May 1, 1862.

JAMES PAGET, Esq., Vice-President, in the Chair.

In accordance with the Statutes, the names of the Candidates recommended for election into the Society were read, as follows:—

George Bentham, Esq.
Henry William Bristow, Esq.
Alexander Ross Clarke, Capt. R.E.
John W. Dawson, Esq.
Frederick J. Owen Evans, Esq.
John Braxton Hicks, M.D.
The Very Rev. Walter Farquhar Hook, D.D.
George Rolleston, M.D.
Charles William Siemens, Esq.
Maxwell Simpson, Esq.
Balfour Stewart, Esq.
Thomas Pridgin Teale, Esq.
Sir James Emerson Tennent.
Isaac Todhunter, Esq.
C. Greville Williams, Esq.

Professor Albert Kölliker, of Würzburg, who was elected a Foreign Member in 1860, was admitted into the Society.

The Croonian Lecture was delivered by Prof. A. Kölliker, For. Memb. R.S., "On the Termination of Nerves in Muscles, as observed in the Frog; and on the disposition of the Nerves in the Frog's Heart," as follows:—

When I was honoured by an invitation to deliver the Croonian Lecture, I at first hesitated to undertake the task, however gratifying to me, because I was not prepared with a subject of discourse which I thought likely to prove of sufficient general interest to the Fellows of this distinguished body, engaged as they are in the pursuit of very various branches of "Natural Knowledge." I felt that on such an occasion it was desirable to lay before the Society the result of some original research, but I feared that the matter I had actually at my command, referring more immediately to a question in Microscopic Anatomy, was scarcely of adequate importance. Knowing, however, that the purpose for which this lecture was instituted is the elucidation of the "Nature and Laws of Muscular Motion," and considering that my researches, although in themselves purely anatomical, have a

decided bearing on that great physiological question, I have felt encouraged to lay them before the Society.

Termination of the Nerves in the Voluntary Muscles.

The investigation of the termination of the nerves in the muscles has for some time occupied the attention of various able inquirers, but the results attained are by no means in mutual accordance. The recent researches of Kühne, in particular, on the muscular nerves of the Frog, have led him to conclusions differing so widely from those of Wagner, Reichert, Schaafhausen, Beale and others, that I was induced to apply myself to the question, in the hope that I might be able to contribute something towards its elucidation*.

While previous observers have been unable to trace the muscular nerves further than the surface of the muscular fibres, Kühne †

* As the more immediate purpose of my present inquiry was to examine into the accuracy of Kühne's recent descriptions, I did not deem it necessary in the Lecture to do more than advert to the labours of previous inquirers. In order, however, to prevent misconception, I think it as well to explain that whilst pale nucleiferous branching fibres have been seen and repeatedly described as the terminal ramifications of sentient nerves, some observers have also described the nerves as ending on muscular fibres by similar pale filaments. Thus Axmann, in 1853, represented the nerves of the cutaneous muscle of the mole as ending in networks of fine fibres; and more recently, Schaafhausen (1859) described the terminations of the nerves in muscles as a very fine network which could be rendered visible by means of carmine. In justice to Dr. Beale also, I must here state that, in the account he has given of his elaborate researches on this difficult point of microscopic anatomy (Phil. Trans. 1860), he describes the nerves of striped muscles as terminating on the sarcolemma in a network of pale fibres connected with nuclei, rendered visible by carmine and chemical reagents. Speaking of these fibres, Dr. Beale observes (p. 616) that their "general appearance and refracting power are the same in every part except where the nuclei are situated"; he adds (p. 617), that "the axis-cylinder gradually loses its hard fibrous character (frog), and the white substance its peculiar refractive power and consistence. The whole fibre, as seen in my specimens, seems to consist of a very transparent and perhaps delicately granular substance, which can be shown to be composed of fatty and albuminous materials," &c. Judging, however, from Dr. Beale's figures, which represent the terminal network of the nerves distributed on the muscular fibres of the mouse, and from his description, I am led to conceive that he has not observed what Kühne and I have seen. He does not mention that he has seen *single* dark-bordered nerve-fibres running out into *simple* and *fine*-branched pale fibres, and, moreover, gives no figures showing such ramifications. It is true Dr. Beale says that the same pale nerve-fibres he has described and figured from the mouse, occur also in the frog; but from what I have seen I cannot admit that pale fibres, of the size and with the arrangement represented in his figures from the mouse, are to be met with in the frog.—A. K.

† Ueber die peripherische Endorgane der motorischen Nerven. Leipz. 1862.

believes he has discovered that the nerve-fibres, on reaching a muscular fibre, penetrate into its interior and end amidst the muscular substance by several pale branches. He states that the nerve-fibre, on reaching the muscular fibre, divides into several branches which retain their characteristic dark contours until they enter the muscular fibre, within which they become pale and faintly outlined. He conceives that the tubular membranous sheath of the nerve-fibres coalesces with the sarcolemma, and that the branches when they enter the muscular fibre lay aside not only their membranous sheath but their white substance, to which they owe their dark outline, and are in fact reduced to mere ramifications of the axis-cylinder or central thread of the original fibre.

