. *e*, masses of germinal matter in the course of nerve fibres becoming developed into ganglion cells. The masses at *c* and *a* are but an early stage of such a ganglion as *c*, *b*, *d*. $\times 700$.

Fig. 6.



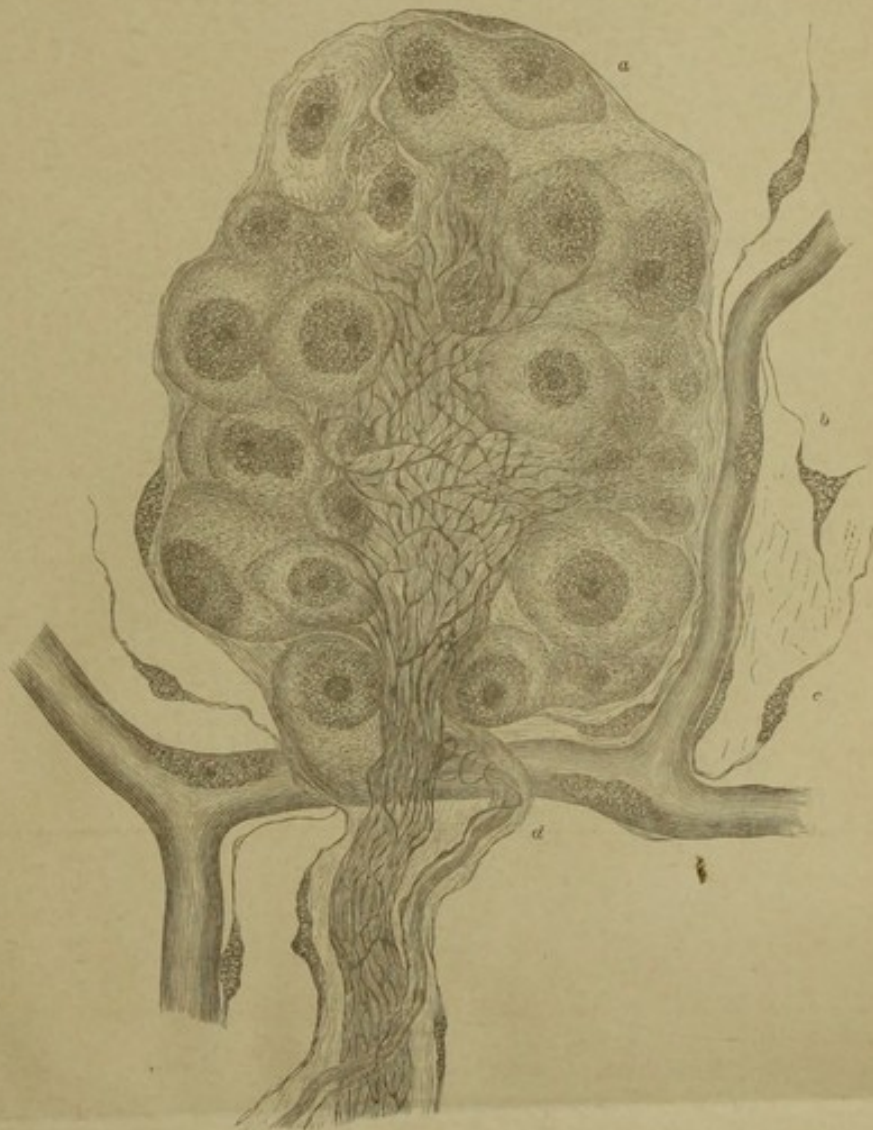
Ganglia and nerve trunks, near iliac artery. Frog. $\times 40$.

Fig. 7.



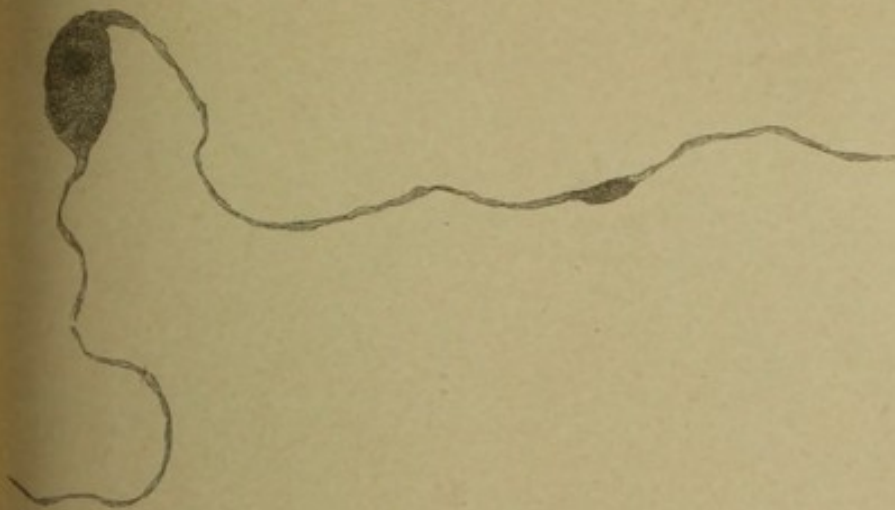
The ganglion cell marked *a* in Fig. 6. $\times 700$ diameters. The mass is undergoing division, and from it a number of separate cells like the groups in Fig. 6 would result.

Fig. 8.



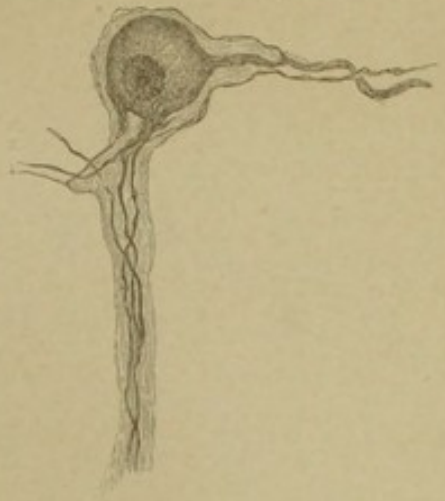
The mass of imperfectly developed ganglion cells at *b*, Fig. 6. *a*, a mass dividing into two. *b*, connective tissue corpuscle. *c*, nerve distributed to capillary vessel. *d*, a more advanced ganglion cell exhibiting straight and spiral fibres; its straight fibre is much thicker than any in the bundle of fine fibres passing into the body of the ganglion. $\times 1800$.

Fig. 9.



