

XXXV. *Further Observations on the Distribution of Nerves to the Elementary Fibres of Striped Muscle.* By LIONEL S. BEALE, M.B., F.R.S., Professor of Physiology and of General and Morbid Anatomy in King's College, London; Physician to King's College Hospital.

Received June 13,—Read June 19, 1862.

THERE are two views with regard to the peripheral distribution of nerves, which are quite incompatible with each other. According to one, it is supposed that nerves end in the tissues to which they are distributed, by free extremities; while the other doctrine is, that free ends or extremities do not exist, and it is supposed that the fibre, after perhaps a very long and circuitous course, is connected with the nervous centre from which it emanated. If this be so, every nerve-cell, central and peripheral, must have at least two fibres proceeding from it, must be bipolar or multipolar. Both these views cannot possibly be true.

That nerves terminate in ends or free extremities is the opinion of many Continental observers, and of late years this view, it may almost be said, has been generally received by anatomists.

The loops and plexuses described by the older observers have since been proved not to be *terminal*. Some of the fibres forming what appears to be a loop, have been seen to divide into finer branches, and these, after having been traced for some distance, become very thin, and are gradually lost. This change occurs abruptly in some situations, but in others a more gradual attenuation is observed.

In some tissues pale fibres have been traced a short distance beyond what appears to be the end of the dark-bordered fibres. But, it will be shown, the dark-bordered fibres differ so very much in diameter, that some of the thinnest are so very fine as scarcely to be distinguishable with very high powers, and in parts they very closely resemble some of the so-called pale fibres. In young animals the fibres corresponding to the dark-bordered fibres closely resemble the pale fibres of fully formed animals. In no tissue has it been more confidently stated that nerves terminate in free ends than in voluntary muscle; and although some differences of opinion exist as to the precise manner in which the nerves end, the existence of these ends is supported by the testimony of so many observers, that it is now almost regarded as an anatomical fact which is settled beyond question.

Yet it may be said that, as plexuses, loops, and networks \* of very fine fibres in young

\* In using the term network, I do not mean to imply that fine nerve-fibres unite with each other after the manner of capillaries, but merely that the *bundles* of fibres are arranged like networks. The fibres composing the bundles do not anastomose. In lace the appearance of a network of fibres is produced; but

tissues are represented by networks and plexuses of coarser fibres in adult tissues, and as plexuses of coarse and fine fibres may be seen in the adult tissues at all periods of life, it is only reasonable to assume the existence of networks composed of fibres so very fine as scarcely to be visible by the highest powers we possess, and so delicate as to be destroyed by the most careful manipulation, or to become disintegrated almost immediately after the death of the animal. All argument, however, must give way to observation; and even if the results of observation are incompatible with conclusions previously regarded as true, the new facts must be received, and our inferences must be modified accordingly. But, on the other hand, it will be admitted, in an anatomical inquiry like the present, that there may be the greatest difference of opinion as to the actual demonstration. The *ends* which one observer may consider to be natural terminations, by another may be held to be merely *apparent ends*, depending upon our being unable to see the continuation of the fibre in consequence of its extreme tenuity. The importance which all observers attach to the process of preparation they follow, is alone sufficient to show that the appearances produced are very different according to the manner in which a specimen is examined; and further, it is quite certain that many points to be readily demonstrated by one process, are quite invisible when another plan is followed. This is one explanation of the many conflicting statements as to facts of observation.

In a paper published in the Philosophical Transactions for 1860, I was led to conclude that many of the so-called connective-tissue corpuscles observed upon the muscular fibres were connected by very delicate granular fibres nearly as wide as the corpuscles, but only to be seen in specimens preserved in fluids which refracted very highly; and I also satisfied myself that these fibres were continuous with the nerve-fibres; and I stated that the nerve-fibres ramified with the capillaries external to the sarcolemma. My conclusions were terribly at variance with those of other observers; for not only was I compelled to infer (1) that the nerve-fibres formed, as it were, a network over the muscular fibres, but (2) that every muscular fibre was supplied with nerves throughout its entire length. It is usually maintained, 1st, that nerve-fibres terminate in free ends on the muscle; 2nd, that nerve-fibres only come into contact with the muscular fibre at very distant points: so that while the fibre, or the entire muscle, is freely supplied with nerves at one situation, the greater part is altogether destitute of nervous supply.

#### *The Views of KÜHNE and KÖLLIKER.*

Since my paper was published, an elaborate memoir on the 'Peripheral Organs at the ends of the Motor Nerves' has been written by KÜHNE; and the same inquiry formed the subject of the Croonian Lecture delivered a month since by Professor KÖLLIKER.

The conclusions of both observers are quite opposed to my own. KÜHNE and KÖLLIKER

every apparent thread is composed of several, each of which pursues a complicated course, and forms but very small portion of the boundary of any one single space. In Plate XLI. fig. 5 a nervous network exists but each cord is compound, and composed of numerous fibres which never anastomose.

agree as to the existence of free ends. The former maintains that these are situated beneath the sarcolemma, and are connected with peculiar organs; the latter, that the free ends lie upon the surface of the sarcolemma. KÖLLIKER has failed to demonstrate the special organs described by KÜHNE. Both observers agree that the muscular fibre receives but a limited supply of nerves, and that the supply is limited to one part of the muscle.

As these observers have worked upon the muscles of the frog, I shall restrict myself entirely to the consideration of the distribution of the nerves to the muscles of this animal, and mainly to the particular muscle which these and most German observers have studied, viz. the thin pectoral muscle.

In many of KÜHNE'S drawings a pale band as broad as (or broader than) the dark-bordered fibre is represented in continuity with it. The outlines of this band are irregular; and in some places it is much wider than in others. This band is five or six times as wide as many fine nerve-fibres which I have seen; and it will be shown that a fibre of the width of these pale fibres in the tissues of the frog generally, is a long distance from its finest divisions. The same observer makes the nerves of insects terminate in a collection of granular matter within the sarcolemma.

1. *The Distribution of Dark-bordered Fibres not so limited as generally supposed.*

With regard to the distribution of the dark-bordered fibres to voluntary muscle, I would remark

That, although some muscles appear to be very sparingly supplied with dark-bordered nerves, the fibres of certain muscles (for example, the inferior muscle of the eye of the frog) are crossed by bundles composed of two or more fibres at intervals of about the fiftieth of an inch\*. The distribution of nerve-fibres to the pectoral muscle is by no means so limited as would appear from cursory examination. It is clear that many branches, resulting from the division and subdivision of some of the large dark-bordered fibres, supply the elementary fibres near the centre of the muscle; and to some muscular fibres four or five of the branches resulting from the subdivision appear to be distributed. These branches divide on the surface of the elementary muscular fibres, but their subdivisions gradually become too fine to be followed. Some branches divide and subdivide into very fine fibres, which are lost amongst the connective tissue upon and between the muscular fibres. But it must not be supposed that all the nerve-fibres of the bundle are arranged thus; for many pursue a much longer course. Bundles composed of two or three dark-bordered fibres leave the large trunk and pursue a long course obliquely across the surface of the muscle. The fibres of each trunk divide and subdivide; and many of the branches which result reach almost to the extremities of some of the elementary muscular fibres. Many pass between the muscular fibres, and, after pursuing a

\* The muscular fibres of the diaphragm of the mouse are crossed by bundles of dark-bordered fibres at short intervals along their whole length, and nerve-fibres may be seen at the points where they are inserted into the central tendon.

very long course, gradually become finer by division, and at last terminate in a lax network of fine fibres which pass in and out between the muscular fibres; while some of the subdivisions are distributed to the elementary muscular fibres, like the set of fibres first alluded to. It appears, therefore, that in various parts of the muscle, not merely near its centre, but also on some of the fibres near their insertions, branches of dark-bordered fibres can be seen to become suddenly attenuated and give off very fine fibres which divide and subdivide on the surface of the sarcolemma, becoming gradually finer until lost, or they leave the surface of the elementary fibre and are lost in the intermuscular connective tissue—and other fibres, which gradually become attenuated and, after very numerous divisions, terminate in a network of fine fibres which may be traced for a long distance amongst the fibres of connective tissue, between or upon the elementary fibres. Many of the bundles of dark-bordered fibres above alluded to can only be detected in well-prepared specimens which have been soaked for some time in glycerine, so that the muscular fibres may be separated from each other without rupture of the nerve-fibres or capillaries.

Again, numerous branches of nerve-fibres, composed of two, three, or four dark-bordered fibres, may be seen ramifying and dividing near the tendinous extremities of the muscular fibres of the mylo-hyoid muscle of the frog. Several branches can be followed from the central tendon as far as the central part of the fibres; and often very fine fibres can be seen passing amongst the fibres for some distance and forming networks or plexuses.

But there is another fact against the view that the nerves are distributed to only a very small portion of the elementary muscular fibres of the frog. In certain parts of the pectoral muscle new muscular fibres are being developed, as KÖLLIKER has mentioned, and here in a comparatively small space may be seen elementary fibres varying very much in length and diameter. The thickest of these narrow fibres, according to my measurements, are often not more than the  $\frac{1}{2000}$ th of an inch in width, and the thinnest not more than the  $\frac{1}{10,000}$ th of an inch in diameter: some are as long as the other muscular fibres; but often single spindle-shaped fibres with two or three nuclei, or more elongated fibres the nuclei of which have divided so as to form a row of perhaps ten or more, may be found. A large nerve-fibre, generally composed of two large dark-bordered nerve-fibres in the same sheath, with finer fibres, can be followed to the oval swelling situated amongst the ordinary muscular fibres; and one or two dark-bordered fibres *leave* the swelling to be distributed on more distant muscular fibres. The dark-bordered fibres divide, and their branches pursue a very tortuous course in the oval swelling, so that one cannot be followed for any great distance; but fine fibres may be seen passing in either direction, and running parallel with the thin growing muscular fibres. Not unfrequently I have seen these nerve-fibres become so fine that they cannot be followed far; but their course can be traced by their nuclei for a considerable distance. In many instances branches of other nerve-fibres pass to these narrow muscular fibres at a point between the oval swelling and the points of insertion of the fibres. The oval swelling itself consists of very young muscular fibres in various stages of development,

and nerve-fibres. My observations therefore agree in the main with those of KÖLLIKER, who has stated that at these oval swellings the development of new muscular fibres takes place in the fully formed muscle. Upon comparing the above description of these very interesting bodies ('nerve-tufts') with that of Prof. KÖLLIKER, some most important differences will be noticed. After describing the very fine transversely striated muscular fibres which exhibit the 'peculiar swellings with the coiled nerve,' he says, "in the situation of the swelling the finer component fibres of the bundle cling fast together, even after the operation of the alkali (strong solution of potash); and a certain amount of striated granular uniting matter is found between them, which may be partly the remains of fine nerve-fibres and capillaries, and some accompanying connective tissue." Prof. KÖLLIKER next states it as his opinion that the fine muscular fibres are generated by the division of thicker muscular fibres, and suggests that "the nerve-tufts arise from a simultaneous growth and division of the nerve-fibre belonging to the parent muscular fibre, in order that each of the young muscular fibres may obtain its branch of nerve." In my specimens there is no evidence of the very fine muscular fibres being formed by the splitting of a coarser fibre. On the contrary, every fine fibre seems to be developed from nuclei, and to grow in two directions from the oval swellings. With these developing muscular fibres are young nerve-fibres; and the latter seem to be carried, as it were, upon the muscular fibres as their length increases. The oval swelling exhibits a most beautiful and elaborate structure, which is not shown in Prof. KÖLLIKER'S drawings\*. The minute anatomy of these 'nerve-tufts' will form the subject of further investigation. Not only do dark-bordered nerve-fibres proceed from the oval swelling and pass to their distribution to fibres at a distant part of the muscle, but fine fibres may be followed in some cases almost throughout the entire length of those very fine muscular fibres, many of which are often equal to the ordinary fibres in length. These very fine nerve-fibres divide into branches as they pass parallel to the muscular fibre; and transverse branches can be seen crossing the fibre at short intervals (Plate XLIV. fig. 30).