In connexion with these internal fibres, Kühne further describes certain bodies which he proposes to name "terminal nerve-buds" (Nervenendknospen). These are attached laterally to the pale fibres, which then may end at some distance beyond in free pointed extremities, while some of the pale fibres appear actually to terminate in these end-buds. The bodies in question are stated to be oval-shaped corpuscles, smaller than the well-known muscular nuclei, usually pointed at their distal extremity, where they bear a minute filamentous tuft. According to Kühne each consists of a little oval mass of finely granular substance, into which a fine filament, apparently derived from the axis-cylinder of the pale nerve-fibre, enters, like a pedicle, at one end, and runs along the middle as a sort of axis-cylinder of the corpuscle, at the free end of which it swells out into a small interior pyriform body containing minute spherules very different in aspect from the granules of the surrounding granular substance. The structure thus described presents, as Kühne observes, some resemblance to that of a Pacinian Body, but yet with marked differences, and he does not lay any great stress on the point.

These observations of Kühne were made with a magnifying power of from 1000 to 1800 linear, on fresh muscular fibres (from the gastrocnemius of the frog) immersed in vitreous humour or blood-serum, also on fibres prepared by macerating a portion of muscle for 24 hours in extremely dilute sulphuric acid, then digesting for an equal time in distilled water at about 100° F., and finally shaking it briskly with a little water in a test-tube so as to separate the tissue into single fibres.

Believing that the wide divergence in the conclusions heretofore arrived at has been owing in great measure to difference in the methods of investigation employed, I made many trials in order to find out reagents which would increase the transparency of the muscular fibres without attacking or at least obscuring the finer fibres of the nerves, and have found the following to be well adapted for the purpose in view. 1. Extremely dilute acetic acid*. 2. Diluted hydrochloric acid in the proportion of 1 part of acid to 1000 of water; but as this reagent eventually softens and destroys the muscles, it is well to observe that the suitable time of exposure to it is from about 12 to 24 hours. 3. Artificial digestive fluid, the use of which for a similar reason requires precaution. 4. Very dilute nitric acid in the proportion of 1 part of acid to 1000 of water.

The object selected for examination was for the most part the cutaneous pectoral muscle of the frog, in which the ramification of the nerves has been so successfully traced and represented by Reichert†. In general I have found it better not to separate the muscular fibres, although I have not omitted also to examine single fibres from the same muscle, and from the gastrocnemius. The magnifying power employed was from 500 to 600 linear, obtained by Hartnach's lenses "à immersion" No. 9 & 10. I have also tried a power of from 1000 to 1500 as used by Kühne, but I could discover nothing by its aid which I did not see equally well with the lower amplification.

In proceeding now to give an account of my own observations, I have first to state that I have been able to confirm the observation of Kühne that in the frog's muscles the nerve-fibres really branch out at their ends into delicate pale filaments—a fact not hitherto recognized by Wagner, Reichert and others, who have investigated the relation of the nerves to the muscles in that animal.

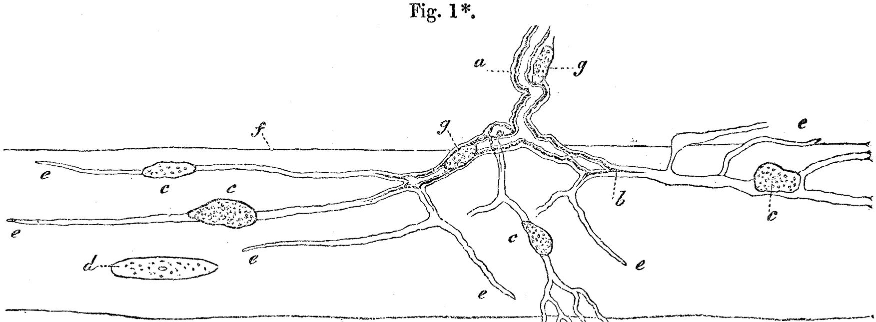
But whilst agreeing with Kühne as to the existence of these pale fibres, I am satisfied that they are situated, not within the muscular fibre but on its surface, as I shall more fully explain hereafter; and that they lie outside the sarcolemma, through which they do not penetrate. As to their nature, Kühne regards them as prolongations

* I find the best proportion to be from 8 to 16 drops of concentrated acetic acid, sp. gr. 1·045, to 100 cubic centimetres ($3\frac{1}{2}$ ounces) of distilled water.

† Müller's Archiv, 1851.

of the axis-cylinder alone; but it decidedly appears to me 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. According to my view, therefore, the delicate membranous sheath does not quit the nerve-fibre and coalesce with the sarcolemma, as Kühne believes, but continues to surround a pale prolongation of the soft contents of the nerve-tube. As to the matter contained in the membranous sheath, it no doubt always comprehends the axis-cylinder, and is chiefly formed by a prolongation of that structure; but I have seen examples in which the contained matter showed slight varicosities and a certain darkness of outline, from which I infer that here and there at least a thin layer of the white substance extends along the pale fibre. But whilst it is easy in most cases to

Fig. 1*.