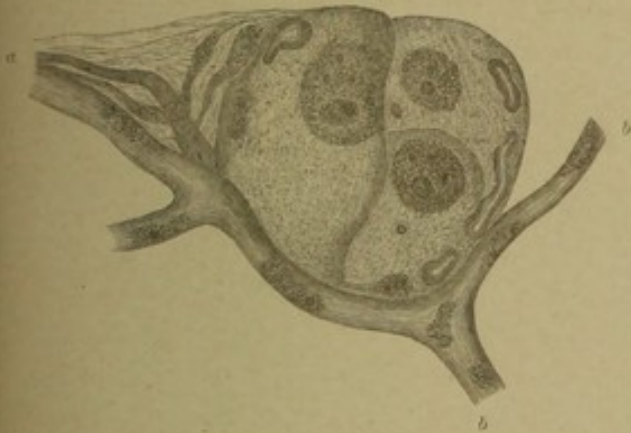
Fine nerve fibre, with cell or nucleus (germinal matter), undergoing development into a ganglion cell. See Figs. 32 to 37. From a bundle of fibres near lumbar nerves, *Hyla*. $\times 1500$.

Fig. 10.



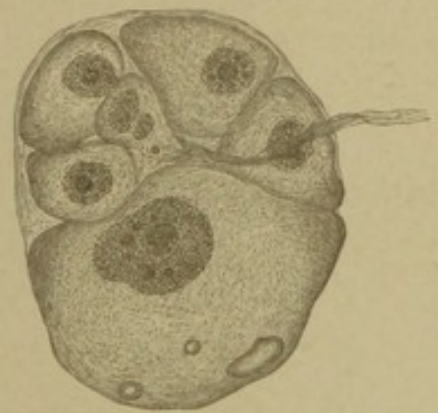
Ganglion cell, with several fibres proceeding from it. Near heart of Frog. $\times 700$.

Fig. 11.



From the ganglion on the posterior root of spinal nerve. *Hyla*. Dorsal region of the cord. Showing the upper surface of a mass, which to a low power appears as one cell, dividing into three. *b* the capillary with its nuclei. At *a* a nerve fibre, which probably comes from one or more of the cells, is seen. $\times 700$. Near the capillary are some oil globules on the surface of the cell.

Fig. 12.



Another mass from the same ganglion as Fig. 11, dividing into six or seven separate cells. $\times 700$. In the lower part of the figure are three oil globules.

Fig. 13.



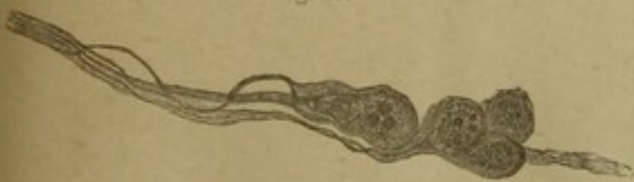
Ganglion cell, with fibres passing in opposite directions. In connective tissue near auricle. Heart of the Frog. $\times 700$.

Fig. 14.



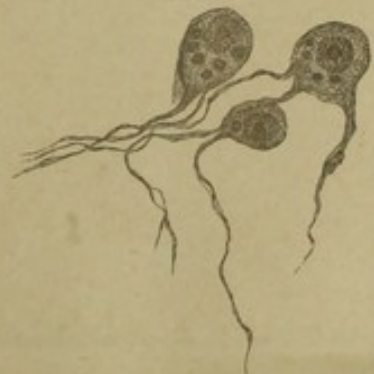
Young ganglion cell. Bladder. *Hyla*. The fibre was very pale. There was no sheath or connective tissue about cell or fibre. $\times 700$.

Fig. 15.



Very young ganglion cells, near iliac artery. Frog. $\times 700$.

Fig. 16.



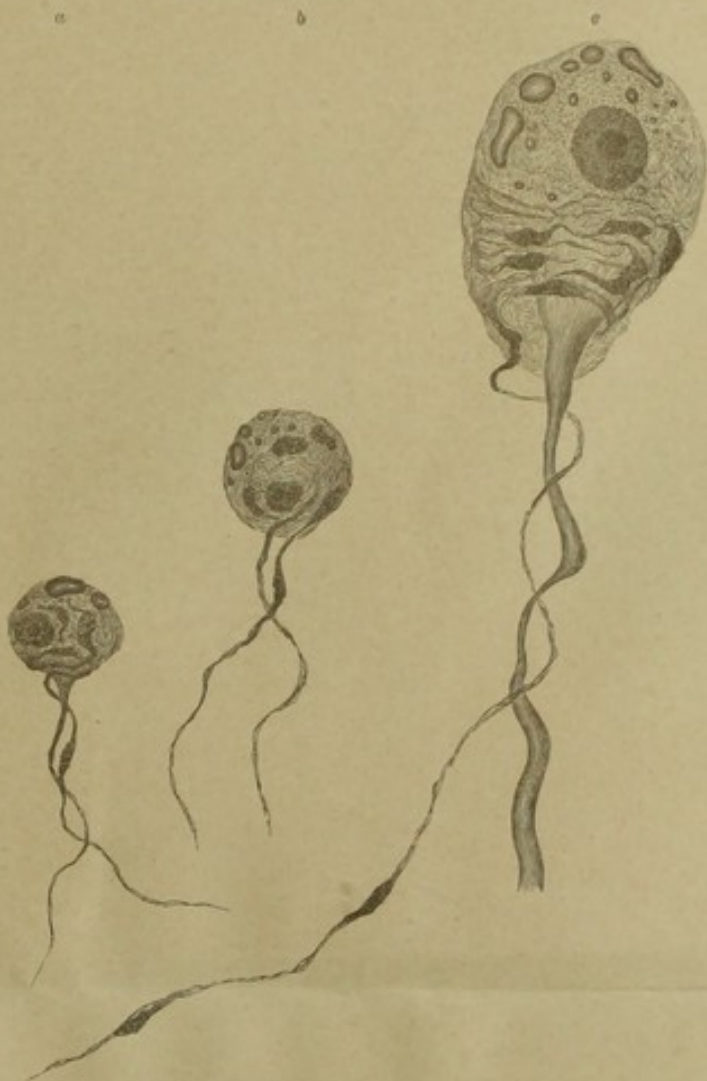
Young ganglion cells, near one of the large arteries of Abdomen. *Hyla*. $\times 700$.



Ganglion cells and nerve fibres in connective tissue. Fig. 17, Bladder. *Hyla*. Fig. 18, near Auricle, Heart. *Hyla*. Fig. 17 is a younger cell than that represented in Fig. 18. The relation of the nerve fibres and cells to the connective tissue corpuscles is seen in this figure. The nerve fibres are not connected with the connective tissue corpuscles.