From these observations I think it probable that the muscular fibre is supplied with nerves in its entire length, and that the branches form a lax network of very fine fibres on the surface outside the sarcolemma. As the muscular fibre increases in size, the finest branches of the nerve are more difficult to demonstrate; and the accumulation of connective tissue external to them increases the difficulty of our seeing these very fine delicate fibres; for it is certain that many active nerve-fibres are much finer than is generally supposed, certainly less than  $\frac{1}{100,000}$ th of an inch in diameter.

2. *The fine Fibres extend further than KÜHNE and KÖLLIKER have traced them.*

With reference to the free terminations of KÜHNE, KÖLLIKER and others, it may be remarked,—

1. That as it is admitted that the nerve-fibre undoubtedly extends beyond the last

\* Proceedings, No. 50, fig. 4, p. 78.

nucleus (Plate XLI. fig. 1, after KÜHNE, figs. 2, 3 *a, b*), it is possible, and indeed probable, that it is continued onwards for a greater distance than it has been followed in KÜHNE'S specimens. As a rule, it becomes too delicate and transparent to be traced further than has been represented in my drawings (figs. 14, 16, 18, 19); but I submit that the evidence adduced in favour of these ends being *actual terminations* of the nerve-fibres is very far from conclusive. Capillaries, when stretched and torn, give rise to a very similar appearance; and it is not uncommon to find an undoubted capillary vessel which gradually becomes fainter and fainter *until every appearance of it is all but lost*, and this even when the tube remains quite perfect. I have proved this in the case of capillaries, distributed to muscle, which had been injected with prussian blue injection, and so stretched that the injection was removed from the tube for a certain distance. In this space the vessel could not be recognized, and all that could be seen was a faint granular appearance. We therefore cannot conclude that nerve-fibre or capillary ceases, merely because we cannot follow it in certain specimens beyond a certain point. It may exist but be quite invisible.

2. In various tissues to which nerves are abundantly distributed, the appearance represented in fig. 3 *a* is common. This looks as if the fibre extended from the nucleus in opposite directions; while the common appearance, represented in fig. 3 *c*, in which two fine fibres are seen running together, is strongly in favour of the view that very fine nerve-fibres run for a considerable distance beyond the point at which the dark-bordered fibre can be demonstrated, without terminating in ends. It will be observed that the fine fibres represented in my figures are not one-sixth of the diameter of KÜHNE'S terminal fibres; and I have seen many fibres much finer than those represented in fig. 3.

3. The finest nerve-fibres visible by the highest powers can often be proved to divide into two fibres, by tracing them to the point where they pass into a fibre running at right angles (fig. 4 *a a*).

4. I have some preparations of the bladder of the frog, in which very distinct networks, composed of very fine nerve-fibres are readily seen. One of these, magnified by a power of 1700 diameters, is shown in fig. 6. This, it might be remarked, is not completely conclusive in favour of nerves forming circuits; for it is possible that fibres may diverge from the bundle with which they run and end in free extremities or in small cells, as represented in fig. 5. Numerous observations are against this view; and I regard certain nuclei from which two or three fibres pass in different directions (figs. 2, 3, *a, b*) as the peripheral and active portion of the nerve-fibre in all cases. Even in the case of the finest fibres, when a nerve joins another branch running at right angles to it, fibres are given off which pursue opposite directions (apparently pursuing opposite courses), towards the centre, and towards the periphery.

5. With regard to the size of the finest nerve-fibres, I have traced fibres from true dark-bordered nerves which are certainly less than the  $\frac{1}{50,000}$ th of an inch in diameter, and these are probably composed of more than two fibres. Still finer fibres of this description have been traced to and from ganglion-cells. The connexion between such very fine

fibres and definite dark-bordered fibres has been demonstrated in many situations (tongue, heart, peritoneum, muscular fibre, and very clearly indeed in the bladder of the frog). I have convinced myself that in many of the ganglion-cells of the frog (abdominal cavity, ganglion on posterior roots of the nerves, heart, bladder) one fibre springs from the central part of the cell, while other fibres are in connexion with its circumference. The latter fibres very frequently are arranged spirally around the central fibre. As already stated, many of the finest fibres are less than the  $\frac{1}{100,000}$ th of an inch in diameter.

It will be said that these fine fibres are composed of connective tissue ; but I shall show that the fibres resulting from the subdivision of those which are the direct continuations of the dark-bordered nerve-fibres exhibit the same characters, and can be distinguished from the fine fibres of yellow elastic tissue. Very many fine fibres which are undoubted nerve-fibres, and which form plexuses and networks, have altogether escaped observation, and their nuclei have hitherto been considered as belonging to the connective tissue. The fine nerve-fibres I have described cannot be seen in specimens immersed in water, or in solutions which refract like water.

*The Division and Subdivision of the Dark-bordered Fibres.*

The numerous divisions and subdivisions of the dark-bordered nerve-fibres have been described and figured by various observers ; but it is necessary to give new drawings of some of these fibres, as their arrangement has not been accurately delineated, and the presence of *very fine nerve-fibres in the sheath* external to the white substance has not been admitted. Fig. 11, Plate XLII. shows that the dark-bordered fibres, even in the trunks, may become so thin as scarcely to be visible as distinct fibres by the  $\frac{1}{12}$ th of an inch object-glass. One of the fibres resulting from the division of *a* may be traced towards the right, and at *d* becomes so thin that it might be easily overlooked, and if recognized would be regarded by most authorities as a fibre of connective tissue in the sheath of the nerve.

Often a fibre resulting from the subdivision of a dark-bordered fibre is seen to pass towards another dark-bordered fibre, and run parallel with it for some distance. This arrangement, which exists in the larger fibres, and which is figured in my last paper, is also observed in the finer ramifications. The terminal dark-bordered fibre very gradually, or more or less abruptly, becomes finer, and divides into two fine fibres ; but there is no *termination* or *cessation* of the white substance, as described by KÜHNE, who states that the *white substance* ceases at the sarcolemma, while the *axis cylinder* only is continued onwards as a pale fibre beneath the sarcolemma. KÖLLIKER states that, "besides the axis cylinder, they are furnished with a prolongation of the membranous sheath ; indeed I have seen this so clearly in a great many favourable instances, that I can have no doubt on the point. . . . . But whilst it is easy in most cases to perceive the membranous sheath and its enclosed matter distinct from each other at the commencement of the pale fibres, yet in their further progress these structures coalesce together, and the terminal fibres then appear as uniform pale filaments."

My specimens lead me to the conclusion that near the periphery the axis cylinder of a nerve-fibre cannot be distinguished as a separate structure from the white substance. The axis cylinder and the white substance seem to be, so to say, incorporated together to form the terminal part of the dark-bordered fibre. The dark-bordered nerve-fibre gradually becomes narrower as we approach its ultimate distribution, and it is resolved into several fine fibres; but even in threads which are so fine as only to be scarcely visible the material appears to be of the same composition as the thicker parts of the fibre, and by the slow action of acetic acid globules of fatty matter are set free (Plate XLI. figs. 7, 8, & 9). I cannot but think that the very abrupt cessation, or sudden breaking off, of the white substance indicated in some of KÜHNE'S drawings is due to the pressure of the thin glass upon the surface of the specimen, which renders comparatively large dark-bordered fibres quite invisible at the point where they cross the convexity of the muscular fibre.

The white substance often diminishes in diameter rather abruptly, but it never ceases in the manner KÜHNE has represented\*; and I have never seen any appearances which lead me to conclude that the axis cylinder is prolonged independently of the white substance; nor do I think that "here and there at least a thin *layer* of the white substance extends along the pale fibre," as KÖLLIKER remarks.

*The ultimate Distribution of the Nerves in the Cutaneous Muscle from the Breast of the Frog.*

Let me now describe more particularly the results of my own observations on the ultimate distribution of the nerves to the muscular fibres of the frog. The fibres resulting from the division of the dark-bordered fibres, which to low powers appear terminal, are often seen to pass over the surface of a muscular fibre, and then become either suddenly attenuated, or gradually thinner as they cross in succession several elementary fibres of the muscle, or pursue a longitudinal course in the intervals between two fibres. In both cases they often give off several branches. In the drawings of KÜHNE the outline of the pale fibres is irregular, and their precise connexion with the dark-bordered fibre is not clearly indicated. In Plates XLII. & XLIII. figs. 11, 12, 13, 14, 15, & 17, it is seen that the dark-bordered fibre divides into two branches, and each branch may be followed for some distance as a definite but very narrow line (less than  $\frac{1}{30,000}$ th of an inch in diameter). This appearance is constant, and exists in every 'terminal' fibre. Nuclei are connected with these fine 'terminal' fibres, which are but the extension of the dark-bordered fibres; and nuclei are also seen at intervals imbedded in the substance of the highly refracting matter of which the dark-bordered fibres are themselves composed. These nuclei are always to be found imbedded in the white substance near the finer divisions of the dark-bordered fibres (Plates XLI.-XLIV. figs. 8, 9, 11, 12, 14, 18, & 31). Around the fine fibres prolonged from the dark-bordered fibre, may be traced for some distance what appears to be the *outline of the sheath* (Plates XLII. & XLIII. figs. 13 & 16);

\* The thickness of the dark-bordered fibre just before it divides, as for example in the case of a fibre in fig. 13, Plate XLII., is often increased by the shortening caused by the *contracted* state of the muscular fibre at the time of preparation.



but these lines may often be seen to divide and subdivide into several very fine fibres, which may run with the prolongation of the dark-bordered fibre, or at once diverge from it (Plate XLIII. figs. 17, 18, & 19; Plate XLIV. fig. 31).