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. They are still, however, to be regarded as tubes; for, in the first place, they are prolongations of a decidedly tubular fibre, and, secondly, when treated with

* Fig. 1. Termination of a dark-bordered tubular nerve-fibre on a muscular fibre, *f*, *f*, of the cutaneous muscle of the frog, seen with Hartnach's Objective "à immersion" No. 10, and Eyepiece No. 1. *a*, Sheath of the nerve-fibre continued at *b* upon the pale terminal fibre; *b*, axis-cylinder and contents of the nerve-tube continued into the pale fibres; *c*, *c*, nuclei of the pale fibres; *d*, a nucleus belonging to the muscular fibre *f*, *f*; *e*, *e*, *e*, *e*, ends of the pale fibres; *g*, *g*, nuclei of the dark-bordered fibres. [The figure shows the continuation of the dark-bordered fibres into the pale filaments, but fails to exhibit the faint outline and characteristic aspect of the latter.]

certain reagents, such as acetic acid, they exhibit a precipitate of fine sparse granules in their interior, as Kühne has also observed; although when examined in the fresh state, or after being treated with hydrochloric acid, or artificial digestive fluid, they appear pellucid and uniform throughout. It is further worthy of remark, that whilst the pale fibres are for the most part rectilinear prolongations of the dark-contoured fibres, instances occur in which a dark fibre ends by dividing at once into two or three pale fibres. More remarkable still are the cases in which a pale fibre comes off laterally, and sometimes at right angles from a dark fibre, or where two pale fibres come off together from opposite sides; because such cases, which Kühne appears not to have seen, or at least has not represented, are well calculated to show that the pale fibres are furnished with a prolongation of the membranous sheath.

The next question of interest arising from Kühne's observation refers to the bodies which he looks upon as peculiar terminal organs, and names the terminal nerve-buds. As regards these corpuscles, I must confess that, after the most careful investigation, I have failed to discover that they possess the peculiar internal structure which Kühne assigns to them. Considering the skill and address in microscopic investigation which Kühne has evinced in his inquiry, and feeling persuaded that he must have met with what seemed to him sufficient indications of the structure he has described, I bestowed the greatest pains on the examination of these so-called end-buds. I studied them in muscles and muscular fibres, both fresh and treated with reagents. I employed the same magnifying powers, and equally good lenses; but the only conclusion to which I could arrive is, that the corpuscles in question are nothing but ordinary nuclei connected with the membranous sheath of the pale nerve-fibres, not essentially differing from those found attached to the sheath of the dark-contoured fibres from which the pale fibres are derived. It is true that some of them show a dark streak in the middle or towards the border, which at first sight might suggest a peculiarity of structure; but the appearance is obviously due to a fold or crease on the surface, and the same thing is seen in the undoubted nuclei of the dark-contoured fibres. Their shape, position, and relative size may be judged of from the figures I have given; and I have only further to remark, that in fresh preparations they are usually very

faint, and therefore somewhat difficult to recognize; but with certain reagents, such as acetic acid, they become darker, more granular, and somewhat shrunken, with an irregular outline; with others, such as hydrochloric acid, they appear more homogeneous and pale. As to their situation, they are attached along the fibres; and I have never seen them at the ends, as Kühne in some instances found, although sometimes they are placed very near the end. Sometimes one is placed in the angle of division of a fibre. They appear to be attached laterally; yet I cannot doubt that they lie within the membranous sheath of the pale fibre, although the prolongation of the latter over them cannot be shown as a separate structure. Were further evidence required concerning the true nature of these corpuscles, I might add that nuclei of precisely the same character exist on the pale terminal fibres of the sensory nerves distributed to muscles, as I shall more fully explain in the sequel, and indeed on the final ramifications of nerves in general, of which we have examples in the skin of the mouse and frog, in mucous membranes, in the cornea, and in the electric organ of the torpedo.

I come now to a more difficult question, namely, whether the pale end-fibres of the nerves really lie within the muscular fibres or not. Important as the determination of this question is in relation to physiology, I can confidently say that I entered upon it without bias, and studiously put aside every consideration which might militate against the notion that the nerves penetrate into the muscular fibres. Indeed I myself at one time thought that in certain parts of the cutaneous pectoral muscle of the frog I had seen muscular fibres penetrated by nerve-fibres. On careful investigation, however, I became convinced that the seeming interior situation of the pale fibres is an illusive appearance, and so many proofs against its reality presented themselves, that I was finally constrained to come to a different conclusion from Kühne on this point also.

According to my view, therefore, the pale terminal ramifications of the nerves lie wholly without the muscular fibres, that is, on the outer surface of the sarcolemma. In support of this opinion I may, without insisting on negative evidence, which may be less regarded, adduce, in the first place, the fact that not unfrequently a pale fibre may be seen running on a muscular fibre towards the border, and then turning round to the other side, obviously outside the sarcolemma. Again

a pale fibre running along the border of a muscular fibre sometimes presents serpentine bendings, which appear alternately under and over the muscular fibre, and in the latter case are clearly exterior to the sarcolemma. Moreover I have observed that the pale fibres derived from one dark fibre are sometimes distributed to two muscular fibres, and must therefore run outside and between them,—an appearance not reconcileable with the descriptions of Kühne, who states that nerve-fibres retain their dark contours until they penetrate the muscular fibre, and that the whole of the terminal pale filaments derived from a nerve-fibre are contained within one muscular fibre.