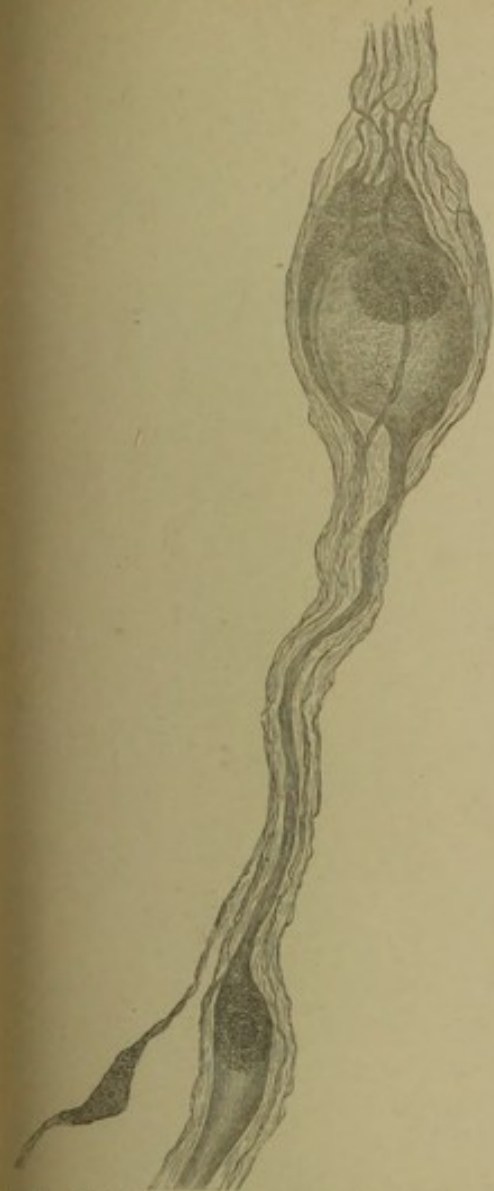
Fig. 19.

Fig. 20.

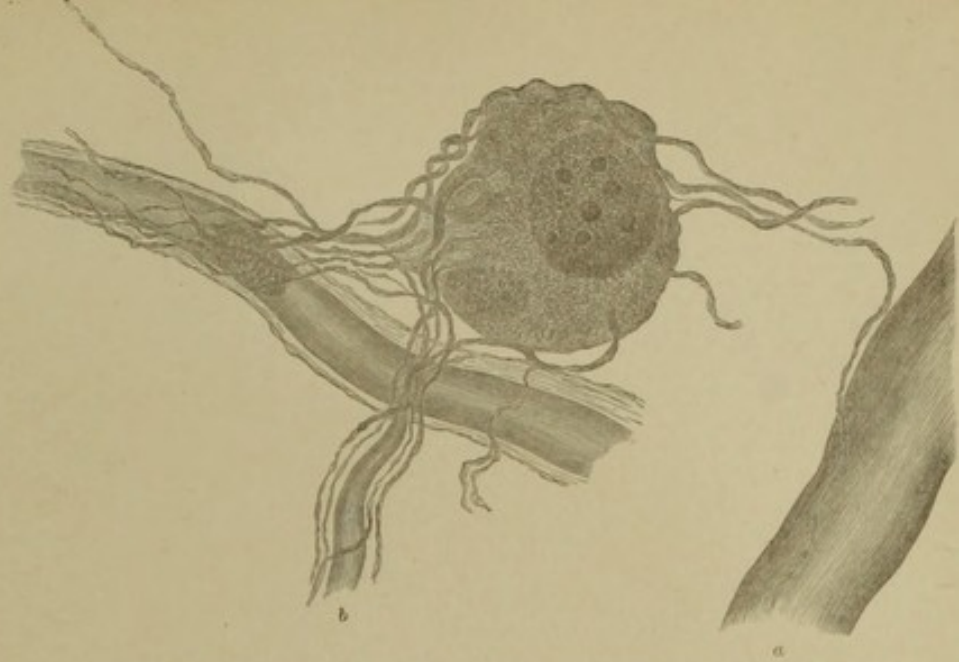


The lower part of a ganglion cell, with the nerve fibres running into it. The spiral fibre divides at the lower part of the figure into a dark twisted fibre.

Three cells of different ages, from the same ganglion. Near lumbar nerves. *Hyla arborea* x 200. The arrangement and connections of the

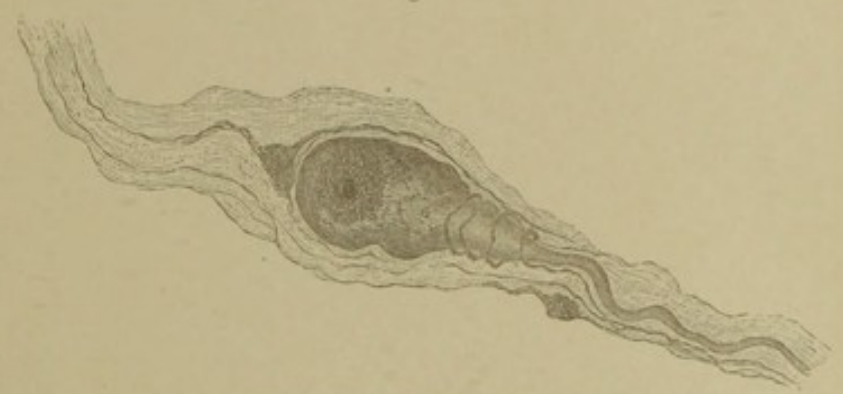


Ganglion cell with fibres, from the bladder of the Hyla. $\times 1800$. It is probable that new cells are being formed in the upper part of the drawing.