Not unfrequently very fine fibres can be traced *external* to what appears to be the outline of the sheath of the nerve, and these form, with the fine fibres already described, a 'pale fibre.' The band or pale fibre divides into smaller bundles, and the fibres composing them gradually become so fine as to be invisible. Nuclei exist in connexion with the finer fibres which I have described, as well as in connexion with the prolongations of the dark-bordered fibres (Plate XLII. figs. 13, 14, & 15). Here, as elsewhere, some fibres appear to be connected with the nucleus, while others pass round it on one side (Plate XLI. figs. 2, 3 *c*). Sometimes fibres pass on both sides of the nucleus. The pale bundles of very fine fibres often give off branches, and these again divide into finer bundles, producing the appearance of a network (Plates XLII. & XLIII. figs. 13, 14, 15, 16, & 17), the meshes of which vary much in diameter. Very often several nuclei are seen at the point where the dark-bordered fibre divides. A very confused appearance often results from the number of nuclei and fibres. As already stated, in specimens examined in aqueous fluids which do not refract highly, it is not possible to trace the course of the separate bundles of fibres and their connexion with the nuclei; but in specimens mounted in glycerine, examined with high powers, the bundles of fine fibres can be separated from each other and followed (Plate XLIII. fig. 21). Some appear to come from the sheath, or are external to it; and others result from the division of the dark-bordered fibre (Plates XLII. & XLIII. figs. 15 & 17). The nuclei and fibres can be very readily demonstrated near the trunks of the dark-bordered fibres, and the network can often be seen in the same situation, but it is not easy to trace the course of the delicate fibres over the muscular fibres for any great distance. The large nerve-fibres prevent the finer ones from being ruptured; but at a distance from the coarse fibres, there being nothing to protect them, the very delicate fibres are generally destroyed by the necessary manipulation, or rendered invisible by the pressure of the thin glass. I have, however, seen such a network very distinctly on the side of some muscular fibres, upon which numerous branches from an adjacent nerve could be traced at intervals for the distance of about one-hundredth of an inch. Indications of the existence of such a network (the nuclei being perfectly distinct) are not unfrequently seen in many parts of the same elementary fibre. Nuclei and fine fibres, resembling those which have been shown to be in connexion with nerve-fibres, can often be seen just at the edge of a muscular fibre, and very frequently a true nerve can be traced, running for some distance near a capillary, and giving off branches with nuclei which are gradually lost on the surface of the muscle or amongst the connective tissue. As these branches pursue the course described, they can hardly be vascular nerves; and there are besides them other branches which lie closer to the vessel, which are probably of this nature. The distribution of very fine fibres can sometimes be traced by the course of the nuclei. In certain cases, in which no fibre connecting nuclei can be detected when the specimen is first prepared, a fibre afterwards

becomes quite distinct. As I have succeeded in following very fine compound fibres for a considerable distance as they passed amongst several adjacent muscular fibres, I feel satisfied that many apparent ends result from the fibres becoming too delicate to be followed beyond this point. Very slight pressure of the thin glass renders even dark-bordered fibres quite invisible; and very moderate stretching renders undoubted nerve-fibres so very fine that they cannot be seen, or, if they remain visible, all characters which would enable us to identify them as nerve-fibres are completely lost. But even if no such appearances as those I have just referred to existed, it would be more in accordance with what we have learnt from many investigations, to conclude that the fibres really extend further than we are able to follow them, than to assume that they absolutely cease at the point at which, having very gradually become finer and finer, they are no longer visible to us. Moreover, as I have already stated, dark-bordered fibres are to be demonstrated in all parts of the muscular fibre, even upon the tendon near its connexion with the muscular fibres. It is hardly likely that this distribution of coarse fibres over the general surface of the muscle should be associated with a very partial and unequal distribution of the fine fibres which result from their division. As the broad pale fibres described by KÜHNE are really composed of several fine fibres (Plates XLII. & XLIII. figs. 14, 16, 18, & 20), which are often connected by transverse branches so as to form a network, and as the fine compound fibres gradually become finer and finer until they cease to be visible, it is still more improbable that what appeared to him and KÖLLIKER to be ends should be real natural terminations, than if the arrangement had been as KÜHNE has described it. It seems therefore to me that the only inference which can be drawn from the facts demonstrated is, that the nerves terminate in a network: but there are still two modes of arrangement possible with regard to the distribution of this network.

1. It may be confined to one part of the muscular fibre.
2. It may extend down the fibre throughout its entire length.

It is true that the network (Plate XLII. figs. 13, 14) which is so readily demonstrable near the plexus of the dark-bordered fibres very soon becomes so faint as to be lost. The meshes are smaller near the large branches of nerve-fibres than further away, and it is at this point that the rupture of the fibres takes place when the muscle is caused to contract violently soon after death. There is therefore no doubt that the fibres of the pectoral muscle receive a greater supply of nerve-fibres near their central part than nearer their extremities; but it is quite certain that the supply of nerve-fibres is not *limited* to this portion of the muscle.

Although I have never been able to demonstrate uninterruptedly the fibres of such a network over more than the  $\frac{1}{100}$ th of an inch of a fully-formed fibre of the breast-muscle of the frog, I have succeeded in doing so several times in the case of fibres undergoing development, and about the  $\frac{1}{2000}$ th of an inch in diameter (Plate XLIV. fig. 30). Upon these I have seen such a network, and I consider that the evidence in favour of the existence of a network extending from one end to the other of the muscular fibre of the voluntary muscle of the frog, though by no means equally distributed over every part

of the fibre, is so strong as to justify me in concluding that such an arrangement is actually present. If the nature of the tissue under examination be considered, and the extreme delicacy of the nerve-structure which has actually been demonstrated be fairly taken into account, no surprise will be felt that the network has not been actually demonstrated throughout the entire length of the large elementary muscular fibres of the frog. The network of fine fibres I have described exactly corresponds in its arrangement with networks which are demonstrated with comparative facility in the palate, bladder (Plate XLI. fig. 6), peritoneum, cornea, skin, and other situations in the frog. In the heart and tongue, networks also exist, but the fibres are very fine, and the meshes are wider. The network, composed of very fine fibres, lies on the same plane as the capillary vessels, and just upon the surface of the sarcolemma. The fine nerve-fibres often lie very near to the capillaries.

The capillaries and the fine nerve-fibres with their nuclei are connected together by a membranous tissue so thin and delicate that its existence can only be proved after it has been coloured, or when some foreign particles have adhered to it. That it is, at least in some places, *distinct from the sarcolemma*, is easily proved in the muscles of the frog, in which animal the sarcolemma is very thick, as it can be stripped off leaving the sarcolemma. I have some specimens in which the muscular tissue has been withdrawn from the tubes of the sarcolemma, so that the nerves can be seen very distinctly. From a part of the surface the thin membrane with nerves and capillaries has been withdrawn, leaving the sarcolemma uncovered. In some specimens, on the other hand, the finest nerve-fibres and their nuclei seem in absolute contact with the sarcolemma, and appear to be adherent to or connected with it; and I incline to the opinion that some of the nuclei which appear imbedded in the sarcolemma are connected with the nerve-fibres.

The pale fibres described by KÜHNE and KÖLLIKER are compound, and are composed of many very fine fibres, and they divide into bundles of fine fibres which form a network. Each 'pale fibre' consists (1) of a very fine fibre prolonged from the dark-bordered fibre, and (2) of very fine fibres continuous with those in the sheath of the nerve. The fibre which is the immediate prolongation of the dark-bordered fibre, as well as the fine fibres amongst which it runs, can be followed to nuclei, and often a lax network can be traced. The dark-bordered fibres are all continued as very fine fibres; and the subdivisions of these, a short distance from the dark-bordered fibre, are too thin to be measured, even when examined by the highest powers made. The subdivisions of all nerve-fibres pass into fibres which have hitherto been included with the fibres of connective tissue.

The same arrangement with regard to the distribution of the nerve-fibres is observed here as elsewhere. The fibres of the network are composed of numerous very fine fibres. Not one individual fibre can be followed for any distance; but certain delicate fibres can be traced from one compound fibre to another, in precisely the same manner as the coarser fibres can be followed in a plexus. In fact, from all that I have observed in examining the finest branches of the nerve-fibres in various tissues, I cannot but conclude that the general disposition of these finest fibres is the same as that of the coarser trunks and fibres. In passing from the trunks towards the ultimate distribution, it might be said that we

meet with finer and still finer plexuses—the finest visible fibres being probably composed of more than a single fibre.

The chief differences observed between the arrangement of the nerves in the muscular fibres of the mouse, described by me in the Philosophical Transactions for 1860, and those of the frog, are, that the fibres are much finer in the latter than in the former, and the fibres themselves, and the nuclei in connexion with them, are much more abundant and closer together in the mouse than in the frog. The position of the fibres with regard to the sarcolemma and the muscular tissue, and their relation to the capillaries, is the same in both.

I now pass on to the consideration of the fine fibres connected with the nerves, and often seen running in the sheath with the dark-bordered fibres, which have already been alluded to in this paper. These fibres have been regarded as fibres of connective tissue, but they have not been carefully studied. The evidence in favour of these being real nerve-fibres is as strong as that upon which the nervous character of the fine fibres, which are the direct prolongations of the dark-bordered fibres, rests.

*Fine Nerve-fibres imbedded in the Sheath.*

The following observations are of the greatest importance with regard to the general question of the mode of distribution of nerve-fibres.

As a dark-bordered nerve crosses the muscular fibres, it often gives off several very fine branches. In Plate XLIII. fig. 19 a nerve is represented from which two branches are seen to proceed and divide upon the surface of the same muscular fibre, and other branches are given off a short distance from the point at which these branches leave the trunks. These fibres are not connected with *those portions of the dark-bordered fibres seen in the figure*, although their arrangement exactly corresponds with the fine fibres prolonged from the dark-bordered fibres. Compare the fibres marked *b, b* in fig. 19 with *b* in figs. 13 & 14. These fine nerve-fibres are very numerous. They often run parallel with the dark-bordered fibres for some distance, perhaps cross them several times, divide and give off fibres which pass off in different directions. The line which appears to be the outline of the tubular membrane of nerve-fibres near their periphery, is frequently found to consist of two or more very fine fibres, which are in many instances connected with nuclei, which, it is generally believed, are the nuclei of the tubular membrane. I have specimens in which five or more very fine fibres can be demonstrated between the dark-bordered fibre and the outline of the tubular membrane (Plate XLI. *et seq.*, figs. 7, 8, 9, *a*, 11, 15, 18, 21, 24, 25, 26, 27, 28, 29, & 31). These branches leave the trunk at intervals and pass to their distribution, or pursue their course with other fibres. Usually two or more pass off at the same point; and in the rare instances in which one fibre passes by itself to its distribution, one can never feel confident that it is really single. In those fortunate specimens in which it can be followed for a short distance, it can be seen to divide into two branches which pursue opposite courses; and very often at the point of division a third fibre can be seen.