In further corroboration of what has been said I may add, that in surface-views of the parts in question the pale nerves always appear above the cross striæ of the muscular fibre, also above its nuclei; which fact would, it is true, not decide whether the pale fibres were outside or inside the sarcolemma, but is sufficient to prove that they do not lie amidst the contractile substance. Further, this contractile substance within the sarcolemma may, by means of dilute hydrochloric acid, be softened and reduced to a fluid state, and nevertheless the pale fibres retain their original position unaltered, even when the liquefied contents of the sarcolemma with the muscular nuclei flow backwards and forwards within the tube. Lastly, when muscular fibres are treated with acetic acid of a certain strength, the whole contents of the sarcolemma are squeezed out in the form of long transversely striated cylinders; so that on cutting across the fibres of a muscle near the part where it receives a nerve, and treating it in the way indicated, the proper substance of the fibres may be examined apart from the sarcolemma, at the place where their nerves reach them. Now, on repeatedly trying this experiment, I have never found a trace of the nerve-fibres on the extruded portions, whilst on the other hand they are still to be seen on the emptied sarcolemma.

It remains for me yet to say a word as to the mode in which the pale nerve-fibres actually terminate, a point on which I confess I have still some doubt. It is true that I have observed apparently free ends as represented by Kühne; but, on the other hand, appearances sometimes present themselves which suggest the question, whether on the muscular fibre, as in the physiologically allied electric organ of the torpedo, there may not be *an extremely fine network*

in which the pale nerve-fibres terminate. Thus in many cases there is an appearance on the pale fibres of numerous short, pointed or blunt, lateral processes, or at least a certain want of definition in their outline, indicating that they may possibly send out still finer offsets. At the same time I have not been able to trace the matter further in this direction; and as regards the few undoubted cases of conjunction of the pale fibres which I have hitherto met with, I am not disposed to interpret them in the above sense. Moreover we can often see the pale fibres so sharply and beautifully defined, and maintaining so long their rectilinear course, that it is difficult not to regard them as the true terminations; so that the above-mentioned appearances to the contrary may perhaps be owing to the effect of the reagents used, which, while they clear up the muscular fibres, may attack more or less the extremely delicate substance of the pale nerve-fibres.

On the Distribution of Sentient Nerves in the Muscles of the Frog.

Having thus laid before the Society the results of my observations on the motorial nerves of the frog's muscles, I have now to speak of the terminations of other nerves which are distributed to the muscles of the same animal, and which are probably sensory in their office. Nerves which are probably of a sentient nature have already been observed in human muscles by myself, and in the cutaneous pectoral muscle of the frog by Reichert, who takes the same view as to their nature. As, however, the mode of termination of these nerves has not heretofore been fully investigated, I have been led to extend my inquiries to that question, and beg leave now to state the principal results.

The sentient nerves of the cutaneous pectoral muscle of the frog are supplied by the common moto-sensory nerve of the muscle (fig. 2, *a a a*), from which they come off at different points as single fibres, and, proceeding to the muscle, branch out upon it in its whole extent, even in parts which are destitute of motorial nerves. As regards the details of distribution, however, there is not even an approach to uniformity in any two muscles, and therefore, instead of attempting a general description, I will refer to fig. 2, which represents an individual case as seen under a low magnifying power, carefully copied from nature.

In this instance the sentient nerves consisted of five principal

Fig. 2*.

* Fig. 2. *a, a, a,* Common trunk and principal branches of moto-sensory nerve.

truncules as they may be called, each, however, being but a single fine fibre ; one of these (fig. 2 *b*), larger than the rest, supplied the upper part of the muscle with branches, two (*c*, *d*) went to the middle, and two rather long ones (*e*, *f*) were distributed on the lower part of the muscle. As to the original source of these truncules, I agree with Reichert in thinking that they are all derived from one principal sentient fibre, which is mixed up with the more numerous motor fibres in the small nerve *a*, *a*, *a*, which is supplied to the cutaneous muscle. It is true that I have not been able, any more than Reichert, actually to trace back these truncules to their parent fibre in the trunk of the common nerve. Nevertheless I feel much confidence in believing that they arise in the way stated; and especially because I have met with cases in which the parent fibre of all the sentient nerve-fibres of the cutaneous muscle escapes from among the motorial fibres of the common muscular nerve at some distance from the muscle ; so that its division into the secondary truncules may be seen. Moreover I have never seen fibres, which from their final distribution may be reckoned as motory, coming from the sentient fibres, nor the latter from the former; although I have sometimes met with a deceptive appearance to the contrary, caused by true motor fibres attaching themselves for a little way to a sentient fibre, and then seeming to come off as branches of it.

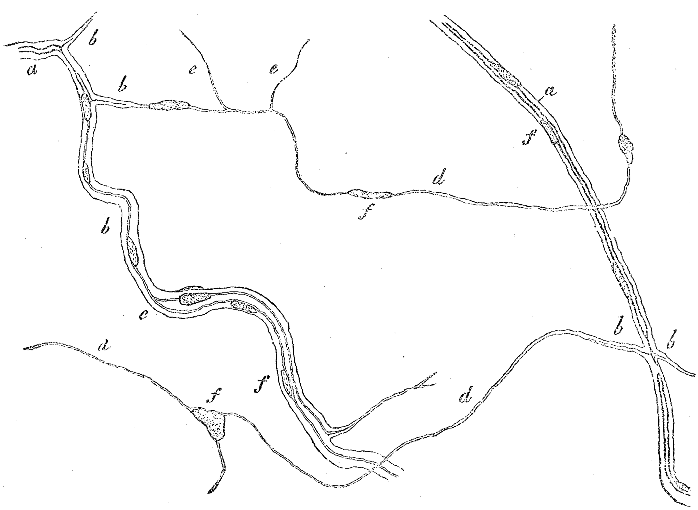
In their progress the dark-bordered sentient fibres for the most part tend towards the outer or cutaneous surface of the thin muscle, on reaching which they branch out upon it underneath a thin fascia, which covers the muscle and forms also the wall of an adjacent lymph-space.