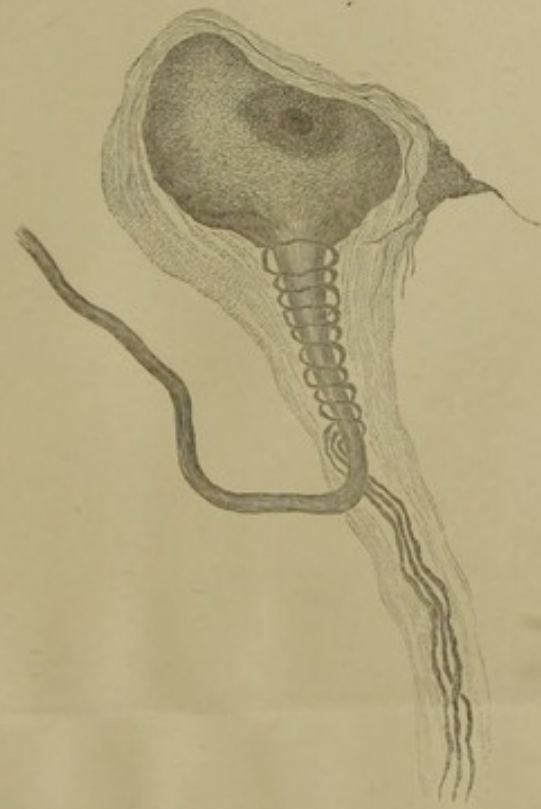
Ganglion cell with fibres connected with it, passing off in three different directions. The large dark-bordered fibre below the cell has no connection with it, and is probably not influenced by it. One of the fibres passing from the cell becomes a fine dark-bordered fibre (b). a is a capillary vessel. From the bladder of the Hyla. $\times 1900$. December, 1892.

Fig. 23.



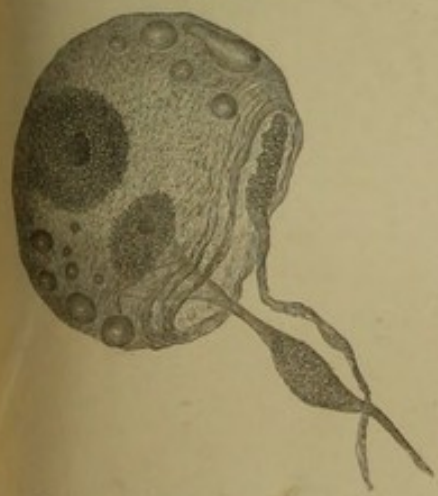
Ganglion cell and fibres in the coat of an artery. $\times 700$. Frog. 1861.

Fig. 25.



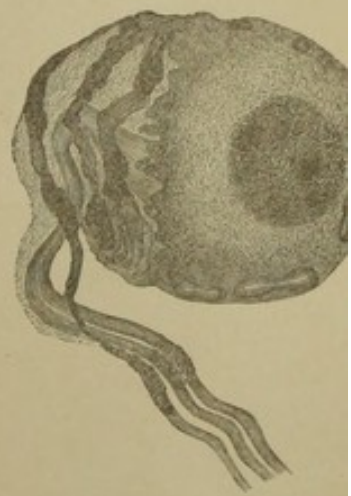
Ganglion cell in connective tissue, near renal artery. Frog. The fibres are seen to pursue opposite directions. $\times 700$

Fig. 21.

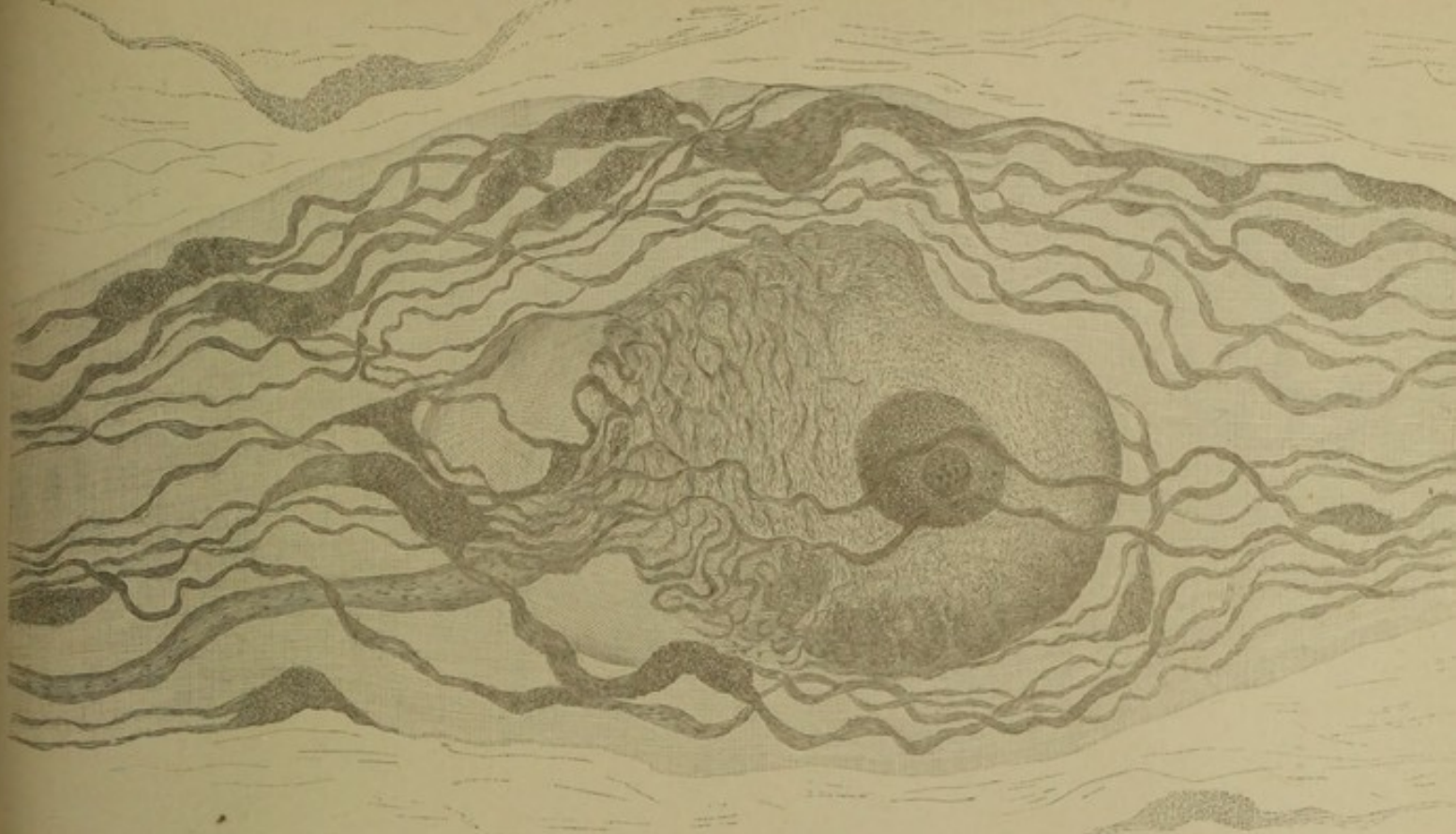


Ganglion cell, from a ganglion close to lumbar nerves. Hyla viridis. $\times 1900$.

Fig. 26.