The fine fibres I have described are very numerous near the point of distribution of the

nerves (Plate XLIV. figs. 27 & 28), and are to be seen in relation with almost all the dark-bordered fibres, distributed not to muscle only, but to the tissues of the frog generally (palate, peritoneum, intestines, skin, heart, tongue, liver, kidney, &c.). I have also seen fine fibres corresponding to these in the mouse, and believe them to exist in vertebrate animals generally; but being so very delicate, they are more difficult to demonstrate in mammals than in the frog. These fine fibres distributed on the muscles of the frog cannot, by any peculiarity in their appearance, be distinguished from the fine fibres which are in direct continuity with the dark-bordered fibres. It has been shown that in many cases, especially in the muscles of the eye, and in those of young frogs generally, and in the palate of the frog at all ages, dark-bordered fibres can be traced, gradually becoming finer and finer until the fibres are too thin to be followed. *Some* of these fine fibres running in the sheath of the nerve, result from the division of the dark-bordered fibres (Plate XLII. fig. 11 *d*), but it is doubtful if all have this origin. At the same time there are many appearances I have seen in various peripheral nerves which are much in favour of this view. I shall be able to express myself more confidently on this question when the researches upon which I am engaged are completed. A great number of these fine fibres with nuclei, running in the same sheath with dark-bordered fibres, are represented in Plate XLIV. fig. 28, from the bladder of the frog; but they are much more numerous in this organ than in connexion with the dark-bordered fibres distributed to striped muscle. I have seen these fine fibres divide in the same direction, that is *from centre towards* periphery, as the coarse fibres; so that in the trunk of the nerve there are dark-bordered fibres which divide as they pass towards the periphery, and finer fibres which divide as they pass in the same direction. In the bladder of the frog there are large bundles of fine fibres passing in the same sheath with the ordinary dark-bordered fibres, as well as numerous trunks composed of fine fibres alone; but in this organ there are many ganglia connected with these fine fibres; so that it is doubtful if the fine fibres I have described in connexion with the muscular nerves are of the same character as the fine fibres in the bladder of the frog. The bundles of fine fibres ramifying in the same sheath with the dark-bordered fibres distributed to the bladder have certainly no connexion with the dark-bordered fibre; but, on the other hand, it is certain that some of the fibres we have been considering are continuous with dark-bordered fibres.

It has been assumed by many observers that a fibre which exhibits the refractive power peculiar to the white substance can alone be regarded as a true nerve; and the point beyond which the white substance cannot be traced has been looked upon as the termination of the nerve. Although pale fibres have been recognized in certain situations, and their continuity with dark-bordered fibres traced, still the general idea seems to be that all true nerves exhibit the dark contours. The pale fibres described by KÜHNE as lying beneath the sarcolemma, and by KÖLLIKER upon this membrane, are regarded as the terminations of dark-bordered fibres with which they are continuous. These pale fibres, which are composed of many fine fibres and have been traced so short a distance from the dark-bordered fibres in certain instances, are, in my opinion, *only*

*the commencement of that portion of the nerve-fibre which influences the muscle and corresponds with the fine fibres composing the network in the bladder of the frog (Plate XLI. fig. 6).* From what I have seen of the distribution of nerves to tissues generally, I feel convinced that the really important part of the peripheral nerve-fibres, by which the various tissues under the control of the nervous system are influenced, really only commences at the point where the white substance seems to cease. Beyond this point, and continuous with the dark-bordered fibres, there is a most extensive system of fine fibres with which nuclei are connected. The fibres are compound, and the arrangement of the bands is such as to produce the appearance of a network, in the meshes of which the active elements of the tissue are situated.

*The relation of Nerve-fibres to the Connective Tissue of Muscle.*

I have shown that the network of delicate compound nerve-fibres on the surface of the muscular fibres is continuous with certain fibres and nuclei which *seem* to belong to the connective tissue around the muscular fibres (p. 892). This connective tissue is thicker in old animals than in young ones, and may be regarded as constituted mainly of the remains of a structure which was active at an earlier period of life. These remarks do not in any way apply to the fascia of a muscle, but only to the indefinite connective tissue beneath it, and in close contact with the sarcolemma and between the muscular fibres.

Many of the fibres delineated by KÜHNE in fig. 15, plate 4 of his memoir, and termed by him fibres of connective tissue, are made exactly to resemble the pale nerve-fibres; and their nuclei are of the same size. The fibres of 'connective tissue' (?) which leave the sides of the dark-bordered fibres represented in his drawings do not accord at all with appearances I have seen, which are much more positive. KÜHNE gives a nucleus lying outside the white substance with indefinite fibrous tissue proceeding from it. In my specimens such a nucleus is seen continuous with definite fibres in the 'matrix' external to the white substance (Plates XLIII. & XLIV. figs. 17, 28, & 31). From the nucleus definite fibres can often be traced in opposite directions; and on one side of it three or four fine fibres may often be demonstrated (fig. 31). It is unnecessary here to repeat the various arguments that have been adduced in favour of the view that these fibres are veritable nerve-fibres, and not mere connective tissue. This important question is decided by some preparations I have made showing the distribution of the nerves in the bladder of the frog\*; and I am sure it will be admitted, at least by those who have seen

\* KÖLLIKER, speaking of the distribution of the nerves, says, "The same mode of termination as in the heart (very fine pointed extremities) prevails in the non-striated muscular tissue of the pharynx and bladder of the frog." I have fully investigated the arrangement of the nerve-fibres in the bladder of the frog, and have given drawings of the appearances I have observed in this paper, and also in No. XII. of the 'Archives of Medicine.' I can follow the finest nucleated fibres for long distances; but they always pass to other fibres, and never terminate in any ends that I can discover. In many situations there is a network with comparatively small meshes, as represented in Plate XLI. fig. 6. Amongst the delicate striped fibres of the auricle of the heart of the frog I have also seen bundles of very fine fibres forming networks with large meshes; but I have never seen ends, and feel sure that free ends do not exist in these tissues.

my specimens, that the appearances represented in the drawings accompanying this paper are incompatible with the conclusion that all the fine fibres I have described are merely fibres of connective tissue.

Since it has been shown that many of the corpuscles in the connective tissue between the muscular fibres, and in other situations which are usually considered to be connective-tissue corpuscles, are really connected with the nerve-fibres, and that the quantity of the connective tissue increases as the muscle advances in age, it remains for those who still maintain that this indefinite connective tissue is a structure developed specially for the support or nutrition of higher tissues, to explain, according to their view, its absence when the tissues are undergoing most active changes, during development, and when they are softest and therefore are in greater need of support, and how and at what period it comes into relation with the nerve-fibres,—why it is more abundant on the muscles of the tongue and diaphragm of the mouse than on the muscles of the limbs,—and many other facts which I have considered elsewhere, and which appear to me to be not only strongly opposed to this view of the origin of this form of connective tissue, but incompatible with it\*.

In adult animals the connective tissue is too thick to permit our seeing the arrangement of the very much more delicate nervous structure beneath it; and the difficulty is further increased by the circumstance that the light must first traverse the muscular fibre itself. The relation of the nerves to the sarcolemma remains constant; but the connective tissue exists in greater quantity and is firmer and more fibrous in old than in young muscles, and forms a fibrous stratum external to the nerve-fibres. If we attempt to tear off this connective tissue in order to see the nerve-fibres beneath it more distinctly, we almost invariably tear away the nerves and vessels also; for these structures are undoubtedly connected with the connective tissue.

It seems to me that many of the appearances observed receive at least a partial explanation from the following considerations. The muscle grows, gradually, until it attains perhaps twenty times the size it exhibited in the young frog. That part of the nerve-fibre which in the young animal might be said to be terminal, would in the larger muscle correspond to trunks from which branches were given off in different directions; and fibres and nuclei which were in contact with the muscular fibres would be removed, as the muscle grew, further and further away from the sarcolemma, but they would still be connected with the new fibres and nuclei which are developed just external to this membrane. Thus we should have a quantity of tissue composed of modified nuclei and wasted nerve-fibres which would accumulate as the muscle advanced in growth, and through which many of the nerve-fibres would be seen to pass. Many of these nuclei and fibres having been originally continuous with the nerve-fibres would still retain connexion with them, but this connexion is not necessarily a physiological one.

Other explanations might be offered, but I desire now only to draw attention to the fact that *all* nerve-fibres at their periphery are continuous with exceedingly delicate

\* "The Structure of the Simple Tissues," Lectures VI. and VII.

fibres which have hitherto been regarded as belonging to connective tissue, but which differ from very fine yellow elastic fibres in their granular appearance, in their mode of branching and the curves which they form, in refractive power, and in the alteration resulting from the prolonged action of dilute acetic acid\*.

It seems quite possible that complete nervous circuits may exist, and the delicate fibres of the plexus may be connected with delicate fibres from the branches of nerve-fibres ramifying in the connective tissue. Although nuclei (connective-tissue corpuscles) appear to be connected with the nerves in great number, it by no means follows that all these are instrumental to the action of the nervous system†. The nerve-currents would of course pursue the shortest route, and as the position of the fibres must become altered in consequence of the development of new ones, some would no longer be traversed by the nerve-current. The nuclei would slowly alter but would still retain a certain anatomical connexion with the fibres, and might still absorb a certain amount of nutrient matter and slowly produce a low form of fibrous tissue.

Many fine bundles of fibres, and fibres which appear to be single, with nuclei connected with them at short intervals, may be seen ramifying in the indefinite connective tissue in all parts of the frog. The fine fibres are generally considered to be fibres of yellow elastic tissue, and the corpuscles are all included under the head of 'connective-tissue corpuscles'. These fibres may be readily followed (especially on the palate, cornea, and bladder) to undoubted nerve-fibres, and it would not be possible to distinguish one of these fibres from the fibre which is the direct continuation of the dark-bordered nerve-fibre in muscle. I am therefore forced to conclude either that nerves terminate in 'connective-tissue fibres,' or that this form of connective tissue itself results from changes occurring in nerve-fibres and the nuclei or cells which take part in their formation. As this form of connective tissue always exists where nerve-fibres are distributed—as it increases in quantity, but at the same time becomes more condensed as the tissue advances in age—as the meshes formed are smaller and less regular as we recede *from* the surface where nerves ramify—as the so-called fibres of yellow elastic tissue in connexion with the nerves become altered like the nerves themselves by the slow action of acetic acid, while other fibres more distant do not undergo this change, and as these facts have been observed, not in one organ or tissue, but in very many (palate, tongue, cornea, mesentery and other parts of the abdominal connective tissue, muscle, skin, pale muscular fibre), as well as in different animals, I venture to conclude that this so-called connective tissue lying immediately beneath sensitive surfaces, and around the elementary fibres of voluntary muscle, and in other situations where nerves are abundantly distributed, is not a tissue specially formed as a medium for con-

\* See some observations on the distribution of nerves to the mucous membrane of the epiglottis of man in No. XII. of the 'Archives of Medicine.'

† KÜHNE has recently stated that the nerve-fibres are connected with the connective-tissue corpuscles of the cornea; but I have some specimens which demonstrate that this view is erroneous. The nerve-tissue is always distinct from other tissues, and possesses its own masses of germinal matter or nuclei of formation.



necting or giving support to higher tissues, but results from changes occurring in the nervous tissue itself, and that the fine fibres of elastic tissue in indefinite connective tissue were actual nerve-fibres at an earlier period of life\*. Thus a low form of tissue, which results from the natural changes taking place during the life and continual growth of the highest tissue, may form a basis of support for the latter. It becomes firmer as the organ or tissue advances in growth, but it does not exist at an early period of development, nor is it a special tissue developed in a certain definite manner like tendon, true yellow elastic tissue, cartilage, muscle, &c.

#### *Conclusions.*

1. In certain muscles of the frog the distribution of dark-bordered nerve-fibres is pretty uniform in every part. Although in the case of the pectoral a greater number of nerve-fibres is distributed to the central part of the muscle, fibres may be traced from the large bundle almost to the extremities of some of the muscular fibres. Many branches which easily escape observation pass between the muscular fibres and their subdivisions and supply neighbouring fibres, or are gradually lost in the connective tissue.