The terminations of these sentient nerve-fibres were not seen by Reichert, and doubtless because he used potash in his examination of them ; but with the aid of some of the reagents already mentioned they may be traced out, although from their extreme tenuity and paleness this is no easy matter. Their mode of termination is on the whole similar to that of the motor nerves, only the pale end-fibres have a more extended distribution and are much finer. The

of the cutaneous muscle ; *b*, *c*, *d*, sentient fibres (truncules) to upper and middle part of muscle, and *e*, *f*, to lower part, all dividing into finer terminal filaments connected with nuclei which are not represented in this general view ; *h*, *h*, *h*, *h*, branches of *f* which went to abdominal muscles ; *i*, *i*, *i*, swollen parts of muscular fibres containing 'nerve-tufts.'

figures will serve better than a long description to give a correct idea of their terminations. Whilst fig. 2, drawn under a low magnifying power, represents their general mode of distribution, fig. 3 shows a small part of their ramification and two or three terminations, highly magnified. It will be seen that the larger fibres divide and redivide into smaller branches, which still retain their dark contours, but give off in their course lateral pale branches, and finally end in pale and numerous prolongations. In the pale fibres, at their commencement the membranous sheath is distinct from the contained fibre, which doubtless consists of the axis-cylinder, with at first some part of the medullary substance; in their progress the sheath becomes blended with the contents, and can no longer be distinguished as a separate structure. Nuclei (*f*, *f*, fig. 3) are seen

Fig. 3*.



all along the pale fibres, and also on the smaller dark fibres. In short, the structural character of the pale sentient fibres is, so far as it can be discovered, essentially the same as the pale terminations of

* Fig. 3. Part of ramifications of the sentient fibres of the cutaneous muscle, as seen with Hartnach's Objective No. 7, and Eyepiece No. 1. *a*, *a*, Dark-bordered fibres with fine sheath and nuclei; *b*, *b*, *b*, pale fibres still having a sheath and pale contents (axis-cylinder); *c*, division of the axis-cylinder of one of these fibres; *d*, *d*, *d*, non-medullated terminal fibres, with nuclei *f*, but on which no sheath can be recognized.

the motor nerves. As already noticed, however, they become smaller in size ; indeed the extreme prolongations are in some places attenuated to the size of filaments of connective tissue. Their fine terminations, moreover, lie quite superficially in the perimysium or sheath of the muscle, and between it and the muscular fibres, and are in a great measure confined to the outer or cutaneous surface of the muscle, although here and there fibres are seen turning to the under surface.

Nerves of the Blood-Vessels.

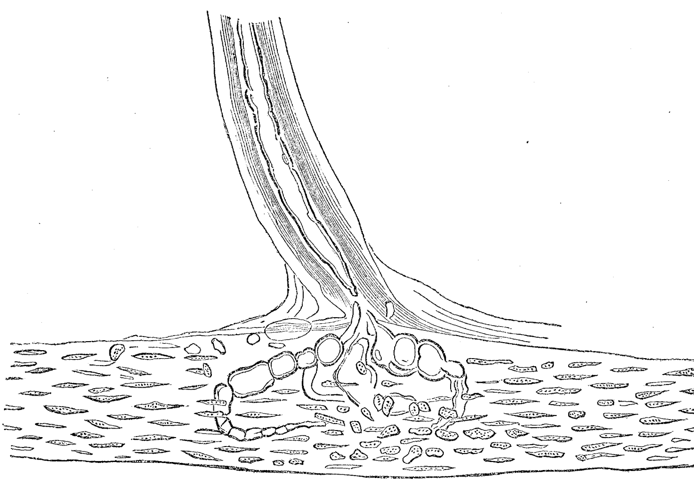
Besides the sentient nerves which I have here described, I have found, in the same cutaneous muscle of the frog, nervous filaments on the blood-vessels, although I have not yet been able fully to satisfy myself as to their source and distribution. These vascular nerves entirely agree in character with the pale sentient fibres, and, like them, are furnished with nuclei. I have found them chiefly on small veins, and on fine vessels on the arterial side of the capillaries, which were, however, destitute of a muscular coat. On these vessels I have traced them a considerable way, passing from one branch to another and often dividing, but have not been able to observe distinct terminations. Now and then also I have recognized them on vessels possessing a decidedly arterial structure; but I am unable to state anything positive as to their arrangement in this case, inasmuch as the nuclei in the outer coat of the small arteries occasion much difficulty in following out pale nucleiferous fibres. Once only I was fortunate enough to trace the origin of one of these vascular fibres from a dark-bordered sentient fibre; and this observation, so far as it goes, together with their distribution to vessels destitute of a muscular coat, favours the notion that the nerve-fibres in question are of the sentient kind.

On the Nerve-tufts in the Cutaneous Muscle of the Frog.