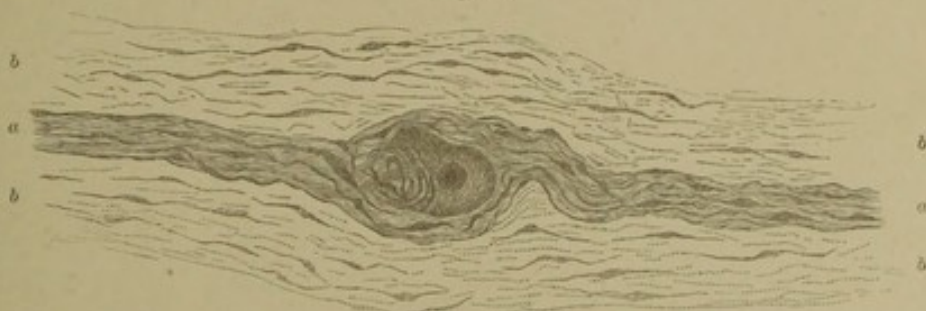


Ganglion cell from ganglion. Posterior root of a spinal nerve. Hyla. $\times 700$.



Single ganglion cell, embedded in a cord of connective tissue, near the lower part of the aorta. Frog. This is the central part of Fig. 28. $\times 1500$.

Fig. 28.



Ganglion cell, with nerve fibres, forming a compound trunk (a) of very fine fibres, embedded in a cord of connective tissue (b), which was more than a quarter of an inch in length. $\times 215$.

Fig. 29.

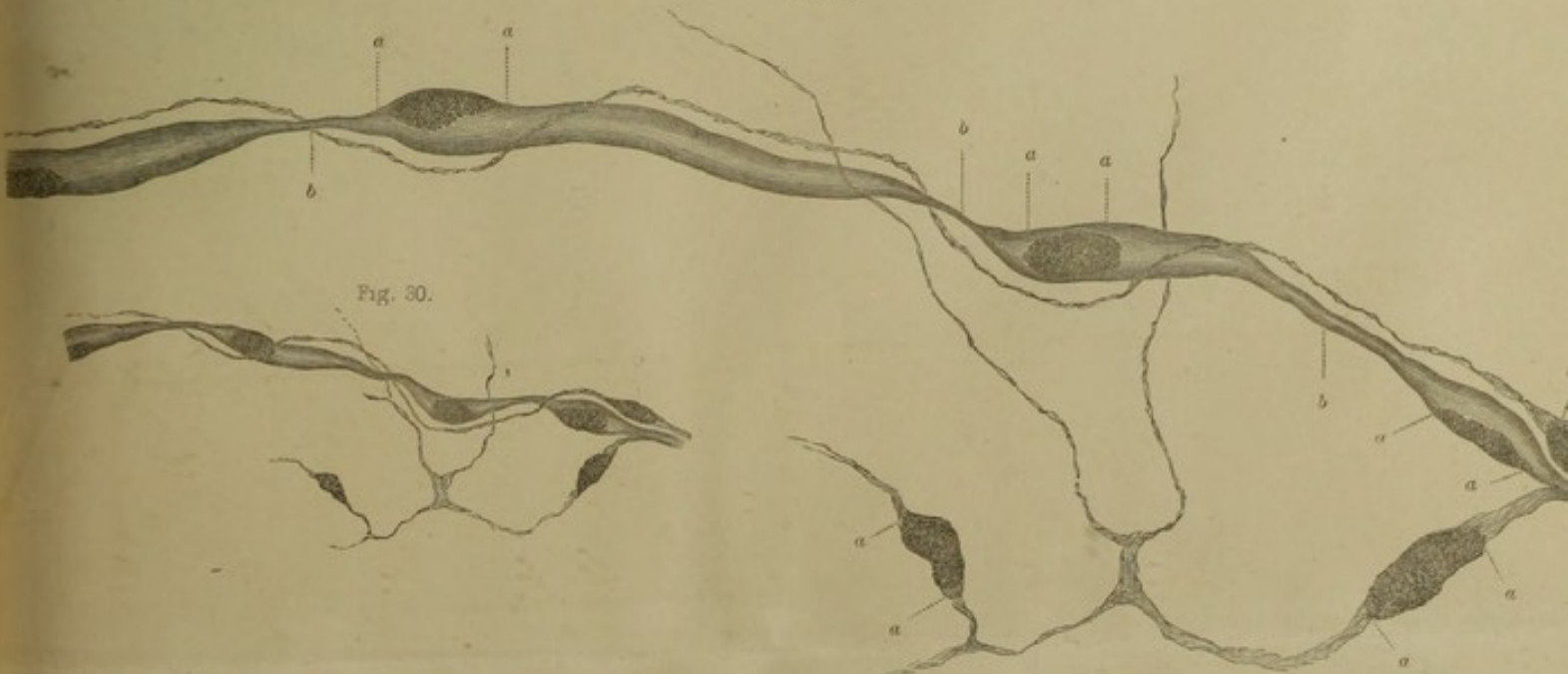


Fig. 30.

Dark-bordered fibre, with fine fibre passing spirally round it. Both fibres are nucleated. The 'nuclei' of the dark-bordered fibres are nearly equidistant, and much closer together than the nuclei of the spiral fibre. The dark-bordered fibre might be said to consist of spindle-shaped cells or elementary parts continuous with each other. The fibre increases at the points marked a, a. The points marked b correspond to the parts of the fibre which were first formed, and are the oldest. Fig. 30 is supposed to represent the same fibres at an earlier period of development. From the bladder of the *Hyla*. $\times 1800$. 1862.