2. Fine nerve-fibres are most easily demonstrated on the external surface of the sarcolemma near the nerve-trunks; but reasons have been advanced in favour of the conclusion that every elementary muscular fibre is more or less freely supplied with nerve-fibres throughout its entire length. Many of these fine nerve-fibres on the surface of the muscular fibre become gradually very faint, until from their extreme tenuity we are no longer able to follow them.

3. Fine nerve-fibres in direct continuation with the dark-bordered fibres, and less than the  $\frac{1}{30,000}$ th of an inch in diameter, have been seen to divide into finer branches which have nuclei in connexion with them.

4. The pale fibres delineated by KÜHNE and KÖLLIKER, and by them considered single terminal fibres, consist of—

*a.* Fibres about the  $\frac{1}{30,000}$ th of an inch in diameter, or less, resulting from the subdivision of the dark-bordered fibre.

*b.* Fibres resulting from the subdivision of fine nerve-fibres ramifying in the sheath of the dark-bordered fibre, or situated external to it.

5. Nuclei are found in connexion with—

*a.* The dark-bordered fibre itself, near its terminal ramifications.

*b.* The fine fibres which are the direct continuations of the dark-bordered fibres.

*c.* The fine fibres in the sheath, or external to it.

6. The nuclei and delicate fibres above referred to are arranged so as to form networks, the meshes of which vary much in size, situated with the capillaries on the external surface of the sarcolemma. The fibres of these networks are compound, and consist of finer fibres, which are distinct from, and do not anastomose with, each other. The

\* "On the Distribution of Nerve-fibres to the Mucous Membrane of the Human Epiglottis," in my 'Archives,' No. XII. 1862.

fine fibres continued from some of the dark-bordered fibres, as well as those ramifying in the sheath of the nerves, may sometimes be followed over six or more elementary muscular fibres, and form, with other fine branches, networks, many of the meshes being as wide as a muscular fibre.

7. Fine nerve-fibres, with nuclei connected with them, exist (not unfrequently to the number of four or five) in the sheath of dark-bordered nerve-fibres near their distribution; and some are also found external to what appears to be the outline of the sheath. Some of these result from the subdivision of a dark-bordered fibre. These fine fibres and their nuclei have been included hitherto under the head of 'connective tissue.'

8. The connective tissue around the elementary muscular fibres, and in connexion with the nerve-fibres, is composed of—

*a.* Nuclei which might have taken part in the formation of the nerve-fibres, but which have degenerated, and a low form of fibrous tissue has alone been produced.

*b.* Fibres and nuclei which were once active and formed an integral part of the nervous system, but which have grown old, and have been replaced by new nuclei and fibres.

*c.* The remains of altered and wasted vessels and nerve-fibres distributed to them, and perhaps wasted muscular fibres themselves.

9. The nerves distributed to the voluntary muscles of the frog do not terminate in free ends, but there is reason for believing that complete nervous circuits exist.

10. In all cases the fibres resulting from the division of the ordinary nerve-fibres are so fine that many cannot be seen with a power magnifying less than a thousand diameters, and there is evidence of the existence of fibres which could only be positively demonstrated by employing a much higher magnifying power. It is probably by very fine fibres alone and their nuclei, that the tissues are influenced. The ordinary nerve-fibres are only the cords which connect this extensive peripheral system (which has been traced in different tissues far beyond the point to which the dark-bordered nerve-fibres can be followed) with the central organs of the nervous system.



11. The facts and conclusions above stated, with reference to the distribution of nerve-fibres to the voluntary muscles of the frog, are in accordance with the arrangement of the finest nerve-fibres demonstrated in many other tissues of the same animal, and agree with many appearances observed by the author in connexion with the peripheral distribution of the nerves, not only in certain tissues of man and the higher animals, but also in invertebrate animals.

12. The distribution of the finest branches of the nerve-fibres can only be demonstrated in tissues which have been immersed in fluids which refract highly, as syrup or glycerine.

## EXPLANATION OF THE PLATES.

The figures represented have been copied from specimens magnified with a twelfth (700 diameters linear) and a twenty-sixth (1700 diameters linear), made by Messrs. POWELL and LEALAND. All the figures, with the exception of figs. 1, 2, 3, 4, & 5, have been carefully copied from nature. The relative sizes of the objects represented have been accurately retained. The dimensions of every object can be ascertained by measuring it upon one or other of the following scales; so that in the text I have considered it superfluous to insert the measurements.

Many of the specimens will retain their characters for some time (probably two or three years at least), and can be examined by any one desirous of seeing them. Some of the drawings were traced from my drawings, on the wood blocks, under my immediate direction, others by myself. They were engraved by Miss POWELL.

1000th   $\times 700$   
 1000th   $\times 1700$

## PLATE XLI.

- Fig. 1. Terminal fibres beneath the sarcolemma, copied from KÜHNE'S paper. The fibre is as broad as the nucleus, appears smooth, and terminates in a pointed extremity.
- Fig. 2. Fine fibres with nuclei, as seen in many tissues of the frog, according to the author's observations. The fine fibres delineated are less than the  $\frac{1}{50,000}$ th of an inch in diameter, and often become so fine that they cannot be followed; but the apparent terminations are not true ends.
- Fig. 3 illustrates the manner in which fine nerve-fibres with nuclei ramify at their distribution. *a*. A nucleus with a fibre passing from either extremity; *b*, fine nerve-fibre branching; *c*, two fibres running parallel to each other.
- Fig. 4. Fine nerve-fibres dividing at the points *a a*, where they meet another fibre, into two branches, which pursue opposite directions.
- Fig. 5. Network of nerve-fibres to show how the finest fibres might possibly terminate in free extremities or in nuclei, consistently with the existence of networks demonstrated by the author.
- Fig. 6. Network of nerve-fibres near the inner surface of the bladder of the frog; each fibre is composed of a number of very minute fibres, which do not anastomose with each other. A dark-bordered fibre was continuous with the fibres of which this network is composed, at a point a little below the lowest fibre represented in the drawing.  $\times 1700$ .
- Fig. 7. 'Termination' of a dark-bordered fibre, showing its continuity with fine fibres arranged to form networks as in fig. 6. A fine fibre (*a*) is seen to run parallel with the terminal part of the dark-bordered fibre (*b*). This is also lost among other fibres of the network. The granular appearance of the fibres in this

specimen results from the slow action of acetic acid. This figure, and figures 6, 8, & 9, show the relation of the fine fibres to the nuclei.  $\times 1700$ .

- Fig. 8. Another terminal 'extremity' of a dark-bordered fibre. A similar fibre (*a*) is seen external to the dark-bordered fibre, as in the last and also in the next specimen. Four nuclei are seen, which exhibit their relation to the bundles of fine fibres.
- Fig. 9. Another terminal portion of a dark-bordered fibre. In figs. 7, 8, & 9 a nucleus is seen in the dark-bordered fibre as well as in connexion with the pale fibres. Figures 6, 7, 8, & 9 are from the bladder of the frog.
- Fig. 10. Portion of muscular fibre from the leg. Several dark-bordered fibres are seen enclosed in the same sheath; and many of these are exceedingly thin, but evidently possess the same structure as the ordinary dark-bordered fibres.  $\times 700$ .

#### PLATE XLII.

- Fig. 11. Dark-bordered fibres. The nucleated dark-bordered fibre *a* is seen to divide into two branches. The one passing in the division which diverges to the right, rapidly becomes so very fine that it can hardly be followed as it runs parallel with another dark-bordered fibre and in the same sheath with it (under *d*). This very fine fibre, in direct continuity with the dark-bordered fibre, cannot be distinguished from the fine fibres seen in the sheath of the nerve on the left side of the specimen (at *b*), which leave the trunk and assist in forming a separate branch at *c*. From the pectoral.  $\times 700$ .
- Fig. 12. Division of dark-bordered fibre in the central part of the pectoral muscle of the frog. The fine fibres resulting from its subdivision may be followed for a considerable distance. Nuclei are connected with them at intervals, and the fibres are arranged to form a network. A more perfect example of this arrangement is represented in figure 43 (not published). This figure shows the course of the very fine fibre which is directly continuous with the dark-bordered fibre in certain cases.  $\times 700$ .
- Fig. 13. Division of dark-bordered fibres on the surface of a muscular fibre, from the central part of the pectoral muscle. The muscular tissue having been removed from the tube of the sarcolemma, the delicate nerve-fibres can be distinctly seen on the *external surface* of this transparent membrane. The pale granular fibres, which are here and there connected by branches so as to form networks, are composed of the delicate fibres which are the immediate continuations of dark-bordered fibres (*a* and *b*), and of finer fibres which are derived from those ramifying in the sheath or external to it. Nuclei are connected with these fibres.  $\times 700$ .
- Fig. 14. Division and subdivision of fine dark-bordered fibres on the surface of muscular fibre, showing numerous fine fibres arranged in the form of a network, and nuclei. Two or three of the delicate compound nerve-fibres may be traced quite to the edge of the muscle. Pectoral muscle.  $\times 700$ .

Fig. 15. Division of dark-bordered fibre with fine fibres ramifying in the sheath of the nerve. From the pectoral muscle.  $\times 700$ .

## PLATE XLIII.

Fig. 16. Distribution of finest dark-bordered fibres on the surface of a muscular fibre from the pectoral muscle. At the edge of the specimen on the left, the delicate nerve-fibres are seen lying, not only upon the external surface of the sarcolemma, but at an appreciable distance from the outer surface.  $\times 700$ .

Fig. 17. Division of dark-bordered fibre and formation of fine networks. Pectoral muscle of the frog.  $\times 700$ .

Fig. 18. Very fine nerve-fibres on the surface of the muscular fibre. From the pectoral of a young frog. Several of these fibres can be followed to the edge of the muscular fibre, where they are lost.  $\times 1700$ .

Fig. 19. Fine fibres from the sheath of the nerve, dividing and subdividing on the surface of two elementary muscular fibres. From muscle of the neck of the frog.  $\times 700$  diameters. Compare the appearance of the fibres represented at *b, b* in the drawing, with fibres *b* in figs. 16, 15, 14, & 20, which undoubtedly come from true dark-bordered nerve-fibres.

Fig. 20. Division of dark-bordered fibre on surface of muscular fibre.

Fig. 21. Fine dark-bordered fibre, and fibres in sheath of the nerve, with nuclei. From muscle of the neck of the frog.  $\times 700$ .

Fig. 22. Fine fibres resulting from the subdivision of a dark-bordered fibre ramifying on a muscular fibre. Pectoral muscle.  $\times 700$ .

Fig. 23. Division of dark-bordered fibres crossing a muscular fibre.

## PLATE XLIV.

Fig. 24. Dark-bordered fibre and fine fibre in the sheath ruptured. From muscle of under jaw of frog.  $\times 700$ .

Fig. 25. Dark-bordered fibre and fine fibres, showing fibres crossing each other and forming very fine branches composed of several finer fibres.  $\times 700$ .

Fig. 26. Dark-bordered fibres and fine fibres in sheath between muscular fibres of the pectoral muscle of the frog.  $\times 700$ .

Fig. 27. Dark-bordered fibre, with fine fibres external to it, ramifying between the elementary muscular fibres of the pectoral muscle of the frog.  $\times 700$ .