In the same muscle of the frog to which I have already made so constant reference, there may be observed, and most commonly about the end of the winter season, from three to five objects of peculiar structure, which at first sight appear to be of the nature of tactile corpuscles or terminal nerve-bulbs, but which really do not belong to that class of organs. The objects in question are indicated in

figure 2 at *i i*, and one is represented on a larger scale in figure 4. They are found on the finer muscular fibres, and appear on a superficial inspection as nodular swellings or somewhat thickened portions of the fibre, marked by a profusion of rather roundish nuclei, and receiving a single very thick nerve-fibre, loosely surrounded by its comparatively wide membranous sheath. On further examination it is found that the nerve-fibre, on reaching the nodule of the muscle, is wound up at one or more spots on the surface into a coil or tuft, in the mean time undergoing repeated division; and for the most part it may be seen to enter the muscular fibre, in which the dark-bordered fibres, becoming finer, are finally lost to view.

Fig. 4 *.

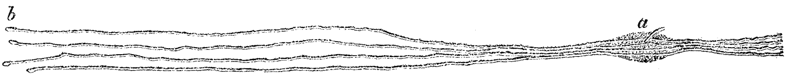


The last-mentioned fact struck me as specially important, inasmuch as it seemed to afford an instance of the penetration of a nerve into the interior of a muscular fibre, as maintained by Kühne. On a careful examination, however, of the structures in question in muscles rendered transparent by acetic acid, I found that the apparently simple muscular fibre bearing the swelling is really a small bundle of from three to seven fine fibres (fig. 5), and that the

* Fig. 4. A nodule or swelling of a muscular fibre (or rather fasciculus), with a large nerve-fibre, nerve-tuft, and nuclei; highly magnified.

apparently penetrating nerve-fibres merely pass between these muscular fibres.

Fig. 5 *.



On tracing the peculiar and seemingly simple muscular fibres towards the ends of the muscle, I found that they there evidently consist of several smaller but still transversely striated fibres, and this brought to my mind the bundles of fine muscular fibres described by Weismann †, and known to me also from actual inspection, which induced that observer to infer the occurrence of longitudinal divisions of the striated fibres. This led me to study these bundles singly by treating the cutaneous muscle with strong solution of potash, and then I found that it is precisely these particular bundles which (appearing as single fibres) exhibit the peculiar swellings with the coiled nerve. In the situation of the swelling the finer component fibres of the bundle cling fast together, even after the operation of the alkali, 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. Now, if it be admitted that the finer muscular fibres composing the bundle are generated by the division of thicker muscular fibres, as Weismann justly concludes, the explanation of the nerve-tufts becomes easy; inasmuch as they may be conceived to 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. The process by which this is effected cannot be satisfactorily studied in consequence of the close cohesion of the fine muscular fibres at the spot, but most probably the original pale terminal fibres of the parent nerve undergo further development by growth and by multiplication of the nuclei, so as finally to supply all the new muscular fibres; and I think it not

* Fig. 5. A small bundle of fine muscular fibres into which an apparently simple (but really longitudinally dividing) fibre has been resolved by means of potash. *a*, Nodule or swelling which contained a nerve-tuft.

† Zeitschr. für rationelle Medicin, 1860, Band x.

unlikely that a part of the numerous nuclei in the neighbourhood belong to the nerve-fibres.

Simultaneously with the increase of its terminal fibres the dark-bordered parent fibre doubtless augments in thickness, which explains the fact, otherwise difficult to understand, that it is invariably of much larger size than the nerve-fibres proceeding to the other muscular fibres.

From what has been stated it will thus be seen that the relation of the nerve to the peculiar structures described does not support the views of Kühne.

On the Termination of the Nerves in the Involuntary Muscles, and on the disposition of the Nerves in the Heart of the Frog.

Having, to the best of my power, investigated the ending of the nerves in voluntary muscles, I thought it right to extend my researches to those of the involuntary muscular organs, respecting the ultimate terminations of which very few, if any, satisfactory observations have been heretofore made known.

The muscles I selected for examination were those of the heart and pharynx of the frog, and the methods of preparing them were the same as for the voluntary muscles.

The nerves of the frog's heart are the two nervi vagi or pneumogastrics, which, having reached the heart at the place where the venous sinus joins with the right auricle, enter the septum between the two auricles, and proceed therein to the ventricle. During this part of their course the two trunks of the vagi, which join together at their entrance into the heart, are almost everywhere beset with numerous ganglionic cells. These cells in some parts form larger masses, well described by Bidder several years ago*. One or two of these masses lie in the upper part of the septum, and may be called the "superior auricular ganglions"; another is situated in the lower part of the septum, near the ventricle, the "inferior auricular ganglion"; and a very remarkable and constant ganglion is seated in each of the two larger valves placed between the ventricle and the auricles,—these are the "ventricular ganglia" of Bidder.

Apart from these larger ganglionic masses on the trunks of the vagi, there are found, although without regular arrangement, gangli-

* Müller's Archiv, 1852.

onic cells, single or in small clusters, on the larger branches distributed to the venous sinus and the auricles, but none on those of the ventricle; so that the ganglionic matter of the ventricle exists only at its venous aperture.