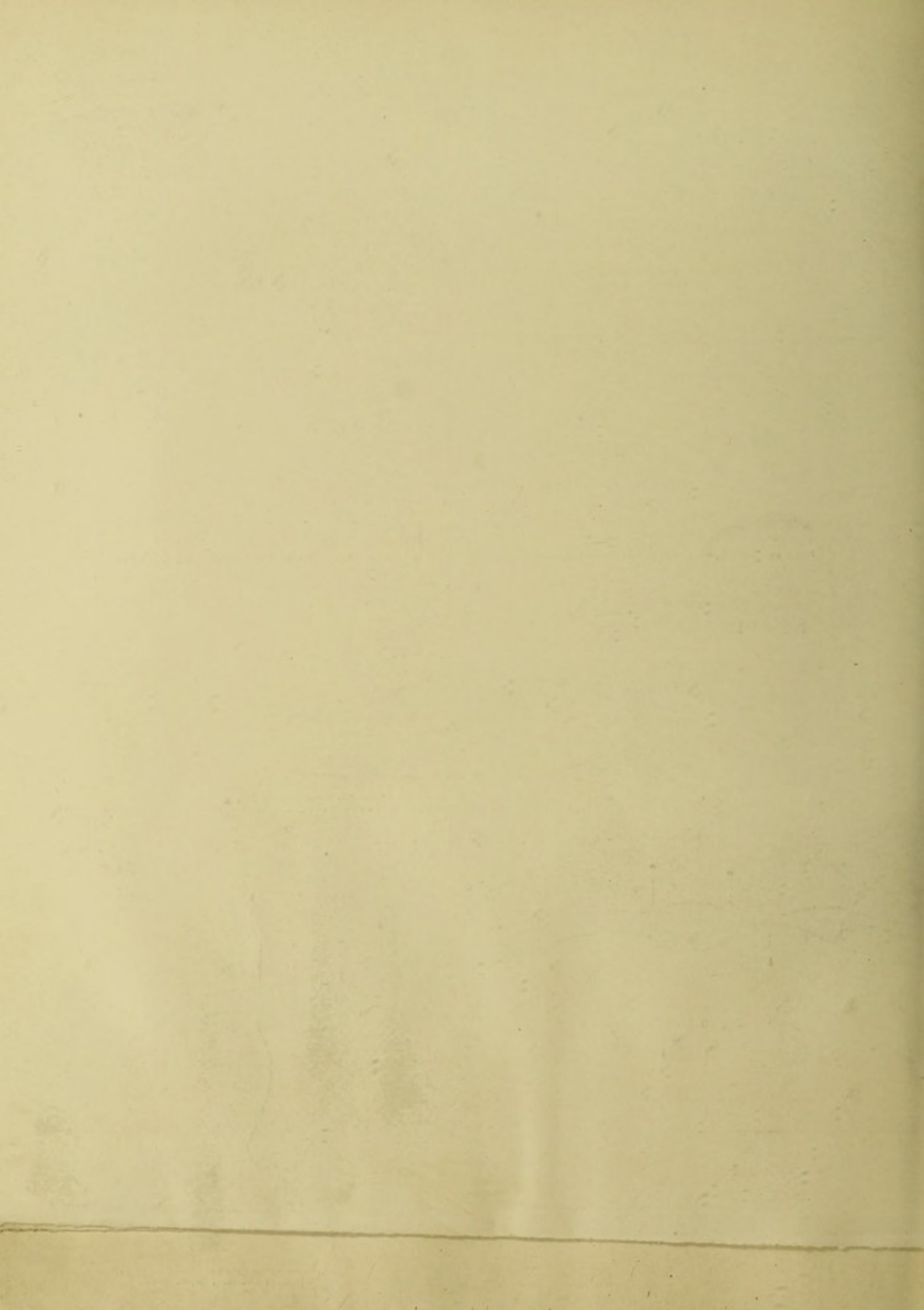


Fig. 31.



Ganglion cell in connective tissue, near iliac artery. Frog. $\times 700$.

Fig. 32.



Fig. 33.



Fig. 34.



Fig. 35.



Drawings to illustrate the successive changes which probably take place during the formation of a ganglion cell, with straight and spiral fibres, from what appears to be the 'nucleus' of a nerve fibre (Fig. 32).

Fig. 36.



Fig. 37.

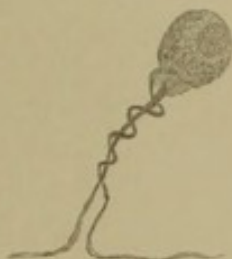
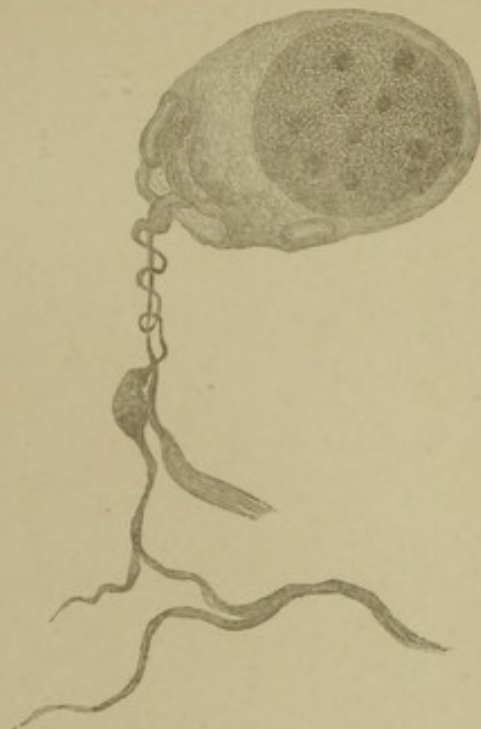


Fig. 38.



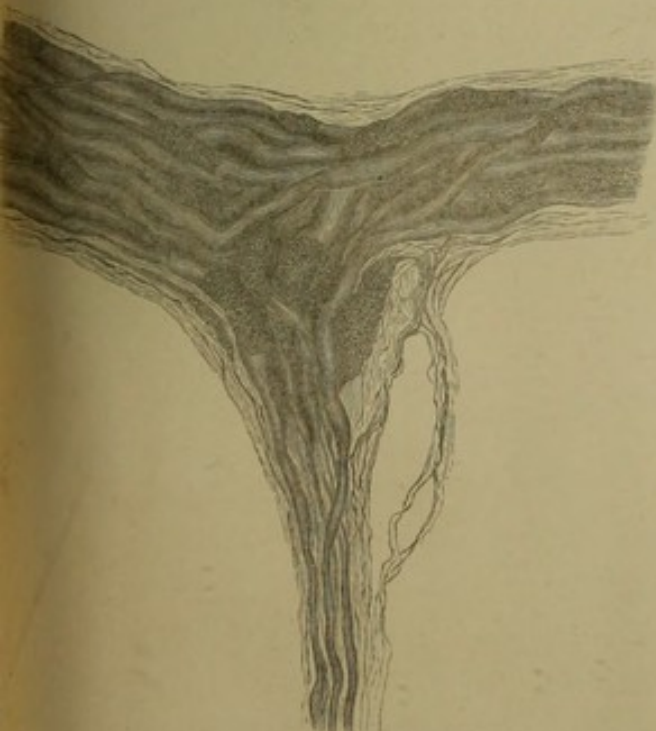
Young ganglion cell near lumbar nerves. Hyla. Observe the great size of the 'nucleus.' The spiral fibre is seen to divide into two branches, one of which runs with another nerve fibre. $\times 1500$.