Fig. 28. Branching and division of dark-bordered nerve-fibre near terminal branches, and bundles of fine fibres. Several nuclei are seen in connexion with both sets of fibres. From the bladder of the frog. At *a* the dark-bordered fibre becomes resolved into several fine fibres.  $\times 700$ .

Fig. 29. Fine fibres continued from a dark-bordered fibre, and the fibres in its sheath crossing a young muscular fibre.  $\times 700$ .

Fig. 30. Young muscular fibre from the pectoral muscle of the frog, near one of the

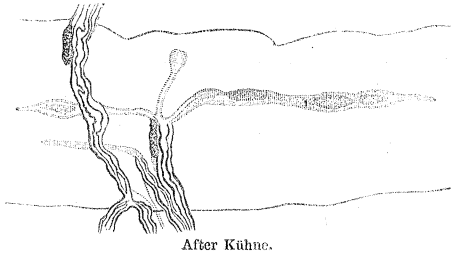
oval swellings. At *a* and *b* are seen the fine fibres which are continuous with the dark-bordered fibres. These are gradually lost amongst very fine fibres. The compound branches divide and subdivide on the surface of the muscular fibre.  $\times 700$ .

*c.* Another fibre at a distance from the oval swelling, showing nuclei with very fine fibres ramifying upon the muscular fibres.  $\times 700$ .

Fig. 31. Dark-bordered nerve-fibre with fine fibres at the side of it. These fine fibres appear in one part like the outline of the tubular membrane, but at a short distance they are seen to give off branches which pass with other fine fibres. It will also be observed that there is no corresponding line on the other side of the dark-bordered nerve-fibre in this case. From bladder of frog.  $\times 700$ .

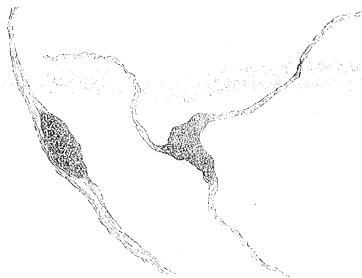
It will be doubted by some if the fine fibres I have figured are true nerve-fibres; but it must be borne in mind, (1) that dark-bordered nerve-fibres divide into fibres as fine as these in the trunks of the nerves near their distribution; (2) that fibres as fine as these form the direct continuation of dark-bordered nerve-fibres themselves; (3) that all dark-bordered nerve-fibres terminate in fine fibres which divide and subdivide into finer branches which run in company with fine fibres apparently derived from the sheath of the nerve or from fibres external to the sheath, but which are probably true nerve-fibres and, at least in some cases, are themselves but the continuation of dark-bordered fibres which run for some distance in the sheath and then diverge.

Fig. 1.



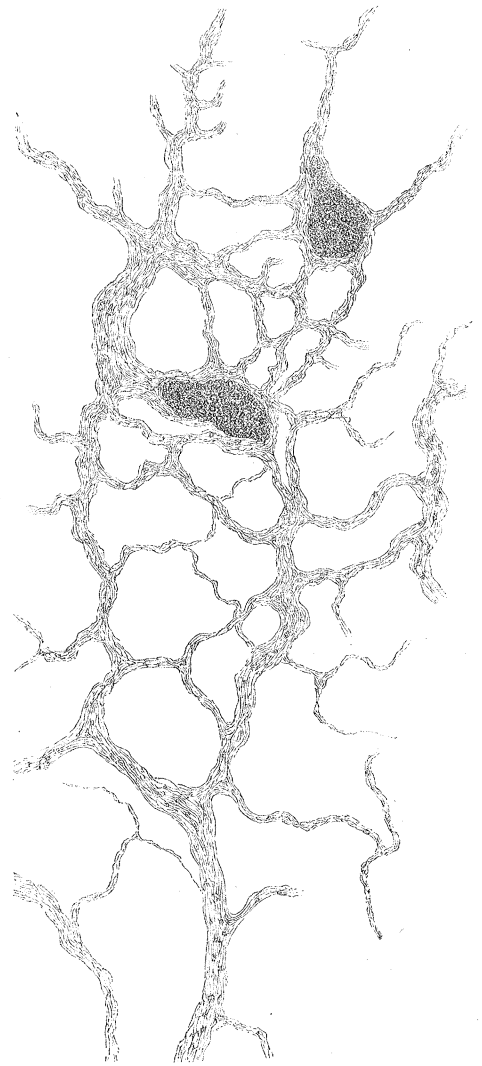
After Kühne.

Fig. 2.



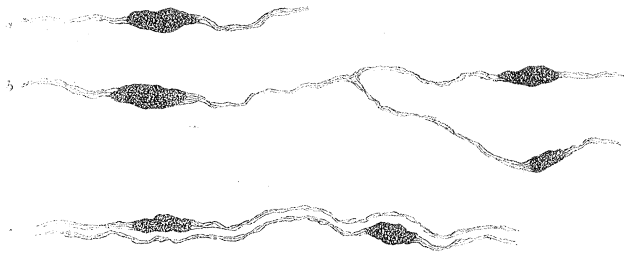
Fine nerve fibres and nuclei.

Fig. 6.



Plexus of finest nerve fibres.—Bladder of frog. × 1700

Fig. 3.



Fine terminal fibres and nuclei.

Fig. 4.

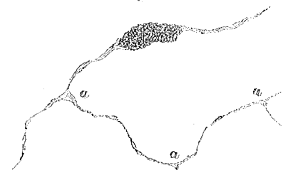
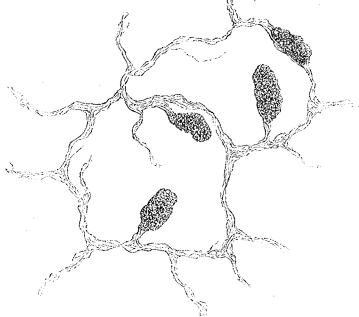
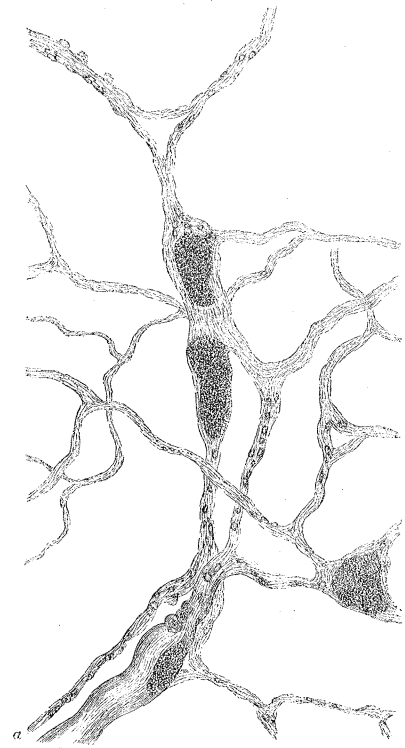


Fig. 5.



Possible mode of termination of finest nerve fibres.

Fig. 7.



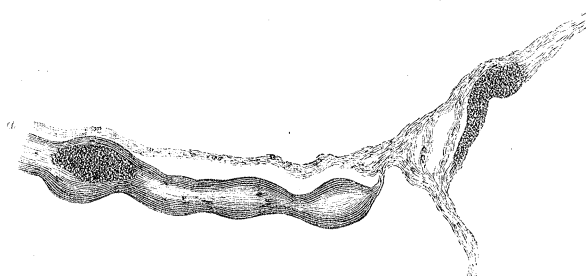
Terminal portion of dark-bordered fibre.—Bladder of frog. × 1700

Fig. 8.



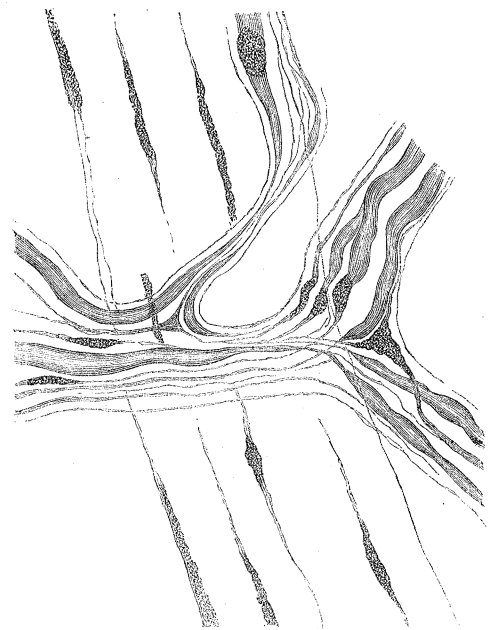
Terminal portion of dark-bordered fibre.—Bladder of frog. × 1700

Fig. 9.



Terminal portion of dark-bordered fibre.—Bladder of frog. × 1700

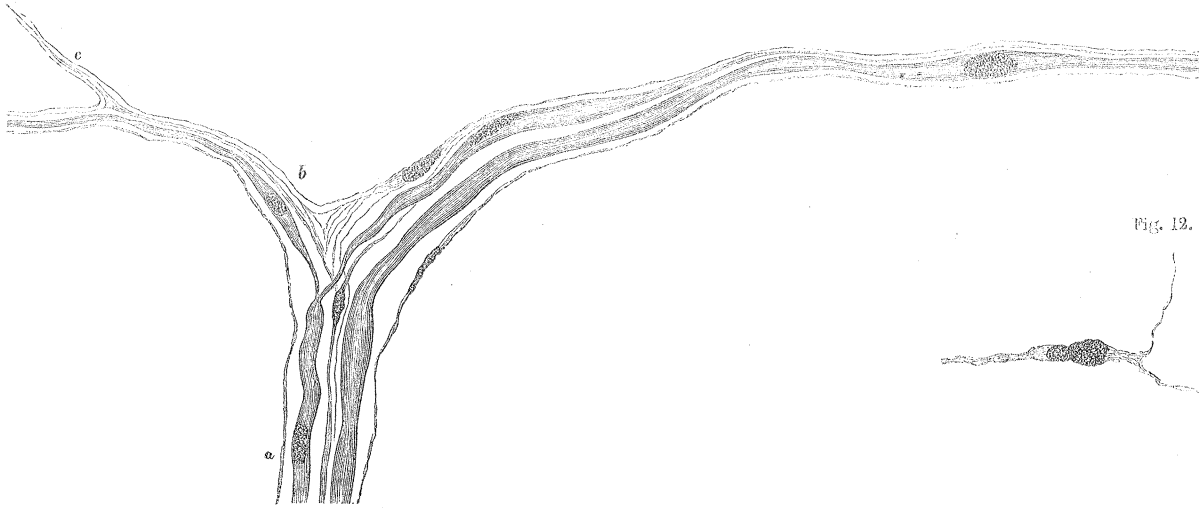
Fig. 10.



Dark-bordered fibres crossing a muscular fibre.—Leg of frog. × 700

1000th × 700

1000th × 1700



Division of dark-bordered nucleated fibre—at *d* a dark-bordered fibre contracts so as to form a very thin scarcely visible line—nuclei in dark-bordered fibres.  $\times 700$

Fig. 12.