Respecting the microscopic structure of these parts, it is known that amongst the ganglionic cells there are many which give origin each to only one nervous fibre, and have therefore been termed unipolar cells, whilst there are others that apparently give off no fibres, and are named apolar cells; but it is as yet altogether unknown whether the proper or radical fibres of the vagi connect themselves with the ganglionic cells of the heart or not, and it is equally uncertain from what immediate source the nerve-fibres proceeding to the muscular substance of the heart are derived.

Most physiologists seem to believe that the fibres of the vagus or pneumogastric are not directly distributed to the muscular fibres of the heart, but that they act only through the medium of the ganglionic cells, and that the fibres derived from these cells are the real motory nervous elements. So far as I know, however, notwithstanding its importance, no one has hitherto examined into this matter.

My own inquiry has had a twofold object: first, to ascertain the relation of the pneumogastric to the ganglionic cells; and secondly, to find out the mode of termination of the ultimate divisions of the nerves on the muscular fibres.

As regards the first question, all my observations tend to show that the nervous system of the frog's heart is constituted on a very simple principle. There are, in fact, two distinct although associated systems of nervous fibres distributed to every part of the muscular walls of the heart: namely, first, the proper or radical fibres of the vagus, which pass through the ganglia of the heart, without, so far as I can discover, connecting themselves with the ganglionic cells, and proceed straightway to the muscular fibres; and secondly, fibres derived from ganglionic cells, which are associated with the original vagus-fibres, and run with them to the muscular tissue.

The obvious bearing of this matter on important questions of physiology requires that I should here explain the grounds on which the conclusion now stated is founded. On this head I have first to state that, in following with the microscope and with the aid of potash the fibres of the vagus as they pass through the several ganglions of the

heart, it is easy to see that they run through these bodies without forming any connexion with the ganglionic cells. Of course I do not pretend to have traced every individual fibre, but I can speak positively of the large majority, and conclude that the same holds good generally, the more so as the ganglion-cells themselves present conditions which corroborate this conclusion. 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 not unipolar cells whose issuing fibre is in some way hidden from view. I may add that, as the cells lie mostly at the side of the vagus and its branches, and not amongst its fibres, their relation to the latter is less difficult to determine.

From what has been said I feel justified in my conclusion that there are in the frog's heart two distinct systems of nervous fibres, one ganglionic, the other directly proceeding from the vagi or pneumogastric nerves.

Before proceeding, in the next place, to describe the terminations of the nerves, I have to explain that the muscular tissue of the frog's heart is entirely made up of short spindle-shaped uninucleated fibres, or fibre-cells, resembling in every respect those described by me in the involuntary muscles generally, except that they have very distinct transverse striæ. These striated fibre-cells, as correctly described by Weismann, are arranged so as to form larger and smaller bundles, and these unite into a network which, in each of the three parts of the heart, is continuous throughout. Now, respecting the nerves, it is easy to show that their smaller branches, composed of dark-bordered fibres from the vagus and the ganglion-cells, also form a general network, with larger and smaller meshes, on or between the secondary muscular fasciculi. As the ramifications become finer the component nerve-fibres gradually lose their medullary sheath, and are finally continued into pale nucleated filaments which lie singly or two or three together in the finest muscular bundles. The last terminations are pale, nucleated fibres, entirely agreeing in aspect with those described as the ends of the sentient nerves in the voluntary muscles.

They enter here and there into the fasciculi of muscular fibre-cells, ramify in these bundles, and end in very fine pointed extremities. The muscular fasciculi are on the whole rather richly supplied with these terminal fibres, so that two or three may be readily found in each bundle by any one accustomed to such investigations. Still it is plain that the nerve-terminations are by no means equal in number to the muscular fibre-cells, so that several of the latter must be governed by one and the same terminal nerve-fibre.

The same mode of nerve-termination as in the heart prevails in the non-striated muscular tissue of the pharynx and bladder of the frog, excepting that the terminal fibres are more scanty; but as these run over a larger extent of the muscular tissue before coming to an end, their comparative rarity may be compensated by their acting at the same time upon a larger number of the muscular fibres.

With these remarks I conclude the account of my anatomical investigation of the terminations of nerves in muscles. It will be obvious to every one conversant with the physiology of the muscular system, that many of the facts on which I have dwelt are of more or less importance in reference to physiological questions; and I would have gladly availed myself of the opportunity now so courteously afforded me of addressing this learned Society, to take up also the physiological side of the question, did I not fear to have already made too large a demand on your patience. I refrain therefore from entering on so large a subject, and shall take leave only to offer the following as what appear to me to be the more interesting physiological inferences from the anatomical facts I have described.

1. As the motor nerves lie outside the sarcolemma, and are confined in their distribution to a comparatively short portion of the muscular fibre, it may be inferred that there must be action at a distance.

2. As the ends of the motor nerves are pale fibres destitute of medullary sheath, it would appear that the latter is of but secondary importance. The same fact may perhaps also afford an explanation of the special action of certain poisonous agents, as the urari, on the ends of these nerves.

3. The muscles have numerous sentient nerve-fibres distributed at their surface, or on the surface of their larger divisions.

4. The heart, at least the heart of the frog, has two distinct sets of nervous fibres, those of the pneumogastric and those from the ganglion-cells, which are both distributed to the muscles. The vagus therefore acts directly on the muscular fibres of the organ, and the well-known experiment of Weber can scarcely be explained through a supposed action of the vagus on the ganglia. On the other hand, the ganglia and their fibres are also motorial organs of the heart, and alone act when it is separated from the body.