Fig. 39.



Part of trunk of pneumogastric, where it passes through an opening in the base of the skull. $\times 700$.

Fig. 40.

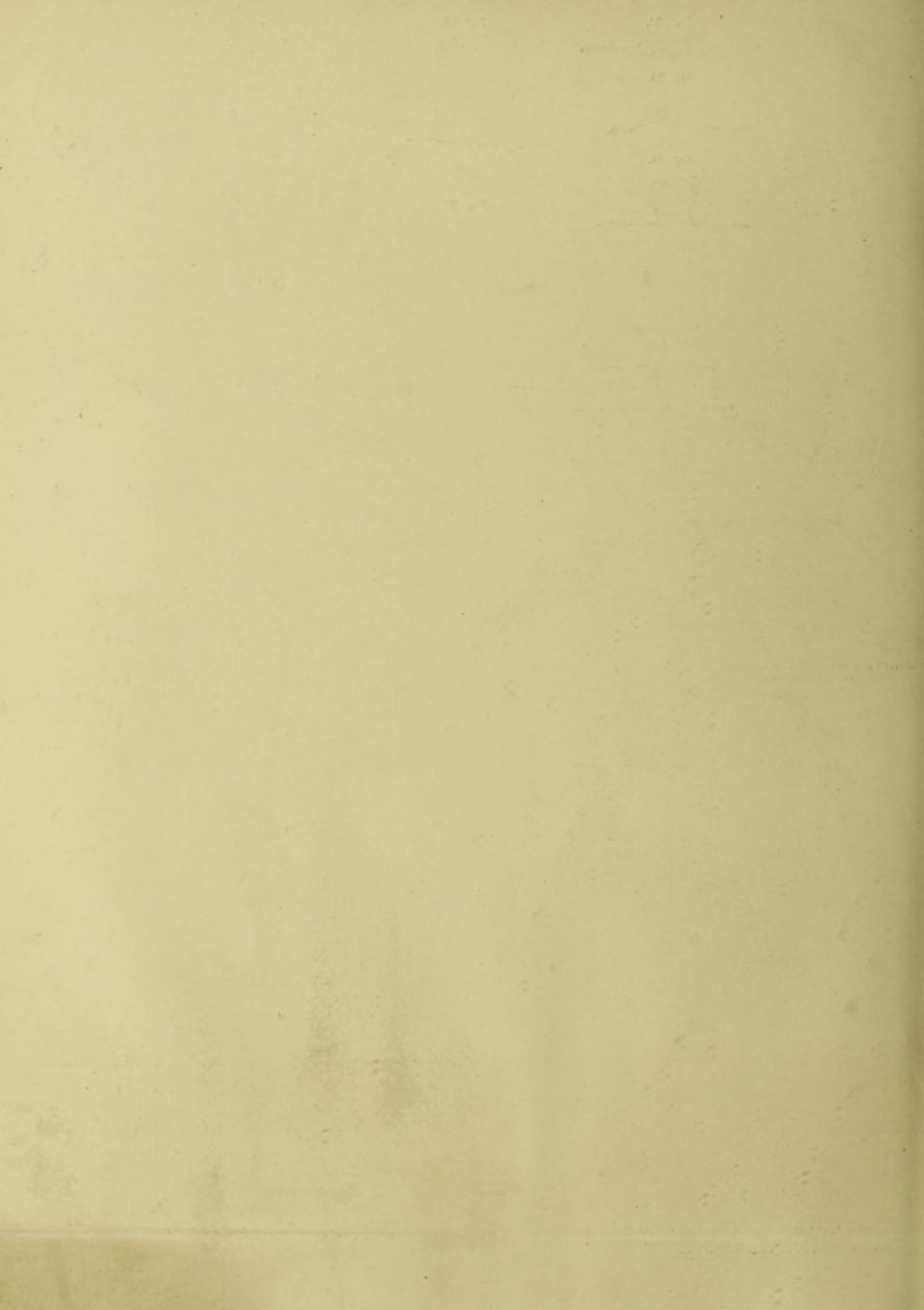


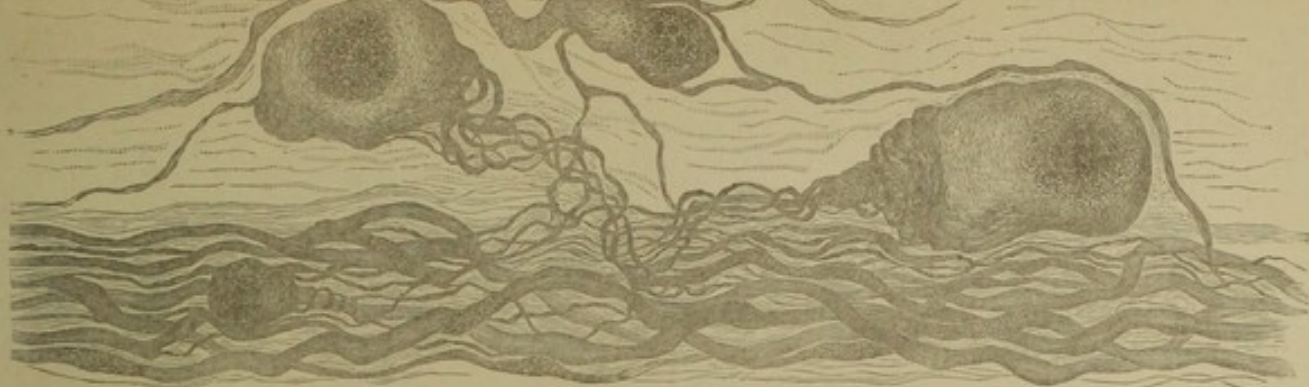
This compound nerve trunk, with a branch coming off at right angles, composed of fibres which pursue opposite courses in the trunk. From the subcutaneous tissue of the Palate. Frog. $\times 700$. 1862.

Fig. 41.



Vagus nerve near the heart. Hyla. a, trunk of the nerve passing towards the heart. b, a branch which connects this with the nerve of the opposite side. The connective tissue, with its corpuscles, is also represented. c, two ganglion cells, more highly magnified in Fig. 42. d, two ganglion cells, the fibres of which, after meeting together, pursue different directions in the trunk of the nerve. $\times 215$.





A portion of the trunk of the vagus, near the heart. *Hyla viridis*. With ganglion cells, the fibres of which are seen to pursue opposite directions in the trunk. It is very difficult to follow the fibres for any distance. In consequence of being so fine, their course is obscured by the larger fibres. $\times 1300$.