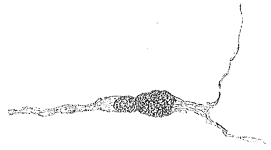
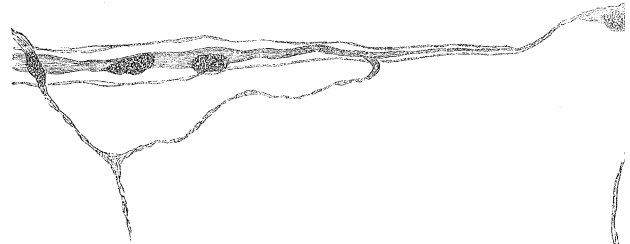


Fig. 13.



Division of dark-bordered fibres on surface of a muscular fibre.  $\times 700$



Division of dark-bordered fibre and fine nucleated fibres.  $\times 700$

Fig. 14.



Fig. 1







Fig. 12.

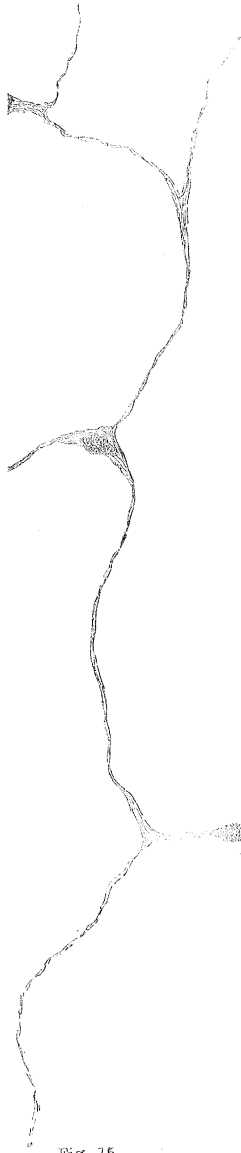
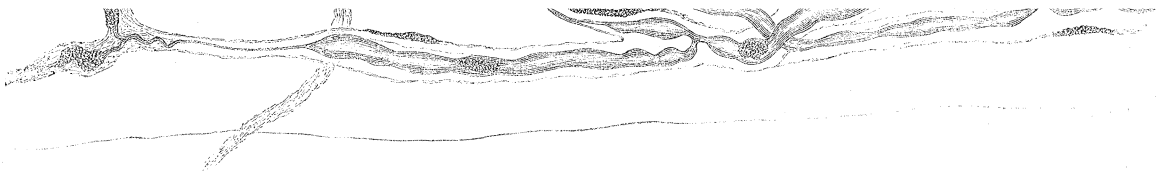


Fig. 15.





Division and sub-division of fine dark-bordered nucleated fibres, and commencing portion of the network of pale nucleated fibres on surface of a muscular fibre. x 700

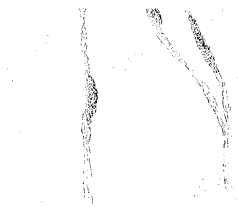
All these figures from the pectoral muscle of the frog.

1000 th  x 700

1000 th  x 1700

L. S. B. ad nat. del.

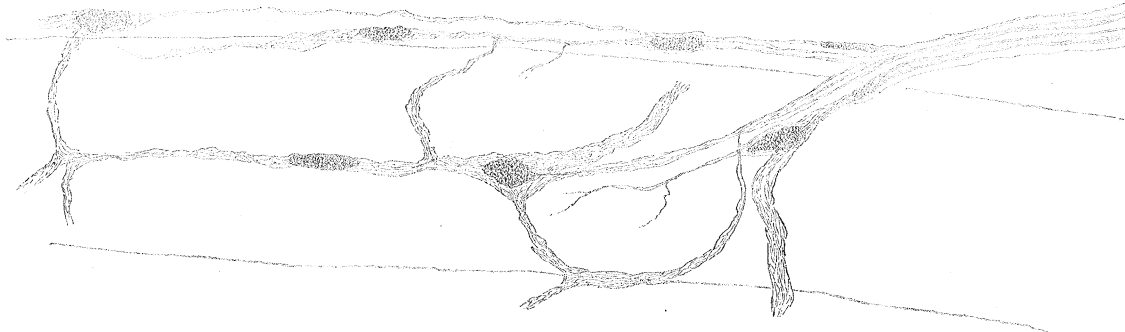
Division  
and pale



Division of dark-bordered fibres  
and pale fibres of sheath.  $\times 700$

[Harrison's fig. 1.]

Fig. 16.



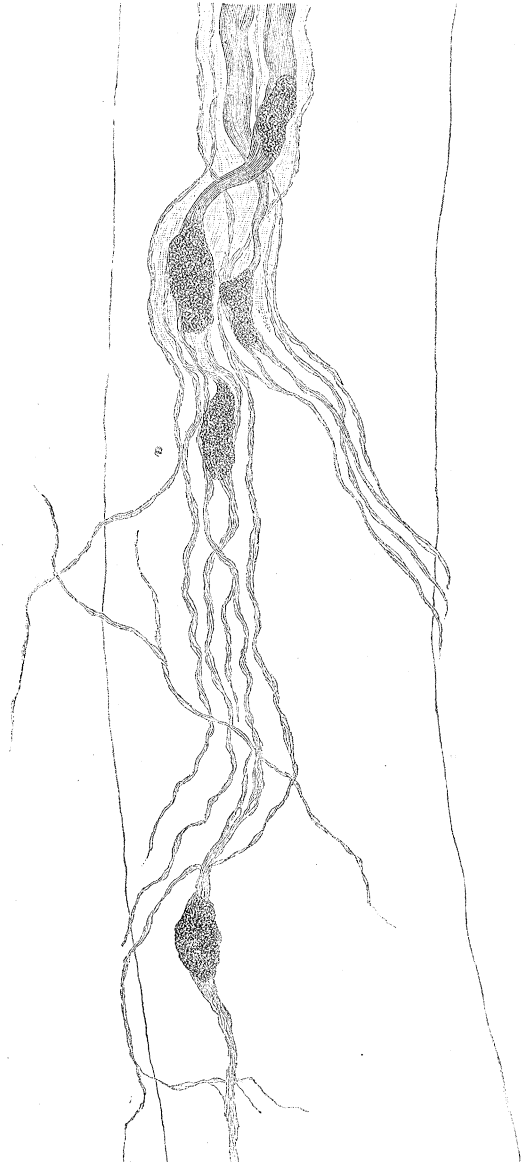
Terminal portion of finest dark-bordered fibres.—Small muscular fibre.—Pectoral. x 700

Fig. 17.



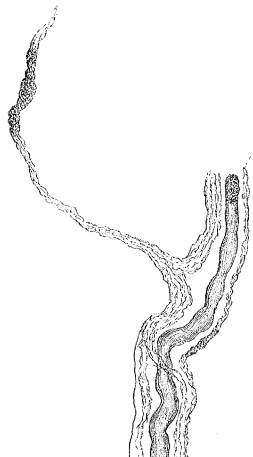
Division of dark-bordered fibre, and fibres of sheath.—Formation of network.—Pectoral. x 700

Fig. 18.



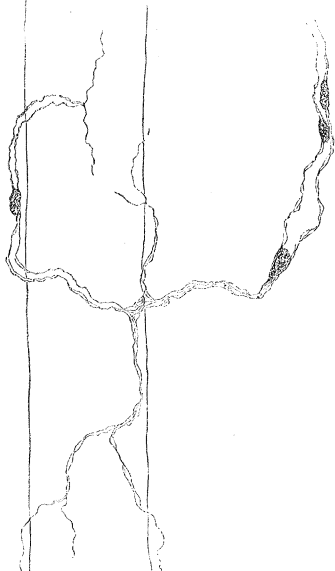
Very fine nerve fibres on small muscular fibre.—Pectoral muscle of a young frog. x 1700

Fig. 21.



Thin dark-bordered fibre.—Fine fibres in sheath, crossing it and forming a branch which leaves the fibre.—From muscle of neck of frog. x 700

Fig. 22.



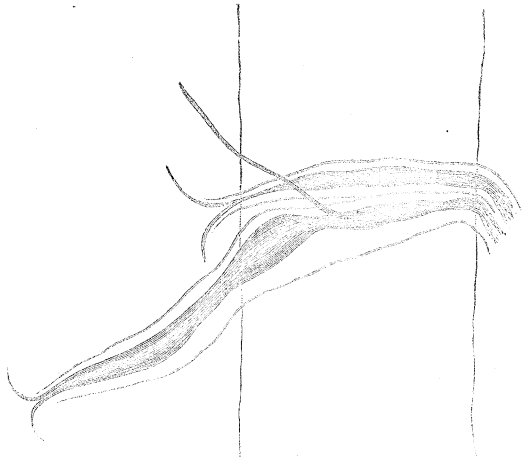
Fine fibres resulting from the sub-division of a dark-bordered fibre. x 700

Fig. 19.



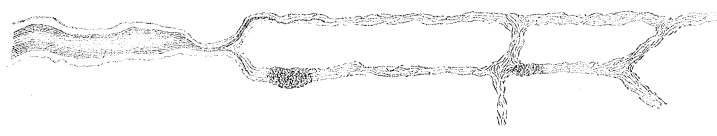
Fine fibres ramifying in sheath, dividing and forming networks.—Muscle from the neck of the frog. x 700

Fig. 23.



Division of dark bordered fibres while crossing a muscular fibre. x 700

Fig. 20.



Division of dark-bordered fibre and network of fine fibres.—Pectoral muscle. x 700

1000 th ..... x 700

1000 th ..... x 1700

Fig. 24.

Fig. 24.



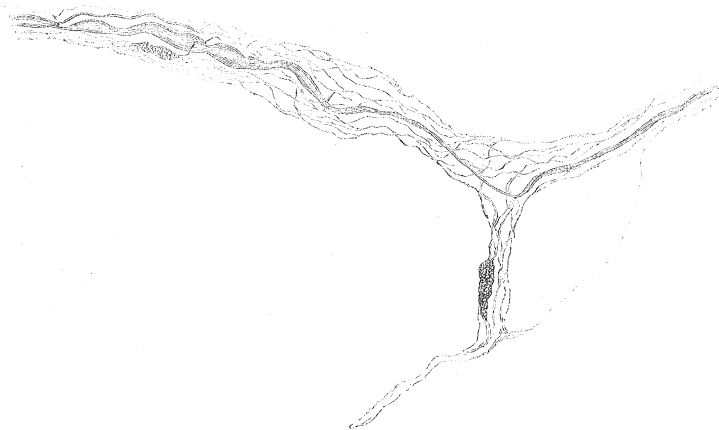
Fine fibre in same sheath with dark-bordered fibre. x 700

Fig. 25.