May 8, 1862.

Major-General SABINE, President, in the Chair.

Heinrich Wilhelm Dove, of Berlin, elected a Foreign Member in 1850, and Henri Victor Regnault, of Paris, elected a Foreign Member in 1852, were admitted into the Society.

The following communication was read:—

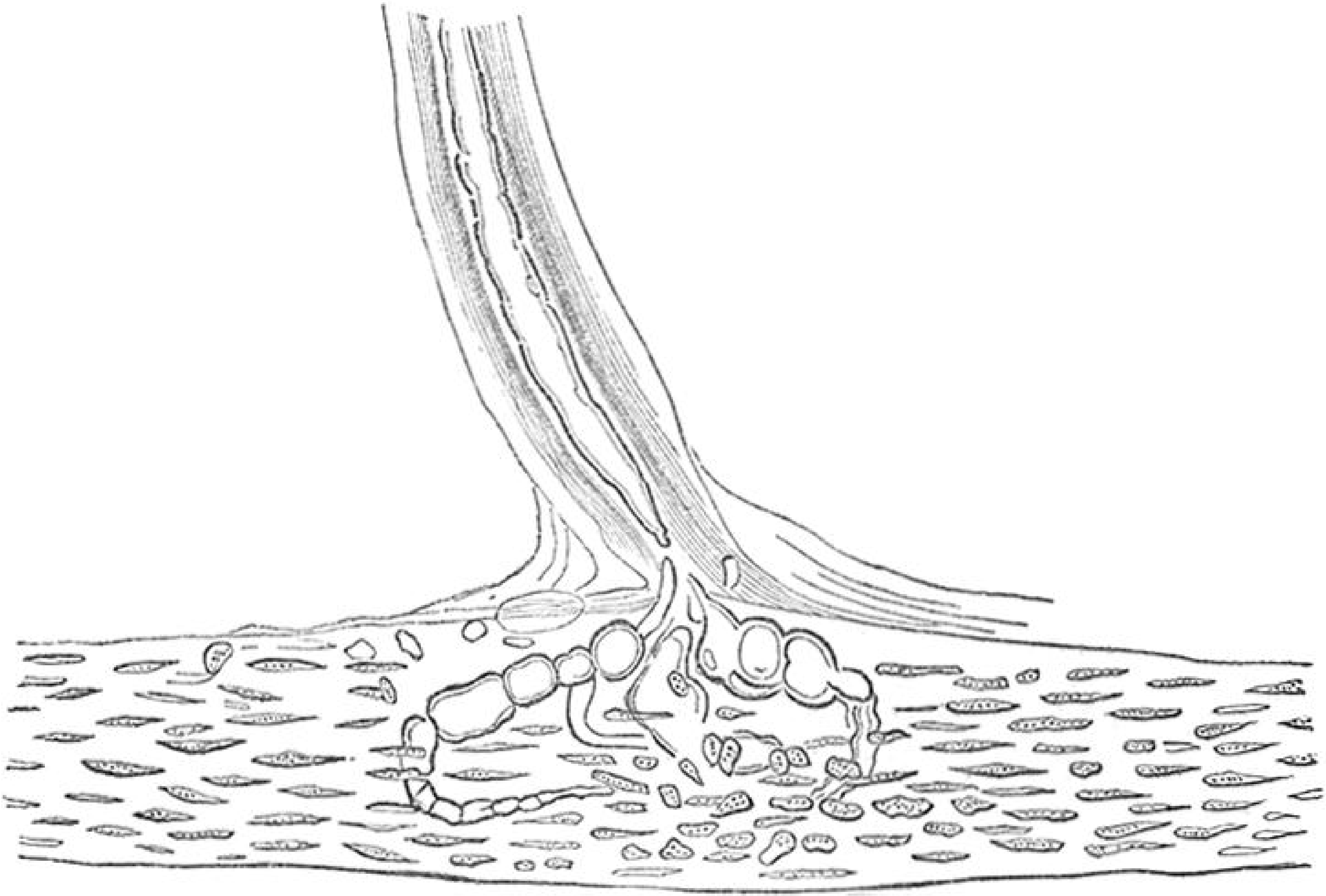
"Appendix to the Account of the Earthquake-Wave Experiments made at Holyhead." By ROBERT MALLET, Esq., C.E., F.R.S. Received March 27, 1862.

(Abstract.)

This communication contributes the sequel of the author's "Report on Earthquake-Wave Experiments" (made at Holyhead), as published in part 3 of the 'Philosophical Transactions' for 1861. At the conclusion of that paper the author expressed his hope of being able soon to lay before the Royal Society some experiments for the determination of the modulus of elasticity of perfectly solid portions of both the slate and the quartz rock formation through which his wave-transit experiments had been made at Holyhead, with a view to throw light upon the relations between the theoretic velocity of transmission (if the rocks were all solid and homogeneous) and the actual velocity as determined by experiment.

He has now determined the elastic modulus for both rocks, and for each rock in two directions, viz. parallel to and transverse to its lamination; and he has extended his determinations to specimens of

Fig. 4 *.



* Fig. 4. A nodule or swelling of a muscular fibre (or rather fasciculus), with a large nerve-fibre, nerve-tuft, and nuclei; highly magnified.