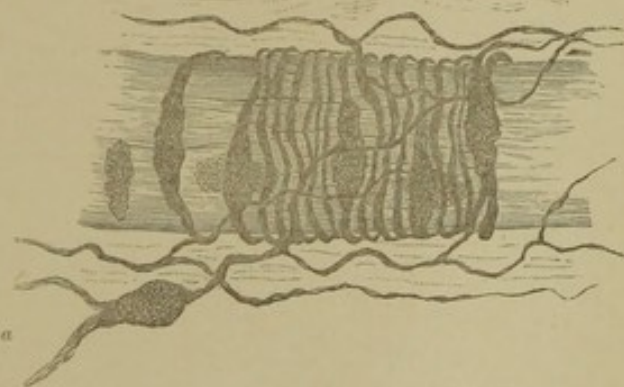
Fig. 43.

Fig. 44.



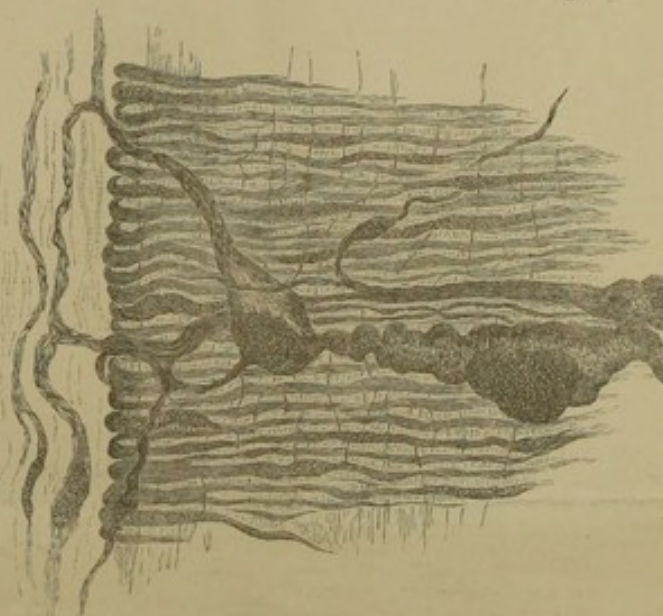
Fine nerves distributed external to a capillary. Bladder of *Hyla*. Observe the nuclei of the nerves and those of the capillary vessel. $\times 700$.

Fig. 45.

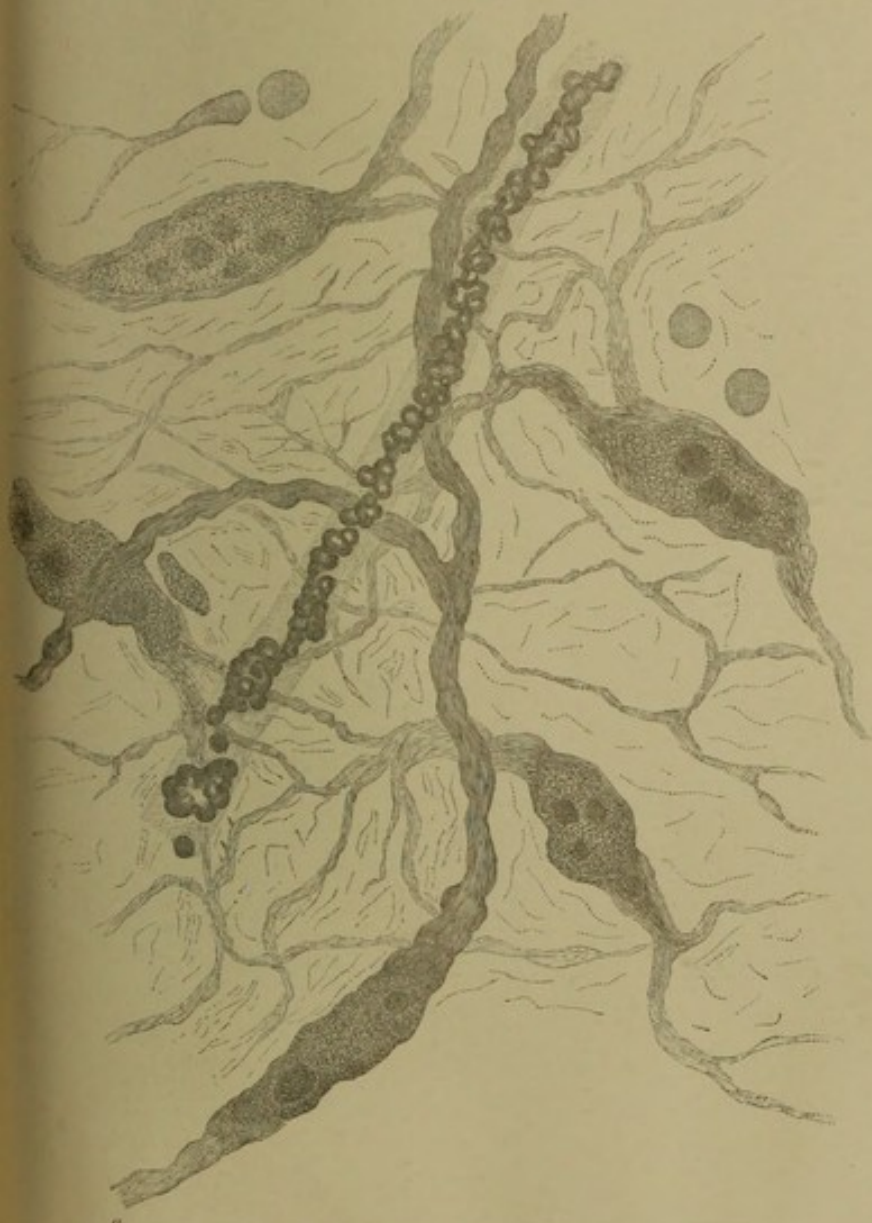


A portion of a very small artery from the bladder of the *Hyla*. The muscular fibre cells, and the nerve fibres, *a*, are well seen. The fibres represented were traced from undoubted nerve fibres beyond *a*.

Fig. 46.



A portion of the coat of a branch of the iliac artery of the Frog. Upon the surface external to the muscular fibres are seen some ganglion cells in process of development, with their fibres which ramify upon the mus.



Very fine nerve-fibre ramifying in the connective tissue at the base of the heart of the *Hyla*. *a*, nerve-fibre with nucleus. Its relation to the connective tissue corpuscles and to the process of a pigment cell is well seen. $\times 2500$.

Fig. 47.