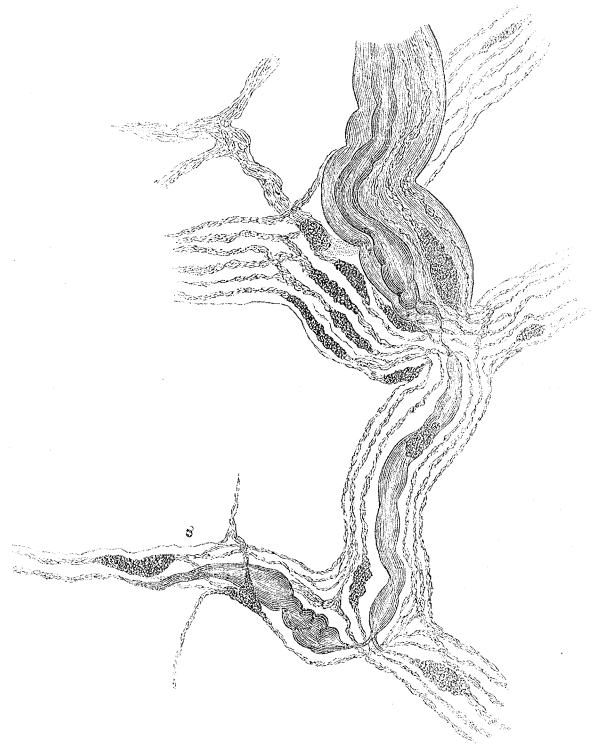
Dark-bordered fibres and fine fibres in sheath. x 700

Fig. 27.



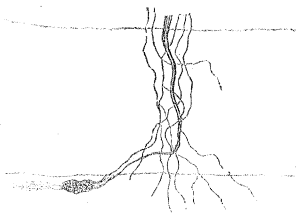
Fine dark-bordered fibre and fine nerve fibres in sheath. x 700

Fig. 28.



Branching and division of dark-bordered fibres and pale fibres in same sheath. —From bladder of the frog. x 700

Fig. 29.



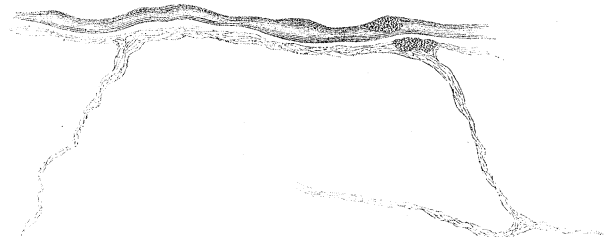
Terminal portion of dark-bordered fibre with fine fibres crossing a young muscular fibre. x 700

Fig. 30.



Young muscular fibres near a nerve swelling.—Pectoral of frog.—Showing division of nerve fibres.—c another fibre at a distance from the nerve swelling. x 700

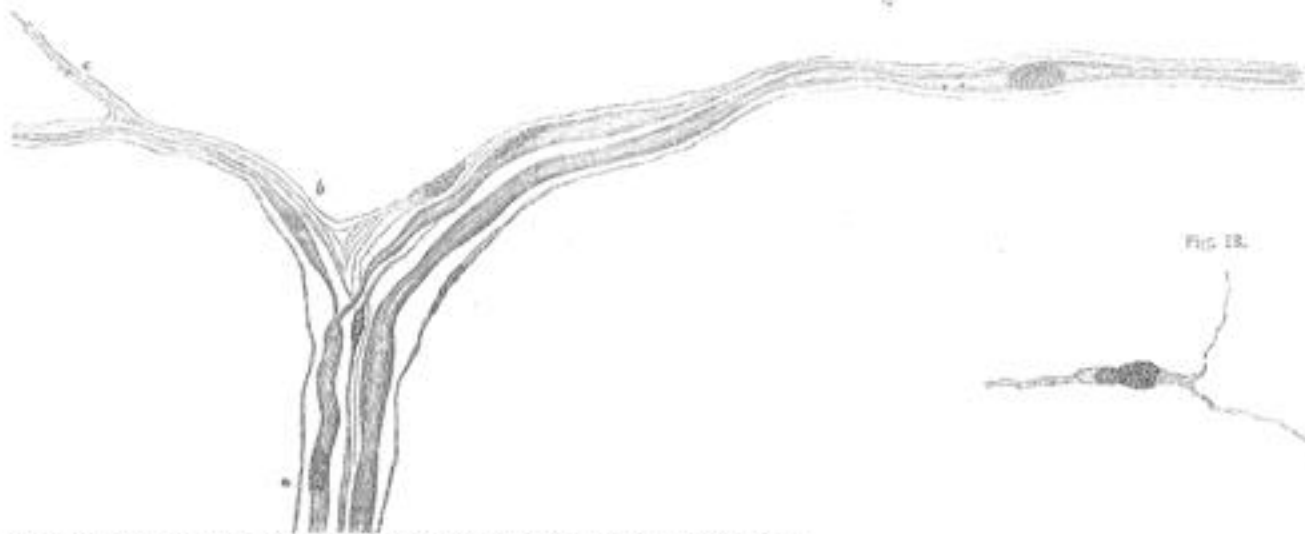
Fig. 31.



Dark-bordered nerve fibre with a bundle of fine fibres by the side of it. Bladder of frog. x 700

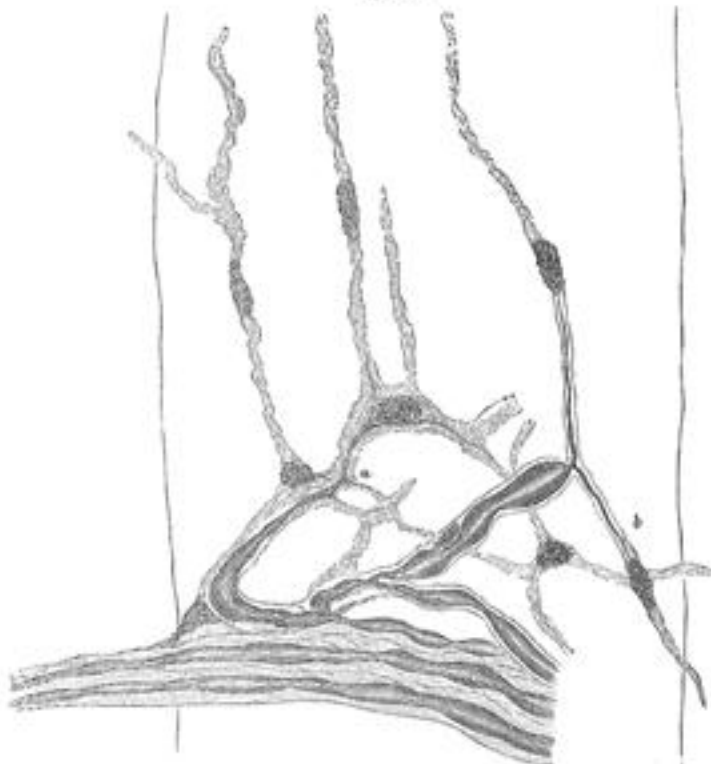
1000th x 700

1000th x 1700



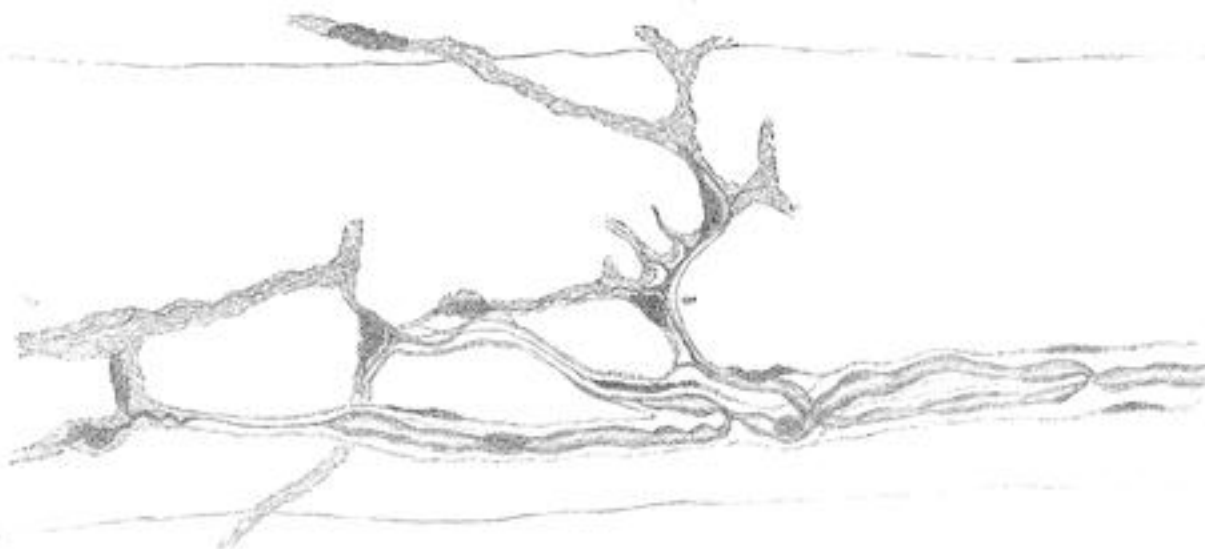
Division of dark-bordered nucleated fibre—*a* dark-bordered fibre contracts so as to form a very thin scarcely visible fibre—*b* in dark-bordered fibres.  $\times 700$

Fig. 13.



Division of dark-bordered fibres on surface of a muscular fibre.  $\times 200$

Fig. 14.



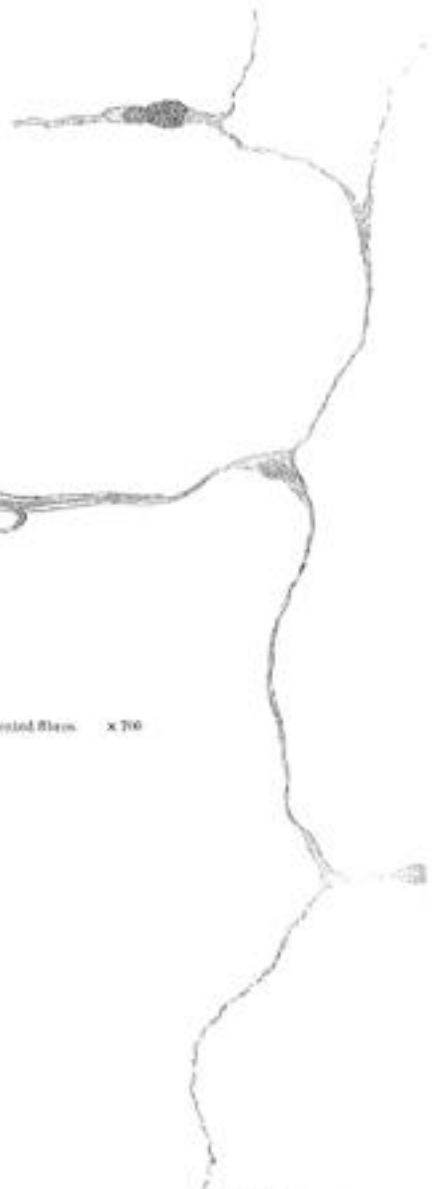
Division and sub-division of fine dark-bordered nucleated fibres, and connecting portions of the network of fine nucleated fibres on surface of a muscular fibre.  $\times 500$

All these figures are in the posterior muscle of the frog.

1000th 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 61, 62, 63, 64, 65, 66, 67, 68, 69, 70

1000th 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 61, 62, 63, 64, 65, 66, 67, 68, 69, 70

Fig. 12.



Division of dark-bordered fibre and fine nucleated fibre.  $\times 700$

Fig. 15.



Division of dark-bordered fibre and fine fibre of sheath.  $\times 700$